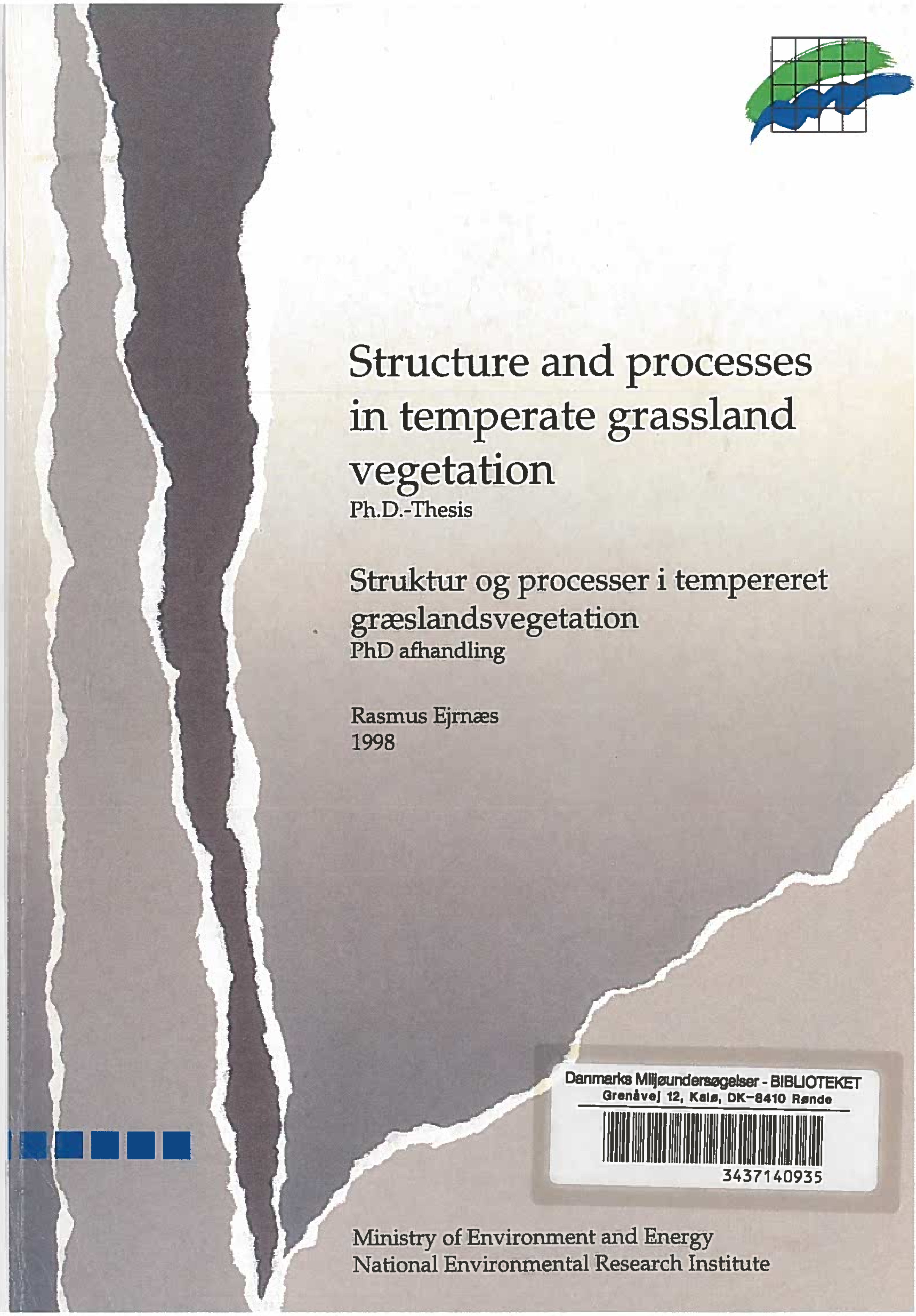

Structure and processes in temperate grassland vegetation

Ph.D.-Thesis

Struktur og processer i tempereret græslandsvegetation

PhD afhandling

Rasmus Ejrnæs
1998

Ministry of Environment and Energy
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to my wife, Anne

Contents

Preface

In Denmark, the grass greens in late March. Perhaps that is the reason why early spring is so well suited to classify grasslands according to conservation value by their colour. When there is no interference by summer drought and autumn litter, a marked difference can be observed between the uniform bluish green colour of a monotonous rye grass sward with white clover and scattered weeds and the yellowish green colour of semi-natural grasslands covered in pleurocarpic mosses and harbouring a diverse array of plant, fungi and insect species. Later, you will maybe also discover how to find the rare species belonging to the fungal genera of *Hygrocybe*, *Entoloma* and *Clavaria*. These occur almost exclusively in the yellowish green, unimproved grasslands, but not everywhere so. In the summer, it is often possible to see that the grass is greener in some parts of a slope or in a hollow - an indication of pressure or ground water enriching the spot. It is moist, but not wet, and that is where you should go and search for fungi mentioned above.

In many situations, such home made rules-of-thumb work quite well, but sometimes they do not, and you get surprised, mystified and maybe intrigued. One day, I realised that within this boring rye grass sward, that I overlooked for years, two species quoted by others as indicators of semi-natural grassland occurred quite frequently, namely *Ranunculus bulbosus* and *Saxifraga granulata*. An even greater arousal occurred after I started to sample grassland vegetation in my MSc.-study and realised that in some grassland localities only 3 species were found on average per 0.1 m^2, whereas in other places more than 20 species were growing together.

Eugen Warming (1841-1924), one of the pioneers of plant ecology, outlined the difference between a floristic and an ecological plant geography. In his book on plant communities (Warming 1895) he begins by listing the tasks for a descriptive floristic plant geography and continues:

"The thoughtful investigator will not remain content with the mere recognition of facts; he will seek after their causes. These are, in part, modern (geognostic, topographical, and climatic), and in part historical. The limits of distribution of a species may depend upon prevailing conditions, upon barriers now existing in the form of a mountain, sea, soil, and climate, which oppose its spread ; but they may also depend upon geohistoric or geological and climatic conditions of ages long past, and upon the whole evolutionary history of the species, the site of this, and the facilities for and means of migration. In addition, problems must be dealt with concerning centres of development, the rise and age of species and genera ; and behind these lies the question of the origin of species."

[This English text (Warming 1909) is a word for word translation of the original Danish text]

The present thesis is the outcome of a three year PhD-study intended to cast light on the occurrence, nature and management of semi-natural grasslands on well-drained soils in Denmark. Rules-of-thumb are merely very simple models, and this study may thus be seen as an attempt to validate, correct or even invent new simple models of relevance for Danish grassland vegetation - and, to give these models an appropriate biological interpretation.

The thesis could not have been formed in a vacuum. The constant exchange of ideas with other researchers is essential, and I am indebted to those of my colleagues who helped me, corrected me and widened my intellectual horizon during the process, notably my supervisors Ib Johnsen, Anna Bodil Hald, my near friend and colleague Hans Henrik Bruun and Hans Tybjerg, Johnny Lund Jeppesen, Anne Jacobsen, Erik Aude, Susanne Mark, Bettina Mogensen, Jonas Lawesson, Jens Reddersen, Kirsten Zaluski, Christian Lange, Jacob Heilmann Clausen, Jens H. Petersen and Jan Vesterholt. The participation in PhD-courses and my visit at Unit of Comparative Plant Ecology at the University of Sheffield constituted invaluable periods. Special thanks to John Philip Grime for his supervision during my visit in Sheffield and for the social and scientific support I received there from Stuart R. Band, Hans Cornelissen, John Hodgson, Ken Thompson, Sarah Buckland, Rosemary Booth, Bryan Booth, Peter Wilson, Suzanne Hubbard, Adriana Carnelli and all the rest of the Unit. Inspiring teachers and students I met during my courses include Anders Dahlberg, Odd Eilertsen, Rune

Økland, David Read, Lauri Oksanen, Peter Kareiva, Illka Hanski, Meelis Pärtel and Mari Moora.

Not least, I acknowledge the coherent and inspiring studies and writing of scientists, that masters the admirable project of creating and pursuing original ideas incorporating research results from within many scientific disciplines. They make it worth carrying on doing research, and for this, I would like to honour John Philip Grime, Stephen Jay Gould, R.H. Whittaker and Eugen Warming.

Dansk resumé

Denne afhandling omhandler græslandsvegetation på veldrænet bund med speciel vægt på en beskrivelse og fortolkning af dansk vegetation. Afhandlingen bygger på 4 manuskripter og en publiceret artikel, som hver for sig berører vigtige problemstillinger af såvel metodemæssig interesse som teoretisk biologisk og forvaltningsmæssig relevans. Datagrundlaget for artiklerne er dels egne analyser af vegetation, jordbund og drifthistorie, dels ældre danske vegetationsanalyser udført med sammenlignelig metode.

Artikel 1 med titlen *A gradient analysis of temperate grassland vegetation on well-drained soil* præsenterer en gradientanalyse af græslandsvegetation på tør bund. Det viser sig, at overdrevsvegetation følger nævnte underliggende komplex-gradienter: 1) En økosystem-gradient fra tørre, basiske skrænter til kølige, udvaskede og sure jorder, 2) En produktivitetsgradient fra tørre, sandede jorder til fugtige lerede, og gerne kalkholdige jorder, 3) En geografisk gradient fra SØ-Danmark til NV-Danmark, 4) En gradient i realiseret produktivitet (konkurrence) fra lavproduktiv eller græsset/forstyrret vegetation til højproduktiv og uforstyrret vegetation.

Artikel 2 med titlen *A classification of Danish grassland on well-drained soil* beskriver og klassificerer de analyserede vegetationsdata fra artikel 1. Fire hovedklasser og 12 typer græslandsvegetation bliver identificeret, beskrevet og sammenlignet med international nomenklatur og phytotaxonomi.

Artikel 3 med titlen *Response curves and pH preferences of grassland plants in Denmark* analyserer enkeltarters responskurver til vigtige miljøvariabler, samt forklaringsevnen af miljøvariabler i forhold til coenokliner identificeret ved ordination. Analysen demonstrerer, at ordination, på trods af hyppige brud på metodens ideale fordring om symmetrisk unimodalt artsrespons, er et effektivt og robust værktøj til at analysere og kortlægge vilkårene for såvel vegetation som enkeltarter.

Artikel 4 med titlen *Cryptogams in Danish grasslands - primary gradients and successional trends over the last 50 years* præsenterer en gradientanalyse af kryptogamer indsamlet i dansk overdrevsvegetation i 1990'erne, og det viser sig at mosser og laver generelt fordeler sig efter de samme gradienter som karplanter. En sammenligning af det indsamlede materiale med materiale fra 40'erne og 50'erne, viser at der stadig findes en værdifuld kryptogamflora tilknyttet dansk græsland, men der kan spores en fremgang for generalister og en tilbagegang for specialister.

Artikel 5 med titlen *Prediction of grassland quality for environmental management* analyserer den relative betydning af drifthistorien (gødskning og opdyrkning) i forhold til andre betydningsfulde miljøvariabler (pH og relativ indstråling) og direkte gradientanalyse anvendes til at udpege potentielle indikatorarter for gamle ugødskede overdrev.

I kapitel 3 perspektiveres resultaterne fra artiklerne, og der fremsættes idéer og hypoteser om vegetationsmodeller og artsdiversitet. Der angives desuden, hvorledes de fremsatte idéer og hypoteser kan valideres og testes. I kapitel 4 defineres og udvikles begrebet naturkvalitet, hvis afklaring er en nødvendig forudsætning for en hensigtsmæssig anvendelse af såvel indikative som prædikative vegetationsmodeller i naturforvaltningen.

I kapitel 5 trækkes konklusionerne fra afhandlingens delkomponenter op, og oplagte videnshuller og forskningsmuligheder i relation til afhandlingens emne påpeges.

1. Introduction

Behind this thesis lies a curiosity regarding perhaps the most fundamental issue in plant ecology:

Why do plants grow where they grow?

Since the very beginning of plant ecology (e.g. Warming 1884) attention has been focused on this fundamental question. The quest for a predictive community ecology (Keddy 1992) has become crucial with the notion of global changes in climate and biogeochemical cycling of carbon and nitrogen (Smith et al. 1997). In order to enter a framework of modelling, the answers to this question will have to be simple, comprehensive and generally valid - and that is a challenge.

Major differences with respect to scale and gradient dimensionality exist between the approaches taken. Warming (1884, 1923) and Raunkiær (1907) were pioneers in the field of classifying plants in *life forms* according to generalised adaptations to important environmental gradients. Warming's classification was based on shoot architecture and life history traits. The outcome was a rather descriptive classification of relevance to gradients in many dimensions, and maybe this complexity was the reason why it gained less wide acceptance than Raunkiær's classification based on the vertical position of the growing points of the shoot during the inactive season (fig.1).

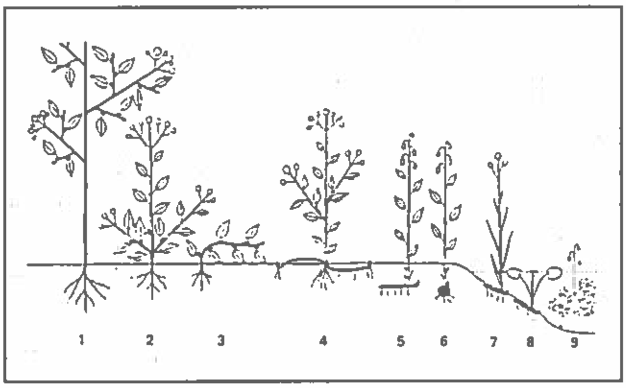


Figure 1. The main types of life forms according to Raunkiær (1907). Light lines denote plant parts dying off in the unfavourable season, heavy lines the parts which persist. Terms in use are: 1, phanerophytes; 2 and 3, chamaephytes; 4, hemicryptophytes; 5 and 6, geophytes; 7, helophytes; 8 and 9, hydrophytes.

The intuitive appeal of this classification lies in the reduction to a few major underlying environmental gradients, particularly *climate*. But, this simplicity is simultaneously the weakness of Raunkiær's life forms - as stated by Grime et al. (1988): *...the life form approach remains essentially a "broad brush" exercise, of greatest value in the hands of phytogeographers, climatologists and ecosystem analysts.*

Grime's (1974, 1979) theory on plant strategies imply the recognition of three major habitat types and the subsequent triangular ordination of plants according to the relative investment in either of three major adaptive strategies, characterised by specific syndroms of life history traits. In this way Grimes CSR-strategy incorporates, in an interpreted model, the early ideas of Warming (1884). It is probably the fate of any low-dimensional model to be questioned, and Austin & Gaywood (1994) also points to the unsatisfactory generalisations of the CSR-theory across totally different ecosystems. As an example Austin & Gaywood mention two species, *Bromus erecta* Hudson and *Athyrium filix-femina* L., that have exactly the same triangular ordination, occur in the same geographical region, and yet would never be found together in the same plant community.

Ellenberg (1974) adopted the simpler approach of summarising the preferences of plants with respect to important simple measurable environmental quantities, e.g. water availability, acidity, and nitrogen availability. This approach is based on a statistical correlation between environment and plants, and although predictions can be derived using the set of species indications, the important "why" in the above question is left unanswered.

A reduction of model complexity can also be achieved by studying the response of vegetation instead of single species. Based on the assumption of a symmetric unimodal response of species to major underlying gradients (Gauch & Whittaker 1972), multivariate methods have been developed (Hill 1973) that enable the extraction of coenoclines. With this tool, gradient analysis advances from the direct approach (Whittaker 1967) to the indirect approach, where unconstrained coenoclines can be extracted and given subsequent interpretations in environmental terms. The process of indirect ordination is not much different from the pattern description and subsequent interpretations of Warming and Raunkiær, except that the reduction in dimensions that is achieved with ordination, and the feasibility of statistical test on personal computers, enables the testing and comparison of large multivariate data-sets without reliance on preconceived ideas.

Object and objectives

The study object of my thesis is grassland vegetation on well drained soils in Denmark. Grassland vegetation is an attractive field for a plant ecologist. As a consequence of the density and diversity of vascular plants, the sampling area can be kept at a minimum, simultaneously satisfying the criteria of homogeneity and representativity (Økland 1990). The short term dynamics of grasslands compared to e.g. forests are also attractive for ecologists describing or experimenting with issues related to vegetation processes.

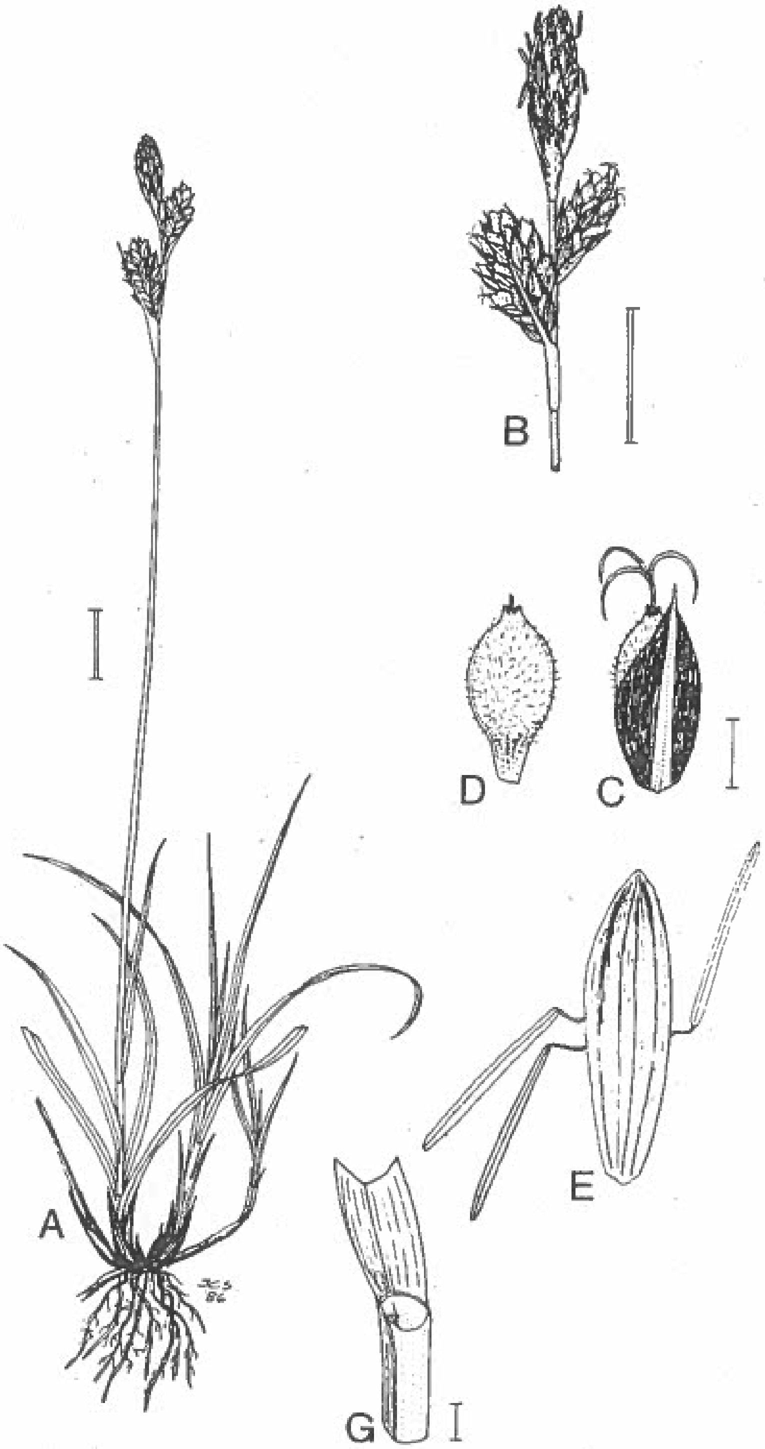
Despite an obvious interest in structure and process in temperate grassland vegetation of northern Europe (e.g. Willems et al. 1993, Grime et al. 1987, Al-Mufti et al. 1977, Mitchley & Grubb 1986) no studies have yet applied contemporary methods of indirect gradient analysis to the range of different grassland types occurring here (but see Gittins 1965, Lloyd et al. 1971). Several studies of dry grassland vegetation in Denmark have left a considerable number of published vegetation samples. The fieldwork of this thesis can thus be seen as a supplementary sampling of Danish grassland vegetation, with the purpose of subsequent indirect gradient analyses. Five major questions constitute the objectives of the study.

1) What are the primary ecoclines in temperate grassland vegetation?
2) Which major plant communities can be recognised?
3) Can the generalisation implicit in the concept of coenoclines (integrated species responses) be justified?
4) Do vascular plants and cryptogams respond to the same complex gradients?
5) Is it possible to substantiate recommendations on the conservation and management of semi-natural grassland with biological arguments?

The thesis falls in three parts. First, five published and unpublished papers investigate the questions stated above. Secondly, a chapter is devoted to future perspectives of the results, including a section of hypotheses and a section of proposed tests and surveys. Last, a chapter containing an attempt to defining the concept of biological quality as a criterium for priorities and methods in the management of seminatural grasslands with special reference to Danish legislation. Finally, a short conclusion recaptures the most important insights reached and the gaps of knowledge revealed. Appendices are included referring to articles published in Danish, and clarifying the role of first and second authors of the included manuscripts.

2. Articles

Article I



Carex caryophyllea Latourr

A gradient analysis of temperate grassland on well-drained soil

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Abstract

This paper presents a gradient analysis of 620 vegetation samples covering the main floristic and environmental variation in semi-natural grassland vegetation on well-drained soils in Denmark. Vegetation was sampled using frequency in subplots. Environmental data for the samples consists of ground inclination, aspect, pH, geographical co-ordinates together with indications of soil type. To facilitate axes interpretations these were supplemented with site calibrations based on weighted averaging of Ellenbergs indicator-values and Grimes CSR-strategy values. A detrended correspondence analysis revealed four coenoclines that could be interpreted in ecological terms. The first coenocline reflected an ecosystem gradient from dry calcareous to humid acidic grasslands. The second responded to an underlying gradient in fertility. The third reflected regional and the fourth reflected a gradient in intensity of competition. We recommend *subset ordination* as a supplement to traditional permutation and correlation statistics for assessment of the consistency of ordination results. DCA$^{1\text{-}2}$ were found to be consistent coenoclines in space and time and were modelled using multiple regression. Ecoclines and species diversity patterns are discussed in a context of plant strategy theory and species diversity models.

Keywords: Europe, Denmark, temperate, semi-natural, unimproved, permanent, ordination, Ellenberg, Grime, competition, diversity, plant strategy theory, statistical modelling.

Nomenclature: Flora Europaea (Tutin et al. 1964-1980).

Introduction

The temperate "semi-natural" grassland vegetation of western Europe is one of the most studied plant communities. One important and lasting focal point has been species diversity and the impact of local scale ecological processes (e.g. Grime 1979, Schmida & Ellner 1984, Tilman 1988, Zobel & Moora 1997). Recently, attention has also been drawn to processes involving larger areas and time spans (Zobel 1992, Pärtel et al. 1996). Despite this obvious research interest, few attempts have been made to present a view of temperate grassland vegetation using contemporary multivariate methods. Studies have generally been restricted to particular grassland types (e.g. Zobel & Kont 1992, Krahulec et al. 1986, on Alvar grasslands) or focused on local successional sequences (e.g. Cramer & Hytteborn 1987, Eilertsen 1991).

Over the last century, but mainly in the period 1940-1960, a couple of quantitative descriptions of Danish grasslands on well-drained soils were published. Tyge W. Böcher studied grassland and forest fringe vegetation on slopes in Denmark (Böcher 1945, Böcher et al. 1946). The aim of Böcher and co-workers in these studies was to find and describe the tiny patches of original Danish vegetation, as little influenced by culture as possible, and through the study of these to deduce an overall picture (Böcher, 1945: p.2). Böcher based his classifications largely on phytogeographical criteria, i.e. differences between relevés with respect to European distribution types of the plants, e.g. continental, oceanic, Mediterranean and boreal. Böcher et al. (1946) recognised the evident importance of topoclimate, pH and erosion for vegetation composition and hypothesised that drought, calcareous soils and erosion could create conditions hostile to tree growth, allowing for the occurrence of patches of natural temperate grassland. However, no thorough environmental interpretation of observed patterns was presented. Vestergaard & Hansen (1989) reported on the distribution of vascular plants in Denmark with special emphasis on regional patterns. They recognised the following key factors for the distribution of grassland and dune species: 1) the main stationary line during the last glacial, 2) regions with high incidences of limestone soils and 3) climatic gradients, mainly reflecting variation in precipitation.

The objective of this study is to analyse and interpret coenoclines in Danish grassland vegetation. We have included in the study all accessible published and unpublished data from Danish grasslands satisfying our selection criteria:

1. Samples of vegetation dominated by herbaceous plants occurring on well-drained soils.
2. Samples of vegetation obtained from a homogeneous area (of app. 10-100 m^2) by "frequency within 10 subplots of 0.1 m^2 each".
3. Studies including measurement of pH, aspect, inclination and indication of soil type.

A separate paper will present a classification based on the same material. The basic questions dealt with in this paper are:

1. What are the most important coenoclines in dry grassland vegetation in Denmark?
2. Can these be interpreted in terms of underlying complex gradients?
3. How do observed patterns in diversity and gradient structure relate to current theories on plant strategies and vegetation processes?

Study areas and sampling objectives

Table 1 lists the studies included in this paper. The data collected by Böcher and co-workers in the 1940's (Böcher, 1945, 1946, 1947, 1957; Böcher et al., 1946, Böcher et al. unpubl., Böcher unpubl.) constitutes the bulk of this material. The unpublished material from Thy/Hanherred and Bornholm was collected in 1942 (supplemented 1945) and 1947 respectively, by Tyge W. Böcher, Tyge Christensen and M. Skytte Christiansen. After the death of Böcher in 1983 it was preserved in the Botanical Library, Copenhagen along with sparse comments (Böcher et al. unpubl., Böcher unpubl.). We have used these tables after revising them with the field notes of T.W. Böcher (also in Botanical Library) and his co-workers (kindly lend to the authors by T. Christensen (†1995) and M.S. Christiansen (†1997).

The sampling rationale of Böcher and co-workers was *documentary*, i.e. vegetation analyses were made in »selected, particularly typical places« (Böcher et al. 1946: 28). In this respect, the approach was very similar to the Braun-Blanquet approach (Westhoff & van der Maarel, 1978). Böcher had a broad view on grassland vegetation and included in his studies also vegetation from edges of forest and scrub as well as from fixed dunes. He selected consciously vegetation as little influenced by man as possible, excluding intensively grazed areas and areas of former cultivation. In our opinion, the choice of stands by Böcher and co-workers was somewhat biased towards stands including rare and semi-rare species.

Mortensen (1953, 1955) sampled vegetation on slopes on Samsø and Hindsholm in the

Table 1. Study area, year of data collection and number of samples and localities for the ten separate studies included here.

Study	Area	Fieldw.y	Samples	Locality
Böcher, 1945	Zealand	1931-42	102	38
Böcher, 1946	Møn	1944-45	17	8
Böcher, 1947	Bornholm	1947	2	1
Böcher, 1957	Bornholm	1947	4	3
Böcher et al., 1946	Himmerland	1943-45	97	32
Böcher, unpubl.	Thy/Hanherred	1942-46	106	28
Böcher, unpubl.	Bornholm	1947	7	3
Fredskild, 1954	Zealand	1951-54	57	6
Mortensen, 1953	Hindsholm	1945-52	24	18
Mortensen, 1955	Samsø	1945-55	31	12
Bruun & Ejrnæs, 1993	Odsherred	1992	20	5
Ejrnæs, unpubl.	Djursland	1994-95	109	29
Wind & Ballegaard, 1995	E-Jutland	1995	6	1

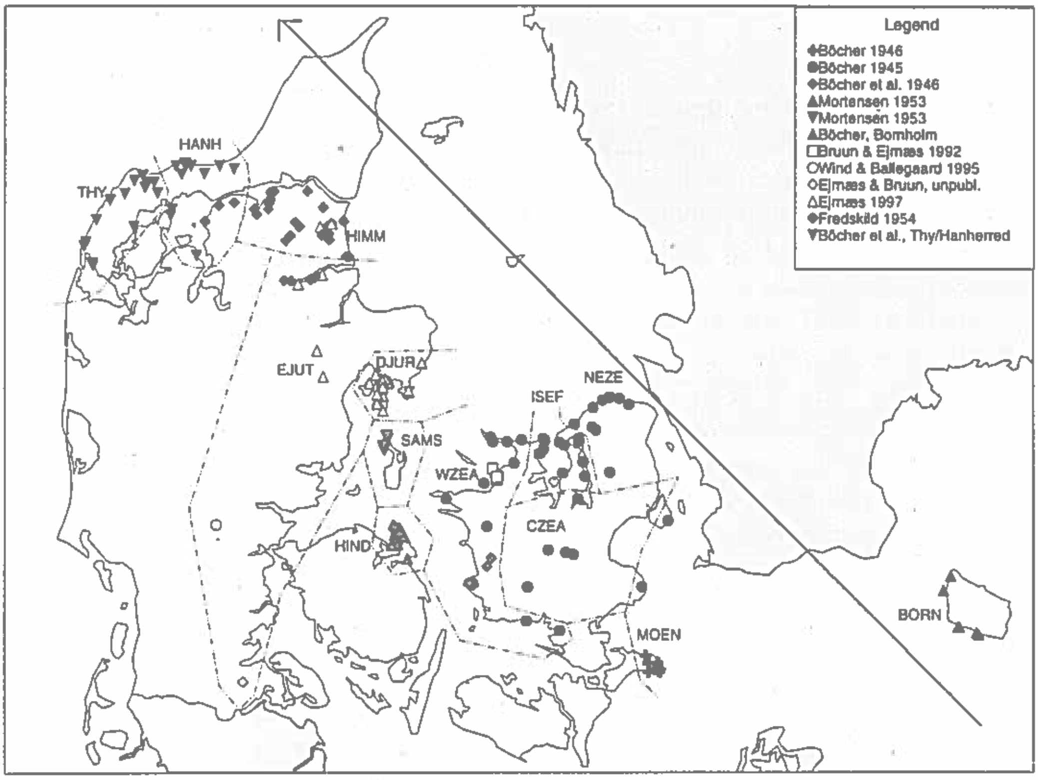

Figure 1. Map showing localities divided on studies. The arrow indicates the geographical SE-NW gradient in the material.

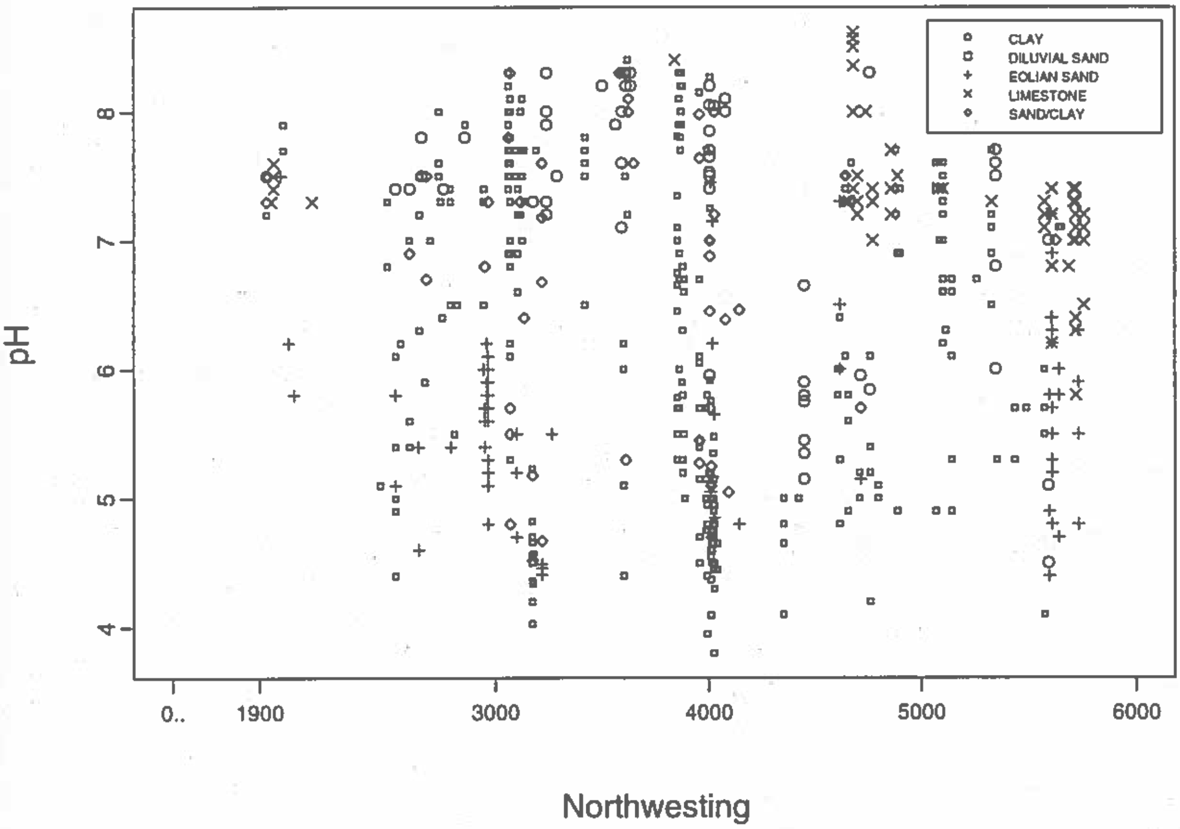

Figure 2. Sampling regime. Vector representing the abscissa (*northwesting*) is indicated on fig.1. A smaller font size is applied to the symbol for diluvial sand, the predominating soil type.

Great Belt region, attempting to extend the studies of Böcher to other parts of Denmark. Fredskild (1954) studied slope vegetation in W-Zealand in an attempt to understand the vegetation on dry sandy slopes in a context of topoclimate and edaphic factors.

The material from the Djursland peninsula, eastern Jutland, was collected 1994-95 using stratified random sampling, by one of the authors. The objective was to sample the floristic gradients present in grasslands with long grazing continuity and without influence of fertilisation. Three small data-sets from NW-Zealand and E-Jutland were collected in similar ways (Bruun & Ejrnæs 1993, Ejrnæs & Bruun 1995, Wind & Ballegaard 1996).

We have excluded 10 samples from forest and white dune (Böcher 1945: tab 1, anal.1-3, tab 3 anal.1, tab 6 anal. 1,2; Böcher et al.1946: Tab.2. anal.1-4), as well as 16 samples from formerly cultivated land (Böcher 1946: locality no 3) leaving us with a material consisting of 180 localities containing 620 vegetation samples and 387 plant species. Figure 1 shows the geographical distribution of the localities and figure 2 shows the distribution of samples on pH-values and soil classes along a SE-NW axis in Denmark.

Sampling method

All vegetation samples were collected using "frequency in subplot" as the abundance measure based on Raunkiær's method (Raunkiær, 1909): According to this method a sample plot is a vegetation stand of undefined size, but most often approximating 100 m^2, that is subjectively judged as homogenous. Vegetation is analysed by recording frequency of species in 10 circular subplots, each of 1/10 m^2, placed at random in the stand. In the published and unpublished studies of Böcher and in the Djursland material an extended version of Raunkiærs method was used including also smaller nested circles (Böcher 1935, Böcher & Weis Bentzon 1958). In the unpublished Djursland material a fixed sample size of 10 m^2 was used within which subplots were placed at random. The resulting abundance scale has the advantage over cover estimation of being objective and little influenced by sampling season. Its disadvantage, especially in Raunkiær's simple version, is the relatively poor resolution in the higher end of the frequency scale (see Böcher & Weis Bentzon 1958). Compared to unweighted measures of cover or biomass, frequency in subplots gives relatively more weight to less frequent species. Frequency in subplots has generally proven useful for subsequent multivariate data treatment including ordination and classification (Økland 1990).

Taxonomic notes

Taxonomy and nomenclature follow Flora Europaea (Tutin et al. 1964-1980), except for the following taxa: *Rumex acetosa* includes *R. thyrsiflorus* FINGERH. and *Hieracium pilosella* includes *H. peleteranum* MIRAT. In a few cases one author distinguished between infra- or microspecies, and others not. For instance Böcher (1945) and Böcher et al (1946) distinguished between the two subspecies of *Heracleum sphondyleum* L., ssp. *sphondyleum* and ssp. *sibiricum* (L.)SIMONKAI, while this distinction was not made in the Djursland material. Here, on the other hand, the subspecies of *Scleranthus annuus* L., ssp. *annuus* and ssp. *polycarpos* (L.)THELL. were distinguished between. The subspecies within Heracleum sphondylium and Scleranthus annuus have similar ecology and were therefore fused into the two broad species. In the Djursland material *Taraxacum* sect. *Erythrospermum* DAHLST. EMEND H.LINDB.FIL. was distinguished from other *Taraxacum* sectios. This was not the case in the rest of the material, although from the field notes we know micro-species of this characteristic sectio to have occurred. This taxon was preserved as it occurs frequently and its ecology is markedly different from other sectios.

The common species *Poa angustifolia* L. and *P. pratensis* L. s.str. was distinguished between in all samples except in the Djursland material. The authors find it unreliable to distinguish between the two species in the field and have therefore decided to fuse them into the broad species Poa pratensis L. s.lat.

Explanatory variables

The number of environmental variables provided are limited, except for Fredskild (1954) and the Djursland material. Table 2 serves the dual purpose of giving a survey of variables included in the gradient analysis and simultaneously providing an environmental characterisation of the grasslands included in the analysis.

Table 2. Summary of variables used in gradient analysis.

Variable	Mean value	Min. value	Max. value	Measurement scale	Missing values
Easting	598200 m	453900 m	878700 m	continuous	
Northing	6233000 m	6091000 m	6335000 m	continuous	
pH	6.4	3.8	8.6	continuous	44
Slope	25	0	50	continuous	22
Relative irradiation March 3	1.09	0	2.37	continuous	22
Relative irradiation June 23	0.94	0.60	1.01	continuous	22
Precipitation May-July	145 mm	130 mm	160 mm	Discrete - 7 levels	
Precipitation y^{-1}	569 mm	450 mm	700 mm	Discrete - 8 levels	
Growth days	200	193	205	Discrete - 5 levels	
Species number	28	2	60	continuous/discrete	
Species density	12.2	0.9	29.7	continuous	
Light^c	7.2	6.0	8.4	continuous	
Temperature^c	5.3	4.0	6.1	continuous	2
Continentality^c	3.6	2.0	5.1	continuous	
Water^c	3.9	2.4	5.4	continuous	1
Acidity^c	5.8	1.8	8.5	continuous	
Nitrogen^c	3.0	1.7	5.8	continuous	
Competition^c	2.9	0.9	6.2	continuous	
Stress^c	6.1	2.2	9.3	continuous	
Disturbance^c	3.0	0.3	5.6	continuous	
Number annual species^c	3.4	0	18	continuous/discrete	
%Density of annuals	10	0	59	continuous	
Coast	Categorical			3 levels	
Soil	Categorical			5 levels	22
Region	Categorical			13 levels	

Fredskild (1954) indicates precisely the pH measuring method, i.e. 0-12 cm topsoil diluted in water (1:2,5) and measured by glass electrode. The Djursland material is comparable; 0-10 cm fresh topsoil mixed with demineralised water (1:2) and stirred and measured after 10 minutes. Böcher (1945) and Böcher et al. (1946) states that pH was measured electrometrically, the soil being "root-soil" and "ca. 0-5 cm." respectively, but nothing is mentioned about dilution medium or soil/liquid ratio. Based on the range of pH values in the data, we assumed that dilution in water was also applied by Böcher and Mortensen.

Aspect and inclination were combined to give values of potential direct irradiation, calculated as the relative daily direct irradiation compared to a horizontal surface at two different days: March 1, in spring, when growth rates increase with temperature and June 23, in mid summer, when drought is a risk. For detailed formulas consult Iqbal (1983), Klein (1977) and Andersen (1980).

Böcher (1945), Mortensen (1953, 1955) and the Djursland material includes subjective classifications of geological substratum whereas Fredskild (1954) includes particle size analysis. In Böcher (1946, 1947) and Böcher et al. (1946) soil type indications are part of the description of localities, and in the Thy/Hanherred similar descriptions are found in the collectors field notes. Based on these sources, samples were assigned to one of 5 soil classes: Limestone (including chalk), clay (clayey till, including marl, colloidal clay and moler), sand/clay, diluvial sand (including gravel) and post-glacial, marine sand (including gravel, shingle, and eolian sand). The soil class limestone often coincides with shallow soils, all other soil classes imply deep soils. 22 samples remained unclassified.

The three levels of "coast" were judged from maps, with *inland* localities being situated more than 1 km from the coast, and the distinction between *bay* and *sea* judged subjectively.

Supplementary to variables working on local scale, a number of regional variables were also included. The geographical position of each sample was read as its UTM coordinates for northing and easting (UTM ED50 estimated with 100 m precision). All localities were assigned to one of 13 regions (fig. 1) delimited subjectively by the authors with respect to differences in predominating geological strata and local climate (Vestergaard & Hansen 1989). All samples were then assigned average values for their particular region with respect to mean annual precipitation, mean precipitation May-July and length of growing season counted as days with a mean temperature above 6 °C (Vestergaard & Hansen 1989).

As an aid in the interpretation of ordination axes (see Persson 1981) we included a set of site calibrations based on the autecological classification of species initiated in the works of Grime (1974) and Ellenberg (1974). Six categories of species indicator values were obtained from Ellenberg et al. (1992) and 3 categories from FIBS (Grime, Hodgson & Hunt, unpub.). We used these to calculate for each sample, averages of each indicator category over all species, weighted by species frequencies. Instead of using the unbalanced CSR-radii given in the FIBS-database, we used the tabulated compound strategy (e.g. *Achillea millefolium* being a CR/CSR-strategist) to calculate a CSR-ratio giving equally abundant species the same weight in the estimate of site condition. In the database each species can take strategy value multiples of halves, thirds, fourths and sixths, leading to 12 points as the smallest common multiple. A species recorded as a CS/CSR-strategist was consequently assigned 5 points for competitive ability, 5 for stress tolerance and 2 for ruderal adaptation as opposed to 3, 3 and 2 in the FIBS-database, whereas a C-strategist was given 12 for competition and zero for stress and ruderal adaptation (6, 0, 0, in FIBS). These "site calibrations" are not to be confused with measured environmental variables and have therefore been assigned a superscript "c" as a suffix to the name.

The last four variables are vegetation descriptors rather than explanatory variables: species number per plot, number of annual species per plot, species density (average number of species per subplot) and annual density (average fraction of annuals per subplot).

Methods of data analysis

Ordinations were run using the data package CANOCO vers.3.12 (ter Braak, 1991). For the purpose of coenocline extraction, DCA with detrending by segments and non-linear rescaling with default options was chosen (CA resulted in a pronounced quadratic distortion of the second axis). Neither weighting nor exclusion of species and samples were applied initially; but see discussion of outliers below. After the warnings regarding ordination instability in CANOCO given by Oksanen & Minchin (1997), all ordinations were rerun using the recommended debugged version of Decorana (Hill 1979, Oksanen & Minchin 1997). In only one data-set the correlation coefficient between the two ordinations were less than 0.999 (0.94 and 0.91 respectively on the third and fourth axes) and for that data-set we used the Decorana ordination instead of the Canoco version. Pearson product moment correlation, multiple regressions and analysis of variance were carried out using functions *cor.test*, *lm*, *aov* and *anova* in S-PLUS vers. 3.3 (Statistical sciences 1995) and Kendall rank correlation was computed using *proc corr* in SAS vers.6.11 (1989). Rank correlation statistics was chosen based on the reasoning that relationships among variables and between axes and variables are not necessarily linear.

To evaluate the consistency of gradients revealed by DCA in the full data-set, eight subsets were also subjected to DCA. These were extracted from the full set as follows:

1. *Common species*, here defined as species present in at least 75 samples (617 samples, 69 species).
2. *Subordinate species*, here defined as species with a maximum average frequency when present of 0.35 (107 species, 450 samples).
3. *Dominant species* here defined as species present in at least 5 samples and with a minimum mean frequency of 0.45 (64 species, 610 samples).
4. *Acidic grasslands* (samples with a pH<6.8, 305 samples, 290 species).
5. *Calcareous grasslands* (samples with pH>6.2, 367 samples, 357 species).
6. *N-Jutland* (samples from Thy, Hanherred and Himmerland, collected 1942-1946; 203 samples, 270 species).
7. *E-Jutland* (Samples from the unpublished Djursland material, collected 1994-1995; 148 samples, 217 species).
8. *Zealand* (Samples from Zealand and Møn, collected 1944-1954; 119 samples, 231 species).

Results

Outliers, although potentially interesting, are unwanted in DCA as they can cause axes distortions resulting in exceptions overruling general patterns. In this study we defined and calculated the isolation of a sample as *the mean distance of that sample to the sixth to 15th closest samples on each axis*. Figure 3 shows the distribution of samples corresponding to different degrees of isolation. The distribution has a long tail, and we decided to omit the six most outlying samples. The effect of omitting outliers was pronounced, especially on axes 3 and 4 (fig. 3). Excluding the next most outlying samples did not affect the DCA-axes markedly. By the same iterative method, we removed from one to six outliers from the eight subsets prior to the ordination reported on below.

Table 3 shows, for all data-sets, eigenvalues, total inertia (TI) and percentage variation explained by DCA$^{1\text{-}4}$. The full data-set was found to have a high TI and only 8.3 % variation explained by DCA$^{1\text{-}4}$. This ratio was apparently influenced by infrequent species: as much as 24.1% of variation was explained in the subsets containing only the common species. Figures for explained variation in the re-

Table 3. Eigenvalues, TI and explained variation in ordination of the full dataset and 8 subsets.

Data	DCA^1	DCA^2	DCA^3	DCA^4	TI	%Expl.var.
	EGV	EGV	EGV	EGV		
Full set	0.44	0.37	0.29	0.23	16.0	8.3
Common species	0.36	0.27	0.16	0.15	3.9	24.1
Subordinate species	0.62	0.49	0.42	0.36	23.3	8.1
Dominant species	0.42	0.32	0.24	0.21	6.7	17.8
Acidic grasslands	0.41	0.31	0.26	0.25	11.0	11.2
Calcareous grasslands	0.44	0.35	0.28	0.21	13.7	9.2
E-Jutland	0.49	0.35	0.20	0.18	6.8	17.8
N-Jutland	0.43	0.34	0.25	0.21	10.3	11.9
Zealand	0.52	0.41	0.25	0.21	9.8	14.1

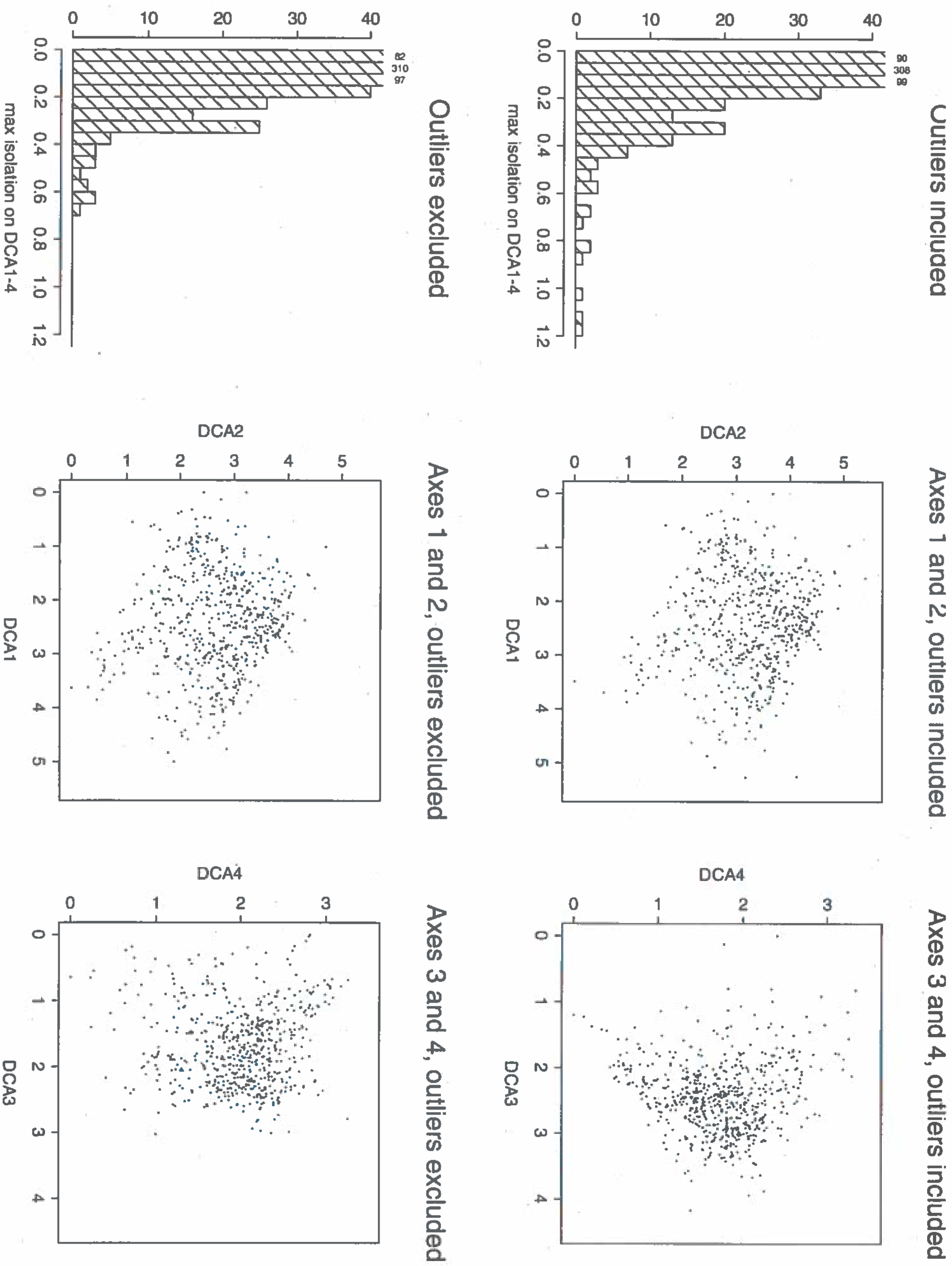

Figure 3. The effect of outliers. The first row shows, for the original set, a histogram of maximum isolation in S.D.units of samples, and scatterplots of the first four DCA-axes. The second row shows the same features after removal of the six most outlying samples.

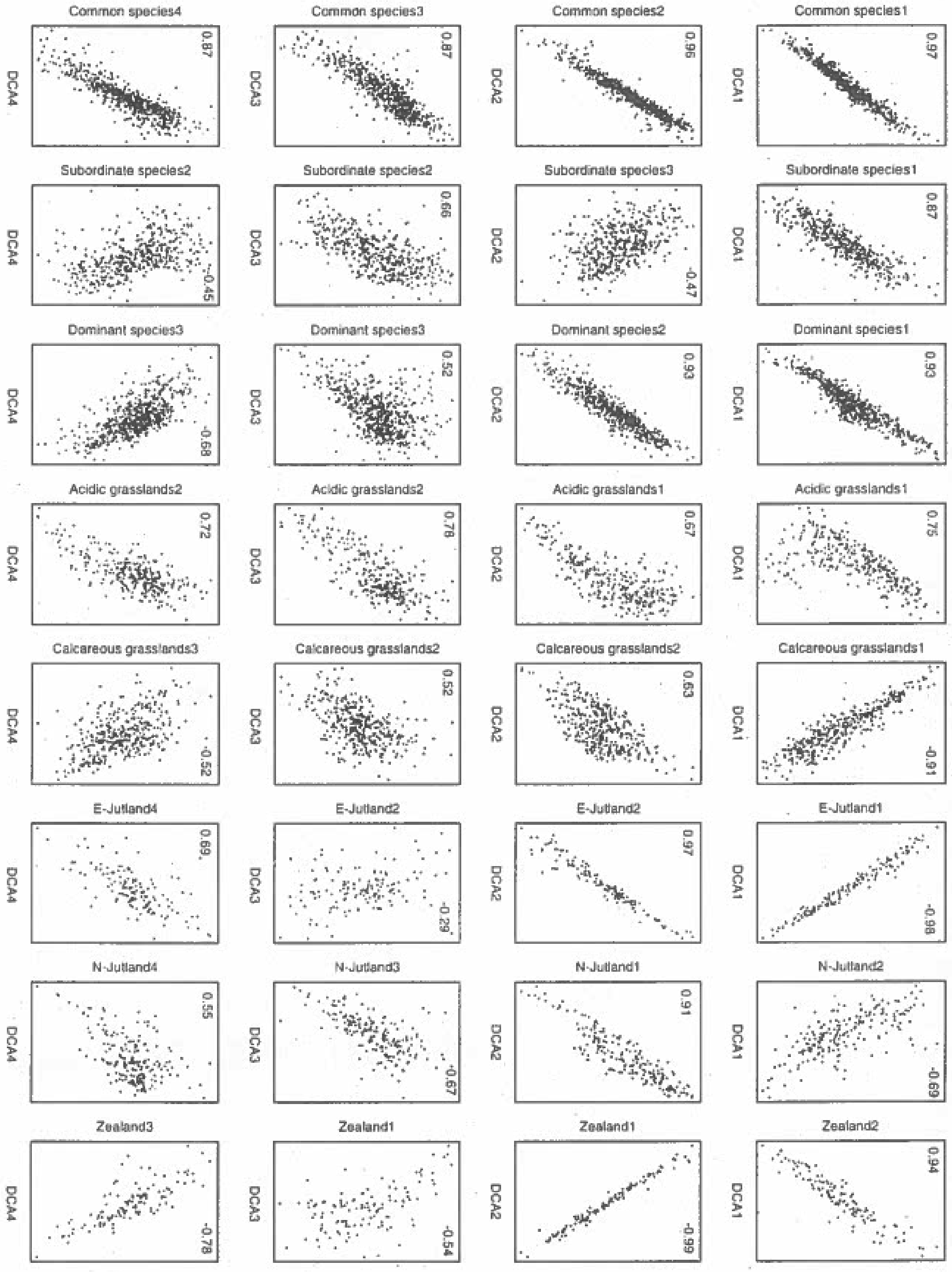

Figure 4. Evaluation of DCA coenoclines by subset ordinations. The four rows represent scatterplots of the four DCA-axes of the full set against the best correlated of the first four DCA axes within the 8 subsets. Coefficients of the Pearson product moment correlation are indicated in the plots.

gional subsets were considerably larger than in the full data-set (tab 3), which indicates that also regional differences constitute part of the residual variation of the full set.

We saw no reasons for initial discarding of any of the four DCA axes as eigenvalues showed a gradual decline from axes one to four and all gradient lengths exceeded 3 S.D.units (unimodal response model justified). No polynomial distortions were detected by visual inspection of axes (fig. 3), and only a tendency of a double sided "tongue effect" could be hypothesised on axes 1-2. CANOCO has no option for extracting more than 4 axes and therefore two alternative fifth axes were extracted by non-standard methods. First, an additional axis was extracted using DCA$^{1-4}$ as covariables. Secondly, DCA^{1} was run as covariable during the extraction of four additional axes, the fourth of which was examined as a potential fifth axis. However CANOCO has no detrending option for covariables, so the first method resulted in a CA-axis with an unrealistic high eigenvalue, exceeding that of DCA^{4}. The latter produced an axis with a reasonably low eigenvalue, but both methods resulted in a fifth axis showing strong rank correlation with standard DCA-axes of higher order, and the fifth axis was therefore left out of further consideration.

A scatterplot matrix of DCA$^{1-4}$ in the full data-set against the best correlated axes in all subsets (fig.4) revealed that the major coenoclines DCA$^{1-2}$ were also prominent in most subsets. Although all correlations were highly significant, DCA^{1} was reproduced less convincingly in the acidic grasslands and in northern Jutland. A clear DCA^{2} was only absent in the subordinate species and the calcareous subsets. The order of the first two axes was reversed for the Zealand and the N-Jutland subsets. DCA$^{3-4}$ were less clearly reproduced although significant elements of these coenoclines were reflected in all subsets.

Table 4 shows a correlation matrix of the explanatory variables including many significant correlations. Some of these are self evident such as the positive correlation between species number and species density. The negative correlation between *northing* and *easting*, needs further explanation: from the site map (fig.1) it appears that sampling has been concentrated in a broad band oriented southeast to northwest.

Table 5. Correlation between explanatory variables and DCA$^{1-4}$. Kendall Rank Correlation .*=P<0.001, *=P<0.0001.

	DCA1	DCA2	DCA3	DCA4
DCA1	1	-0.03	0.1*	-0.01
DCA2	-0.03	1	-0.01	-0.02
DCA3	0.1*	-0.01	1	-0.05
DCA4	-0.01	-0.02	-0.05	1
pH	-0.55**	0.29**	-0.19**	0.07
pH^{c}	-0.47**	0.42**	-0.28**	-0.04
CONTINENTALITY^{c}	-0.50**	0.15**	-0.31**	-0.1*
SLOPE	-0.26**	0.28**	-0.09	0.00
WATER^{c}	0.39**	0.35**	0.14**	-0.17**
IRRADIATION 1/3	-0.38**	-0.23**	-0.06	0.04
LIGHT^{c}	-0.38**	-0.22**	-0.05	0.19**
TEMP^{c}	-0.43**	-0.26**	-0.01	0.08
IRRADIATION 23/6	-0.02	-0.39**	0.00	0.0
COMPETITION^{c}	0.01	0.09*	0.07	-0.57**
NITROGEN^{c}	-0.05	0.39**	0.23**	-0.37**
STRESS^{c}	0.22**	-0.03	-0.23**	0.33**
DISTURBANCE^{c}	-0.29**	-0.05	0.26**	0.00
EASTING	-0.18**	-0.09*	0.07	-0.15**
NORTHING	0.27**	0.02	-0.17**	0.08
PRECIPITATION * Y^{-1}	0.25**	0.03	-0.27**	0.12**
PRECIPITATION MAY-JULY	0.16**	0.08	-0.24**	0.12**
GROWTH DAYS	-0.04	-0.11*	0.50**	-0.01
ANNUALS	-0.52**	-0.14**	0.04	0.22**
PERCENT ANNUALS	-0.50**	-0.18**	-0.00	0.23**
SPECIES NUMBER	-0.03	0.30**	0.01	0.22**
SPECIES DENSITY	0.09	0.22**	0.09*	0.32**

Table 6. Inclusion order and F-values of factor variables in A OVAs with respect to DCA$^{1-4}$. For comparison with continuos variables, factor conversions of two of the most influential co tinuos variables are included for each axis. Number of factor els in parenthesis. Levels of significance: *=P<0.001, **=P<0.0

	DCA1		DCA2		DCA3		DCA4	
	No	F	No	F	No	F	No	
SOIL (5)	4	2	1	**99****	1	**123****	3	28
REGION (13)	3	17**	5	4**	2	39**	4	6
COAST (3)	5	1	4	13**	4	9**	5	
PH(3)	1	**562****	3	24**	3	31**		
IRRADIATION1/3 (3)	2	**177****						
IRRADIATION23/6 (3)			2	51**				
GROWTH DAYS (5)					5	0.05		
COMPETITION (3)							1	**34**
NITROGEN (3)							2	29

Table 4. Correlation among explanatory variables. Kendalls tau is given together with levels of probability *= 0.001,**=0.0001. Correlations with tau > 0.3 are in bold. The presence of four clusters of inter-correlated variables is indicated in bold frames.

	pH	pH^{c}	Contin.^{c}	Slope	Water^{c}	Irra1/3	Light^{C}	Temp^{C}	Irra23/6	Compet^{C}	N^{C}	Stress^{C}	Disturb^{C}	East	North	PrecY^{-1}	PrecM-J	Gdays	Annuals	Dens.ann.	Sp.N.
pH	1																				
pH^{c}	**0.60****	1																			
Contininentality^{c}	**0.45****	**0.53****	1																		
Slope	**0.35****	**0.32****	0.24**	1																	
Water^{c}	-0.12**	-0.03	-0.20**	-0.01	1																
Irradiation 1/3	0.16**	0.12**	0.18**	0.11*	**-0.39****	1															
Light^{c}	0.21**	0.08	0.20**	0.06	**-0.39****	-0.28**	1														
Temperature^{c}	0.21**	0.08	0.17**	0	**-0.41****	**0.38****	**0.40****	1													
Irradiation 23/6	-0.16**	-0.17**	-0.06	-0.53**	-0.23**	**0.33****	0.11**	0.25**	1												
Competition^{c}	-0.02	0.08	0.09*	0.01	0.25**	-0.03	-0.13**	-0.08	-0.01	1											
Nitrogen^{c}	0.13**	0.23**	0.09	0.13**	**0.41****	-0.16**	-0.19**	-0.14**	-0.21**	**0.42****	1										
Stress^{c}	-0.14**	-0.14**	-0.13**	-0.03	-0.12**	-0.07	-0.14**	-0.19**	-0.02	**-0.46****	**-0.46****	1									
Disturbance^{c}	0.19**	0.09	0.08	0.03	-0.03	0.12**	0.29**	0.31**	0.04	0.02	0.25**	**-0.57****	1								
Easting	0.03	0.01	0.05	-0.01	-0.19**	0.04	0.14**	0.15**	0.03	0.12**	-0.03	-0.11**	0.06	1							
Northing	-0.13**	-0.07	-0.07	-0.05	0.17**	-0.10*	-0.17**	-0.18**	0	-0.09	-0.04	0.18**	-0.16**	**-0.62****	1						
Precipitation*Y^{-1}	-0.13**	-0.05	-0.04	-0.09	0.17**	-0.07	-0.17**	-0.18**	0.04	-0.12*	-0.09	0.23**	-0.22**	**-0.52****	**0.63****	1					
Precipit. May-July	-0.06	0	-0.02	-0.09	0.08	-0.1	-0.13**	-0.12*	0.03	-0.12**	-0.12**	0.24**	-0.24**	-0.22**	**0.39****	**0.69****	1				
Growth days	-0.06	-0.15**	-0.22**	-0.11*	-0.04	0.01	0.05	0.14**	0.07	0.03	0.06	-0.16**	0.20**	0.27**	**-0.38****	**-0.47****	**-0.34****	1			
Number of annuals	**0.33****	0.17**	0.18**	0.12**	-0.38**	0.31**	0.39**	0.49**	0.11*	-0.24**	-0.08	-0.16**	0.42**	0.12**	-0.18**	-0.21**	-0.16**	0.11*	1		
Annual percentage	**0.32****	0.15**	0.18**	0.09	-0.38**	0.33**	0.42**	0.53**	0.13**	-0.24**	-0.11**	-0.18**	0.45**	0.10*	-0.17**	-0.18**	-0.15**	0.1	**0.75****	1	
Species number	0.14**	0.19**	0.01	0.10*	0.05	-0.13**	-0.03	-0.07	-0.16**	-0.21**	0.04	0.09	0.05	-0.02	0.04	0.05	0.13**	-0.07	0.21**	0.07	1
Species density	0.04	0.05	-0.11**	-0.02	0.10*	-0.16**	-0.04	-0.08	-0.11*	-0.30**	0.01	0.11**	0.1*	-0.18**	0.13**	0.12*	0.09	0.01	0.15**	0.06	**0.63****

The strongest of the remaining correlations were grouped in what we recognised as four main clusters: 1) *pH and continentality*, 2) *water availability and topoclimate*, 3) *fertility and competition* and 4) *regional features* (table 4). The correlation between water^{c} and nitrogen^{c} constitute a link between the second and third cluster.

Table 5 and 6 show correlations between DCA$^{1-4}$ sample scores and the variables. DCA^{1} was correlated with pH & continentality^{c} and topoclimate, ranging from warm and dry calcareous slopes with many annuals and species with a subcontinental European distribution to cool and humid, acidic grasslands with predominance of species with a relatively oceanic European distribution. Along DCA^{2}, pH and water^{c} combined in the opposite way. With low scores were found relatively fertile grasslands on clay, limestone and occasionally diluvial sand with good water supply, and in the opposite end were found the notoriously infertile, dry grasslands on marine and eolian sand (see also fig.5). It should be acknowledged that Ellenbergs N-value should be interpreted as a general fertility indication, rather than as a precise index of nitrogen availability (Ellenberg et al. 1992).

DCA$^{3-4}$ were less consistent across the subsets and should be interpreted with caution. DCA^{3} correlated with soil type and region (tab.6 & fig.5), the one extreme being characterised by grasslands of high pH on infertile marine sand and limestone with a continental element in the vegetation, and the other by grasslands of lower pH on relatively fertile sand and clay. Being fitted fifth in the ANOVA (table 6), *number of growth days* were found to be almost completely aliased to *region*, suggesting that local climate could be re-

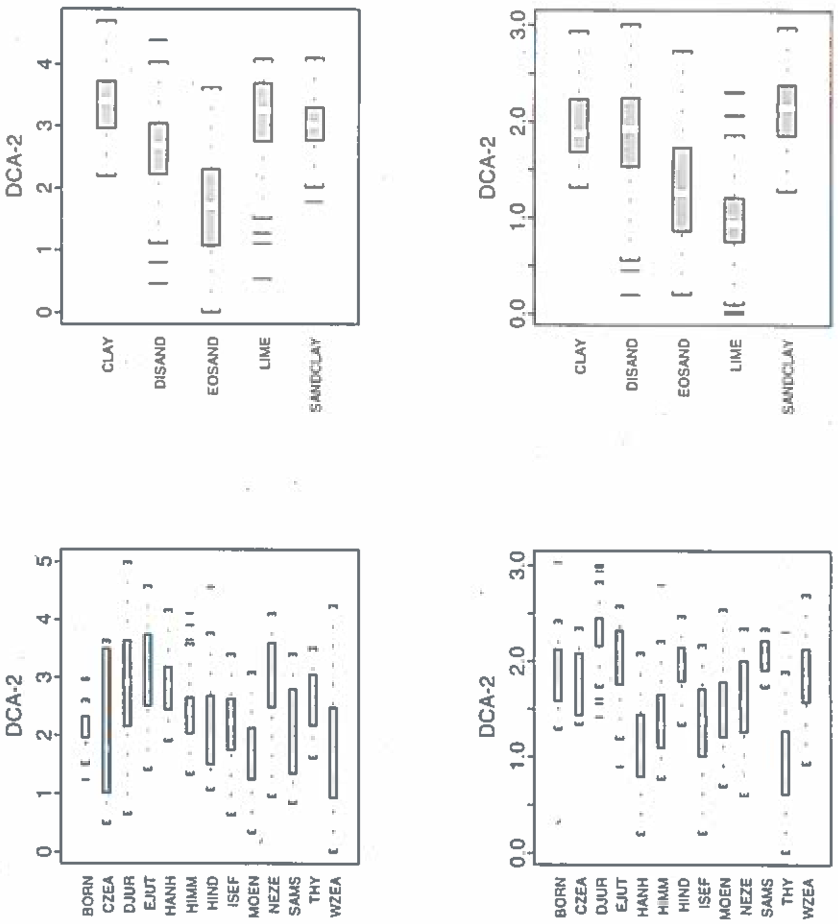

Figure 5. Factor plots of soil and region with respect to relevant DCA-axes (cf. table 6). The boxes cover the interquartile range, and the whiskers (dotted lines) extend to the extreme values or 1.5 x the interquartile range, whichever is less. Horizontal ticks indicate samples with extreme values.

sponsible for some of the regional element in DCA^3. DCA^4 was highly negatively correlated with competition^c and nitrogen^c and positively with stress^c (tab. 5).

The vegetation descriptive variables were also related to ordination axes: The ecocline along DCA^1 was of very significant importance for the annuals, and the coenoclines of DCA^1, DCA^2 and DCA^4 produced conspicuous species density patterns (fig 6). No significant patterns were detected along DCA^3. Species density was modelled in terms of the most influential calibrated variable along each axis (continentality^c, nitrogen^c and competition^c) and graphed along with the matching histograms of the number of Danish grassland

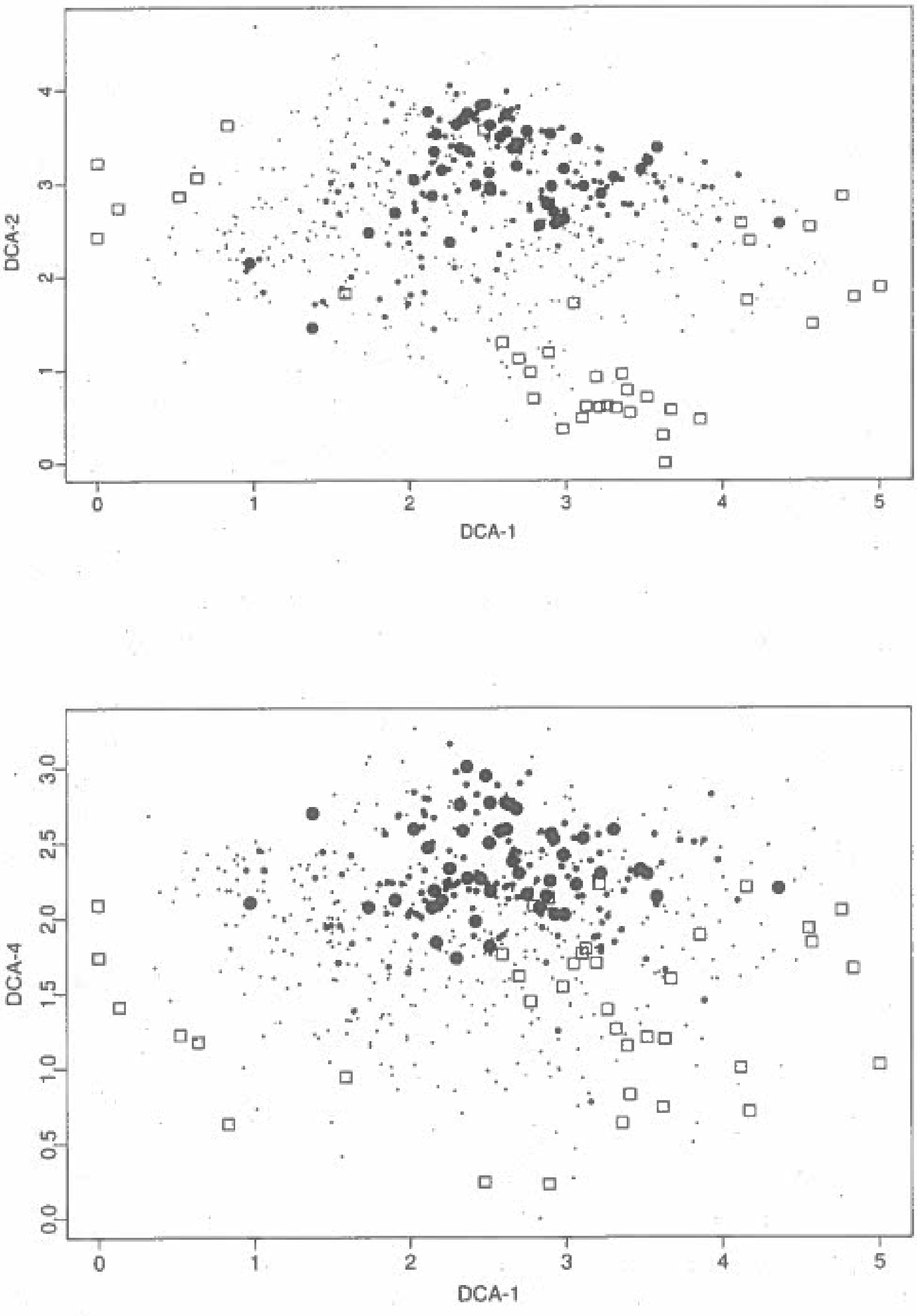

Figure 6. Species density in coenoplanes. Only DCA 1, 2 and 4 are shown, DCA 3 did not correlate with species density. Open quadrates correspond to samples with an average of less than 5 species per 0.1 m2, small dots correspond to an average of between 5 and 15 species, medium dots indicate more than 15 species and large dots more than 20 species.

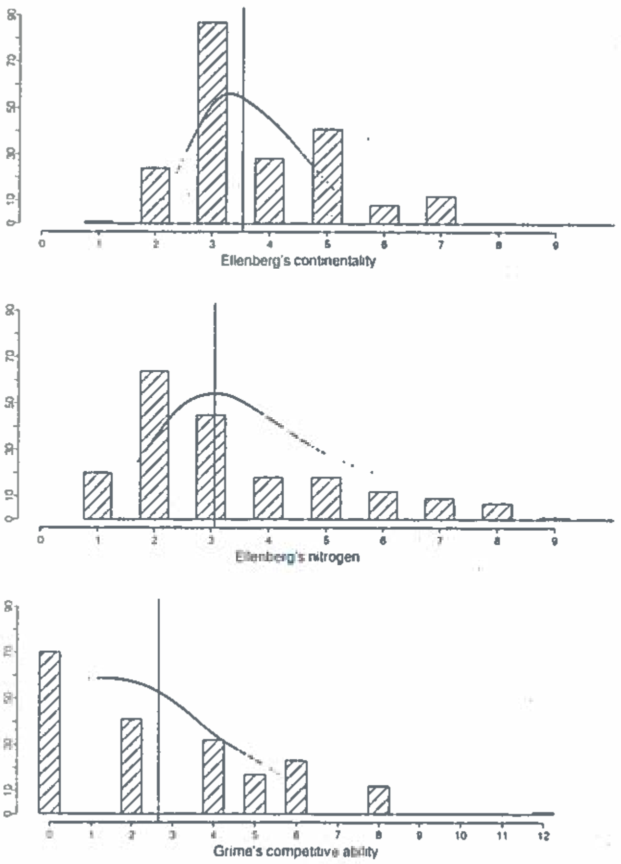

Figure 7. Species density. Histograms show the number of grassland species (only species with more than 5 occurrences included) corresponding to the different levels of the relevant variable. Superimposed curves show predictions of species density corresponding to that indicator variable (augmented by a factor 4), based on a model allowing a smoothed response. A vertical line indicates the weighted average of all species indicator values weighted by their number of occurrences in the data-set.

species corresponding to the levels of these variables (fig. 7). A marked coincidence was found between predicted species density and actual number of grassland species (regional species pool) along these three gradients.

The consistency of the first two coenoclines across species groups, study areas and study years, encouraged us to model these in environmental terms. Most relationships were found to be linear, and a simple transformation of pH justified the use of multiple linear regression. Table 7 shows ANOVA tables, comparing for each coenocline models including one to four terms added sequentially by forward selection from all variables (with the exception that closely related measured variables were preferred to calibrated variables when of comparable strength). The tables also include r^2 for the fit of each model. Figure 8 and 9 show plots of the models and their fitted single terms (for factor variables compare with figure 5). the model of DCA^1 was convincing: as much as 70% of sample score variation was explained by only two environmental variables, pH and irradiation March 1 (tab.7). Continentality was partly aliased to pH and irradiation, which somewhat masked its strong correlation with DCA^1. DCA^2 was less clear - first we needed to incorporate a calibrated variable in the model (nitrogen^c), and after fitting four variables, approximately one third of the variation in sample scores still remained unexplained (tab.7). The less convincing fit of this model might be due to the lack of precise indications of site fertility, a difficult variable to cope with.

Table 7. ANOVAs comparing successively more complicated multiple regression models including up to the four most important variables (selected by forward selection). Fraction of variation explained by fit (r^2) in last column. Degree of freedom, sum of squares, F-values and probability levels relate to the added variable.

Response: DCA^1

Terms	Test	Df	SS	F Value	Pr(F)	r^2
1/pH		1	279.5	1848	< 0.00001	0.56
1/pH + irradiation 1/3	**+irrad 1/3**	1	71.6	473	< 0.00001	0.71
1/pH + irradiation 1/3 + continentality^c	**+cont**	1	26.5	175	< 0.00001	0.76
1/pH + irradiation 1/3 + continentality + region	**+region**	12	36.4	20	< 0.00001	0.83

Response: DCA^2

Terms	Test	Df	SS	F Value	Pr(F)	r^2
Nitrogen^c		4	138.3	175.6		0.39
Nitrogen^c + soil type	**+soil**	4	65.8	83.5	< 0.0000	0.59
Nitrogen^c + soil type + (irradiation23/6)^2	**+(irrad 23/6)^2**	2	19.9	50.6	< 0.0000	0.66
Nitrogen^c + soil type + (irradiation23/6)^2 + pH	**+pH**	1	6.4	32.5	< 0.0000	0.69

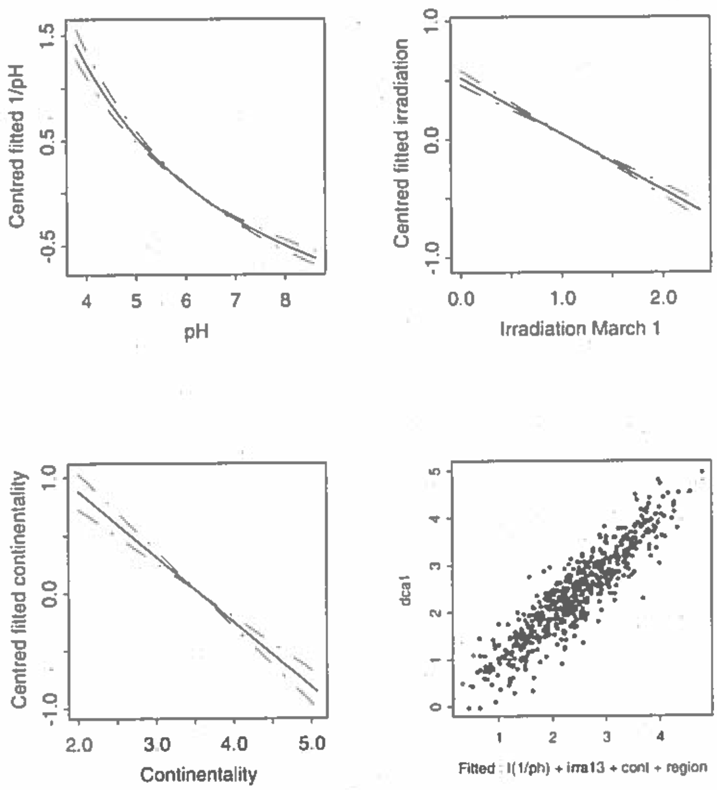

Figure 8. Fits of three centered single terms of the linear model of DCA¹, including pointwise twice standard error bands, and DCA¹ plotted against the fitted model.

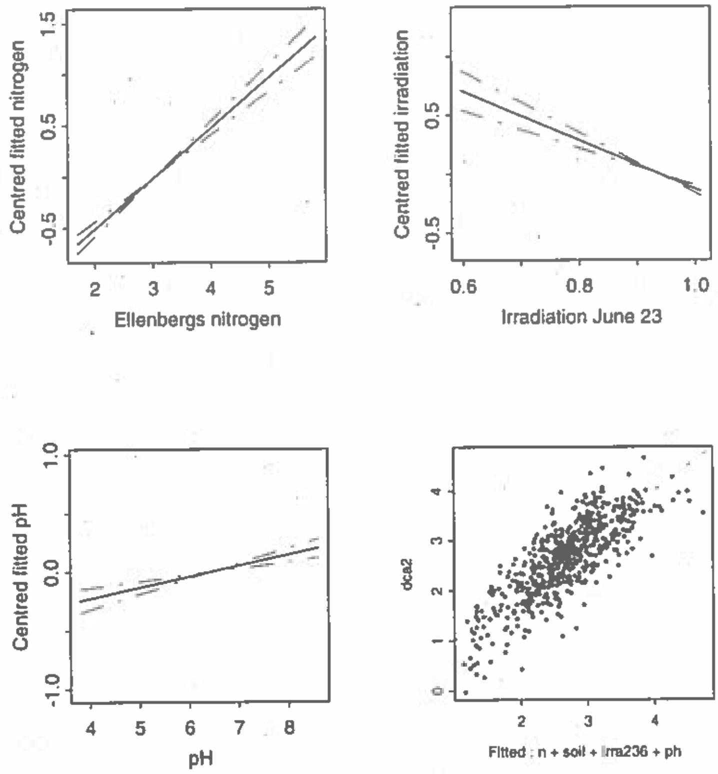

Figure 9. Fits of three single terms of the additive linear model of DCA² including residuals, and DCA² plotted against the fitted model.

Discussion

Methods

Lately, Canonical correspondence analysis (CCA) has gained in popularity and is held by many ecologists as the most powerful tool for gradient analysis purposes (e.g. ter Braak & Prentice 1988, Palmer 1993). We support the alternative view stated by Økland (1996), that indirect methods, like CA and DCA, are fundamentally different from CCA, and that choice of method should depend on the objective of the study. CCA deliberately discards the very important residual variation by constraining coenoclines to be linear combinations of variables. This could easily lead to distortion of the complex gradients present in the vegetation data, especially if the environmental data are sparse. Secondly, as demonstrated in this study, relationships between environmental variables and major coenoclines are not necessarily linear. Therefore, when general gradient analysis is the objective, indirect methods should be the first choice.

The high total inertia (TI) compared to the eigenvalues of DCA$^{1-4}$ questions the multivariate approach to vegetation science adopted in this study. However, the ordination has been shown to make ecological sense, resulting in consistent and interpretable grassland coenoclines, and it is thus the large TI that calls for an explanation. The decrease in residual variation in regional subsets and subsets excluding uncommon species, indicates that "noise" is generated by local species pools and stochasticity in species occurrences (especially regarding uncommon species). In addition, polynomial distortions (detrending is only performed with respect to axis 2-4) and species responses differing from the assumed unimodal symmetrical response (e.g. Austin et al. 1994) are likely to contribute considerably to TI.

In large data-sets, correlation between coenoclines and environmental variables (including permutation statistics in CCA) tend to be extremely significant, and this condition is not changed substantially by applying e.g. Bonferoni corrections. A highly significant correlation does not however guarantee that the result can be reproduced under slightly different conditions. We therefore support the idea of Lawesson (1997) that subsets of species data can be used to validate or moderate conclusions obtained in gradient analysis, and in this study we extend subset ordination to include also geographical and ecological subsets of the data.

Ordination

Earlier attempts to interpret ordination axes within the framework of plant strategy theory has been fruitful (del Moral 1983, Oksanen & Ranta 1992). In this study DCA$^{1-2}$ did not reproduce the CSR-strategy theory as defined by Grime (1974). DCA^{1} did show significant correlation with disturbance^{c}, but disturbance^{c} was confounded with the better correlated variables *irradiation* and *pH*.

The turnover along the axis from continental to oceanic species accompanied by increased moisture and acidification is a striking feature of the axis, leading to the suggestion of a "trans-ecosystem" gradient behind DCA^{1}: in the dry, calcareous axis end, topoclimate and mineral soils favour the continental type grasslands with high species turnover rates, and frequent drought episodes allowing for annuals as a major vegetation component. In the opposite end, the relatively oceanic grass heath is favoured. This coincidence of relatively continental species and dry calcareous soils is rarely discussed in current ecological literature, but Sterner (1922) gave it a comprehensive treatment. The significance of continentality in the flora was also recognised by Böcher (1945), who based his classification of grassland vegetation largely on the occurrence of species with a characteristic geographical distribution, e.g. subcontinental or oceanic.

Surprisingly, no correlation with stress^{c} or competition^{c} was found along the fertility ecocline (DCA^{2}). As a partial explanation we suggest that most of the sampled communities has been influenced by grazing; especially the relatively fertile grasslands, that would grow into scrub without grazing. Grime (1979) defines grazing as a disturbance and grazing is therefore predicted to reduce the intensity of competition. However, grazing is not predicted to increase stress levels, so in this particular case our results conflict with CSR-strategy theory, lending some support to alternative views (e.g. Oksanen & Ranta 1992) suggesting a different role for grazing. We would suggest that moderate grazing acts to reduce the benefits of the pure C, S and R strategies: Relative fast regrowth following a defoliation is advantageous, yet fast growing, erect growth forms will be eliminated. The effect of grazing will of course depend on the intensity and frequency of grazing, but we suggest, that moderate repeated grazing favours the stress tolerators relative to the competitors and ruderals in unimproved temperate grasslands.

The regional element in DCA^3 makes this ecocline less obvious to interpret in a plant strategy context. Along the fourth coenocline (DCA^4), a strong expression of competition^c and stress^c was found, accompanying nitrogen^c as expected from theory. The low rank of competition as a vegetation structuring force found in this study, is hypothesised to result from the comparatively low fertility of dry unimproved grasslands. In many of these grasslands the first C-strategists to appear in a successional sequence will be shrubs and trees, and they are not represented in our analyses.

Seen in a local scale perspective, the diversity response along DCA^2 and DCA^4 are consistent with expectations based on theory (Grime 1979) and experiments on productivity gradients (Campbell and Grime 1992, Tilman 1993): high α-diversity was found with low intensity of competition (DCA^4) and the diversity pattern along the *fertility ecocline* (DCA^2) is in accordance with the expectation of a positive effect of fertility in the lower end of the productivity range (Grime 1973, Al-Mufti et al. 1977). The diversity response along the *continentality ecocline* (DCA^1) is harder to interpret in terms of local interactions, although it could be argued, that *dominance* in terms of biological control over nutrient cycling could explain the low α-diversity in humid acidic grassland, and a harsh environment with frequent episodes of drought could account for the low α-diversity in the "continental type grassland".

Figure 7 suggests a very simple alternative explanation of α-diversity, that is in accordance with the species pool hypothesis (Taylor et al. 1990, Zobel 1997). The striking coincidence between predicted species density and the estimated size of the regional species pool, almost seems to render local scale explanations superfluous. It makes biological sense to interpret the diversity patterns along DCA^1 in terms of species pool size, but figure 6 indicates that the species pool hypothesis cannot stand alone. Along DCA^2 we see a positive effect of fertility, whereas the opposite is the case along DCA^4. The biological interpretation of this apparent contradiction is clear: we should expect the highest species density to occur in moderately fertile grasslands - as long as the intensity of competition is kept low, e.g. by grazing!

The present study demonstrates the benefits of both the *local scale* and the *species pool* perspective, and we believe that both viewpoints are necessary to reach an understanding of the mechanisms behind diversity. Experimental studies investigating their relative importance should be encouraged, together with the formulation of a consistent species pool theory incorporating ecological, historical and evolutionary explanations of species pool size.

Acknowledgements

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Literature

Al Mufti, M.M., Sydes, C.L., Furness, S.B., Grime, J.P. & Band, S.R. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *J. Ecol.* 65: 759-792.

Andersen, P. 1980. Comments on "monthly average insolation on tilted surfaces" by S.A. Klein. *Solar Energy. Vol* 25: 287.

Austin, M.P., Nicholls, A.O., Doherty, M.D. & Meyers, J.A. 1994. Determining species response functions to an environmental gradient by means of a β-function. *J.Veg.Sci.* 5: 215-228.

Bruun, H.H. & Ejrnæs, R. 1993. *Naturtypen overdrev - vegetationen og dens forudsætninger.* M.Sc. thesis, Department of Botany, University of Copenhagen.

Böcher, T.W. 1935. Om en Metode til Undersøgelse af Konstans, Skudtæthed og Homogenitet (Summ.: On a method for investigating constancy, shoots density and homogeneity). *Bot.Tiddskr.* 43: 278-303.

Böcher, T.W. 1945. Beiträge zur Pflanzengeographie und Ökologie dänischer Vegetation. 11. Über die Waldsaum- und Graskrautgesellschaften trockner und halbtrockener Böden der Insel Seeland mit besonderer Berücksichtigung der Strandabhange und Strandebenen. *Kgl.Dan.Vidensk.Selsk., Biol.Skr.IV*, 1. 1-163.

Böcher, T.W.. 1946. Græs-Urte-Vegetationen paa Høje Møn (Summ.: Grassland communities of »Høje Møn«). *Bot.Tidsskr.* 48: 1-45.

Böcher, T.W. 1947. Festuca polesica Zapal., its Chromosome Number and Occurrence in Denmark. *Botaniska Notitser* 1947(4): 353-360.

Böcher, T.W. 1957. *Jordbund og skræntvegetation ved Bornholms sydkyst*. Bornholms naturhistoriske forening, udgivet i anledning af 25 års jubilæet.

Böcher, unpubl. *Field notes on slope vegetation on the island of Bornholm*. (Bot. Centralbibl., Copenhagen).

Böcher, T.W., T.Christensen, M.S.Christiansen. 1946. Slope and Dune Vegetation of North Jutland. I. Himmerland. *Kgl.Dan.Vidensk.Selsk., Biol.Skr.IV*, 3. 1-78.

Böcher, T.W., T.Christensen, M.S.Christiansen. Unpubl. Slope and Dune Vegetation of North Jutland. II. *Manuscript (Bot. Centralbibl., Copenhagen).*

Böcher, T.W. & Weis Bentzon, M. 1958. Density determination in plant communities. *Oikos* 9:1, pp 35-56.

Campbell, B.D. & Grime, J.P. 1992. An experimental test of plant strategy theory. *Ecology* 73: 15-29.

Cramer, W & Hytteborn, H. 1987. The separation of fluctuation and long-term change in vegetation dynamics of a rising seashore. *Vegetatio* 69: 157-168.

del Moral, R. 1983. Vegetation ordination of subalpine meadows using adaptive strategies. *Can. J. Bot.* 61: 3117-3127.

Eilertsen, O. 1991. Vegetation patterns and structuring processes in coastal shell-beds at Akerøya, Hvaler, SE Norway. *Sommerfeltia* 12: 90 p.

Ejrnæs, R. & Bruun, H.H. 1995. Prediction of grassland quality for environmental management. *J. Env. Mgmt*. 43: 171-183.

Ellenberg, H., 1974. Zeigerwerte der Gefässpflanzen Mitteleuropas. *Scripta Geobotanica* 9: 122 p.

Ellenberg, H, Weber, H.E., Düll R.., Wirth, V., Werner, W., Paulissen, D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica vol 18*. Datenbank.

Fredskild, B. 1954. Ecological and Floristic Studies on Dry Sand Slopes in Western Sealand. *Oikos* 5: 205-235.

Grime, J.P., 1973. Control of species density in herbaceous vegetation. *J. Env. Mgmt.*, 1: 151-167.

Grime, J.P., 1974. Vegetation classification by reference to strategies. *Nature* 250: 26-31.

Grime, J.P. 1979. *Plant strategies and vegetation processes*. Chichester: Wiley.

Grime, J.P., Hodgson, J & Hunt, R. Unpubl. FIBS: *An extended version of the Electronic Comparative Plant Ecology*. NERC, University of Sheffield, 1996.

Grime, J.P., Mackey, J.M.L., Hillier, S.H. & Read, D.J. 1987. Floristic diversity in a model system using experimental microcosms. *Nature* vol. 328: 420-422.

Hill, M.O. DECORANA: *A FORTRAN program for detrended correspondence analysis and reciprocal averaging*. Cornell University, Ithaca, NY.

Iqbal, M. 1983. *Introduction to solar radiation*. Academic Press.

Klein, S.A. 1977. Calculation of monthly average insolation on tilted surfaces. *Solar Energy* vol. 19: 325-329.

Krahulec, F. Rosen, E. & Van der Maarel, E. 1986. Preliminary classification and ecology of dry grassland communities on Ölands Stora Alvar. *Nord. J. Bot*. 6: 797-809.

Lawesson, J. 1997. Effects of species partition on explanatory variables in direct gradient analysis - a case study from Senegal. *J. Veg. Sci*.8:409-414.

Mortensen, M.B. 1953. Urtesamfund på skrænter på Hindsholm (Summ.: Grassland Communities on the Slopes of Hindsholm). *Bot.Tidsskr*. 49: 239-259.

Mortensen, M.B. 1955. Urtesamfund på skrænter på Nord-Samsø (Summ.: Grassland Communities on Slopes in Northern Samsø). *Bot.Tidsskr*. 52: 85-112.

Oksanen, J. & Minchin, P. 1997. Instability of ordination results under changes in input data order: explanations and remedies. *J.Veg Sci*. 8: 447-454.

Oksanen, L. & Ranta, E. 1992. Plant strategies along mountain vegetation gradients: A test of two theories. *J. Veg. Sci* 3:175-186.

Palmer, M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* 74: 2215-2230.

Pärtel, M., Zobel, M., Zobel, K. & van der Maarel, E. 1996. The species pool and its relation to species richness: evidence from Estonian plant communities. Oikos 75: 111-117.

Persson, S. 1981. Ecological indicator values as an aid in the interpretation of ordination diagrams. *J.Ecol.* 69: 71-84.

Raunkiær, C. 1909. Formationsundersøgelse og Formationsstatistik. *Bot.Tidsskr.* **30**: 20-132 (Chapt.VI. *Investigations and statistics of plant formations*, in: C. Raunkiær. 1934. *The Life Forms of Plants and Statistical Plant Geography, being the collected papers of C.Raunkiær.* Oxford University Press; p. 201-281).

SAS Institute Inc. 1989. *SAS/STAT User's Guide*, Version 6, Fourth Edition, Vol. 1, Cary, NC: SAS Institute Inc., 846 pp.

Schmida, A. & Ellner, S. 1984. Coexistence of plants with similar niches. *Vegetatio* 58, 29-55.

Statistical Sciences 1995. Inc. *S-PLUS version 3.3 for Windows*. Seattle: Statistical Sciences, Inc.

Sterner, 1922. The continental flora of South Sweden. Geografiska Annaler 4: 221-441.

Taylor, D.R., Aarsen, L.W., Loehle, C: 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. Oikos 58: 239-250.

ter Braak, C.F.J. 1991. *CANOCO - a FORTRAN program for Canonical Community Ordination*. Version 3.12. Microcomputer Power, Ithaca NY.

ter Braak, C.F.J. & Prentice, I.C. 1988. A theory of gradient analysis. *Adv.Ecol.Res.*18: 271-317.

Tilman, D. 1993. Species richness of experimental productivity gradients: How important is colonization limitation? *Ecology* 74: 2179-2191.

Tutin, T.G. et al. 1964-1980. *Flora Europaea*. Cambridge University Press, Cambridge.

Van der Maarel, E., Noest, V. & Palmer, M.W. 1995. Variation in species richness on small grassland quadrats: Niche structure or small-scale plant mobility? *J.Veg.Sci.* 6: 741-752.

Vestergaard P & Hansen, K. (eds.) 1989. Distribution of vascular plants in Denmark. *Opera Botanica* 96.

Westhoff, V. & Van der Maarel, E. 1978. *The Braun-Blanquet approach*. In: Whittaker (ed.) Classification of plant communities, pp. 287-399. Junk, The Hague.

Wilson, J.B., Sykes, M.T. & Peet, R.K. 1995. Time and space in the community structure of a species-rich limestone grassland. *J.Veg.Sci.* 6: 729-740.

Wind, P. & Ballegaard, T. 1996. *Overvågning af overdrev 1995*. Arbejdsrapport fra DMU nr. 21. Naturovervågning. Miljøministeriet.

Zobel, M. 1992. Plant species coexistence - the role of historical, evolutionary and ecological factors. *Oikos* 65: 314-320.

Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in ecology and evolution*: 266-269.

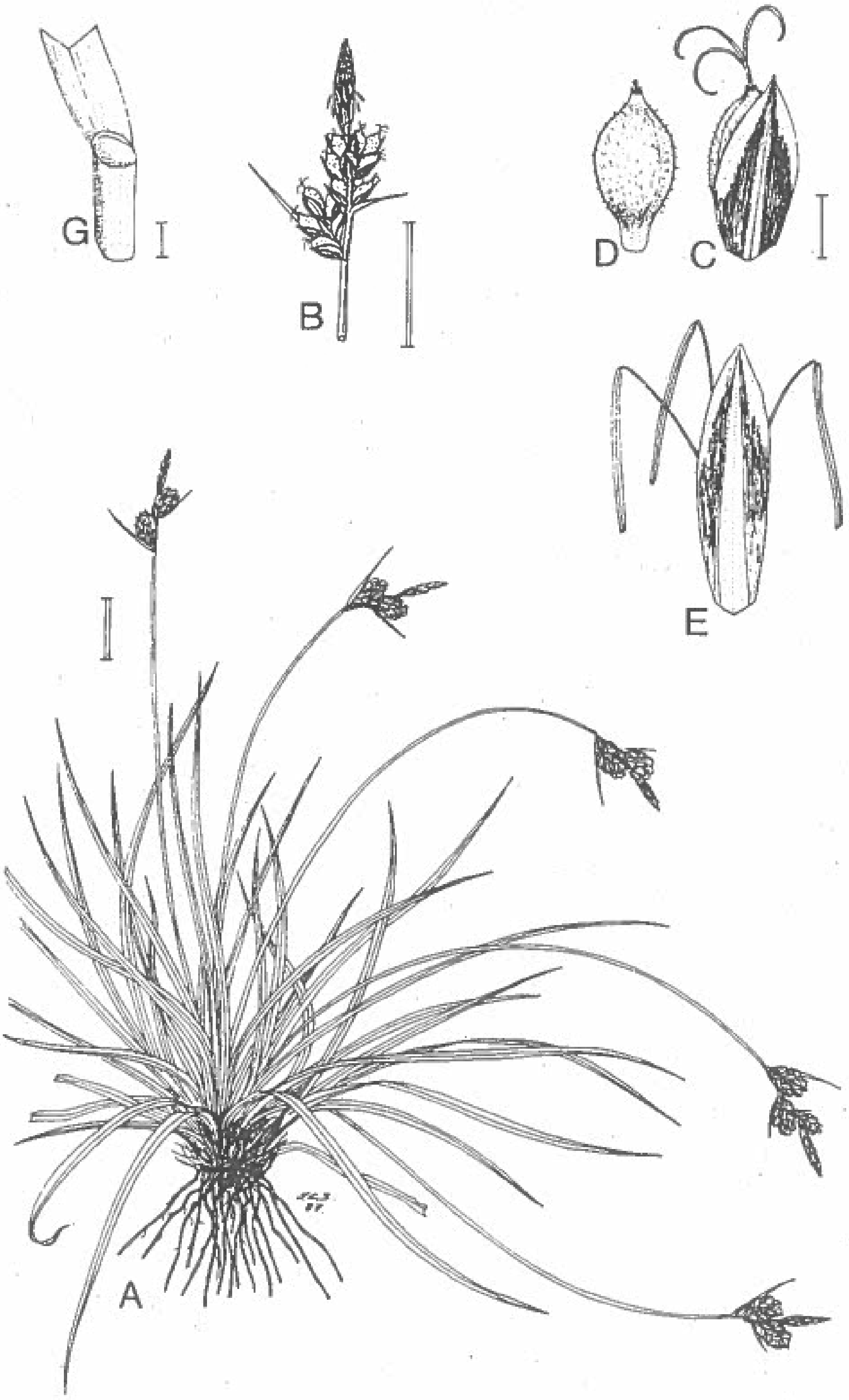
Zobel, M. & Kont, A. 1992. Formation and succession of alvar communities in the Baltic land uplift area. *Nord. J. Bot.*: 249-256.

Zobel, M. & Moora, M. 1997. Plant species coexistence in the interactive environment: arbuscular mycorrhiza should not be out of mind. *Oikos 78*: 202-208.

Økland, R.H. 1990. Vegetation Ecology: Theory, methods and applications with reference to Fennoscandia. *Sommerfeltia* suppl. vol 1.

Økland, R.H. 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? *J. Veg Sci.* 7(2): 289-292.

Article II



Carex pilulifera L.

A classification of Danish grasslands on well-drained soils

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Abstract

A hierarchic classification of Danish natural and semi-natural grassland vegetation on well-drained soils is constructed by TWINSPAN on the basis of 614 samples from vegetation with continuous coenoclines, yet total turnover in species composition in more dimensions. The optimal hierarchic level, and indirectly the size of clusters, are determined by Indicator Species Analysis. The classification is interpreted in terms of variables relating to abiotic ment and vegetation structure and to major ecoclines as identified in a previous gradient analysis. The twelve final clusters are compared to syntaxa of formal phytosociology and to communities in the British Vegetation Classification. It is discussed how to achieve floristically homogeneous clusters without sacrificing the ecological interpretability and validity of the clusters in time and along geographical gradients.

Keywords: Acidic, calcareous, Europe, plant community, temperate, continuum, Trifolio-Geranietea sanguinei T.Müll. 1961, Koelerio-Corynephoretea Klika ap. Klika et Nowák 1941, Festuco-Brometea Br.Bl. et R.Tx. 1943, Calluno-Ulicetea Br.Bl.& R.Tx.1943.

Nomenclature: Flora Europaea (Tutin et al. 1964-1980).

Introduction

Faced with the diverse array of approaches to the classification of vegetation (e.g. Whittaker 1978), a fundamental question arises: why classify vegetation? Shimwell (1971) posed the question and answered simultaneously that classification is an inherent and intuitive act of the human race. There are, however, strong differences among approaches, ranging from those who believe to identify real communities, to those who classify for practical reasons. Parallel contrasts exist with respect to the methods applied; from ideal true cluster seeking (e.g. Noy-Meir & Whittaker 1977) to pragmatic continuum segmentation. Agglomerative clustering algorithms imposed on coenoclines have been coined continuum segmentation, and so has the division of CA-axes by means of indicator species in Two-Way-INdicator-SPecies-ANalysis (TWINSPAN, Hill 1979) (van Groenewoud 1992).

A related fundamental question of vegetation classification is whether to optimise within-cluster floristic homogeneity or maximum reflection of the environment. The Braun-Blanquet approach (Westhoff & van der Maarel 1978) seems to favour very narrow communities (associations) defined solely in terms of floristic composition, whereas the majority of vernacular designations of vegetation types, e.g. dune, heath, forest, are abstractions implying differences in vegetation structure, edaphic and climatic conditions, and not necessarily a certain composition of species. An approach with narrow clusters demands the erection of equal clusters for vegetation apparently stable for centuries as well as for successional stages only existing for a few years, whereas an approach based solely on measured environmental variables demands an *a priori* selection of relevant variables, which might be wrong.

The aim of the present paper is to present a classification of Danish grassland communities on well drained soils based on a compromise between cluster homogeneity and reflection of environmental conditions. High priority will be given to achieve consistency of clusters in time (succession) and space (a larger region, i.e. Denmark).

Danish grassland classification

Since Eugenius Warming described the world biomes as 'plant communities' (Warming 1895) and Christen Raunkiær introduced the statistical approach to vegetation description focusing on ecoclines rather than ecotones (Raunkiær 1909, 1918), the tradition in Danish vegetation ecology has been to use broadly circumscribed units defined from vegetation structure and dominant life-form rather than from exact floristic composition. Many attempts to classify vegetation in accordance with this 'vegetation reflects environment'-view were carried out, resulting in a 'Danish school' of vegetation classification (Shimwell 1973: 229-234). These two pioneers did hardly treat Danish dry grasslands. Warming considered temperate grassland vegetation merely a product of culture, without much ecological interest (Warming, 1895: p.275), except for the dune communities which he monographed (Warming 1909). Raunkiær (1909, 1913) only described grassland from very acidic soils. Grøntved (1927), following Raunkiær, described the grassland vegetation on Danish commons, and later Sørensen (1948) reanalysed Grøntved's data demonstrating his Quotient of Similarity.

Tyge W. Böcher's classifications of communities from grassland (e.g. Böcher 1945; Böcher et al. 1946) and heathland (e.g. Böcher 1941, 1943) have quite a different location on the conceptual continuum from emphasis on cluster homogeneity to reflection of the environment. Böcher defined communities by constancy of species, yet rejected the character species of the Braun-Blanquet approach. Instead Böcher replaced these with groups of diagnostic species based on a combination of phytogeographic type and autecology (see Shimwell 1973: 234). The approach of Böcher was apparently compatible with the Braun-Blanquet approach as some of his vegetation entities were formally named and typified into syntaxonomy by other workers (e.g. Vaccinion vitis-ideae Böch.1943 emend.Schub.1960).

Material and methods

The floristic material treated here is the same as in Ejrnæs & Bruun (subm.), viz. a compilation of all published and unpublished datasets selected by two criteria: Standardised sampling, and herbaceous vegetation from old and unimproved sites. The studies selected is Böcher (1945, 1946, 1947, 1957, unpubl.), Böcher et al. (1946, unpubl.), Mortensen (1953, 1955), Fredskild (1954), Ejrnæs (unpubl.), Ejrnæs & Bruun (1995) and Wind & Ballegaard (1996) - see Ejrnæs & Bruun (subm.) for details. The six most outlying samples were omitted prior to classification, yielding a dataset of 387 species in 614 samples. This study is consequently more comprehensive than any of the above mentioned, implying a unique opportunity to synthesise a new classification on a more objective basis.

Choice of clustering method

Aiming at a classification based on floristic composition, and yet interpretable in terms of environmental conditions, a method based on ordination seemed optimal. An additional advantage of an ordination is its noise-reducing effect, which was desirable since a major part of the floristic variation in the data could be considered noise (normal for vegetation data, see Ejrnæs & Bruun subm. for a discussion). A further advantage is the approximately linear relationship between ecological distance and floristic dissimilarity along non-linearly rescaled DCA-axes (Økland 1986; Ejrnæs & Bruun subm.). Gauch & Whittaker (1981) proposed the method 'Ordination Space Partitioning' (OSP, e.g. DCASP), dividing the primary coenoplane into a number of clusters either by a divisive algorithm or by hand. Gauch (1982) stated that at least four criteria could be independently optimised by any one division: a) equal space, b) compactness, c) equal numbers, and d) division in sparse regions. Gauch (1982) recommended to optimise equal space and compactness, to a lesser degree equal numbers, and to adjust subsequently according to sparse regions. We find this reasoning sensible, though the compactness criterion would not solve much in the present case, since compactness in the primary coenoplane (Ejrnæs & Bruun, subm.: fig. 3) tends to increase towards the centre where divisions necessarily must take place to optimise equal space and numbers. Likewise, the primary coenoplane does not show sufficient disjunctions or sparse regions to make a division by hand into 'natural clusters' feasible. We tried to make divisions in the ordination hyperspace made up of the four interpretable axes using Euclidean distance as dissimilarity measure and a simple non-hierarchic clustering method (SAS Institute Inc. 1990: proc fastclus), but the outcome was difficult to interpret in ecological terms.

The best alternative proved to be TWINSPAN. The method is i) based on Correspondence Analysis, ii) employing a divisive algorithm (less noise sensitive than agglomerative; Gauch 1982), and iii) being polythetic as opposed to the intentional polythetic but in practise monothetic Braun-Blanquet approach (syntaxa above the level of association are often defined from presence of single character species; Feoli 1977). A drawback of all hierarchic methods is that they do not optimise the compactness and separation of clusters since divisions are constrained by preceding divisions or junctions (Gauch 1982), and we therefore felt free to rearrange end-clusters within the tree a posteriori (this is only expressed in the naming though).

TWINSPAN synthesis

TWINSPAN-classification in the version of Oksanen & Minchin (1997) with superstrict convergence criteria was run by means of the package PC-ORD 3.0 (McCune & Mefford 1997). The maximum possible number of cutlevels (5) was used, resulting in a somewhat coarser abundance scale than in the original data but still an acceptable resolution (0.1-0.2, 0.3-0.4, 0.5-0.6, 0.7-0.8 and 0.9-1.0). The maximum number of indicators per division was set to 15, as the data set was believed to be sufficiently large and the samples sufficiently species rich for that. Altering the mentioned options did not markedly affect the output. We did not try to change the input order as Jari Oksanen's program for that - CEPSHUFL - does not accept a dataset of this size (Oksanen & Minchin 1997). It is worth noting that all but one of the datasets tested by Oksanen & Minchin (1997) were very small, and that the only large set (roughly half the size of the present) produced stable solutions even with more lax convergence criteria than used here.

Divisive clustering was allowed to proceed to level 5 (32 end-clusters) and this preliminary tree was evaluated by the Species Indicator Analysis, proposed by Dufrêne & Legendre (1997) and available in PC-ORD 3.0 (McCune & Mefford 1997), in order to select the appropriate stop level. Dufrêne & Legendre (1997) compute for each species in a data set an indicator value for a given a priori classification by multiplying its relative abundance (average abundance of the species in a given group of samples over the average abundance of that species in all samples) with its relative frequency (fraction of samples in given group where the species is present), and they test the obtained values by a permutation test. They argue that the sum of significant indicator values will increase with cluster homogeneity, hence more and smaller clusters, and that it will increase with species fidelity to clusters, hence large and few clusters. From this follows that the sum of significant indicator values will reach a maximum somewhere between 1 and N clusters. In a dichotomous tree, the number of clusters is doubled in every level with respect to the previous level. In the non-hierarchic k-means-clustering method applied by Dufrêne & Legendre (1997) can provide clusterings with any desired number of clusters, also a series of clusterings with the number of clusters increasing by one. Although we turn the focus from the optimal number of clusters to the optimal hierarchical level, the method is useful. In the case of our dichotomous TWINSPAN tree the sum of significant indicator values (1000 Monte Carlo permutations) was maximal at level 2 (results not shown). We decided to make a few adjustments to the tree: there were no significant indicators for the subdivision of cluster 4 (*sand grassland*), and we decided not to divide this cluster further. As we did not want to treat different successional stages as different communities, the subdivision of cluster 7 (within *xeric grassland*) was avoided. These refinements yielded a tree similar to that shown in fig. 1, except that all "new" clusters in level 4 were further subdivided to level 5. In a new Species Indicator Analysis the sum of significant indicator values was maximal at level 4 in the tree (fig. 1), and it was decided to omit level 5.

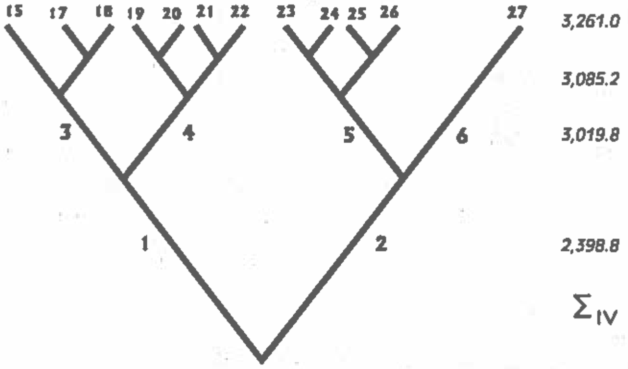

Figure 1. TWINSPAN tree with 12 end-clusters. The number of samples is shown next to each node, and the sum of significant indicator values used to assess the optimal level is shown to the left at the four levels. The similar sum for level 5 (not shown) is 3011.

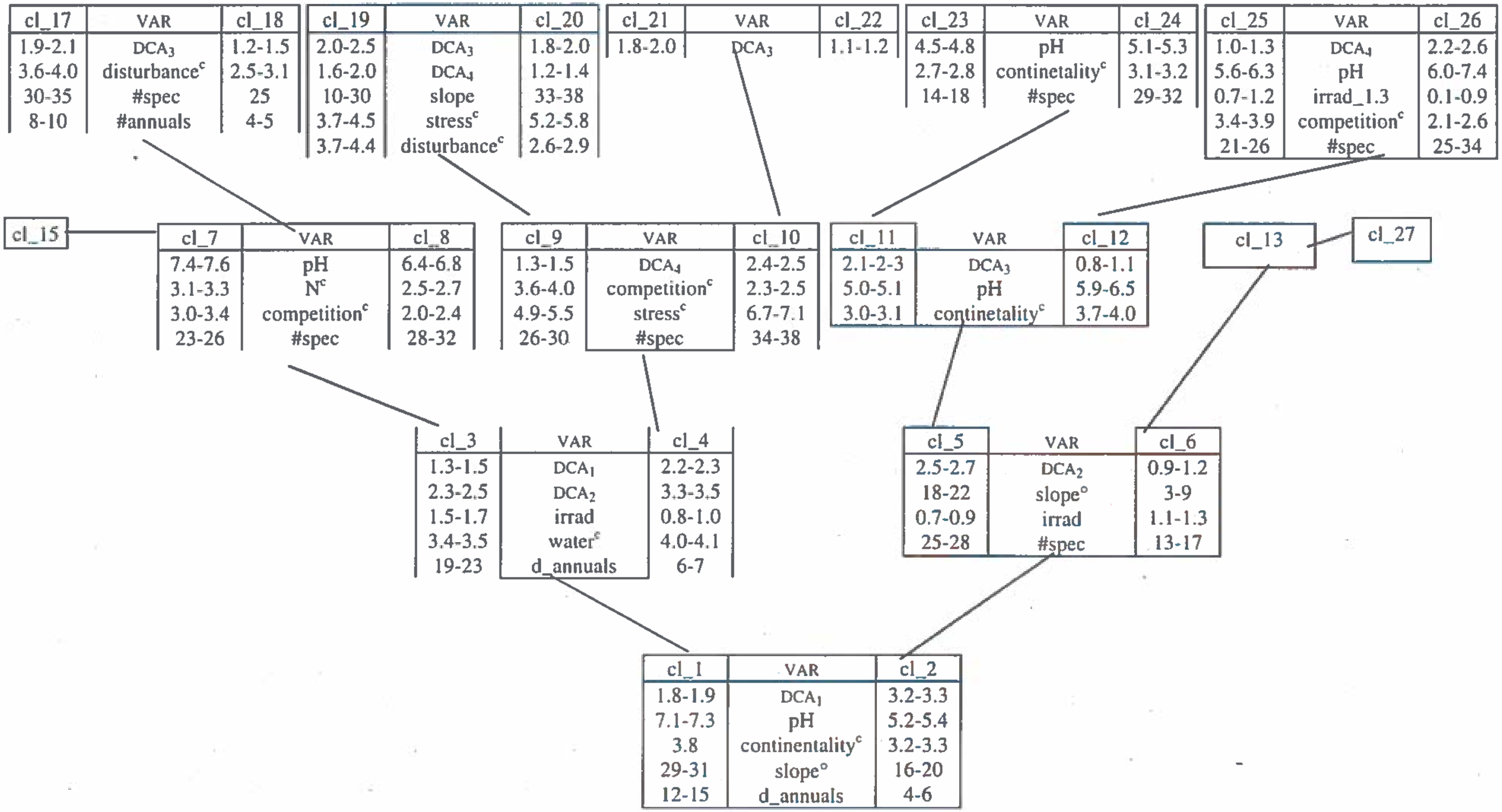

Figure 2. TWINSPAN tree with 12 end-clusters. Differences regarding score on $DCA_{1\text{-}4}$ and explanatory variables are indicated for each dichotomous division as 99% confidence intervals. Irradiation on March 1 ranges from 0-2. Values calibrated from the species composition are denoted with a ^{c}.

Table 1. Indicator Species Analysis of the TWINSPAN tree. For each species is shown two figures separated by a slash: its relative abundance in each cluster (average abundance in the cluster over the average abundance in all samples) and its relative frequency (fraction of samples in the cluster where the species is present), both expressed as percentages (the value 0/0 not shown). The first two columns show the maximum Indicator Value over all clusters and the statistical significance of it computed by 1000 MonteCarlo permutations. 163 species with nonsignificant indicator values and low absolute frequencies have been omitted. Allegedly symmetric indicators (IV_{max}>55%) are shown in bold.

species	IV max	tw15	tw17	tw18	tw19	tw20	tw21	tw22	tw23	tw24	tw25	tw26	tw27
Poa compressa	35 ***	**55/47**	7/18		26/15	2/4	0/3	9/11		0/1			
Festuca trachyphylla	19 ***	**67/24**	11/12	15/7				6/2	1/3	0/1			
Bromus sterilis	10 ***	**100/10**											
Alyssum alyssoides	8 ***	**76/10**	24/4										
Melilotus alba	6 **	**100/6**											
Papaver argemone	5 **	**84/6**	16/2										
Anchusa officinalis	4 *	**84/5**	16/2										
Bromus erectus	4 *	**40/7**	14/2			21/4	25/6			1/1			
Melampyrum arvense	4 **	**55/7**									45/3		
Lithospermum arvense	3 *	**100/3**											
Artemisia campestris	57 ***	**33/73**	**25/63**	**30/74**	1/8	1/4	0/3	4/17	1/8	1/3			5/19
Bromus hordeaceus coll.	49 ***	**20/56**	**39/78**	**11/44**	13/46	1/6	11/32	0/2	0/3	4/9	0/3	0/7	
Arenaria serpyllifolia	42 ***	**19/56**	**36/75**	**10/37**	6/23	1/4	15/48	11/29		0/3		2/13	0/2
Sedum acre	41 ***	**16/53**	**28/82**	**31/96**		0/2	4/13	4/20		1/7	3/17	2/20	10/35
Convolvulus arvensis	34 ***	**45/48**	**27/25**	**12/15**	11/31	2/4				2/2			
Phleum phleoides	30 ***	**29/37**	**30/33**	**26/33**		3/6	3/3	8/13		1/2			
Potentilla argentea coll.	24 ***	**19/25**	**46/45**	**8/15**	2/8	6/6	18/6			2/3			
Trifolium campestre	23 ***	**14/27**	**35/51**	**20/22**	10/8	0/2	10/19	1/5		5/14	3/3		3/8
Myosotis ramosissima	19 ***	**27/27**	**26/25**	**1/4**	35/23	1/2	6/6			2/2			
Acininos arvensis	18 ***	**40/33**	**22/12**	**12/19**		2/2		26/18					
Allium vineale	14 ***	**38/16**	**41/20**	**5/11**		11/8				4/3			
Veronica arvensis	14 ***	**17/18**	**36/33**		29/23	1/2	12/23	0/1		5/5			
Medicago minima	13 ***	**33/13**	**67/20**										
Vicia hirsuta	11 ***	**21/13**	**38/24**	**14/11**	6/8	10/10	4/3	4/3		0/1			3/2
Echium vulgare	7 **	**39/11**	**41/8**					19/1					
Sedum telephium coll.	4 *	**30/7**	**11/2**	**24/11**		6/2				4/2	22/3		3/2
Seseli libanotis	4 *	**42/7**	**29/4**			28/4							
Valerianella locusta	4 *	**20/8**	**19/2**		54/8		8/3						
Trifolium striatum	35 ***	3/4	**77/45**		5/15	2/2	10/10			4/2			
Aira caryophyllea	21 ***	6/2	**76/27**	2/4			7/3	1/1		6/4	2/3	0/7	
Erophila verna	20 ***	11/13	**57/35**	3/7		1/4	16/19	6/8		8/7			
Saxifraga granulata	15 **	5/12	**32/45**		15/31	3/8	18/32	1/5		23/32		2/7	
Myosotis stricta	12 *	26/8	**66/18**			4/2				4/2			
Petrorhagia prolifera	10 **	32/8	**66/16**			2/2							
Arabidopsis thaliana	5 *	13/5	**69/8**				16/6			2/1			
Cerastium semidecandrum	41 ***	13/40	**46/80**	**17/44**	6/8		5/19	2/8	2/5	8/17	1/7	1/7	1/4
Trifolium arvense	35 ***	9/17	**39/53**	**33/63**			1/3			2/7	11/17		5/17
Helichrysum arenarium	18 ***	14/14	**29/25**	**49/37**					1/3				7/13
Vicia lathyroides	14 ***	7/8	**35/25**	**33/19**	7/15	4/4	3/3		1/3	4/3		2/7	4/8
Armeria maritima	13 ***	2/7	**15/43**	**18/41**	2/15	1/6	10/45	3/7	1/5	7/17	19/41	15/33	7/17
Dianthus deltoides	12 ***	1/2	**24/24**	**31/19**	2/8	2/2	17/10	0/1		13/14	4/7	5/7	2/2
Erodium cicutarium	7 **	1/1	**64/10**	**34/4**						1/1			
Lychnis viscaria	5 *	6/3	**23/14**	**29/7**		20/12		2/3		20/9			
Trifolium dubium	5 *	2/1	**31/16**	**3/4**	17/15		22/13	3/1		10/7	10/7		
Veronica verna	5 **	2/1	**83/6**	**15/4**									
Pulsatilla pratensis	49 ***	2/6	8/12	**62/78**		2/4	1/13	2/6	2/3	2/3			18/23
Thalictrum minus coll.	14 ***	2/2	8/6	**48/30**		4/10	12/10	6/5		2/2	12/10		6/8
Veronica spicata	12 **		19/10	**62/19**		4/2	2/3	8/3			2/3		4/4
Silene otites	7 *			**96/7**									4/2
Scleranthus perennis	6 *		2/2	**44/15**	8/8				22/3				24/4
Dactylis glomerata coll.	68 ***	**14/88**	**8/63**	**1/15**	**23/100**	**16/90**	**17/97**	**12/75**		2/22	3/24	4/27	
Galium verum	51 ***	**10/90**	**12/98**	**14/96**	**7/69**	**5/72**	**12/97**	**8/82**	1/35	7/73	11/90	5/73	8/69
Avenula pratensis	49 ***	**6/42**	**20/80**	**9/52**	**2/38**	**8/48**	**20/77**	**23/89**	0/8	7/40	1/3	2/7	2/13
Centaurea jacea	48 ***	**12/47**	**7/25**	**0/7**	**25/62**	**20/76**	**11/55**	**22/67**		1/7	0/3		
Medicago lupulina	47 ***	**7/39**	**10/37**	**3/19**	**21/69**	**2/22**	**24/74**	**24/82**		0/2	0/3	8/33	
Centaurea scabiosa	33 ***	**23/41**	**2/10**		**12/54**	**23/40**	**6/23**	**33/46**		1/4		0/7	
Phleum pratense ssp. bertolonii	33 ***	**13/40**	**16/41**	**2/11**	**28/85**	**3/16**	**25/65**	**10/33**		2/15			0/2
Ononis repens	31 ***	**12/44**	**13/45**	**5/22**	**20/46**	**9/38**	**20/42**	**12/37**	1/11	7/24		1/7	
Daucus carota	23 ***	**11/27**	**4/6**		**45/46**	**7/16**	**4/13**	**29/43**		0/2		0/7	
Filipendula vulgaris	23 ***	**6/21**	**10/24**	**8/15**	**8/23**	**17/36**	**25/45**	**18/39**		8/23			
Anthyllis vulneraria	18 ***	**6/16**	**12/35**	**3/19**		**1/6**	**15/42**	**15/44**		1/7	6/10	39/47	2/6
Silene nutans	16 ***	**20/21**	**14/18**	**10/15**		**13/18**	**10/6**	**24/25**	1/5	7/7		0/7	0/2

Hypericum perforatum	15 ***	**29/32**	**9/12**	**6/4**		**28/28**	**4/6**	**13/17**	1/3	11/11			
Geranium sanguineum	13 ***	**6/13**	**10/18**	**11/26**		**20/32**	**12/19**	**11/20**		1/4	27/45		1/8
Origanum vulgare	10 ***	**26/11**				**45/22**		**29/16**					
Fragaria viridis	9 ***	**12/10**	**24/14**		**41/23**	**12/12**	**8/13**	**2/2**		1/1			
Scabiosa columbaria	8 ***	**31/17**	**9/4**	**16/4**		**12/4**	**4/3**	**27/8**		0/1			
Allium oleraceum	7 ***	**21/15**	**13/8**		**49/15**	**14/8**		**1/1**		2/2			
Prunus spinosa	6 **	**45/12**	**10/4**			**29/12**	**8/3**	**4/2**		3/5			
Geranium molle	4 **	**31/6**	**30/8**			**2/2**	**37/10**						
Helianthemum nummularium coll.	4 *	**17/4**	**4/2**	**9/7**		**17/8**	**16/3**	**29/8**		9/4			
Silene vulgaris ssp. vulgaris	3 *	**32/7**	**5/2**		**21/8**	**38/4**				4/2			
Phleum arenarium	2 *	**28/4**	**25/4**	**12/4**				**36/1**					
Bellis perennis	40 ***				**64/62**		33/29	0/2		2/5			
Lolium perenne	32 ***	2/3	5/10		**51/62**		37/48			4/9			
Elytrigia repens	28 ***	8/23	16/33	1/4	**45/62**	16/24	5/10	1/2		5/9	4/10		
Potentilla reptans	27 ***	8/11	2/6	4/7	**49/54**	12/26	14/26	5/11		1/5	5/3		
Lathyrus pratensis	24 ***	0/1			**52/46**	15/18	7/6	9/7		2/2	1/3	14/7	
Carex hirta	23 ***	2/3	3/4		**60/38**	7/8		3/2	10/8	15/13	1/3		
Ranunculus repens	23 **	2/2			**74/31**	14/12					10/3		
Agrimonia eupatoria	18 ***	6/10			**40/46**	16/22	28/29	7/10		2/6	1/3		
Geranium dissectum	14 **				**93/15**		7/3						
Vicia sativa ssp. nigra	14 ***	18/19	20/22	7/11	**36/38**	5/8	2/3	1/2		10/11	1/3		1/2
Myosotis arvensis	9 **	35/2			**61/15**					4/1			
Equisetum telmateia	8 *				**100/8**								
Galium palustre	8 *				**100/8**								
Juncus inflexus	8 *				**100/8**								
Potentilla anserina	8 *				**100/8**								
Rubus sect. Rubus	8 *				**100/8**								
Sonchus arvensis	8 *				**100/8**								
Thlaspi caerulescens	8 *				**100/8**								
Capsella bursa-pastoris	6 *				**83/8**					17/1			
Cirsium vulgare	6 *	6/1			**78/8**	4/2	7/6	5/2					
Festuca arundinacea	14 ***	6/4	1/2		**36/23**	**34/20**	13/3	10/3		0/1			
Rubus caesius	14 ***	4/3			**18/8**	**74/18**				4/2			
Anthriscus sylvestris	8 **	6/2	2/2		**9/8**	**76/10**				6/2			
Picris hieracioides	5 **				**21/8**	**79/4**							
Tanacetum vulgare	5 *	7/2	0/2			**66/8**				9/2		17/7	
Tragopon pratensis coll.	4 *	2/1	5/2		**56/8**	**15/6**	6/3	12/3		2/2		2/7	
Arrhenaterum elatius	20 ***	21/17	2/8		3/8	**49/42**	3/6	8/14	8/5	6/6			
Galium mollugo	17 ***	8/6	1/2			**67/26**		21/3	2/3				
Heracleum sphondylium coll.	17 **					**86/20**		10/5		4/2			
Campanula persicifolia	15 **	4/4	4/4			**48/32**	14/6	22/13		7/3			
Hedera helix	11 **	6/2				**94/12**							
Vincetoxicum hirundinaria	10 **	15/7	1/2	2/4		**71/14**		12/3					
Brachypodium sylvaticum	6 *	19/3				**80/8**		1/1					
Clinopodium vulgare	6 *					**100/6**							
Stellaria holostea	6 *					**100/6**							
Primula veris	38 ***	0/1	1/4		**13/23**	**17/64**	**29/58**	**15/44**	0/5	5/20	7/17	13/33	
Cirsium acaule	36 ***	0/1	1/2		**15/31**	**4/20**	**30/48**	**31/52**		3/8		18/33	
Carex flacca	35 ***	0/1	0/2		**13/31**	**8/30**	**23/45**	**27/52**		3/11	3/14	23/53	
Viola hirta	24 ***	3/6			**17/15**	**31/26**	**21/32**	**27/25**		1/1			
Leucanthemum vulgare	23 ***	3/3	5/8		**23/8**	**11/24**	**8/19**	**36/45**		11/9		4/7	
Taraxacum sp.	20 ***	2/7	4/22	9/26	**19/77**	**5/28**	**15/52**	**11/40**		6/22	3/14	25/73	1/6
Festuca pratensis	19 ***	2/4	2/2		**31/15**	**17/16**	**20/23**	**26/24**		0/1	1/3		
Plantago media	19 ***	2/4			**9/8**	**3/10**	**27/39**	**16/37**		3/4	1/7	39/40	
Senecio jacobaea	19 ***	13/19	3/6		**28/23**	**7/16**	**6/19**	**41/33**		1/3	1/3		
Knautia arvensis	18 **	4/14	5/18	2/11	**12/31**	**12/34**	**11/35**	**20/41**	2/8	20/46	5/14	6/20	1/2
Avenula pubescens	16 ***	3/7	8/18	5/11	**17/23**	**25/28**	**22/45**	**9/18**	1/5	8/13	1/3	0/7	0/2
Trifolium pratense	15 ***				**20/31**	**0/2**	**29/45**	**12/23**		5/13	6/24	29/40	
Fragaria vesca	12 ***	2/1			**24/8**	**28/18**	**4/3**	**36/15**	4/8	3/2			
Ranunculus acris	12 **				**15/23**	**13/24**	**10/16**	**12/20**	0/3	8/17	20/21	23/33	
Leontodon hispidus	11 ***					**15/14**	**42/19**	**23/18**	2/3	18/8			
Tussilago farfara	5 **	3/1			**16/8**	**26/4**	**34/6**	**21/6**					
Inula salicina	2 *					**57/2**		**43/3**					
Ranunculus bulbosus	27 ***	4/28	12/55	5/26	15/54	2/22	**30/90**	12/52	0/3	15/63	0/10	5/27	
Cynosurus cristatus	23 ***	0/1	2/6		42/54	1/4	**38/61**			17/28			
Cerastium fontanum ssp. triviale	21 ***	1/5	4/16	4/7	19/38	2/16	**28/74**	5/25		15/46	8/31	11/27	3/13
Thymus pulegioides	18 ***	15/33	13/24	4/4		5/12	**44/42**	10/9		9/16			
Trifolium repens	14 **		3/6	7/11	25/38	1/4	**32/45**	1/6		12/23	12/28	3/13	5/8
Taraxacum sect. Erythrosperma	11 **	1/2	16/16	1/4	24/31	2/2	**37/29**	1/2	1/5	12/12			4/4
Astragulus danicus	6 *	4/3	16/4		28/8		**49/13**			4/2			
Potentilla cinerea	6 *	13/1	11/6				**58/10**			18/2			

Briza media	44 ***	1/4	3/12	2/7	5/31	5/26	**38/74**	**31/64**		8/20	2/3	5/20	
Carex caryophyllea	21 ***	3/12	12/27	3/11	1/8	6/24	**27/55**	**24/51**		24/46			
Arabis hirsuta	14 ***	14/9	7/8	2/4		5/6	**21/16**	**48/25**		2/2			
Succisa pratensis	10 **					4/2	**14/6**	**43/23**	6/8	33/18			
Euphrasia stricta	5 *		5/4	18/4			**7/3**	**40/13**		17/6		0/7	13/2
Geum rivale	4 *						**20/3**	**62/6**		19/1			
Koeleria pyramidata	35 ***	2/2	7/8	12/7		1/2	7/6	**71/49**					
Campanula glomerata	20 ***					11/8	5/3	**84/24**					
Sanguisorba minor ssp. minor	12 **	2/1	3/2			16/6	2/3	**78/16**					
Polygala amarella	11 **							**100/11**					
Crepis praemorsa	9 **							**100/9**					
Hieracium lactucella	7 *							**73/9**		27/6			
Polygonatum multiflorum	6 *							**100/6**					
Brachypodium pinnatum	5 *					31/2		**69/7**					
Festuca rubra	37 n.s.	**3/41**	**6/65**	**5/59**	**13/92**	**8/76**	**13/97**	**10/85**	**3/59**	**7/77**	**12/97**	**15/100**	**4/63**
Poa pratensis	34 n.s.	**7/61**	**8/73**	**9/59**	**8/92**	**10/66**	**12/77**	**4/39**	**8/68**	**10/75**	**16/100**	**7/40**	**2/15**
Plantago lanceolata	30 n.s.	**4/42**	**10/75**	**5/52**	**13/77**	**4/48**	**18/77**	**7/63**	**0/3**	**16/87**	**10/59**	**12/53**	**0/4**
Deschampsia flexuosa	66 ***	0/1	0/2					1/3	**72/92**	20/42	3/7		3/6
Galium saxatile	44 ***						1/3	1/1	**85/51**	13/11			
Carex pilulifera	30 ***								**80/38**	20/13			
Agrostis vinealis	16 ***		9/12			3/2		1/1	**55/30**	22/23			9/4
Genista anglica	7 *								**49/14**	36/5			15/2
Holcus mollis	19 ***	0/1				1/2			**69/27**	**30/18**			1/2
Lathyrus montanus	17 ***						28/10		**11/11**	**61/23**			
Anemone nemorosa	15 ***					1/2		5/3	**51/19**	**43/16**			
Vaccinium myrtillus	8 **								**20/5**	**80/9**			
Equisetum pratense	4 *								**46/8**	**54/3**			
Hypericum pulchrum	4 **								**10/3**	**90/5**			
Nardus stricta	4 *								**43/3**	**57/5**			
Carex panicea	3 *								**59/5**	**41/2**			
Stellaria graminea	20 ***		5/6			14/8	5/10	1/1	6/3	**64/31**	2/3		3/4
Rumex acetosa	42 ***	2/17	5/22		2/31	9/42	14/55	5/18	**18/59**	**28/70**	**11/45**	**7/20**	
Danthonia decumbens	34 ***	0/1	3/12	0/4		2/8	13/32	5/13	**13/32**	**33/51**	**4/28**	**26/33**	0/2
Veronica officinalis	30 ***	0/1	0/2			0/2	5/13	3/6	**7/14**	**26/40**	**35/52**	**21/20**	2/6
Potentilla erecta	29 ***						1/3	2/3	**29/30**	**43/36**	**20/14**	**5/13**	
Trifolium medium	23 ***	1/2	1/10		28/31	13/20	13/19	4/11	**5/11**	**32/51**	**4/7**		
Polygala vulgaris	18 ***	0/1		3/4			25/23	8/10	**1/3**	**44/35**	**4/7**	**15/20**	
Equisetum arvense	11 **	2/4	0/2		29/23	5/8	13/16	0/1	**9/8**	**16/20**	**23/17**	**2/7**	
Hypericum maculatum	6 **	1/1				14/4		6/2		**34/10**	**28/7**	**17/7**	
Rosa pimpinellifolia	42 ***		2/2	2/4				1/1		2/2	**77/55**	14/13	1/6
Ammophilia arenaria	36 ***	1/1		13/19							**54/66**	3/13	28/38
Veronica chamaedrys	22 ***		1/4	2/7	14/31	18/24	6/19	2/8	4/8	11/32	**40/55**	1/7	1/2
Linaria vulgaris	19 ***	3/4	1/2			1/4		1/1			**60/31**	24/7	10/4
Polypodium vulgare	16 ***								32/8	8/2	**57/28**		3/2
Silene vulgaris ssp. maritima	10 ***										**100/10**		
Calamagrostis epigeios	9 **	4/2	3/2	12/4		22/12		2/1		3/1	**54/17**		
Pimpinella saxifraga	36 ***	3/19	4/33	2/30	2/31	7/46	6/52	12/75	3/32	7/50	**23/79**	**28/87**	3/17
Lotus corniculatus	23 ***	1/7	4/20	7/33	3/31	2/14	7/45	16/60	0/3	8/37	**17/59**	**28/67**	6/21
Holcus lanatus	17 ***	0/1	1/4		8/15	9/10	10/13		0/3	16/23	**20/34**	**35/33**	
Salix repens coll.	16 ***							4/1	4/3	4/2	**47/17**	**42/20**	
Vicia cracca	16 ***	0/2			1/8	9/22	6/13	18/30	3/8	8/20	**38/38**	**13/27**	3/4
Hippophae rhamnoides	12 ***	3/2		4/4				4/1			**47/21**	**35/7**	7/4
Potentilla tabernaemontani	8 ***	1/1	19/12	1/4		1/2	19/6	7/7		3/2	**33/17**	**16/13**	1/2
Equisetum hiemale	5 **			47/4							**53/10**		
Cochlearia officinalis	4 *									29/1	**24/7**	**47/7**	
Plantago maritima	56 ***			1/4				5/10		0/1	16/45	**65/87**	13/27
Solidago virga-aurea	50 ***	2/11	0/2			9/16	2/6	8/23	2/5	2/9	16/38	**58/87**	2/4
Antennaria dioica	37 ***						1/3	1/3		7/5	7/7	**80/47**	3/2
Agrostis stolonifera	36 ***					2/4	13/6	9/7		0/1	7/7	**67/53**	2/4
Linum catharticum	35 ***	0/2			1/8	1/10	24/52	26/57		3/9		**44/80**	1/2
Senecio integrifolius	34 ***							25/26				**72/47**	3/2
Empetrum nigrum	29 ***							3/2	7/3		29/14	**54/53**	7/10
Prunella vulgaris	29 ***	0/2			9/15	0/2	26/45	13/33		8/18	0/3	**44/67**	
Carlina vulgaris	27 ***	0/1		2/4	6/15	3/6	12/19	23/38		3/5		**51/53**	
Galium sterneri	27 ***		3/6	4/11		1/6	2/19	32/61		10/17	5/10	**41/67**	2/6
Gentianella amarella	26 ***							19/11				**77/33**	4/2
Leontodon autumnalis	22 ***		2/2			1/4	9/13	4/5		28/21	3/10	**47/47**	7/8
Erigeron acre	21 ***	13/5	2/2							1/1	13/10	**64/33**	6/6
Draba incana	13 ***							9/2				**64/20**	27/2
Hypochoeris maculata	13 ***		9/8	4/7		5/2	2/3	7/3		3/2	18/7	**47/27**	4/8
Papaver dubium	12 **							14/1				**86/13**	
Botrychium lunaria	10 **			10/4		9/2						**74/13**	6/2
Centaurium erythraea	6 *	1/1						7/2				**91/7**	

Omalotheca sylvatica	6 *									11/1		89/7	
Luzula campestris	59 ***	1/10	7/55	6/48	2/38	2/22	17/84	3/28	13/84	23/89	11/59	10/67	4/42
Agrostis capillaris	58 ***	1/14	11/65	5/52	5/31	4/28	11/77	1/11	17/81	28/94	11/62	5/33	2/23
Anthoxanthum odoratum	47 ***	2/10	8/31	7/22	2/15	5/32	17/61	1/8	7/38	33/89	6/45	9/33	3/17
Festuca ovina	42 ***	1/15	12/67	9/52	1/8	2/22	17/81	12/68	14/73	21/88		5/33	6/44
Hieracium pilosella	42 **	8/72	11/86	8/81	7/54	1/16	13/90	9/75	6/57	14/89	5/41	12/93	8/65
Achillea millefolium	39 **	6/62	9/76	3/26	11/77	7/64	12/90	8/62	4/32	15/92	16/97	9/67	1/13
Campanula rotundifolia	39 ***	1/14	3/22	3/26	2/23	8/60	12/84	16/84	8/62	14/79	9/62	20/87	4/25
Viola canina	34 ***	0/1	0/2	1/7		6/10	13/26	7/10	8/24	26/47	12/38	10/20	18/44
Hypochoeris radicata	30 ***	0/2	3/10	1/7	4/8	0/2	5/6	2/1	7/14	37/48	16/24	14/13	10/19
Calluna vulgaris	28 ***	1/2	0/2				1/3	2/3	56/49	24/36	4/7	4/7	8/19
Rumex acetosella	24 ***	1/5	19/41	9/26			3/6	0/1	29/49	23/33	2/7		14/29
Aira praecox	18 ***	1/2	31/31	1/4			7/10		16/14	37/36	2/3	1/7	4/8
Teesdalia nudicaulis	4 *		34/10	3/4					31/5	23/7			8/4
Corynephorus canescens	71 ***			14/19					2/3		2/7		82/73
Carex arenaria	64 ***	1/6	2/18	26/74		1/6	1/3		9/32	7/20	17/79	4/27	32/92
Jasione montana	49 ***	4/6	15/20	22/30					1/3	1/4	8/14		49/60
Hieracium umbellatum	48 ***	1/3	0/2	6/22	1/8	1/10	3/13	4/16	12/32	5/20	7/31	29/73	30/69
Thymus serpyllum	39 ***	1/6	7/24	26/74		0/2	1/13	13/45	0/3	3/11	8/34	18/60	22/69
#samples		103	51	27	13	50	31	87	37	123	29	15	48

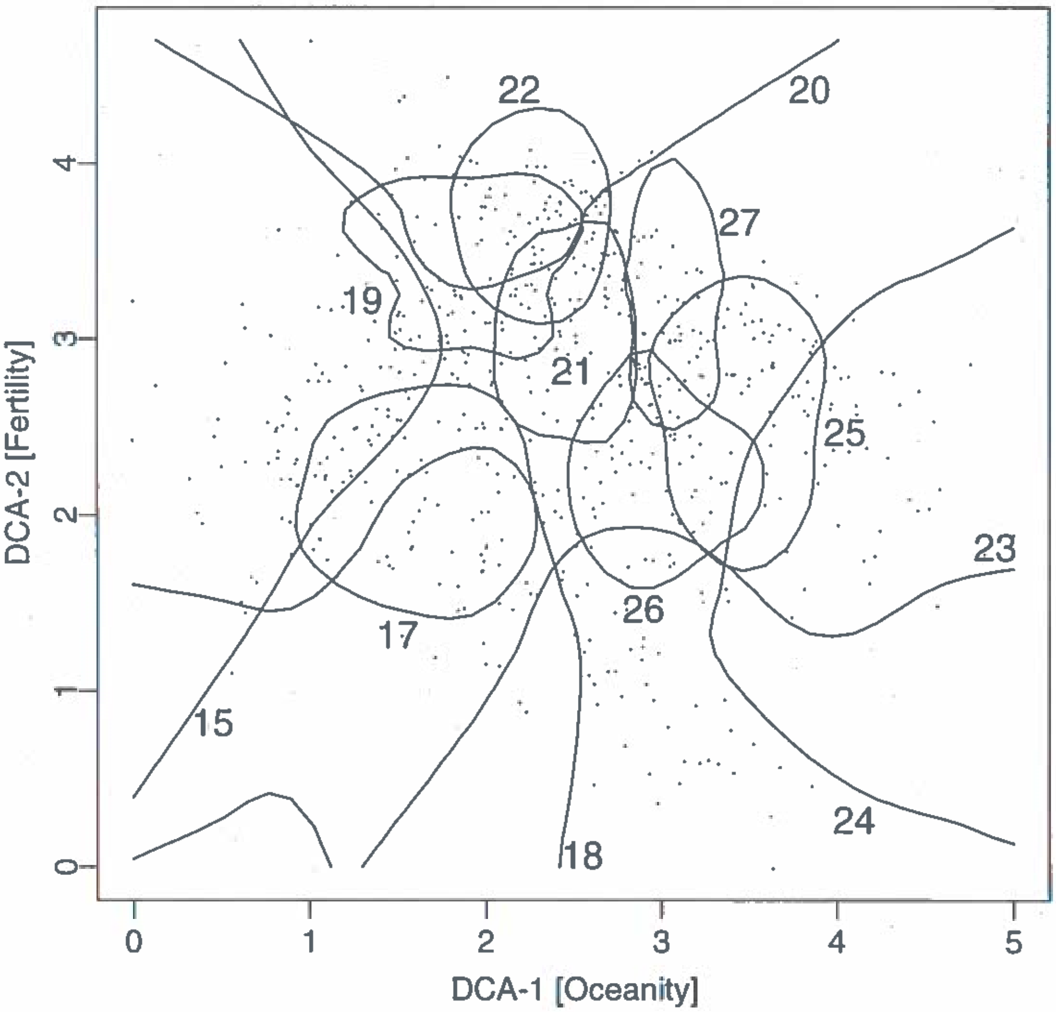

Figure 3. Prediction of optima of the twelve end-clusters on the primary coenoplane (DCA$_2$ vs. DCA$_1$) based on a logistic model of cluster occurrence in terms of the two axes. The coenoclines correspond to complex gradients in pH and drought (DCA$_1$) and fertility (DCA$_2$). The contour lines delimit for each cluster an area with a probability of meeting that cluster being three times the fraction of that cluster out of all samples. Cluster numbers are indicated on the figure with numbers placed at outer margins of cluster areas. Except for the central cluster 21, where the number is placed inside the cluster area. Dots show the actual position of samples, and plot regions without points should be interpreted as combinations of the ecoclines unlikely to be found with grassland vegetation in Denmark.

Results

A hierarchic structure with 12 final clusters emerge from the clustering procedure (fig. 1). The first dichotomy divides the most important coenocline (DCA_1; 5.19 SD units) which runs from open vegetation on south-facing slopes with calcareous soil to humid leached acidic grasslands (fig. 2). The two dichotomies at level 2 both divides the second most important coenocline (DCA_2; 4.71 SD units) which mainly reflects productivity running from relatively fertile grasslands on clay, limestone and occasionally diluvial sand with good water supply, to infertile dry grasslands on marine or eolian sand (Ejrnæs & Bruun, subm.). The division of cluster 1 also follows DCA_1 to some extent. The significant indicator species for the divisions appear from table 1.

Description of main types

Four main clusters emerge from the first two divisions, and they correspond to the poles of the two main ecoclines and are centred towards the four corners of the almost rhombic configuration of sample points in the primary coenoplane. At this level the sum of significant indicator values is close to its maximum (93%), which means that these clusters are relatively homogeneous and well suited as main grassland vegetation types. The optima and variation of the main types and the end-clusters with respect to the primary coenoplane appear from fig. 3.

Cluster 3 XERIC GRASSLANDS (181 samples)

This is relatively open vegetation - often rich in annual species - occurring on drought-exposed soil. The soil pH ranges from approximately 5 to well above 8 (mean 7.1). Apart from the species indicative of both cluster 3 and 4, e.g. *Dactylis glomerata, Galium verum, Avenula pratensis,* character species for this cluster are *Artemisia campestris, Bromus hordeaceus, Arenaria serpyllifolia, Sedum acre, Convolvulus arvensis* and *Phleum phleoides.*

Cluster 4 CALCAREOUS GRASSLANDS (181 samples)

This is closed species-rich vegetation on limestone soil or moraine soil containing calcite $CaCO_3$ (pH ranging from below 6 to 8.5 with a mean of 7.3). It less often occurs on south-sloping terrain, and then the soil has a significant content of clay. Besides *Dactylis glomerata, Galium verum, Avenula pratensis* which are also indicative of cluster 3, the most prominent indicators are *Primula veris, Cirsium acaule, Carex flacca, Viola hirta* and *Leucanthemum vulgare.*

Cluster 5 ACIDIC GRASSLANDS (160 samples)

This is closed vegetation on north-facing slopes and other sites which are not exposed to drought, and where the soil is well below neutrality and often leached and acidic - pH below 4 to 7 (mean 5.2). Besides the species indicative of both cluster 5 and 6 - *Luzula campestris, Agrostis capillaris* and *Anthoxanthum odoratum,* the strongest indicators are *Rumex acetosa, Danthonia decumbens, Veronica officinalis* and *Potentilla erecta.*

Cluster 6 SAND-GRASSLANDS (48 samples)

This cluster is not divided further and it is described below as cluster 27.

It is striking how many (sub-) continentally distributed taxa which are indicative of cluster 1, the dry and/or calcareous grasslands. This is to some degree an expression of the fact that a dry and warm local climate produces a high base saturation of the soil. But calcareous substrates appear to be preferred by continentally distributed taxa also in the absence of a dry local climate. We have anecdotal evidence that some species which are calcicolous in northwest Jutland tend to be less pH-limited in the subcontinental region, e.g. *Avenula pratensis, Filipendula vulgaris, Geranium sanguineum, Origanum vulgare, Scabiosa columbaria* and *Helianthemum nummularium.* This phenomenon is also relevant along a latitudinal gradient in Europe (Etherington 1975: 278).

Description of end-clusters

The twelve end-clusters are described in terms of their characteristic flora and significant features of their local environment with due reference to the gradient analysis (Ejrnæs & Bruun, subm.). The descriptions follow a scheme: The most prominent indicator species (character species) are listed first (all significant indicator species appear from table 1). Then frequency-dominant species are mentioned, i.e. species with abundance >0.95 in more than 50% of the samples in the cluster. These species need not be dominant in terms of biomass, as even small stature species occurring scattered in a species dense vegetation can reach high frequency counts. Then come constant species, i.e. species which occur in more than 50% of the samples in a cluster. Species names are followed by the number (in brackets) of samples in the cluster where the species is present.

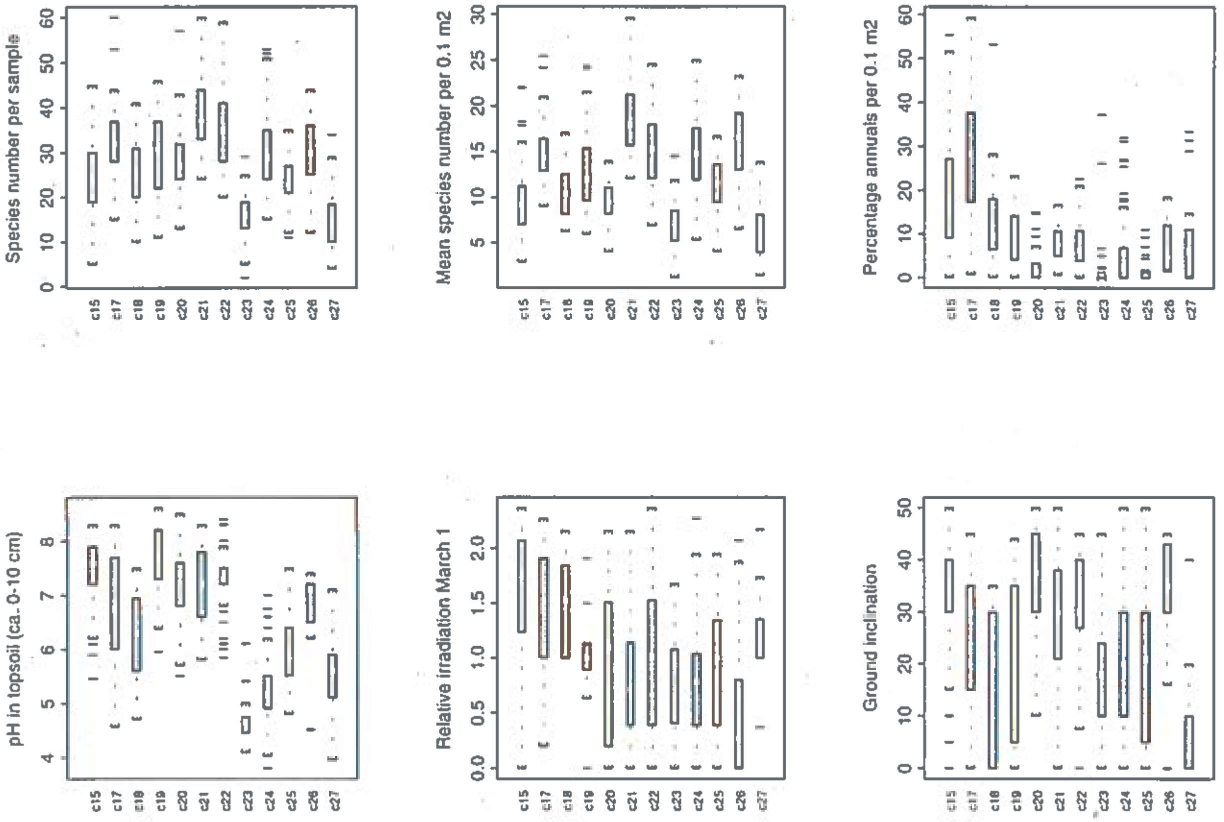

Figure 4. Diversity and local environment in the twelve end-clusters. Number of species per sample, species density, percentage of annuals in the species density, soil pH, incident radiation on March 1, and angle of slope. The dark boxes are the 3. quartiles below and above the median (white bar), the thin vertical bars are the 99% confidence limits and the horizontal bars each represent an outlier.

Two measures of species diversity are used: species number per sample (1 m^2 in 10 subplots randomly distributed in a homogeneous stand) and species density (average no of species per subplot of 0.1 m^2) (fig. 4). For clusters where the vegetation is rich in annuals, the per cent contribution of these to the species density is indicated.

Diversity figures as well as figures for soil pH are followed by 99% confidence intervals in parentheses. The local environment is described by the most significant explanatory variables (fig. 2 and 4), though soil pH and relative irradiation on March 1 are mentioned without exception (see Ejrnæs & Bruun subm. for details on available variables). Distribution of soil types in the clusters appear from table 2. For all types the prose description is accompanied by a dot-map of Denmark see appendix I. The maps should be interpreted as documentation of the type rather than distribution of the type. The reason for this is a biased sampling in certain regions, especially favouring calcareous and sand-grasslands Böcher (1945) and Böcher

Table 2. Percentages of crude soil types within the twelve end-clusters.

	cl 15	cl 17	cl 18	cl 19	cl 20	cl 21	cl 22	cl 23	cl 24	cl 25	cl 26	cl 27
Clay	11	4	0	54	22	33	10	0	9	0	0	0
Sand/clay	15	2	5	15	13	27	1	0	11	0	7	0
Diluvial sand	72	83	27	15	51	33	38	97	68	17	0	19
Eolian sand	1	0	15	0	0	0	0	0	1	59	7	23
Alluvial sand or shingle	1	8	30	0	2	0	0	3	11	7	0	46
Limestone	1	2	14	15	11	7	51	0	0	17	87	11

Table 3. Comparison of the twelve end-clusters with the closest unit of formal syntaxonomy (mainly Schubert et al. 1995; Dierβen 1996) and the classification of British Plant Communities (Rodwell 1993). Brackets indicate doubtful assignments.

syntaxon (North Germany)	cluster	British Plant Communities
(Plantagini-Festucion ovinae Passarge 1964)	15	
Plantagini-Festucion ovinae Passarge 1964 (espec. Helichryso-Phleetum phleoidis (Böcher 1945) Dierβen 1996)	17	CG7 Festuca ovina-Hieracium pilosella-Thymus pulegioides grassland
Plantagini-Festucion ovinae Passarge 1964 *OR* Koelerion glaucae (Volk 1931) Klika 1935	18	(U1 Festuca ovina-Agrostis capillaris-Rumex acetosella grassland / Erodium cicutarium-Teesdalia nudicaulis sub-community)
(Trifolio medii-Agrimonietum T.Müll.1962)	19	MG5 Cynosurus cristatus-Centaurea nigra grassland / Lathyrus pratensis subcommunity
Geranion sanguinei (Galio borealis-Geranietum sanguinei R.Tx.1967 *AND* Geranio-Trifolietum alpestris T.Müll.1962)	20	
(Bromion erecti Br.Bl.& Moor 1938)	21	MG5 Cynosurus cristatus-Centaurea nigra grassland / Galium verum subcommunity *AND* CG2 Festuca ovina-Avenula pratensis grassland
Bromion erecti Br.Bl.& Moor 1938 (e.g. association Solidagini-Helictotrichetum Will.,Delft et Rijke 1981)	22	CG2 Festuca ovina-Avenula pratensis grassland
Violion caninae Schwick.1944	23	U2 Deschampsia flexuosa grassland / Festuca ovina-Agrostis capillaris subcommunity
Violion caninae Schwick.1944 *AND* Vaccinio-Callunetum Büker 1942	24	U4 Festuca ovina-Agrostís capillaris-Galium saxatile grassland / Lathyrus montanus-Stachys betonica and Holcus lanatus-Trifolium repens subcomunities *AND* U1 Festuca ovina-Agrostis capillaris-Rumex acetosella grassland / Galium saxatile-Potentilla erecta subcommunity
	25	
	26	
Corynephorion canescentis Klika 1934	27	

et al. (1946). Nevertheless, most clusters seem to be rather evenly distributed over the sampled area. Exceptions to this picture are mentioned below.

A comparison of the end-clusters to formal syntaxonomy and to the British Vegetation Classification (Rodwell 1992) is shown in table 3. Differences in data collection introduce some noise to the comparison: our data are frequencies, which have a non-linear relationship to ramet density, but hardly any relationship to cover, which forms the base of the mentioned approaches. But, most complications regarding a comparison owes to the Danish climate and the available pool of grassland plant species being considerably different from Central Europe and Great Britain. Furthermore, South Scandinavia is only superficially treated in the phytosociological literature.

The naming of clusters constituted a specific challenge. We decided to combine the names of two constant species that, preferably each, but alternatively in combination, characterise and distinguish one community from the other. In addition, the first species was chosen to indicate the relationship of the cluster to main grassland types: Artemisia campestris indicate xeric grassland, Dactylis glomerata indicate calcareous grassland, Rumex acetosa indicate acidic grassland and Carex arenaria indicate sand-grassland.

Cluster 15 ARTEMISIA CAMPESTRIS-POA COMPRESSA GRASSLAND (103 samples)

The significant indicator species are the clonal grasses *Poa compressa* (48) and *Festuca trachyphylla* (25), and the annuals *Bromus sterilis* (10) and *Alyssum alyssoides* (10). Weaker indicators are the ruderal species *Melilotus alba* (6) and *Papaver argemone* (6), and *Melampyrum arvense* (7). The vegetation often has a low total cover, thus there are no frequency-dominants, although *Galium verum* rather often gain high abundance. Constant species are *Galium verum* (93) and *Dactylis glomerata* (91), and to a smaller extent *Artemisia campestris* (75), *Hieracium pilosella* (74), *Poa pratensis* (63), *Bromus hordeaceus* (58) *and Sedum acre* (55). Also *Achillea millefolium* (64) and *Arenaria serpyllifolia* (58) are rather constant, but never with high frequencies.

The vegetation is relatively species poor, 24 (±2) species per sample on average and 9.4 (±0.8) species per subplot, but rich in annuals - 20% (±3) of the species density. The local environment is characterised by very high pH (7.5 ±0.2) and very high incident radiation. Drought is the major limit to productivity, and cessation of grazing leads only to a succession in a very slow speed towards scrub often dominated by *Prunus spinosa*. This type of grassland occur predominantly in the precipitation-poor regions of Denmark: along the coasts of the Great Belt and the eastern Baltic Sea.

Cluster 17 ARTEMISIA CAMPESTRIS-TRIFOLIUM STRIATUM GRASSLAND (51 samples)

The significant indicator species are all annual species occurring in less than 50% of the samples - viz. *Trifolium striatum* (23), *Aïra caryophyllea* (14) and *Erophila verna* (18). *Saxifraga granulata* (23) is a weaker indicator; it is probably at lot underestimated in the data as the majority of Böcher's surveys were undertaken during summer. Another weak indicator is *Petrorhagia prolifera* (8) which also occurs in cluster 15. The tussocky grass *Avenula pratensis* (41) is the only frequent dominant. The constant species are *Galium verum* (50), *Hieracium pilosella* (44), *Sedum acre* (42), *Avenula pratensis* (41), *Cerastium semidecandrum* (41), *Bromus hordeaceus* (40), *Achillea millefolium* (39), *Arenaria serpyllifolia* (38), *Plantago lanceolata* (38), *Poa pratensis* (37), *Festuca ovina* (34), *Agrostis capillaris* (33), *Festuca rubra* (33), *Artemisia campestris* (32), *Ranunculus bulbosus* (28), *Trifolium arvense* (27) and *Trifolium campestre* (26). Also *Dactylis glomerata* (32) and *Luzula campestris* (28) are constant, but always with low abundance unlike in other clusters.

The vegetation is species rich - on average 32 (±3) species per sample, 14.9 (±1.2) per subplot, and rich in annuals - 20% (±3) of the species density. A moderate soil pH (6.8 ±0.4) combined with high irradiation indicates noncalcareous unleached soils.

Cluster 18 ARTEMISIA CAMPESTRIS-CAREX ARENARIA GRASSLAND (27 samples)

Significant indicator species are *Pulsatilla pratensis* (21), *Thalictrum minus* (8), and weaker *Veronica spicata* (5). *Galium verum* (26) is the only frequency dominant species. Constant species are *Sedum acre* (26), *Hieracium pilosella* (22), *Carex arenaria* (20), *Thymus serpyllum* (20), *Trifolium arvense* (17), *Festuca rubra* (16) and *Poa pratensis* (16). Also rather constant, but always at low abundance is *Artemisia campestris* (20), *Agrostis capillaris* (14), *Avenula pratensis* (14), *Festuca ovina* (14) and *Plantago lanceolata* (14).

The vegetation is relatively species poor - on average 25 (±4) species per sample, 10.5 (±1.6) per subplot, but relatively rich in annuals - 13% (±5) of the species density. The type mainly occurs on post-glacial marine sand and shingle deposits, in north-west Jutland on drought prone fixed dune sites though. Often the substrate have been calcareous, but now being somewhat leached, though never acidified (pH 6.2 ±0.4), and the irradiation is high. The vegetation share some characteristic species with cluster 27, e.g. *Corynephorus canescens* (5). The presence in northern Jutland of continentally distributed species in calcareous fixed dune grasslands is unique in Europe (Böcher 1954).

Cluster 19 DACTYLIS GLOMERATA-LOLIUM PERENNE GRASSLAND (13 samples)

Significant indicator species are *Bellis perennis* (8), *Lolium perenne* (8), *Elytrigia repens* (8), *Potentilla reptans* (7), *Lathyrus pratensis* (6), *Carex hirta* (5), *Agrimonia eupatoria* (6) and *Vicia sativa ssp. nigra* (5). The only frequency dominant species is *Festuca rubra* (12). Constant species are *Dactylis glomerata* (13), *Poa pratensis* (12), *Phleum pratense ssp. bertolonii* (11), *Achillea millefolium* (10), *Plantago lanceolata* (10), *Taraxacum sp.* (10), *Galium verum* (9), *Medicago lupulina* (9), *Centaurea jacea* (8), *Centaurea scabiosa* (7), *Cynosurus cristatus* (7), *Hieracium pilosella* (7) and *Ranunculus bulbosus* (7).

Diversity is variable but may be very high - on average 30 (±9) species per sample, and frequently very species dense: 13.9 (±5.1) species per subplot, despite the prevalence of species potentially capable of dominance. The soil is clayey, either moraine clay or Eocene (plastic) clay, the pH is very high (7.6 ±0.7), and moderate irradiation and oozing subsoil water makes sites less susceptible to drought and potentially productive. Our information on grazing in the old data sets is inadequate but we hypothesise that grazing controls the competitive species and allow for the co-occurrence of less competitive species. Despite the occurrence of species typical for improved pastures, the type is unimproved and contains numerous species indicative of absence of fertilisation and cultivation.

Cluster 20 DACTYLIS GLOMERATA-ARRHENATERUM GRASSLAND (50 samples).
Significant indicator species are *Arrhenaterum elatius* (21) and *Galium mollugo* (13), and weaker but significant *Heracleum sphondylium* (10), *Campanula persicifolia* (16), *Hedera helix* (6) and *Vincetoxicum hirundinaria* (7). Frequency dominant species *Festuca rubra* (38), and occasionally characteristic forbs like *Geranium sanguineum* (16) or *Vincetoxicum hirundinaria*. Constant species are *Dactylis glomerata* (45), *Centaurea jacea* (38), *Galium verum* (36), *Poa pratensis* (33), *Achillea millefolium* (32), *Primula veris* (32), *Campanula rotundifolia* (30). The coarse grass species like *Arrhenaterum* and *Dactylis* only rarely dominate the vegetation.

The vegetation is not species poor - on average 28 (±3) species per sample, but with a low species density, 9.6 (±0.8) species per subplot. This is probably a reflection of the larger plant modular size, i.e. dominance. The vegetation is supposedly ungrazed or lightly grazed, but the steepness of the slopes (36° on average) makes scrub encroachment take place at a very slow rate. Soil pH is high (7.2 ±0.3), and the irradiation moderate.

Cluster 21 DACTYLIS GLOMERATA-RANUNCULUS BULBOSUS GRASSLAND (31 samples)
Significant indicator species are *Ranunculus bulbosus* (28), *Cynosurus cristatus* (19), *Cerastium fontanum ssp. triviale* (23) and *Thymus pulegioides* (13). Frequency dominant species are *Festuca rubra* (30) and less often *Avenula pratensis* (24). Constant species are *Dactylis glomerata* (30), *Galium verum* (30), *Achillea millefolium* (28), *Hieracium pilosella* (28), *Campanula rotundifolia* (26), *Luzula campestris* (26), *Festuca ovina* (25), *Agrostis capillaris* (24), *Plantago lanceolata* (24), *Poa pratensis* (24), *Briza media* (23), *Medicago lupulina* (23), *Phleum pratense ssp. bertolonii* (20), *Anthoxanthum odoratum* (19), *Primula veris* (18), *Carex caryophyllea* (17), *Centaurea jacea* (17), *Rumex acetosa* (17), *Linum catharticum* (16), *Pimpinella saxifraga* (16) and *Taraxacum sp.* (16).

The vegetation is very species rich - 39 (±5) species per sample, and 19.1 (±2.2) per subplot. The soil pH is high (7.2 ±0.4), the soil is sandy moraine deposits, of which some contain calcite and some are decalcified with pH just below 7. The irradiation is relatively low, the sites often being north faced slopes. This cluster is somewhat transitional to acidic grassland.

Cluster 22 DACTYLIS GLOMERATA-KOELERIA PYRAMIDATA GRASSLAND (87 samples)
Significant indicator species are *Koeleria pyramidata* (43), *Campanula glomerata* (21), and weaker but significant *Sanguisorba minor ssp. minor* (14), *Polygala amarella* (10) and *Crepis praemorsa* (8). Only *Avenula pratensis* (77) is a frequency dominant species. Constant species are *Festuca rubra* (74), *Campanula rotundifolia* (73), *Galium verum* (71), *Medicago lupulina* (71), *Dactylis glomerata* (65), *Hieracium pilosella* (65), *Pimpinella saxifraga* (65), *Festuca ovina* (59), *Centaurea jacea* (58), *Briza media* (56), *Plantago lanceolata* (55), *Achillea millefolium* (54), *Galium sterneri* (53), *Lotus corniculatus* (52), *Linum catharticum* (50), *Carex flacca* (45), *Cirsium acaule* (45), *Ranunculus bulbosus* (45) and *Carex caryophyllea* (44).

The vegetation is very species rich - 35 (±2) species per sample on average, and 15.2 (±1.1) species per subplot. Soil pH is high (7.3 ±0.1) and irradiation moderate. Within Denmark all of the significant indicator species occur almost exclusively in northern Jutland, where also the geographic centre of the cluster is. Vegetation resembling the core of the type occur scattered in the precipitation-poor region. The substrate in northern Jutland and on the isle of Møn is slopes of Cretaceous chalk, more or less covered by sandy moraine deposits. In the rest of the country the substrate is calcite-rich sandy moraine.

Willems et al. (1981) investigated Danish vegetation similar to this community with traditional phytosociological methods, and described the association Solidagini-Helictotrichetum Will.,Delft et Rijke 1981 (in the alliance Bromion erecti Br.Bl.& Moor 1938). Their relevées could surely be ascribed to cluster 22, but the remaining part of cluster 22 and the whole of cluster 21, which also fits with the diagnostic species of Mesobromion, cannot easily be assigned to Solidagini-Helictotrichetum.

Cluster 23 RUMEX ACETOSA-DESCHAMPSIA FLEXUOSA GRASSLAND (37 samples)

Significant indicator species are *Deschampsia flexuosa* (34), *Galium saxatile* (19), *Carex pilulifera* (14) and *Agrostis vinealis* (11). *Deschampsia flexuosa* is almost always dominating the vegetation. Constant species are *Luzula campestris* (31), *Agrostis capillaris* (30) sometimes codominant, *Festuca ovina* (27), *Poa pratensis* (25), *Campanula rotundifolia* (23), *Festuca rubra* (22), *Rumex acetosa* (22), *Hieracium pilosella* (21), *Calluna vulgaris* (18) and *Rumex acetosella* (18).

The vegetation is species poor - 16 (±3) species per sample and 7.1 (±1.2) per subplot. The soil is very acidic (pH 4.6 ±0.2), and often podzolised. The type occur predominantly on level terrain to north-facing slopes with low incident radiation. The type can be seen as a transition to the dwarf-shrub heath, though chamaephytes play only a minor role. The apparent concentration of the cluster on the Mols peninsula, Eastern Jutland, is probably a sampling artefact. This grassland type is underrepresented in Böcher's samples, and is known to be common, especially in the precipitation-rich regions.

Cluster 24 RUMEX ACETOSA-AGROSTIS CAPILLARIS GRASSLAND (123 samples)

The only significant indicator species for this the largest cluster is *Stellaria graminea* (38). This apparent paradox arises as the cluster represents the middle of the primary coenoplane - or "normal" grassland vegetation. Frequency dominant species are *Agrostis capillaris* (116) and *Festuca ovina* (108). Constant species are *Achillea millefolium* (113), *Hieracium pilosella* (110), *Luzula campestris* (110), *Anthoxanthum odoratum* (109), *Plantago lanceolata* (107), *Campanula rotundifolia* (97), *Festuca rubra* (95), *Poa pratensis* (92), *Galium verum* (90), *Rumex acetosa* (86), *Ranunculus bulbosus* (78), *Danthonia decumbens* (63), *Trifolium medium* (63) and *Pimpinella saxifraga* (62). These species are among the most common grassland species.

The vegetation is species rich - 31 (±2) species per sample, and 15.0 (±1.0) per subplot-and occurs mainly on level to north-facing ground. It is related to cluster 23 but the soil pH is a little higher (5.2 ±0.1) which has profound impact on the number of species.

Cluster 25 CAREX ARENARIA-FESTUCA RUBRA GRASSLAND (29 samples)

Significant indicator species are *Rosa pimpinellifolia* (16), *Ammophila arenaria* (19), *Veronica chamaedrys* (16), *Linaria vulgaris* (9), *Polypodium vulgare* (8) and *Silene vulgaris ssp. maritima* (3). The only frequency dominant species is *Festuca rubra* (28), and constant species are *Poa pratensis* (29), *Achillea millefolium* (28), *Galium verum* (26), *Carex arenaria* (23), *Pimpinella saxifraga* (23), *Agrostis capillaris* (18), *Campanula rotundifolia* (18), *Lotus corniculatus* (17), *Luzula campestris* (17), *Plantago lanceolata* (17) and *Veronica officinalis* (15). Chamaephytes such as *Calluna vulgaris* and *Vaccinium myrtillus* are absent.

The vegetation is relatively species poor - 23 (±3) species per sample and 11.5 (±1.5) per subplot. The substrate is eolian sand, often previously calcareous but now decalcified, yielding a soil pH of 6.0 (±0.5). This type mainly occurs in north-western Jutland, but similar vegetation without *Rosa pimpinellifolia* is found in the precipitation-poor region.

Cluster 26 PLANTAGO MARITIMA-SOLIDAGO VIRGA-AUREA GRASSLAND (15 samples)

Significant indicator species are *Plantago maritima* (13), *Solidago virga-aurea* (13), which are also constant, and *Antennaria dioica* (7), *Agrostis stolonifera* (8), *Linum catharticum* (12), *Senecio integrifolius* (7), *Empetrum nigrum* (8), *Prunella vulgaris* (10), *Carlina vulgaris* (8), *Galium sterneri* (10), *Gentianella amarella* (5), *Leontodon autumnalis* (7), *Erigeron acre* (5), *Draba incana* (3) and *Hypochoeris maculata* (4). Some of these species are widespread and often occur in habitats other than grassland, but at least *Agrostis stolonifera, Dactylis glomerata, Solidago virga-aurea, Anthyllis vulneraria* and *Hypochoeris maculata* seem to have specialised ecological races on the sampled localities (e.g. Böcher 1961: *Dactylis*; Lampinen 1990: *Anthyllis*). *Festuca rubra* (15) is the only frequency dominant species. Constant species are *Hieracium pilosella* (14), *Campanula rotundifolia* (13), *Pimpinella saxifraga* (13), *Galium verum*(11), *Hieracium umbellatum* (11), *Taraxacum sp.* (11), *Achillea millefolium* (10), *Lotus corniculatus* (10), *Luzula campestris* (10), *Thymus serpyllum* (9), *Carex flacca* (8) and *Plantago lanceolata* (8).

The vegetation is species rich - 30 (±6) species per sample and 16 (±1.3) per subplot. The type is found on steep north-facing slopes of limestone, more or less overlaid by eolian sand. The eolian sand contains varying amounts of calcite as it is partly produced by the seas erosion of calcareous cliff. These circumstances, which are limited to north-westernmost Jutland, results in a very variable soil pH (6.7

±1.0). Typical for the cluster is also a very low irradiation. The geographic range corresponds to that of this peculiar mixture of limestone and eolian sand. Only one, apparently misclassified, sample from outside this area has been included in the cluster.

The cluster seems somewhat misplaced in the first division, where it was separated from the *calcareous grassland* (it shares many species with cluster 22) and fused with acidic grassland, but the odd mixture of species give it a transitional status. This type bears obvious ecological similarities to the English chalk heath (Grubb et al. 1969) and limestone heath (Etherington 1981) although the particular species are different.

Cluster 27 CAREX ARENARIA-CORYNEPHORUS CANESCENS GRASSLAND (48 samples)
Significant indicator species are *Corynephorus canescens* (35), *Carex arenaria* (44), *Jasione montana* (29), *Hieracium umbellatum* (33) and *Thymus serpyllum* (33). No frequency dominant species are found. Constant species apart from the indicator species are *Galium verum* (33), *Hieracium pilosella* (31) and *Festuca rubra* (30).

The vegetation is species poor - 15 (±3) species per sample and 6.2 (±1.3) per subplot. It occurs on postglacial marine deposits all over the area north of the isostatic line where the coastline has retreated during the last 5000 years. The largest areas of such deposits are found in northern Jutland. The soil pH is low (5.5 ±0.2) and irradiation is moderate. The texture of the substrate makes the sites very susceptible to summer drought, which is likely to be a major constraint on productivity and species composition. The cluster contains a transition towards the vegetation of the 'white' dune - a few samples having species like *Ammophila arenaria* and *Lathyrus japonicus*, suggesting a former sand-drift.

Discussion

A gradient analysis (Ejrnæs & Bruun subm.) showed that the floristic variation in these dry grasslands was continuous and with an almost complete turnover of species from one axis end to the other along at least two axes. The replacement of species were judged from the length of DCA-axes scaled in SD-units, assuming the average species to appear, reach its optimum and disappear in 6 SD-units (Minchin 1987), and it should be taken into account that the applied abundance scale favours presence over abundance, which is reported to shorten DCA-axes (Eilertsen et al. 1990). No natural clusters were obvious in a plot of samples in the primary coenoplane (fig. 3), except for a weak disjunction between cluster 3 *acidic grassland* and cluster 4 *sand grassland*. This observation lends support to the view that species basically behave individualistically, and that communities are not discrete units in the ecological space (cf. Austin 1990). Despite this continuous variation, the clustering procedure yielded a number of floristically and ecologically well-defined clusters. This leads us to conclude that vegetation classification often, if not always, is continuum segmentation (van Groenewoud 1992 on TWINSPAN), but nevertheless feasible and useful, both to scientific research and to nature management and conservation.

There is always a certain stochastic element in a species' abundance, and especially regarding its absence and presence at a site. In dynamic plagioclimax vegetation, species regional dynamics (sensu Eriksson 1996) lead to an interaction between species and landscape, and hence to stochastic differences in grassland species pools. A site of calcareous grassland surrounded by heathland is likely to have a somewhat different composition of subordinate species than a similar site surrounded by other calcareous grasslands, due to the mass effect. In order to achieve a classification acknowledging that sites with a similar environment can have vicarious species, some within-cluster floristic heterogeneity should be allowed for. The breadth of our clusters seems to be suitable to avoid as much stochasticity as possible.

Vegetation succession implies events of local extinction and colonisation, further raising the element of stochasticity, and reducing the predictability of species composition in terms of the local environment. This relationship suffers even further if the vegetation is under strong influence by man. The classification approach taken in formal syntaxonomy and the British Vegetation Classification emphasising within-cluster floristic homogeneity and simultaneously aiming to cover the entire gradient in human interference with vegetation implies the description of separate entities of vegetation created or strongly influenced by man and of short-lived successional stages, e.g.

formal syntaxonomy and the British Vegetation Classification. What such an approach to vegetation classification might gain in precision of vegetation description, is lost in a weak correspondence between associations/communities and local environment. In the hierarchic formal syntaxonomy this problem is further accentuated by the assignment of successional phases to very different syntaxonomic levels depending on vegetation type (see van der Maarel 1996 for examples). We support the original idea of Böcher (1945) to classify only vegetation with low human interference and our clusters have deliberately been made sufficiently broad to include short-lived stages characterised by reversible overgrowing by coarse grasses, forbs and scattered shrubs. It is striking that the syntaxonomic parallels of our clusters are exclusively found on the level of alliance, the associations being much too narrow. Rodwell (1992) states that the British communities have been delimited in attempt to obtain a breadth similar to that of syntaxonomic associations. However, common communities, e.g. MG5, have a breadth similar to our clusters, but the rarer ones being much narrower.

The comparison of the final clusters to phytosociological classifications from adjacent countries leaves 4 clusters without direct parallels, and 2 clusters without any equivalent. Cluster 25 (Carex arenaria-Festuca rubra grassland) has affinities to Hieracio-Empetretum Libbert 1940, but it also contains calcicolous species like *Geranium sanguineum*. Cluster 26 (Plantago maritima-Solidago virgaaurea grassland) has some affinity to Gentianello-Pimpinelletum saxifragae R.Tx. 1967 described from south Norwegian calcareous fixed dunes, due to constant species as *Festuca rubra* and *Pimpinella saxifraga*, and rare subordinate species as *Draba incana*. But this association does not show the intimate mixture of calcifuges and acidifuges characteristic of cluster 26. It thus seems likely that the distribution of the communities typified as clusters 25 and 26 are limited to southern Scandinavia.

The recently proposed Indicator Species Analysis (Dufrêne & Legendre 1997) has proven useful for vascular plant frequency data, by guiding the breadth of clusters, and by providing the classification with a synoptic determination key (table 1). Dufrêne & Legendre (1997) distinguish between asymmetric and symmetric indication. Symmetric indicator species are indicating the true cluster membership, and their presence are likely in all members of that cluster, while asymmetric indicators only have the former feature. According to Dufrêne & Legendre (1997) the limit between asymmetric and symmetric indication correspond to 55% of perfect indication. This value is not, however, supported in our data: *Carex arenaria, Luzula campestris* and *Agrostis capillaris* are occurring rather frequently and abundantly outside the cluster for which they should be symmetric indicators.

Some vegetation classifications contain an a priori division of the data according to soil type or other environmental features, but the justification is not always evident. The division in the British Vegetation Classification (Rodwell 1992) into calcifugous, mesotrophic and calcicolous grasslands, allegedly determined by the presence of conspicuous elements of calcifugous or calcicolous species (mesotrophic grasslands having neither), gives the impression of a division along a gradient in soil acidity. The argument appears circular, though, since the soil acidity preference of species probably is judged from their presence in communities traditionally coined calcicolous or calcifugous. The cluster of ours having the most 'mesotrophic' vegetation (cluster 19) occur on calcareous soil with very high soil pH, and the same goes probably for its British parallel MG5. Furthermore, communities combining calcifugous *and* calcicolous species (e.g. our cluster 26 and the British chalk heath) does not easily fit into the pattern.

The common treatment of 'dune vegetation' as a separate vegetation type, due to eolian sand being its substrate (e.g. Warming 1909), is not supported by the present classification considering the dispersion of eolian sand over the clusters (tab. 2). The mentioned approaches to classification are analogous to the direct approach to gradient analysis (see also Carleton et al. 1996). The gradient analysis of the present data set showed the vegetation to respond to a set of ecological gradients in a complex manner that could not be predicted by the single gradients (Ejrnæs & Bruun subm.). A classification of samples based on the two most important explanatory variables, soil pH and relative irradiation, resulting in the four combinations of acidic/basic vs. moist/dry, would only poorly reproduce the classification presented here.

Similarly, the present classification in combination with the gradient analysis of the same data indicate that a simple division according to soil types would also sacrifice the floristic homogeneity of clusters. In conclusion, the best way to simultaneously optimise precision of the vegetation description and ecological validity is an 'indirect' approach to classification.

Acknowledgements

Lecturers Henning Adsersen and Anders Michelsen are thanked for helpful comments on the manuscript.

Literature

Austin, M.P. 1990. Community Theory and Competition in Vegetation, in: J.B. Grace & D. Tilman. *Perspectives on Plant Competition*, pp. 215-238. Academic Press.

Böcher, T.W. 1941. Beiträge zur Pflanzengeographie und Ökologie Dänischer Vegetation, I. Über die Flechtenheiden und Dünen der Insel Läsö. *Kgl.Dan.Vidensk.Selsk., Biol.Skr.* 2(1), 38 pp.

Böcher, T.W. 1943. Studies on the plant geography of the North-atlantic heath formation. *Kgl.Dan.Vidensk.Selsk., Biol.Skr.* 2(7), 130 pp.

Böcher, T.W. 1945. Beitrage zur Pflanzengeographie und Ökologie dänischer Vegetation. II. Über die Waldsaum- und Graskrautgesellschaften trockner und halbtrockener Böden der Insel Seeland mit besonderer Berücksichtigung der Strandabhange und Strandebenen. *Kgl.Dan.Vidensk.Selsk., Biol. Skr.* 4(1) 163 pp.

Böcher, T.W.. 1946. Græs-Urte-Vegetationen paa Høje Møn. *Botanisk Tidsskrift* 48: 1-45.

Böcher, T.W. 1947. Festuca polesica Zapal., its Chromosome Number and Occurrence in Denmark. *Botaniska Notiser* 1947(4): 353-360.

Böcher, T.W. 1954. Studies on the European Calcareous Fixed Dune Communities. *Vegetatio* 5-6: 562-570.

Böcher, T.W. 1957. Jordbund og skræntvegetation ved Bornholms sydkyst. Bornholms naturhistoriske forening, udgivet i anledning af 25 års jubilæet.

Böcher, T.W. 1961. Experimental and Cytological Studies on Plant Species. VI: *Dactylis glomerata* and *Anthoxanthum odoratum*. *Botanisk Tidsskrift* 56: 314-335.

Böcher, T.W., T. Christensen, M.S. Christiansen. 1946. Slope and Dune Vegetation of North Jutland. I. Himmerland. *Kgl.Dan.Vidensk.Selsk., Biol.Skr.*4(3), 78 pp.

Böcher, T.W., T. Christensen, M.S. Christiansen. Unpubl. Slope and Dune Vegetation of North Jutland. II. *Manuscript (Bot. Centralbibl., Copenhagen)*

Carleton, T.J., R.H. Sitt & J. Nieppola. 1996. Constrained indicator species analysis (COINSPAN): an extension of TWINSPAN. *J.Veg.Sci.* 7: 125-130.

Dierβen, K. 1996. *Vegetation Nordeuropas*. Ulmer, Stuttgart.

Dufrêne, M. & P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67: 345-366.

Ejrnæs & Bruun (ms). A gradient analysis of temperate grasslands on well-drained soils. subm. to JVS.

Eilertsen, O., R.H. Økland, T. Økland & O. Pedersen. 1990. Data manipulation and gradient length estimation in DCA ordination. *J.Veg.Sci.* 1: 261-270.

Eriksson, O. 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos* 77: 248-258.

Etherington, J.R. 1975. Environment and Plant Ecology. Wiley, London.

Etherington, J.R. 1981. Limestone heaths in south-west Britain: their soils and the maintenance of their calcicole-calcifuge mixtures. *J.Ecol.* 69: 277-294.

Fredskild, B. 1954. Ecological and Floristic Studies on Dry Sand Slopes in Western Sealand. *Oikos* 5: 205-235.

Gauch Jr., H.G. 1982. Multivariate analysis in community ecology. Cambr.Stud.Ecol. 1: 1-298.

Grøntved, J. 1927. Formationsstatistiske Undersøgelser paa nogle danske Overdrev. *Botanisk Tidsskrift* 40: 1-71.

Grubb, P.J., H.E. Green & R.C.J. Merrifield. 1969. The ecology of chalk heath: its relevance to the calcicole-califuge and the soil acidification problems. *J.Ecol.* 57: 175-212.

Hill, M.O. 1979. *TWINSPAN: a FORTRAN Program for Arranging Multivariate Data in an Ordered Two-way Table by Classification of the Individuals and Attributes*. Cornell University, Ithaca NY.

Lampinen, R. 1990. Anthyllis vulneraria subsp. danica, subsp. nova (Fabaceae) from Denmark. *Ann.Bot.Fennici* 27: 217-220.

McCune, B. & M.J. Mefford. 1997. *PC-ORD. Multivariate Analysis of Ecological Data*, version 3.0. MjM Software Design, Gleneden Beach OR.

Minchin, P. 1987. Simulation of multidimensional community patterns: towards a comprehensive model. *Vegetatio* 71: 145-156.

Mortensen, M.B. 1953. Urtesamfund på skrænter på Hindsholm (Summ.: Grassland Communities on the Slopes of Hindsholm). *Botanisk Tidsskrift* 49: 239-259.

Mortensen, M.B. 1955. Urtesamfund på skrænter på Nord-Samsø (Summ.: Grassland Communities on Slopes in Northern Samsø). *Botanisk Tidsskrift* 52: 85-112.

Noy-Meir, I. & R.H. Whittaker. 1977. Continuous multivariate methods in community analysis: some problems and developments. *Vegetatio* 33: 79-98.

Økland, R.H. 1986. Rescaling of ecological gradients. I. Calculation of ecological distance between vegetation stands by means of their floristic composition. *Nord.J.Bot.* 6: 651-660.

Økland, R.H. 1992. Studies in SE Fennoscandian mires: relevance to ecological theory. *J.Veg.Sci.* 3: 279-284.

Oksanen, J. & P.R. Minchin. 1997. Instability of ordination results under changes in input data order: explanations and remedies. *J. Veg.Sci.* 8: 447-454.

Raunkiær, C. 1909. Formationsundersøgelse og Formationsstatistik. *Botanisk Tidsskrift* 30: 20-132 (Chapt.VI. Investigations and statistics of plant formations, in: Raunkiær. 1934. pp 201-281).

Raunkiær, C. 1916. Formationsstatistiske Undersøgelser paa Skagens Odde. *Botanisk Tidsskrift* 30: 20-132 (Chapt.VIII. Statistical investigations on the plant formations of Skagens Odde (The Skaw), in: Raunkiær. 1934. pp 303-342).

Raunkiær, C. 1918. Recherches statistiques sur les formations vègètales. Kgl.Dan.Vidensk. Selsk., Biol.Medd. 1(3) (Chapt.XI. Statistical researches on plant formations, in: Raunkiær. 1934. pp 379-424).

Raunkiær, C. 1934. *The Life Forms of Plants and Statistical Plant Geography*, being the collected papers of C.Raunkiær. Oxford University Press.

Rodwell, J.S. (ed.). 1992. *Grasslands and Montane Communities. British Plant Communities*, vol. 3. Cambridge University Press.

SAS Institute Inc. 1990. *SAS/STAT® User's Guide*, ver. 6, 4th ed.

Schubert, R., W. Hilbig & S. Klotz. 1995. *Bestimmungsbuch der Pflanzengesellschaften Mittel- und Norddeutschlands*. Gustav Fischer Verlag, Stuttgart.

Shimwell, D.W. 1971. *The Description and Classification of Vegetation*. Sidgwick & Jackson, London.

Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. *Kgl.Dan.Vidensk.Selsk., Biol.Skr.* 5(4), 34 pp.

van Groenewoud, H. 1992. The robustness of Correspondence, Detrended Correspondence, and TWINSPAN analysis. *J.Veg.Sci.* 3: 239-246.

Warming, E. 1895. *Plantesamfund. Grundtræk af den økologiske Plantegeografi*. P.G.Philipsens Forlag, København.

Warming, E. 1909. *Dansk Plantevækst. 2. Klitterne*. Gyldendal, København & Kristiania.

Westhoff, V. & E. van der Maarel. 1978. The Braun-Blanquet approach, in: Whittaker, R.H. (ed.) *Classification of plant communities.*, pp 287-399. Junk, The Hague.

Whittaker, R.H. (ed.) 1978. *Classification of plant communities*. Junk, The Hague.

Willems, J.H., J.M.E. van Delft & M.J. de Rijke. 1981. Observations on North-West European Limestone Grassland Communities: IV. Phytosociological notes on chalk grasslands in Denmark. *Folia Geobot.Phytotax.* 16: 391-406.

Appendix I. Dot-maps of end-clusters in Denmark.

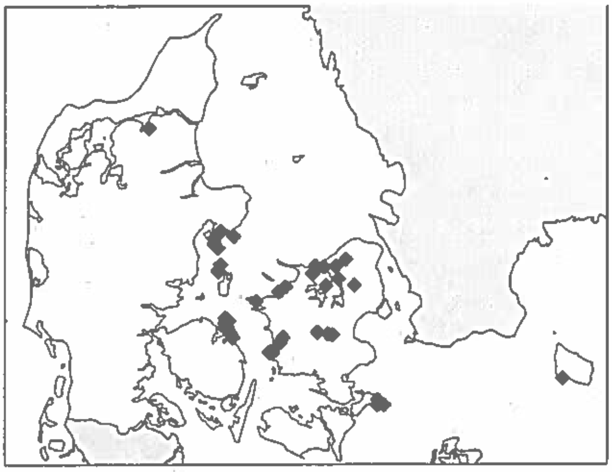

Figure 5. Sites of cluster 15 Artemisia campestris-Poa compressa grassland

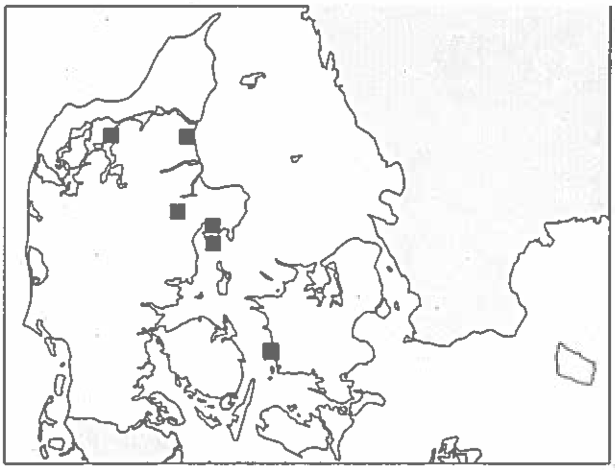

Figure 8. Sites of cluster 19 Dactylis glomerata-Lolium perenne grassland

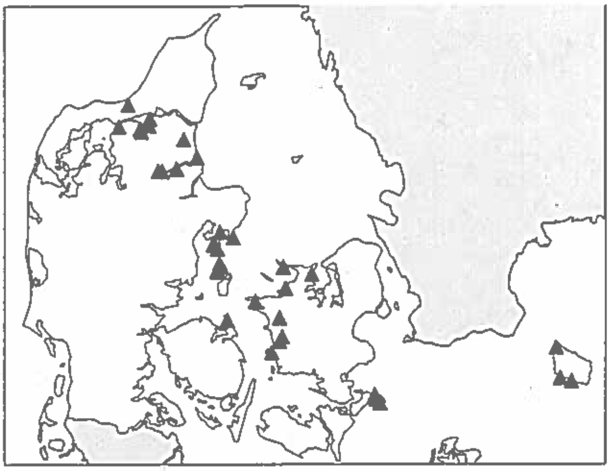

Figure 6. Sites of cluster 17 Artemisia campestris-Trifolium striatum grassland

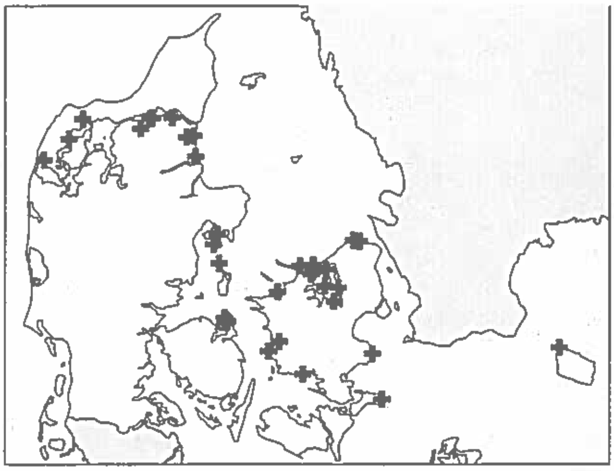

Figure 9. Sites of cluster 20 Dactylis glomerata-Arrhenaterum grassland

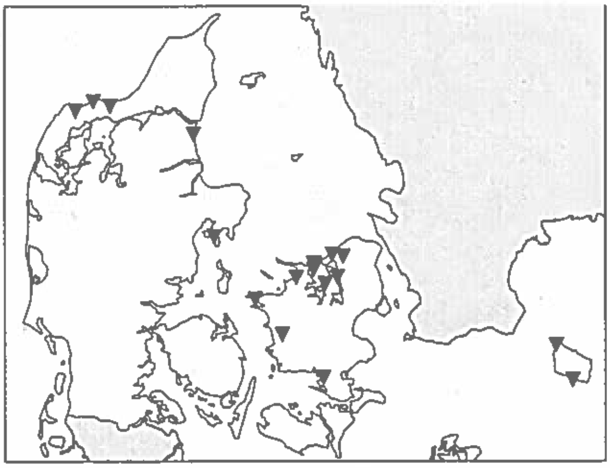

Figure 7. Sites of cluster 18 Artemisia campestris-Carex arenaria grassland

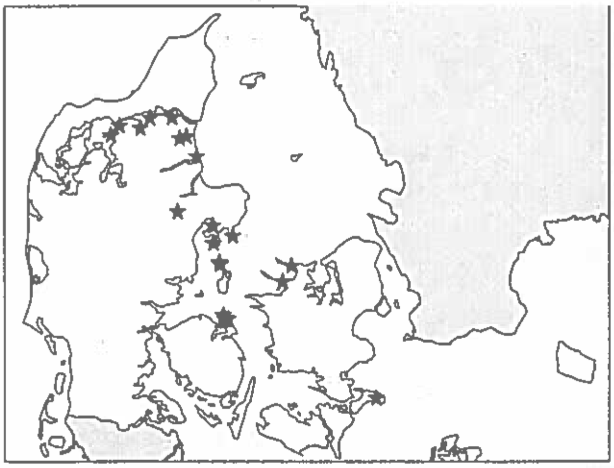

Figure 10. Sites of cluster 21 Dactylis glomerata-Ranunculus bulbosus grassland

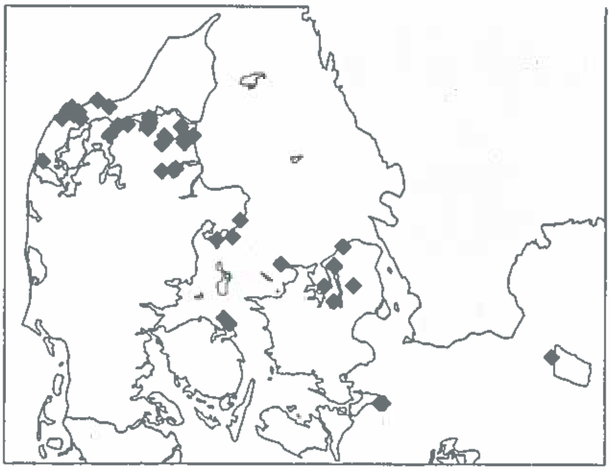

Figure 11. Sites of cluster 22 Dactylis glomerata-Koeleria pyramidata grassland

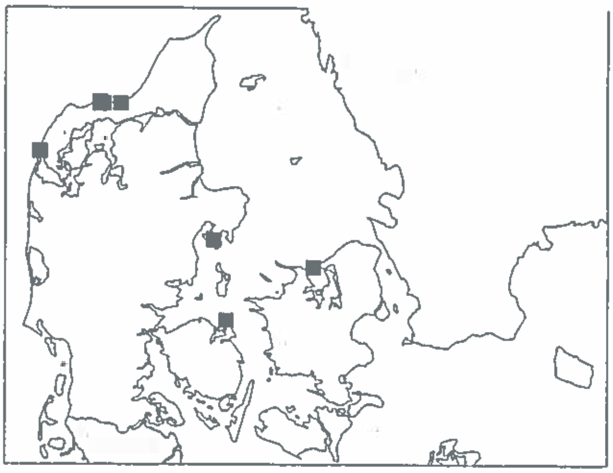

Figure 14. Sites of cluster 25 Carex arenaria-Festuca rubra grassland

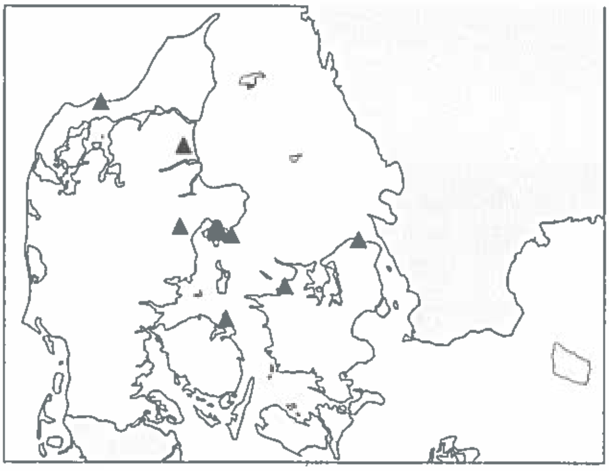

Figure 12. Sites of cluster 23 Rumex acetosa-Deschampsia flexuosa grassland

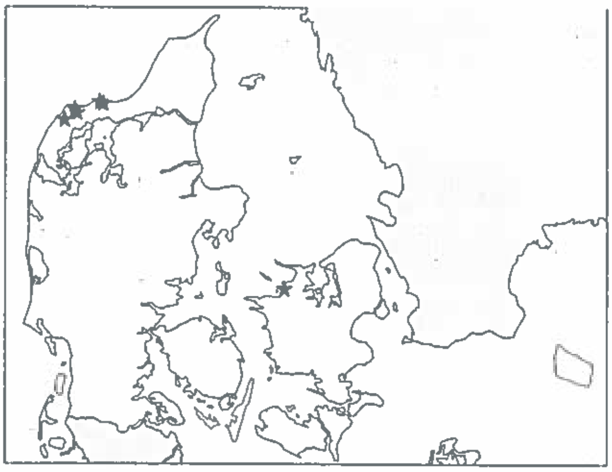

Figure 15. Sites of cluster 26 Plantago maritima-Solidago virga-aurea grassland

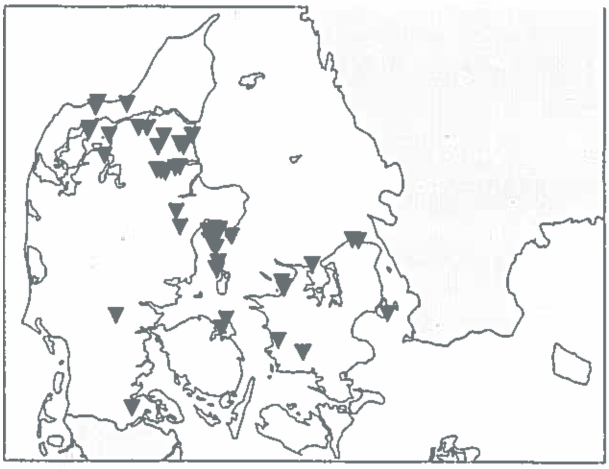

Figure 13. Sites of cluster 24 Rumex acetosa-Agrostis capillaris grassland

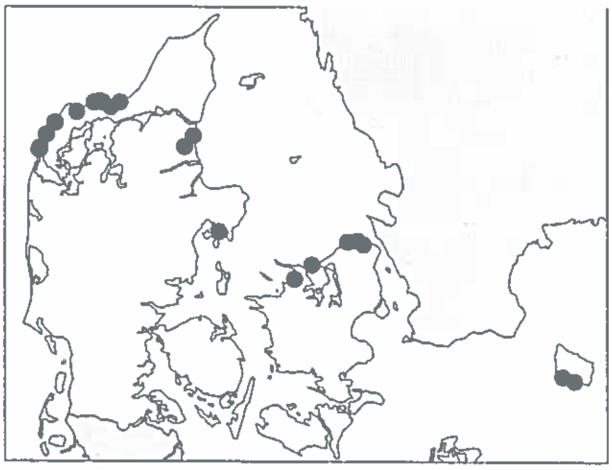

Figure 16. Sites of cluster 27 Carex arenaria-Corynephorus canescens grassland

Article III

Carex montana L.

Response curves and pH preferences of grassland plants in Denmark

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Abstract

I investigate the response of grassland plants to environmental gradients. I show that species responses to pH can be symmetric unimodal, asymmetric unimodal and bimodal. Discontinuous bimodal distributions disappear in more environmental dimensions and along the two major ecoclines revealed by correspondence analysis, but the asymmetric response type remains frequent. Consequently multivariate methods based on weighted averaging are burdened by biased estimates of species optima. Though not always assuming the correct response function, I demonstrate that detrended correspondence analysis produce coenoclines interpretable in meaningful environmental terms, that have a high explanatory power with respect to species occurrences. I therefore recommend extensive use of indirect ordination as evaluation tool of the realism of any predictive model of vegetation based on measured variables.

I present indicator values of pH optima and amplitude are presented for 146 species and show that they correlate with, yet differ considerably from, indications from Central Europe.

Introduction

The development of predictive tools in plant ecology is a lasting challenge (see e.g. Keddy 1992). Autecological knowledge is a basic prerequisite and the extraction of simple, yet reliable measures of important species characteristics, has been a major field in plant ecology. Autecological information in the form of indicator values (e.g. Ellenberg 1974, 1992) has received much attention and has been used for estimating site conditions (e.g. Persson 1980). Grime (1973, 1974 & 1977) suggested reducing the plant environment to a disturbance and a productivity gradient, leading to three major adaptive strategies in plants; of which the pure forms are known as *competitors*, *stress tolerators* and *ruderals*. Methods for extracting relevant autecological information have also been studied. Gauch & Whittakers (1972) continuum theory provided a theoretical basis for the prediction of species distribution and vegetation composition. Hill (1973) introduced indirect gradient analysis by *correspondence analysis*, based on unimodal species responses to plant ecology, and ter Braak (1986) added to this the direct gradient analysis tool *canonical correspondence analysis*.

Austin et al. (1984) and Austin (1987) studied the distribution of Eucalypt species in southern New South Wales and found that ideal bell shaped curves were not universal, and Austin (1994) therefore questioned the validity of approaches based on weighted averaging of species responses to environmental gradients, including e.g. ordination by correspondence analysis. This is in conflict with Øklands (1990: 141-155) recommendations based on a thorough discussion of shortcomings and potentials of CA and DCA. Økland concludes that detrended correspondence analysis (DCA), despite its faults, is a useful ordination method, that has been the basis for a considerable number of successful gradient analysis studies. A major concern to vegetation ecologists should therefore be whether indirect gradient analysis using an ordination method with a potentially incorrect assumption of response function should be given up in favour of the more flexible modelling of single species responses in terms of measurable environmental gradients.

Ordination methods are bound to extract general coenoclines, based on a common model for species responses, ignoring differences among species with respect to shape and intensity of the response. This constraint is potentially severe, especially if many species deviate from the assumed model of species response, e.g. by having bimodal or skewed response curves when a symmetrical unimodal response is assumed, or if species generally respond to different gradients.

Austin's alternative approach of modelling single species responses (Austin et al. 1994) is a direct gradient analysis and consequently relies on prior knowledge about the composition of major environmental gradients. This demand does not necessarily cause any problems when gradients are strong and simple but could be troublesome when complex gradients in multiple dimensions are present. In this study of gradients and response curves of Danish grassland plants, I aim:

1) To investigate species response curves to environmental gradients in dry grassland.
2) To compare the potential of coenoclines extracted by correspondence analysis with gradients modelled using measured variables, with respect to predicting species occurrences in dry grassland.
3) To present pH indications for Danish grassland plants.

Study area and data collection

The data consists of 620 samples (387 species) of herbaceous grassland vegetation originating from 180 localities in Denmark (figure 1). Sampled plant communities includes slopes, uplifted marine deposits and stabilised dunes, but previously fertilised or cultivated plots were consciously avoided. This material covers the major gradients in grasslands on well drained soils, but some of the species occur frequently outside the sampled gradients, e.g. *Anemone nemorosa L.* in forests, *Carex flacca Schreber* in fens and *Calluna vulgaris (L.) Hull* in dwarf shrub heaths. The data was obtained by sampling in the 40s, 50s and 90s by different researchers applying comparable methods: species occurrences were recorded in 10 randomly spaced subplots of 0.1 m^2 each, within a homogenous stand of approximately 10-100 m^2. Sampling included measurements of pH, slope and aspect, together with geographic position and field classification of soil type (table 1). I used slope and aspect to calculate relative daily values of direct irradiation on March 1 and June 23 (ignoring influence from the atmosphere, and shading from the surroundings). Soil was divided in four classes: Dilluvial sand and gravel, alluvial sand and gravel (including eolian sand), clay (including sandy clay, clayey sand and silt) and limestone. The material was divided in five geographical regions (figure 1). Frequency in subplot data was used in response smoothing and calculation of indicator values, whereas only presence/absence data were used in modelling. Only species having 25 or more records, 146 species in all, were included in the single species parts of the study. For a more detailed description of the material see Ejrnæs & Bruun (subm.).

Methods

I used the debugged version of DECORANA (Oksanen & Minchin 1997) for ordinations and S-PLUS vers. 3.3 (Statistical sciences 1995) for modelling species responses. I applied detrended correspondence analysis (DCA) with detrending by segments and non-linear rescaling in order to extract unrestricted general coenoclines of the data. No initial exclusion nor downweighting of species or samples was applied, but six problematic outlying samples caused distortion of ordination axes 3 and 4 and were consequently omitted during the

Table 1. Summary of variables used in gradient analysis.

Variable	Mean value	Min. value	Max. Value	Measurement scale	Missing values
pH	6.4	3.8	8.6	continuous	44
Slope	25	0	50	continuous	22
Relative irradiation March 3	1.09	0	2.37	continuous	22
Relative irradiation June 23	0.94	0.60	1.01	continuous	22
Precipitation y^{-1}	569 mm	450 mm	700 mm	Discrete - 8 steps	
Soil				Categorical, 4 levels	22
Region				Categorical, 5 levels	13

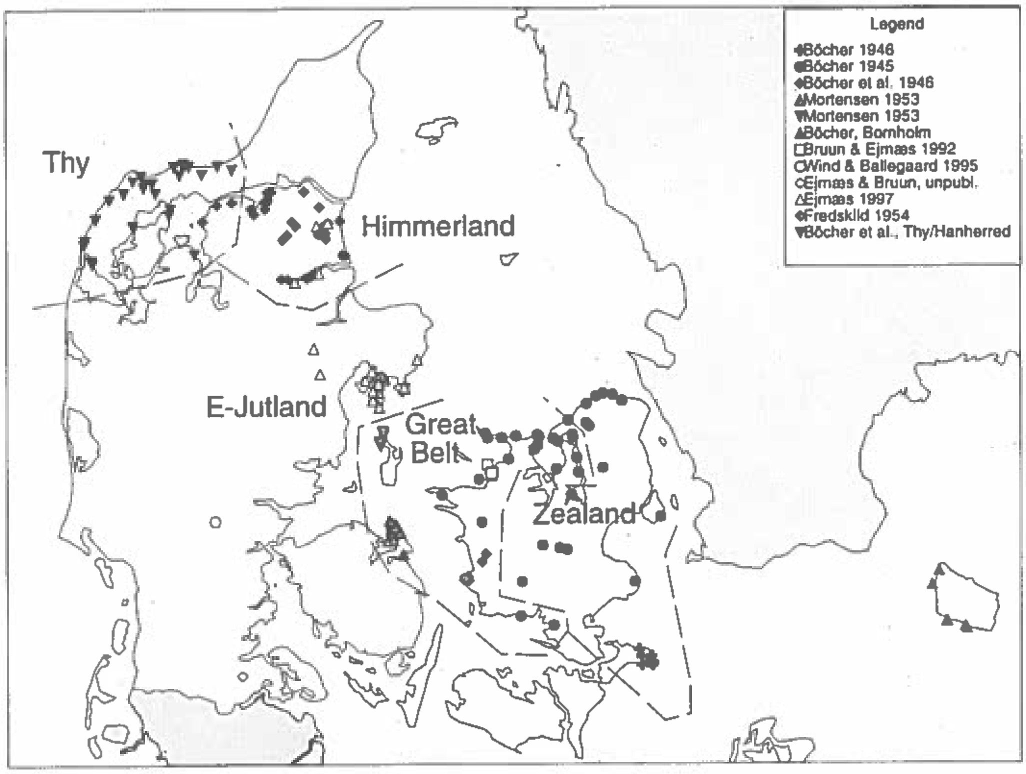

Figure 1. Location of sites and regions included in the analysis.

analysis (for discussion see Ejrnæs & Bruun, subm.). To avoid circularity in the part of the analysis involving coenocline fitting to species occurrences, separate DCA analyses were run with respect to each species that were subjected to subsequent modelling, excluding that particular species from the DCA.

To describe species responses to the pH-gradient, a kernel smoother (weighted running averages) was used with the available *triangle* kernel and the minimum *bandwith* resulting in relatively smooth curves locally (function =*ksmooth*, kernel=*triangle*, bandwith=1). In order to determine the predictive potential of coenoclines versus measured variables, a logistic multiple regression was applied in terms of a generalised additive model with stepwise selection of variables and opportunities for both linear and smoothed responses of species to single terms (function=*gam and step.gam*, family=*binomial*). The functions *predict.gam* and *expand.grid* was used to graph two-dimensional probability surfaces for selected species. The sample plots span a pH-gradient from 3.8-8.6, but the shorter interval 4.3-8.3 was chosen for the pH-gradient part of the study, as only 10 samples had pH-vaalues outside this range.

Results

Four major types of response curves to pH were observed (fig. 2):

1) Symmetrical unimodal, e.g. *Dianthus deltoides L. , Koeleria pyramidata (Lam.) P.Beauv., Lotus corniculatus L.*
2) Asymmetrical unimodal, e.g. *Medicago lupulina L., Deschampsia flexuosa (L.)Trin., Daucus carota L. ssp.carota.*
3) Bimodal, e.g. *Campanula rotundifolia L., Succisa pratensis Moench., Cerastium semidecandrum L.*
4) Broad ranging/indifferent, e.g. *Galium verum L., Achillea millefolium L., Festuca ovina L.*

These twelve species were selected for subsequent multiple logistic regression of presence/absence data. Table 2 summarises the results. Generally the residual deviance of the two model approaches are of comparable strength, and a paired T-test did not reveal significant

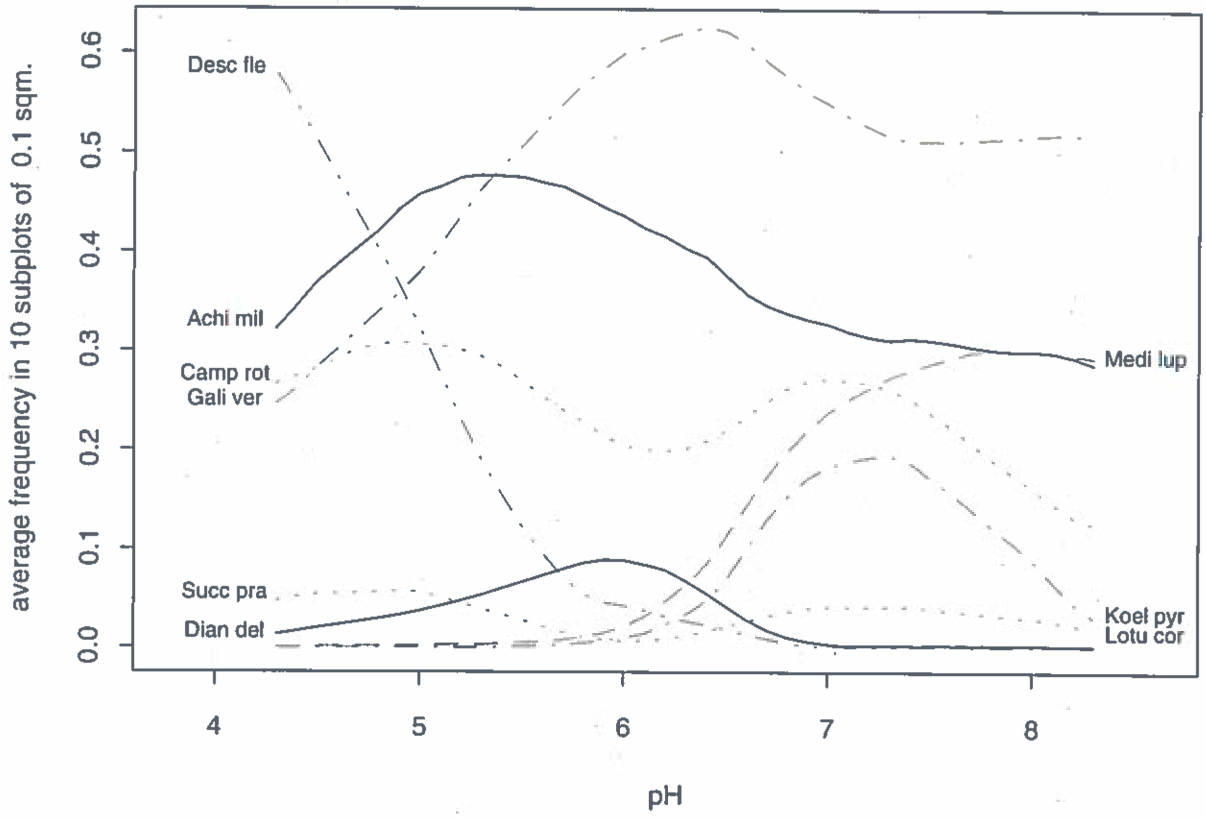

Figure 2. Types of Responses to pH. Species shown are: Achillea millefolium (Achi mil), Campanula rotundifolia (Camp rot), Deschampsia flexuosa (Desc fle), Dianthus deltoides (Dian del), Galium verum (Gali ver), Koeleria pyramidata (Koel pyr), Medicago lupulina (Medi lup), Succisa pratensis (Succ pra).

Table 2. A comparison of additive GAM-models based on measured variables and DCA-coenoclines respectively. Variables were selected stepwise (forward and backward) from pools of 6 measured variables and 4 DCA-coenoclines, and the best model in terms of the AIC-statistics was selected. The number of variables/coenoclines included and the residual degrees of freedom is shown in parenthesis. Predicted range corresponds to maximum and minimum predictions.

Species	Measured variables		DCA-axes	
	% Residual variance	predicted range	% Residual variance	predicted range
Dianthus deltoides	60 (6, 529)	0.00-0.58	64 (3, 531)	0.00-0.51
Lotus corniculatus	84 (5, 530)	0.06-0.87	79 (4, 533)	0.00-0.90
Senecio integrifolius	37 (3, 532)	0.00-0.87	43 (4, 536)	0.00-0.95
Daucus carota	76 (5, 535)	0.00-0.85	71 (4, 534)	0.00-0.99
Deschampsia flexuosa	35 (6, 529)	0.00-1.00	46 (4, 530)	0.00-0.99
Medicago lupulina	54 (5, 524)	0.00-0-96	56 (4, 527)	0.00-0.96
Campanula rotundifolia	79 (5, 533)	0.08-0.97	70 (4, 530)	0.00-0.97
Cerastium semidecandrum	72 (5, 524)	0.00-0.87	64 (4, 533)	0.00-0.95
Succisa pratensis	60 (5, 524)	0.00-0.83	61 (4, 533)	0.00-0.83
Achillea millefolium	89 (3, 535)	0.00-0.98	79 (3, 534)	0.00-0.98
Festuca ovina	80 (6, 526)	0.00-0.97	68 (4, 530)	0.00-1.00
Galium verum	84 (4, 530)	0.00-0.96	79 (3, 534)	0.00-0.95

differences between the model approaches with respect to mean ratio of residual to null deviance. Exceptions are *Deschampsia flexuosa* for which the measured variables model has a marked better fit and *Campanula rotundifolia, Cerastium semidecandrum, Achillea millefolium* and *Festuca ovina* for which the coenocline model has the best fit. For most species the coenocline model is simpler regarding number of included terms and has more residual degrees of freedom than the measured variables counterpart.

I graphed the predicted distribution of species in two dimensions based on the two different approaches in order to investigate the bimodal response to pH observed for some species, and to compare the two modelling approaches in a different setting. The gradients chosen were DCA$^{1-2}$ and the two most important measured variables for each species, selected by forward selection. The species chosen were the three bimodal species of table 2 as well as *Galium verum*, the most constant species in the dataset. The diagrams shown in figure 3 and 4 confirm, that with this dataset and only two allowed dimensions, coenoclines are better predictors of species distributions than measured variables. Furthermore, both approaches resulted in weakening or disappearance of bimodality.

Based on measured variables (fig. 3), the probability of finding *Campanula rotundifolia* is predicted to increase from dry calcareous via dry siliceous to moist grasslands of a wide pH range. *Cerastium semidecandrum* is predicted to occur mainly in relatively dry conditions avoiding low pH and northern aspects. A slight bimodality with respect to pH remains,

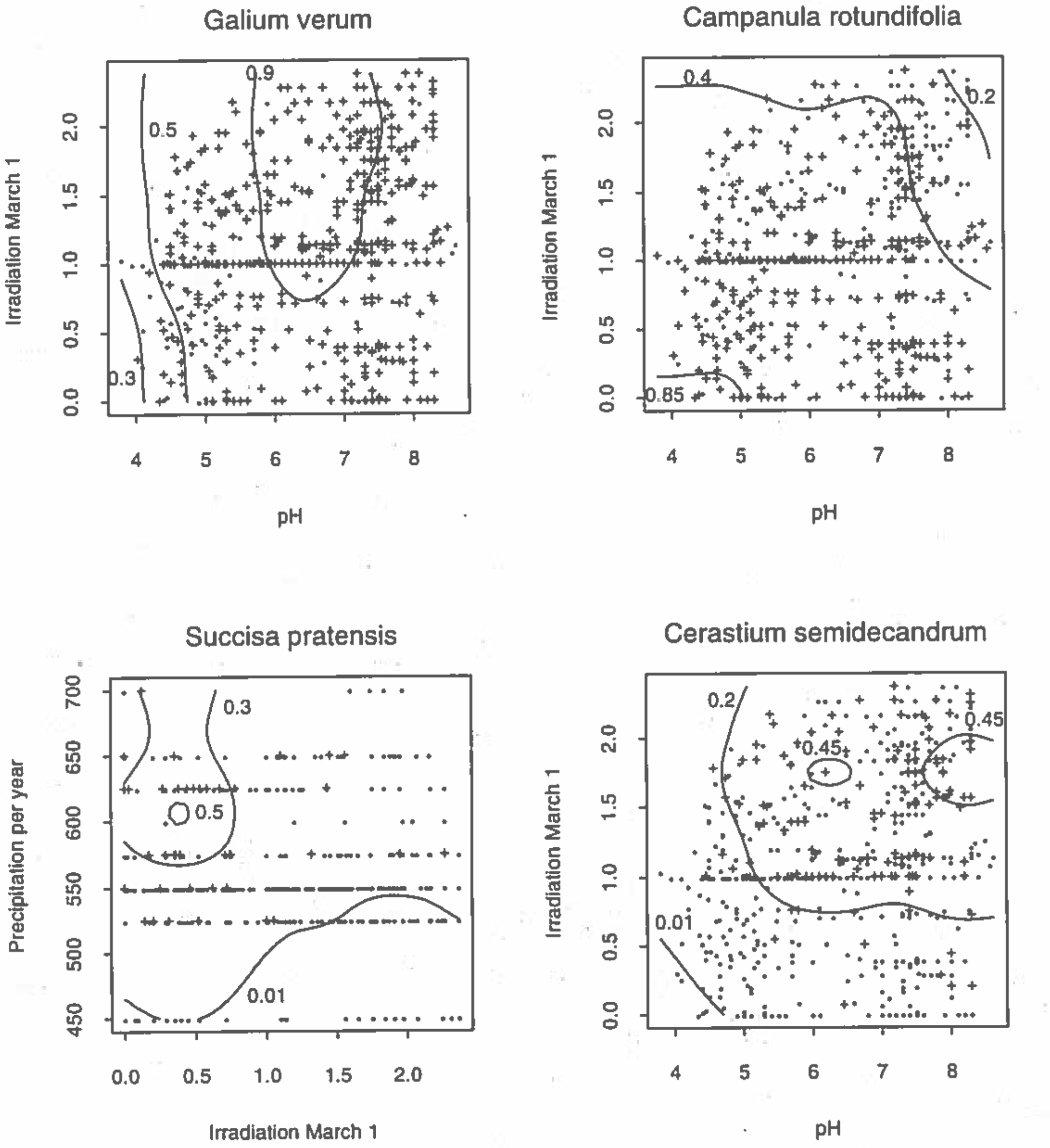

Figure 3. Two-dimensional contour plots of species along two environmental gradients. The plottet points correspond to the distribution of sample plots in gradient plane, "+" indicate presence of the species. Contour lines correspond to minimum and maximum predicted probability (rounded to nearest 0.05) within the sampled area, and a level corresponding to app. half of maximum, fixed for each species in figures 3 and 4.

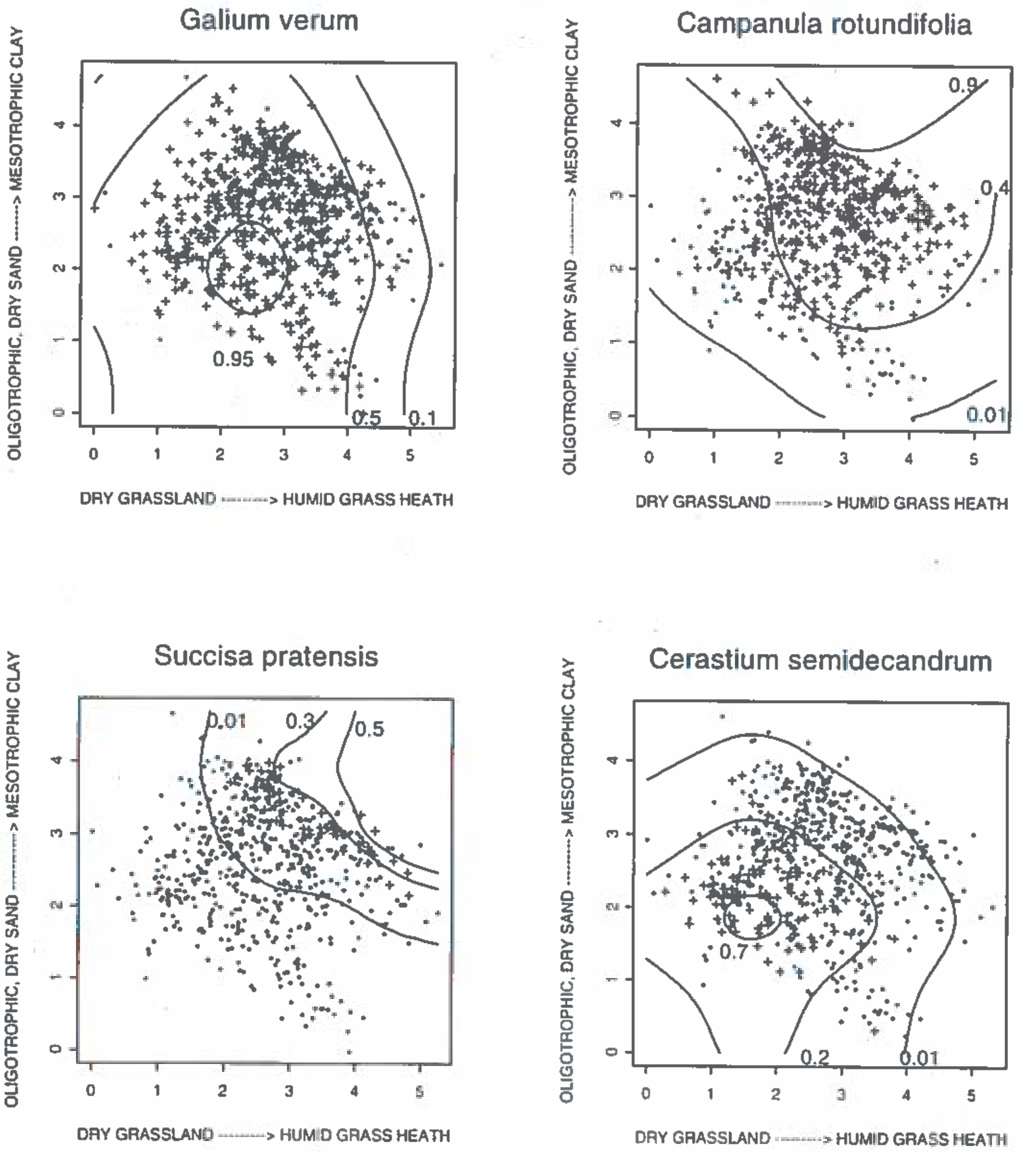

Figure 4. Two-dimensional contour plots of species in the grassland coenoplane. The plottet points correspond to the distribution of sample plots in the coenoplane, "+" indicate presence of the species. Contour lines correspond to minimum and maximum predicted probability (rounded to nearest 0.05) within the sampled area, and a level corresponding to appr. half of maximum, fixed for each species in both fig. 3 and 4.

but the distribution is clearly continuous. *Succisa pratensis* is predicted better by annual precipitation and irradiation than by pH, and should be found in regions of high precipitation, combined with conditions of low irradiation. *Galium verum*, showed little response to irradiation, but should occur less frequently in acidic than in calcareous grassland.

The response surfaces with respect to coenoclines (fig. 4) contain additional information. None of the species responses were bimodal with respect to these gradients, and *Campanula rotundifolia*, *Cerastium semidecandrum* and *Galium verum* were predicted more clearly with a wider range of probabilities. Ejrnæs & Bruun (1997, submit.) interpreted DCA^1 as the vegetation component in an "ecosystem ecocline" ranging from grasslands with warm and dry topoclimate and high pH, with many annuals and subcontinental species, to acidic grasslands with cool and humid topoclimate and more oceanic species. DCA^2 was interpreted as a response to a fertility gradient ranging from notoriously infertile grassland on dry eolian sand to naturally productive grasslands on relatively moist calcareous clay. *Succisa pratensis* was predicted to prefer acidic grasslands with a cool, humid topoclimate and relatively fertile grasslands. *Cerastium semidecandrum* was predicted to prefer infertile grasslands and a warm and dry topoclimate. *Campanula rotundifolia* was predicted to prefer relatively moist and fertile conditions, and *Galium verum* was dicted to prefer infertile and moderately dry grasslands.

Appendix I lists the pH preferences of 146 species. The pH optimum was found as the value corresponding to maximum value of the species response predicted by Kernel smoothing. The weighted mean was found as the mean of all pH-classes weighted by the species response in that class predicted by Kernel smoothing. The pH amplitude was the range within which 90 % of the occurrences were predicted to occur. I have chosen to include local optima for 24 species having marked bimodal responses (see also App. II). I found a pH-amplitude of less than 2 pH-units for 27 species, and they all had optima at either extreme of the pH gradient, and these are consequently suggested as good indicator species with respect to pH in Danish grasslands. For 23 species, fitting pH did not significantly improve a model of species distribution after fitting irradiation March 1, and the pH indications of these species should be used with caution. I strongly advice against using the biased weighted average optima for environmental calibration. For many species the two values differ by more than 1 pH-value, generally so that a less extreme optimum is suggested by weighted averaging. Of the 123 species with significant response to pH listed in this study, 73 are also assigned pH-optima on an ordinal scale from 1-9 in Ellenberg (1992). Figure 5 shows the relation between the two sets of values, and though a significant positive correlation can be seen, large differences between the two sets of values are obvious. I also compared site calibrations of pH based on weighed averages of Ellenbergs reaktionszahl with site pH, and found this measure to be considerably more reliable than the single species values. Linear regressions of single species pH-optima and site pH predicted by Ellenberg numbers gave figures for r^2 of 0.49 and 0.66, respectively.

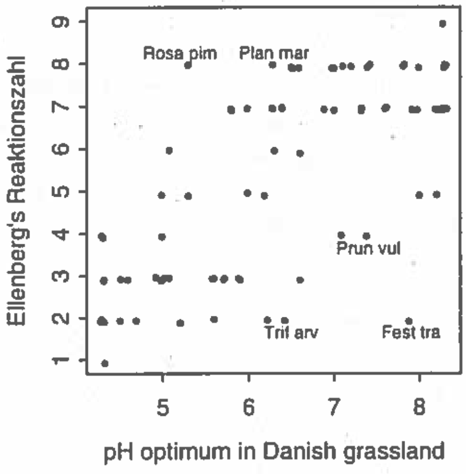

Figure 5. Plot of Ellenbergs "Reaktionszahl" against the pH optima found in this study, for 73 common grassland species (r^2=0.49). Abbreviated names of species with the most divergent indicator values are plotted on the diagram: Fest tra=Festuca trachyphylla, Rosa pim=Rosa pimpinellifolia, Trif arv= Trifolium arvensis, Plan mar=Plantago maritima, Prun vul=Prunella vulgaris.

Discussion

Soil reaction (pH), though not a resource for plants, is known as one of the measurable quantities that is best correlated with grassland vegetation, and it is typically reflected in grassland classifications (e.g. Rodwell et al 1992). Among the four observed types of responses to pH, the asymmetric unimodal and the bimodal responses are problematic with respect to regression and calibration based on weighted averaging (Austin 1994). The two dimensional response surfaces shown in fig. 3, suggest that the strikingly bimodal response curves observed for some species with respect to pH, should be interpreted as covariance patterns rather than responses of species to gradients. In this way our results support the view of Austin et al. (1984) that observed bimodality does not necessarily imply ecotypic differentiation or competitive exclusion. For example the observed pH-bimodality of many of the species preferring moist conditions (e.g. *Ranunculus acris L.* and *Leontodon hispidus L.*) merely suggests a coincidence, and maybe a causal link, in dry grasslands, of high soil moisture and pH-values corresponding to moderately acidic siliceous soils and moderately alkaline calcareous soils. Both conditions could arise for example as the result of oozing ground water on slopes.

The comparison between models based on measured variables versus coenoclines led me to the following concluding remarks with respect to the use of correspondence analysis in vegetation ecology:

1) Though many species do not fit the ideal unimodal symmetric response curve, DCA

is a robust ordination method (given appropriate data) enabling the extraction of meaningful coenoclines.

2) DCA is a powerful tool for dimensionality reduction, eventually leading to the suggestion of new overlooked environmental variables or combination of variables.
3) Vascular plant species generally respond to the same major gradients.

The observation that the first two DCA-axes actually correlated with both of the two most influential measured variables (pH and water availability), but in different ways (Ejrnæs & Bruun, subm.) can serve as an exemplification of the second of the above statements: Irradiation and pH correlated positively with axis 1 along an ecosystem ecocline from a continental type grassland to an oceanic type of grass heath. On the second axis, pH and water availability combined in a fertility ecocline. The fertility ecocline of axis 2 does not represent a surprise, whereas the ecosystem ecocline on axis 1, seem to have been largely overlooked in recent ecological studies in temperate grasslands, but see Sterner (1922).

The importance of the third statement lies in the notion that gradient analysis is a useful part of vegetation ecology: Predictions generated from gradient analysis of vegetation are not just insignificant averages of multiple different species responses, but have significance for single species too.

Recently, the indirect approach of correspondence analysis has been largely abandoned in favour of the direct approach offered by canonical correspondence analysis (Økland 1996). It should be acknowledged off course, that when the objective is to create predictive models for species occurrences, indirect gradient analysis can not substitute the direct analysis of vegetation responses to measurable properties of the environment. But, DCA provides a very useful way of testing the validity of a model based on modelling of species responses in terms of measured variables, and only unrestricted (indirect) gradient analysis can serve the purpose of an open minded search for overlooked complex gradients, and hence lead to new ecological insight and better predictions.

Although skewed response curves were found frequently in this study, the critical view of Austin (1994) upon ordination methods based on weighted averaging is not fully supported. On the contrary it is suggested that the incompleteness of measured variables can have an equal or greater negative impact on the goodness of fit than the incorrectness of the assumed symmetric unimodal response of ordination methods based on weighted averaging. This statement applies to correspondence analysis more than to canonical correspondence analysis, as the latter also relies on prior understanding of underlying gradients.

On the other hand, the marked differences found between response optima obtained by kernel smoothing and by weighted averaging indicates that DCA could be improved by substituting the weighted averaging algorithm used to calculate species optima with a density probability algorithm based on the more realistic and flexible assumption of unimodal, but not necessarily symmetric response curves.

The pH amplitude values presented here, indicates that not only is the physiological amplitude of species with respect to pH pronounced (Ellenberg 1992), the realised response to pH is generally also of great amplitude. Soil pH is not a plant resource but acts both as a direct variable influencing plant physiology (Austin & Smith 1989), and an indirect variable through the influence on microbial activity and hence nutrient cycling. The pH optima of a species should thus be expected to be influenced by other factors of importance to fertility and pedogenesis, leading to variations in pH optima for species occurring in different ecosystems and geographical regions. It is therefore not surprising that major discrepancies can be found between pH-optima of species in unimproved, dry grassland of Denmark and pH indications for species encompassing both natural and more perturbed habitats of Central Europe.

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References

Austin, M.P. 1987. Models for the analysis of species' response to environmental gradients. Vegetatio 69: 35-45.

Austin, M.P., Cunningham, R.B. & Fleming, P. M. 1984. New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. Vegetatio 55: 11-27.

Austin, M.P., Nicholls, A.O., Doherty, M.D. & Meyers, J.A. 1994. Determining species response functions to an environmental gradient by means of a β-function. J.Veg.Sci 5: 215-228.

Austin, M.P. & Smith, T.M. 1989. A new model for the continuum concept. Vegetatio 1983: 35-47.

Ejrnæs, R. & Bruun, H.H. A gradient analysis of temperate grassland on well-drained soil. Subm.

Ellenberg, H. 1974. Zeigerwerte der Gefäss-pflanzen Mitteleuropas. Scripta Geobotanica 9.

Ellenberg, H, Weber, H.E., Düll R.., Wirth, V., Werner, W. & Paulissen, D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica vol 18.

Gauch, H.G. & Whittaker, R.H. 1972. Coenocline simulation. Ecology 53: 446-451.

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242: 344-347.

Grime, J.P. 1974. Vegetation classification by reference to strategies. Nature 250: 26-31.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111: 1169-1194.

Hill, M.O. 1973. Reciprocal averaging; an eigenvector method of ordination, J. Ecol. 61: 237-249.

Keddy, P.A. 1992. Assembly and response rules: Two goals for predictive community ecology. J.Veg.Sci.: 157-164.

Oksanen, J. & Minchin, P.R. 1997. Instability of ordination results under changes in input data order: explanations and remedies. J.Veg.Sci. 8: 447-454. [downloaded "debugged, strict version of DECORANA" from: http://www.helsinki.fi/~jhoksane/].

Persson, S. 1980. Succession in a south Swedish deciduous wood - a numerical approach. Vegetatio, 43:103-122.

Rodwell, J.S. (ed.), Pigott, C.D., Ratcliffe,D.A., Malloch, A.J.C., Birks, H.J.B., Proctor, M.C.F., Shimwell, D.W., Huntley, J.P., Radford, E., Wigginton, M.J. & Wilkins, P. British Plant Communities vol.3. Grasslands and montane communities. Cambridge 1992.

Statistical Sciences, Inc. S-PLUS version 3.3 for Windows, Seattle: Statistical Sciences, Inc., 1995.

Sterner, R. 1922. The continental flora of South Sweden. Geografiske Annaler IV: 221-390.

ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.

Økland, R.H. 1990. Vegetation Ecology: theory, methods and applications with reference to Fennoscandia. Sommerfeltia supplement vol. 1, 233 pp.

Økland, R.H. 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? J. Veg Sci. 7(2): 289-292.

Appendices

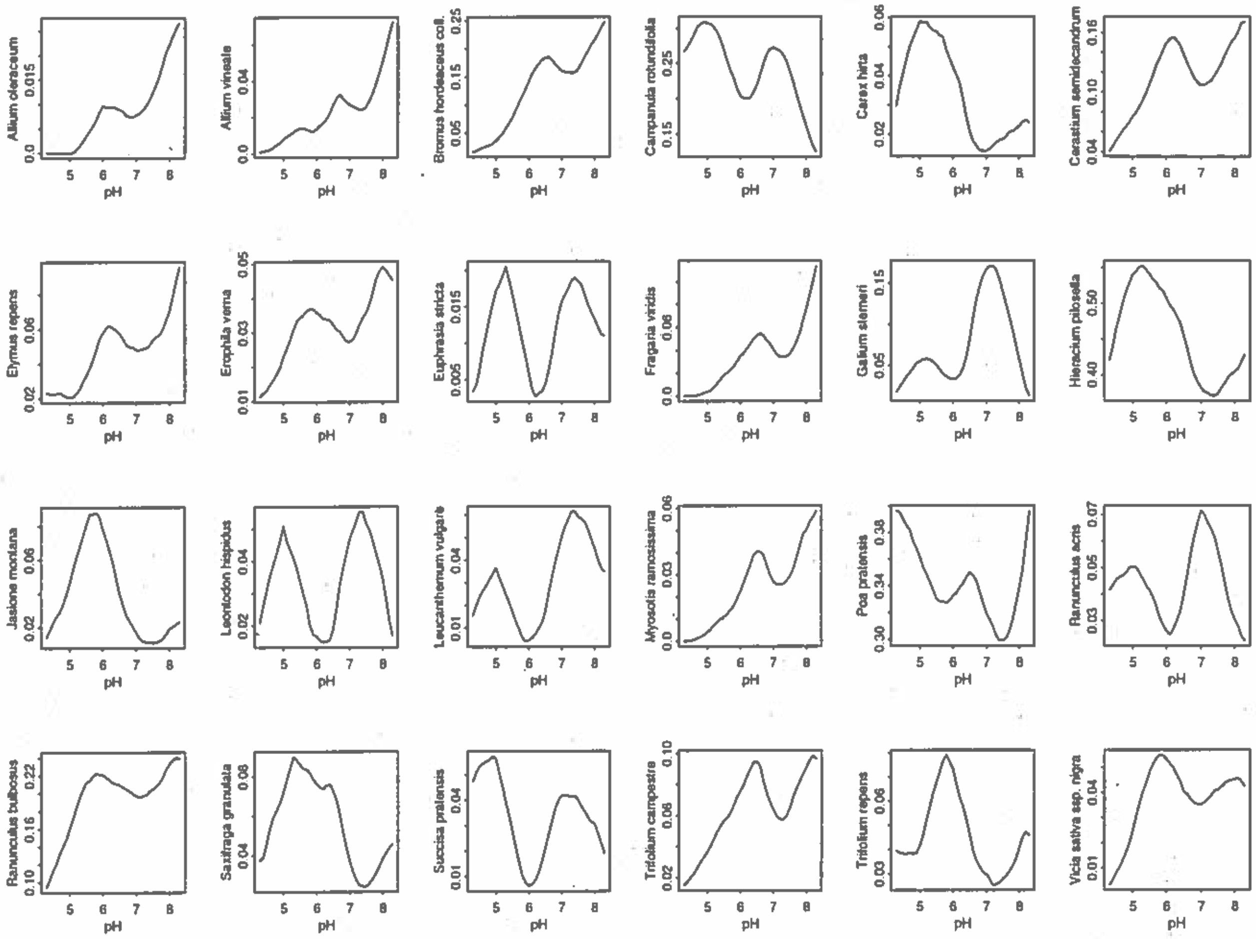
Appendix 1. **Indicator value with respect to pH of 146 common Danish grassland species.** Species with insignificant response to pH after fitting relative irradiation on March 1, have values followed by a question mark. Two values are presented when two peaks of near equal importance were observed. Weighted averages were obtained by weighting of evenly spaced pH-intervals by kernel smoothing probability estimates. Range was defined as the minimum range including 90 % of the estimated species population. The pH values corresponding to conspicuous, but subordinate, peaks are indicated in the last column. The curves of these bimodal species are presented in fig. 5. Values for species with insignificant response to pH after fitting irradiation are shown in parenthesis.

Species	pH-optimum	weighted mean	pH-amplitude	Local optima
Achillea millefolium	5.5	6.1	4.3-7.8	
Acininos arvensis	8	7.5	6.8-8.3	
Agrimonia eupatoria	8.3	7.2	5.9-8.3	
Agrostis capillaris	4.6	5.5	4.3-6.7	
Agrostis stolonifera	(6.6)	(6.5)	4.8-7.9	
Agrostis vinealis	4.3	5	4.3-5.9	
Aira caryophyllea	(5.9)	(6.2)	4.5-7.9	
Aira praecox	4.7	5.3	4.3-6.3	
Allium oleraceum	8.3	7.2	5.9-8.3	6.0
Allium vineale	8.3	7.1	5.4-8.3	6.7
Anemone nemorosa	4.3	5	4.3-6	
Anthoxanthum odoratum	5	5.6	4.3-6.8	
Anthyllis vulneraria	8.3	7	5.7-8.3	
Arabis hirsuta	7.1	7.1	6.2-8.3	
Arenaria serphyllifolia	8.2	7.1	6.0-8.3	
Armeria maritima	6.2	6.1	4.3-7.4	
Arrhenaterum elatius	7.6	6.9	5.3-8.3	
Artemisia campestris	8.2	7	5.6-8.3	
Avenula pratensis	7	6.8	5.3-8.3	
Avenula pubescens	6.5	6.7	5.3-8.3	
Bellis perennis	8.2	7.1	5.8-8.3	
Briza media	7.2	7	5.8-8.3	
Bromus hordeaceus coll.	8.3	6.9	5.6-8.3	6.4
Calluna vulgaris	4.3	4.9	4.3-5.6	
Campanula glomerata	7.3	7.3	6.6-8.1	
Campanula persicifolia	6.6	6.8	5.9-8.1	
Campanula rotundifolia	4.9	6.1	4.3-7.7	7.0
Carex arenaria	5.6	6.6	4.3-6.6	
Carex caryophyllea	(6.5)	(6.2)	4.3-7.8	
Carex flacca	7.2	7.1	6.1-8.3	
Carex hirta	5.2	5.9	4.3-8.3	8.2
Carex pilulifera	4.3	4.9	4.3-5.7	
Carlina vulgaris	7.2	7.1	6.2-8.3	
Cerastium fontanum ssp. triviale	5.7	6.1	4.3-8.3	
Centaurea jacea	8.3	7.2	6.1-8.3	
Centaurea scabiosa	7.4	7.4	6.6-8.3	
Cerastium semidecandrum	8.3/6.1	6.6	5.1-8.3	6.1
Cirsium acaule	7.4	7.2	6.3-8.3	
Convolvolus arvensis	8.3	7.3	6.0-8.3	
Corynephorus canescens	5.6	5.5	4.4-6.4	
Cynosurus cristatus	6	6.3	4.8-8.3	
Dactylis glomerata coll.	8.3	7	5.7-8.3	
Danthonia decumbens	5	5.5	4.3-6.7	
Daucus carota	8.3	7.4	6.6-8.3	

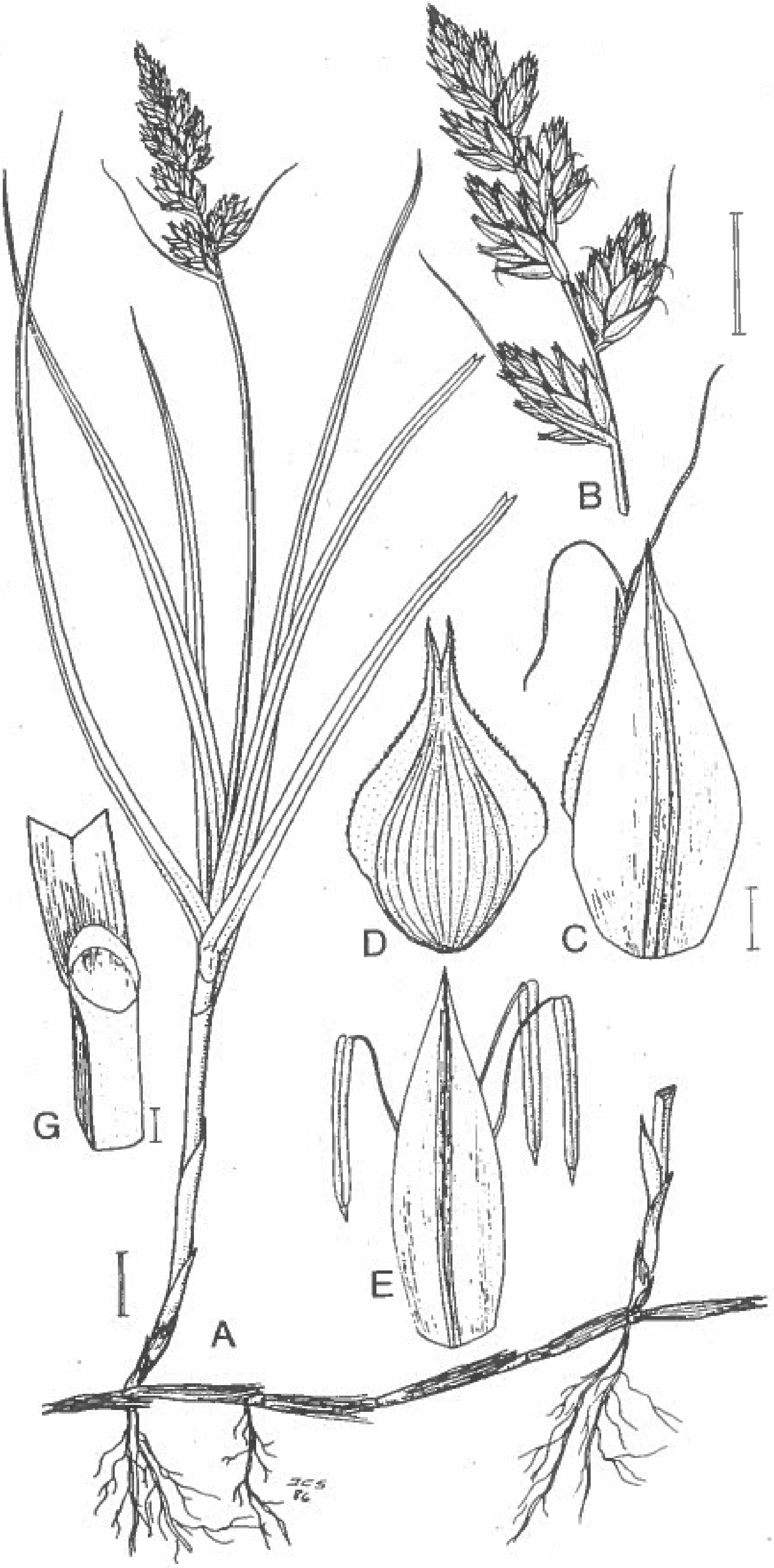
Deschampsia flexuosa	4.3	4.9	4.3-5.6	
Dianthus deltoides	5.9	5.8	4.6-6.6	
Echium vulgare	8.2	7.5	6.3-8.3	
Elymus repens	8.3	6.7	4.3-8.3	6.1
Equisetum arvense	(5.5)	(5.8)	4.3-8.3	
Erophila verna	8/5.8	6.5	5.0-8.3	5.8
Euphrasia stricta	(5.3/7.4)	(6.4)	4.6-8.3	7.4
Festuca arundinacea	8.2	7.7	7.0-8.3	
Festuca ovina	5	5.8	4.3-7.4	
Festuca pratensis	7.3	7.3	6.6-8.3	
Festuca rubra	(6.9)	(6.4)	4.3-8.3	
Festuca trachyphylla	7.9	7.3	6.3-8.3	
Filipendula vulgaris	6.5	6.6	5.4-8.3	
Fragaria vesca	7.5	7.3	6.4-8.3	
Fragaria viridis	8.3	7.1	5.9-8.3	6.6
Galium mollugo	7.4	7.2	6.4-8.3	
Galium saxatile	4.3	4.9	4.3-5.6	
Galium sterneri	7.1	6.6	4.7-8.0	5.2
Galium verum	6.3	6.4	4.9-8.3	
Geranium sanguineum	6.5	6.6	5.4-8.3	
Helichrysum arenarium	8	7	5.7-8.3	
Helianthemum nummularium coll.	6.4	6.8	5.7-8.2	
Hieracium pilosella	(5.3)	(6.2)	4.3-8.3	8.3
Hieracium umbellatum	4.3	5.6	4.3-7.1	
Holcus lanatus	4.3	5.8	4.3-7.2	
Holcus mollis	4.3	4.9	4.3-5.6	
Hypericum perforatum	8.3	6.7	4.3-8.3	
Hypochoeris maculata	(6.3)	(6.2)	4.5-7.6	
Hypochoeris radicata	5	5.2	4.3-6.3	
Jasione montana	5.6	6	4.5-8.3	8.3
Knautia arvensis	(6.9)	(6.2)	4.3-7.8	
Koeleria pyramidata	7.3	7.2	6.5-8.1	
Lathyrus montanus	4.9	5.3	4.3-6.2	
Lathyrus pratensis	7	7.2	6.4-8.3	
Leontodon autumnalis	5	5.7	4.3-7.4	
Leontodon hispidus	7.3	6.3	4.3-8.2	5
Leucanthemum vulgare	7.3	6.6	4.4-8.3	5
Linaria vulgaris	(5.8)	(6.2)	4.7-7.8	
Linum cartharticum	7.4	7.2	6.4-8.3	
Lolium perenne	(8.2)	(6.8)	5.5-8.3	
Lotus corniculatus	6.4	6.4	4.7-7.9	
Luzula campestris	4.5	5.6	4.3-7	
Lychnis viscaria	6.2	5.8	4.5-6.8	
Medicago lupulina	8	7.4	6.6-8.3	
Medicago minima	8.3	7.6	6.8-8.3	
Myosotis ramosissima	8.3	7	5.8-8.3	6.4
Ononis repens	8.2	6.8	5.1-8.3	
Origanum vulgare	8.3	7.5	6.7-8.3	
Petrorhagia prolifera	8.3	7.3	5.5-8.3	
Phleum pratense ssp. bertolonii	8.3	7.1	6.0-8.3	
Phleum phleoides	7.8	6.9	5.7-8.3	
Pimpinella saxifraga	7	6.3	4.5-8.0	
Plantago lanceolata	(5.7)	(6.1)	4.3-7.7	
Plantago maritima	6.3	6.5	5.4-7.7	
Plantago media	7	7.1	6.2-8.3	

Poa compressa	8.3	7.6	6.7-8.3	
Poa pratensis	(4.3)	(6.2)	4.3-8.3	6.5 8.3
Polygala vulgaris	5	5.5	4.3-8.2	
Potentilla argentea coll.	6.6	6.6	4.3-8.1	
Potentilla erecta	4.9	5.2	4.3-6.2	
Potentilla reptans	8.3	7.2	5.9-8.3	
Potentilla tabernaemontani	6.3	6.3	5.0-7.8	
Primula veris	7	7	5.6-8.3	
Prunella vulgaris	7.4	6.8	5.3-8.3	
Pulsatilla pratensis	6	6.1	4.7-7.7	
Pulsatilla vulgaris	(5.1)	(6)	4.3-7.6	
Ranunculus acris	7	6.3	4.3-8.0	5
Ranunculus bulbosus	5.8	6.5	4.9-8.3	8.2
Rosa pimpinellifolia	5.3	5.7	4.3-7.0	
Rumex acetosella	4.5	5.3	4.3-6.4	
Rumex acetosa	4.3	5.6	4.3-7.1	
Saxifraga granulata	5.3	6	4.3-8.3	8.3
Scabiosa columbaria	7.8	7.3	5.9-8.3	
Sedum acre	8.3	6.8	5.5-8.3	
Senecio integrifolius	7.1	7.1	6.4-7.9	
Senecio jacobaea	7.6	7.5	6.8-8.3	
Silene nutans	7.9	6.9	5.1-8.3	
Solidago virga-aurea	6.8	6.6	4.3-8.3	
Stellaria graminea	4.3	5.3	4.3-6.3	
Succisa pratensis	4.9	6	4.3-8.2	7
Taraxacum sp.	7.1	6.6	4.6-8.3	
Taraxacum sect. Erythrospermum	(6.4)	(6.3)	4.3-8.0	
Thalictrum minus coll.	6	6.2	4.9-7.4	
Thymus pulegioides	8.3	6.9	5.3-8.3	
Thymus serpyllum	5.8	6.2	4.7-7.8	
Tragopon pratensis coll.	(7)	(6.8)	5.5-8.3	
Trifolium arvense	6.4	6.6	5.4-8.3	
Trifolium campestre	8.2	6.6	5.2-8.3	6.5
Trifolium dubium	(6)	(6.5)	5.3-8.3	
Trifolium medium	5.3	5.7	4.3-7.2	
Trifolium pratense	7	6.8	5.5-8.3	
Trifolium repens	(5.8)	(6.2)	4.3-8.3	8.1
Trifolium striatum	6.2	6.5	5.4-8.3	
Veronica arvensis	(6.6)	(6.5)	4.7-8.1	
Veronica chamaedrys	(5.2)	(5.9)	4.3-7.6	
Veronica officinalis	5.2	5.4	4.3-6.6	
Vicia sativa ssp. nigra	(5.9)	(6.5)	5.2-8.3	8.1
Vicia cracca	(7)	(6.4)	4.5-7.8	
Vicia hirsuta	6.4	6.9	5.8-8.1	
Vicia lathyroides	(5.7)	(6.4)	4.9-8.0	
Viola canina	5.1	5.7	4.3-7.0	
Viola hirta	8.3	7.4	6.6-8.3	

Appendix II. Response curves of species with a markedly bimodal response to pH.



Article IV



Carex arenaria L.

Cryptogams in Danish grasslands

- primary gradients and successional trends over the last 50 years

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Abstract

A detrended correspondence analysis of grassland cryptogams is presented. The analysis is based on 160 10 m^2 sample plots covering a range from acidic to calcareous grasslands on different soil types and different slopes and aspects. The ordination is compared with an ordination of the same plots based on vascular plants. Cryptogams were generally found to respond to the same major gradients as vascular plants, and the possible explanations and implications are discussed. The most important two-dimensional ecological space was defined and graphed for the 12 most common cryptogams, among which both specialists and generalists were found.

A comparison with three inventories of Danish grasslands from the period 1945-1955 revealed significant differences regarding both species richness and single species frequencies. Two generalist bryophytes were found to be more frequent in the recent material whereas two specialist bryophytes were more frequent in the old material. These differences are discussed in relation to a reported impoverishment of the cryptogam flora in Dutch and British chalk grasslands.

Keywords: Bryophytes, mosses, liverworts, hepatics, lichens, DCA, coenoclines, vegetation, fugitives, Denmark, semi-natural, unimproved, diversity, conservation.

Nomenclature: Mosses follow Andersen et al. (1976), Lichens follow Alstrup & Søchting (1989), and Hepatics follow Smith (1990).

Introduction

It is a tradition to include cryptogams in phytosociological and ecological studies in Danish grasslands (Böcher 1945, Böcher et al 1946, Mortensen 1953, Fredskild 1954, Ejrnæs & Bruun 1995). Despite this, cryptogams have only received little attention in the proceeding data treatments, and Fredskild (1954) stated, that mosses and lichens are nearly always insignificant in the dry grassland ecosystem.

Cryptogams in chalk grassland have come into focus after the findings of an impoverishment over the last 40 years of the bryophyte and lichen flora in Dutch (During & Willems 1986) and the lichen flora in British (Gilbert 1993) chalk grassland. Temperate grassland is a plagioclimax ecosystem, and many simultaneous changes have taken place over the last decades, on local (dereliction, fertilisation) as well as landscape scale (deposition of atmospheric oxides of nitrogen and sulphur). The interpretation of changes in the cryptogam flora therefore relies on autecological information.

Cryptogams differ from vascular plants - in particular with respect to size and relative growth rates. A fugitive or opportunistic strategy is common among cryptogams, but by no means universal (Slack 1982, During 1979). In cryptogam communities without noticeable competition from phanerogams, or under conditions of tolerated phanerogam induced stress, a diverse array of life forms and life history strategies may partition the *niche hyperspace* (Slack 1982, Muotka & Virtanen 1995). A point of some debate has been whether cryptogams respond to the same environmental gradients as vascular plants. It has been shown that cryptogam ecoclines differ from vascular plant ecoclines in oligotrophic mires (Økland, 1990) and boreal forests (Carleton, 1990), where shortages of nutrients and light lead to a concentration of vascular plants in locally more productive parts of the ecosystem. Herben (1987) found that the distribution of grassland bryophytes was determined largely by other factors than the vascular plants, but permanent grid studies demonstrated strong correlation between vascular plants and bryophytes with respect to spatial pattern and dynamics in Dutch chalk grasslands (During & Lloret, 1996). In a comprehensive survey of the lichens of British chalk grassland, Gilbert (1993) stated, that lichens specific to open grassland, rely heavily on regular disturbances creating suitable regeneration gaps. The objectives of the present study are:

1) To describe the ecoclines most relevant to cryptogams and compare these with the vascular plant ecoclines.
2) To describe the preferences of common grassland cryptogams.
3) To compare the grassland cryptogam flora of 1995-97 with that of 1945-1955.

Study area and data

In May-June 1997, a field inventory was carried out, collecting mosses, hepatics and lichens in 138 sample plots in 30 localities distributed in Eastern Jutland, with a concentration in S (fig.1). The localities cover a major part of the variation in Danish grasslands with respect to soil type, pH, topography and grazing regimes, and all were old, permanent grasslands, that never experienced fertiliser treatment. Samples of vascular plants and soil were obtained from the same plots in 1994-1995.

The sample plot was a circle of 10 m^2, and all cryptogams in the plot were recorded as either present or dominant, the latter corresponding to a cover of at least 20%. The cover of bare soil was estimated on a percentage scale. Presence of vascular plants were recorded within10 subplots of 0.1 m^2 placed randomly within the plot.

In 1994-1995, soils were sampled to 10 cm depth, analysed for pH and classified in one of 5 classes: *Limestone* (including chalk), *clay* (clayey till, including marl, colloidal clay and moler), *sand/clay*, *diluvial sand* (including gravel) and *postglacial, marine sand* (including) gravel, shingle, and eolian sand). The soil class *limestone* coincides with shallow soils, all other

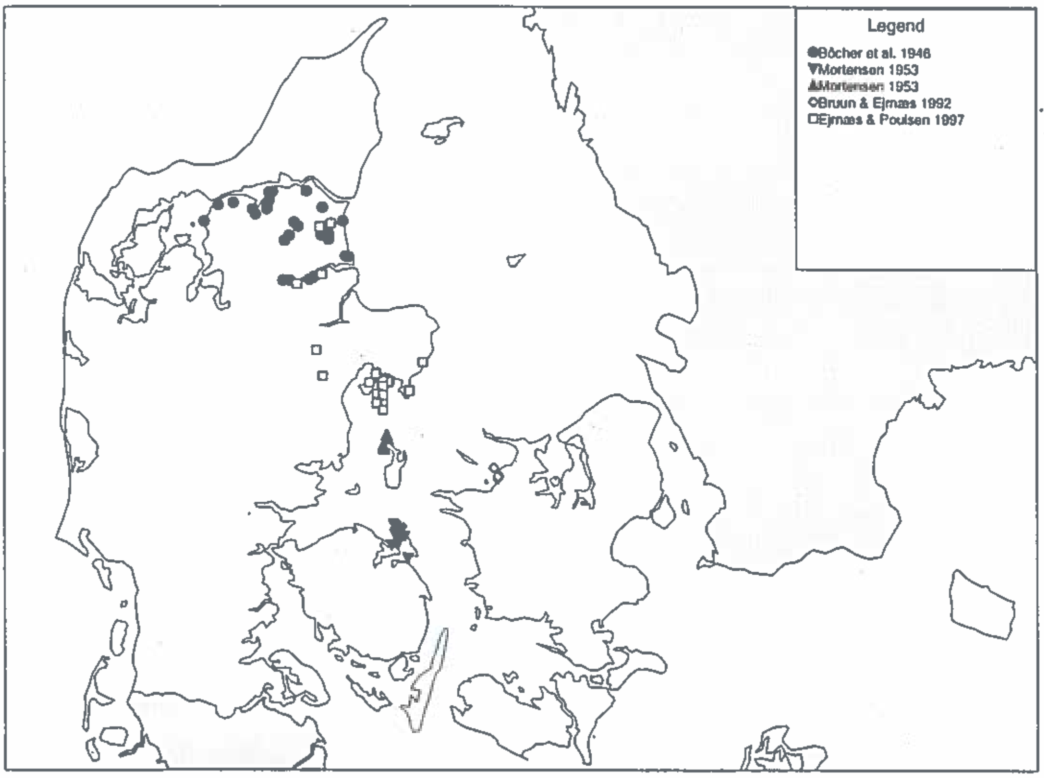


Figure 1. A site map showing the distribution of sites belonging to the new and old studies.

soil classes are characterised by deep soils. Topography was recorded as *slope* and *aspect*, when slope exceeded 5 degrees, and converted to an irradiation index corresponding to relative values of irradiation (ignoring the influence of an atmosphere) on two arbitrary dates: March 1 and June 23 (see Ejrnæs & Bruun, subm.). Grazing was estimated from current practice and land use history on a 5 point scale: 1=ungrazed for 15-40 years, 2=ungrazed or very lightly grazed for the last 10 years, 3=light grazing regime, 4=moderate grazing regime, 5=intensive grazing regime. In addition, indicator values for each site were obtained by weighted averaging of Ellenberg-values (Ellenberg et al. 1992) and Grime's CSR-values (Grime et al., unpubl.) with the frequency of the vascular plant species (see Ejrnæs & Bruun, subm.). By definition we write these site indications with a small superscript "c", to keep in mind that they represent estimates based on autecological accounts from the literature, rather than real measured quantities. Table 1 gives a survey of included variables.

A subset from Ejrnæs & Bruun (1995) of old unimproved grasslands from NW Zealand was included in our study, as both cryptogam and soil sampling was similar to the Jutland data. The combined material consists of 158 samples including 63 mosses, 20 lichens and 5 hepatics, with the majority of samples in the pH range from 4-6. A list of species found in these two recent inventories is given in appendix I.

For comparison with data from the 40's and 50's, we used cryptogam data published from Himmerland (Böcher et al. 1946) and from Hindsholm and Samsø (Mortensen 1953, 1955). We did not include data from Böcher (1945) or Fredskild (1954) since these lists appeared incomplete in comparison with the other material, probably due to less intensive sampling or suboptimal sampling seasons. We did only use presence/absence data, as these were believed to result in a more robust comparison, less influenced by differential sampling techniques. The old material consists of 157 samples including 64 species of mosses, 34 lichens and 4 hepatics, with the majority of samples in the pH range from 6-8.

Taxonomic notes

For the identification of *Cladonia spp.* standard chemical spot tests and UV-lights were used. Species of the *Cladonia chlorophaea group* (including *C. fimbriata (L.) Fr.*) are difficult to distinguish between, and except for typical *C. fimbriata* we used the collective name *Cladonia chlorophaea agg.* Typical *C. pyxidata* (L.) Hoffm. was not found in this study.

Böcher et al. (1946) included in their study both epilithic and epiphytic species (the latter presumably growing on shrubs, fallen twigs or exposed roots). These were not inclu-

Table 1. Variables used in coenocline interpretation and response modelling.

Variable	Mean value	Range	Measurement scale	Missing values
pH	5.7	3.8 - 8.6	continuous	
Slope	18 °	0° - 44°	continuous	
Relative irradiation March 3	1	0 - 2.2	continuous	
Relative irradiation June 23	0.94	0.75 - 1	continuous	
Species number	27	2 - 60	continuous/discrete	
Species density	13	1.2 - 13.4	continuous	
Light^{c}	7.2	6.0 - 7.7	continuous	
Temperature^{c}	5.2	4.0 - 6.1	continuous	2
Continentality^{c}	3.2	2.0 - 4.9	continuous	
Water^{c}	4.1	3.2 - 5.4	continuous	1
Acidity^{c}	4.5	1.8 - 7.9	continuous	
Nitrogen^{c}	3.2	1.9 - 5.8	continuous	
Competition^{c}	2.9	1.5 - 5.1	continuous	
Stress^{c}	5.9	2.2 - 8.5	continuous	
Disturbance^{c}	3.2	0.3 - 5.6	continuous	
Number of annual species^{c}	3	0 - 18	continuous/discrete	
% density of annuals	8.7	0 - 59	continuous	
Grazing			5 levels	
% bare soil	11	0 - 68	continuous	
Soil			5 levels	

ded in the comparison between the old and recent inventories. Interpretation of names in the old material did generally not cause problems. However, Böcher et al. (1946) used the name *Mnium cuspidatum (L.) Neck. neque Hedw.*, which we interpret as being identical with *Plagiomnium affine (Funck) Kop.* found in the recent material. *Webera sp.* found by Mortensen (1953, 1955), is hypothesised to include *Pohlia nutans (Hedw.) Lindb.*.

Critical material is deposited in the second authors private herbarium.

Methods

For the purpose of searching for ecoclines, the debugged version of DECORANA (Hill 1979, Oksanen & Minchin 1997) was used to carry out detrended correspondence analysis (DCA) with default options. Outlying samples were omitted after visual inspection of DCA-axes 1-4. We used *logistic regression* in the form of *generalised additive modelling* for the analysis of single species niche preferences (Chambers & Hastie 1993), and *G-test for independence* for the analysis of differential number of single species records in the new and old datasets (Sokal & Rohlf 1981). A two-sided T-test was applied to test for differences in mean species numbers per sample between the old and new dataset. S-Plus ver.3.3 (Statistical sciences 1995) was used for generalised additive modelling of the DCA coenoclines in ecological .terms (function=gam, step.gam), for modelling of single species occurrences (function=gam, step.gam, *family=binomial*), for graphing species preferences in contour plots (function=predict.gam, *type="response"* and function=contour), for testing differences in single species occurrences between the recent and old data set (function=fisher.test), and for testing differences in species number per plot (function= t.test).

Results

The eigenvalues of cryptogam DCA axes 1-4 were 0.58, 0.39, 0.24 and 0.21 respectively, and total inertia amounted to 7.9. Corresponding eigenvalues for the vascular plant ordinations were 0.48, 0.35, 0.20, 0.17 with total inertia amounting to 7.1. Visual inspection of simple xy-plots revealed no signs of interactions between environmental variables and axes 3-4 of neither dataset, and these subordinate axes were therefore left out of further consideration.

Grassland ecoclines

The best generalised additive models of cryptogam coenocline 1 and 2 in terms of environmental variables are summarised in table 2 and figure 2, together with the corresponding models for phanerogam coenoclines 1 and 2. There is a striking agreement between the models of phanerogam and cryptogam coenoclines. The dependency on pH and continentality^c along DCA-1 is shared by cryptogams and vascular plants, and irradiation for vascular plants and temperature^c for cryptogams are obviously related. On the second axis, soil type, irradiation, nitrogen^c and disturbance^c make up a complex fertility gradient for vascular plants. Irradiation and water^c are important for cryptogams and these could also be hypothesised to make up a complex fertility - of relevance to the cryptogam layer.

Table 1 includes a model of cryptogams in terms of the phanerogam coenoclines and vice versa. The models of cryptogam coenoclines in terms of phanerogam coenoclines were found to be better than the corresponding models based on environmental variables, whereas cryptogam coenoclines were inferior predictors of phanerogam coenoclines compared to measured variables. A Pearson product moment correlation did not reveal any correlation between the number of vascular plants and the number of cryptogams per sample.

Table 2. Comparison of models of cryptogam and phanerogam coenoclines, respectively (response = DCA axes 1-2). Two types of models are reported on: a model in environmental terms, and a model in terms of the coenoclines of the other vegetation layer. Goodness of fit is reported by r^2; refer to fig. 2 for fit of single terms.

Response	Cryptogams		Phanerogams	
	Terms in model	r^2	Terms in model	r^2
DCA1	pH + continentality + temperature	0.75	pH + continentality + irradiation	0.89
DCA2	Irradiation + water	0.49	Soil + irradiation + disturbance + nitrogen	0.68
DCA1	Phanerogam1 + phanerogam2	0.80	Cryptogam1 + Cryptogam2	0.78
DCA2	Phanerogam1 + phanerogam2	0.55	Cryptogam1 + Cryptogam2	0.62

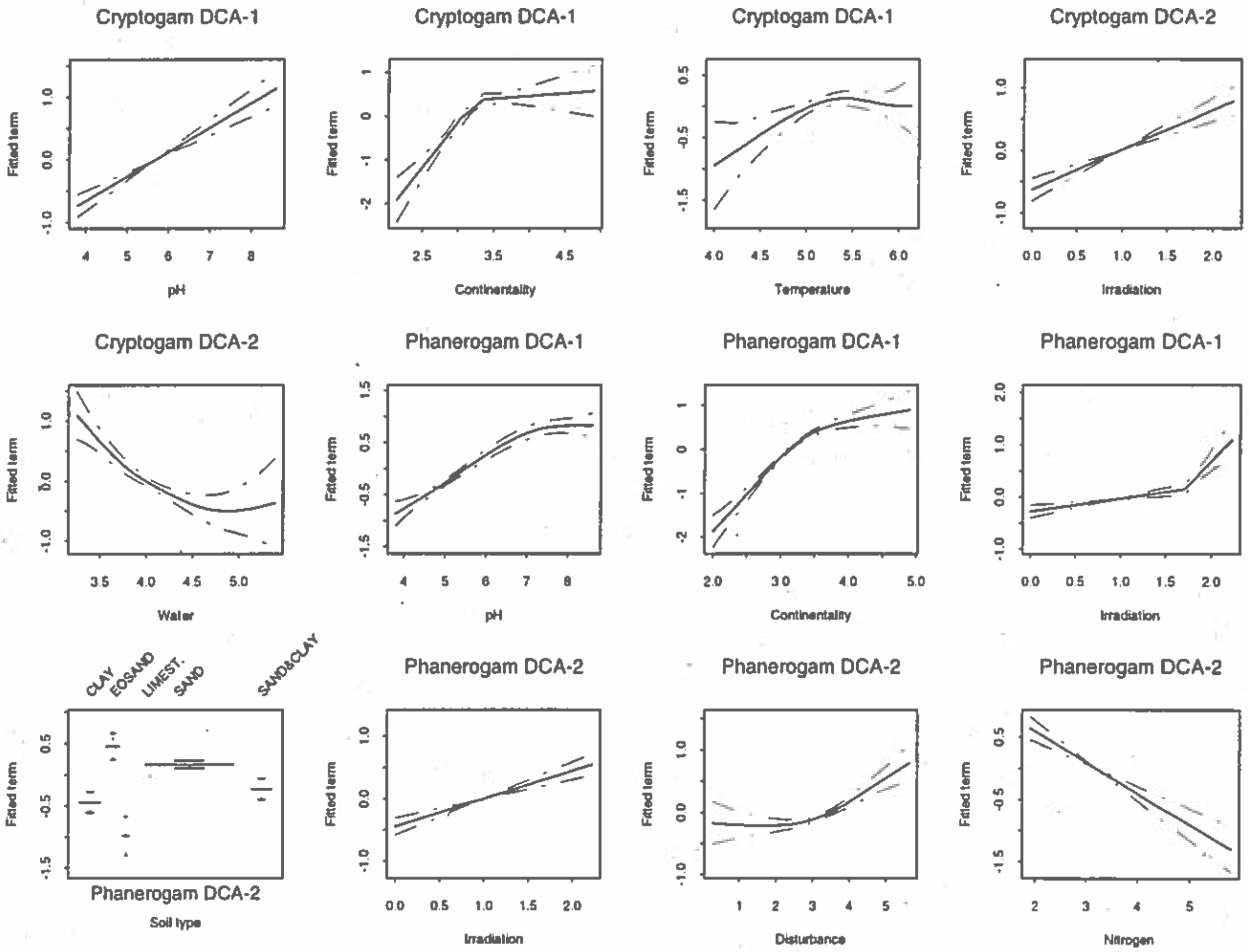
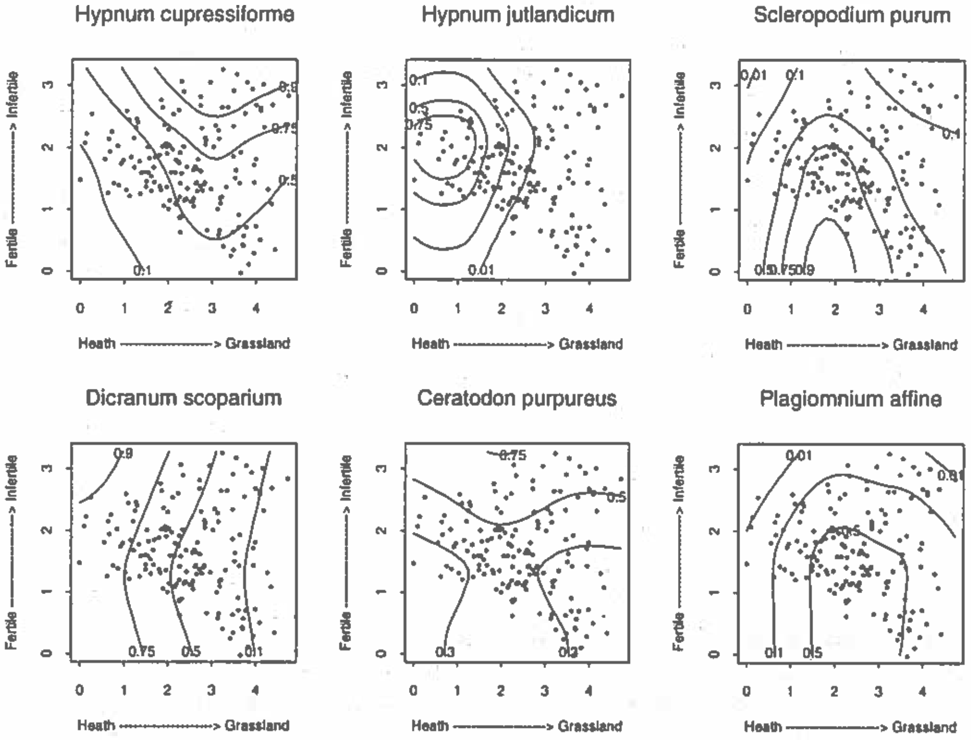


Figure 2. The centred fitted terms of the models based on environmental variables reported on in table 2. Broken lines indicate pointwise standard error estimates corresponding to an approximate 95 % *t* interval for the variation in the slope. Scale on the abscissa is fixed for each model, enabling a comparison of the single term contributions to the model.



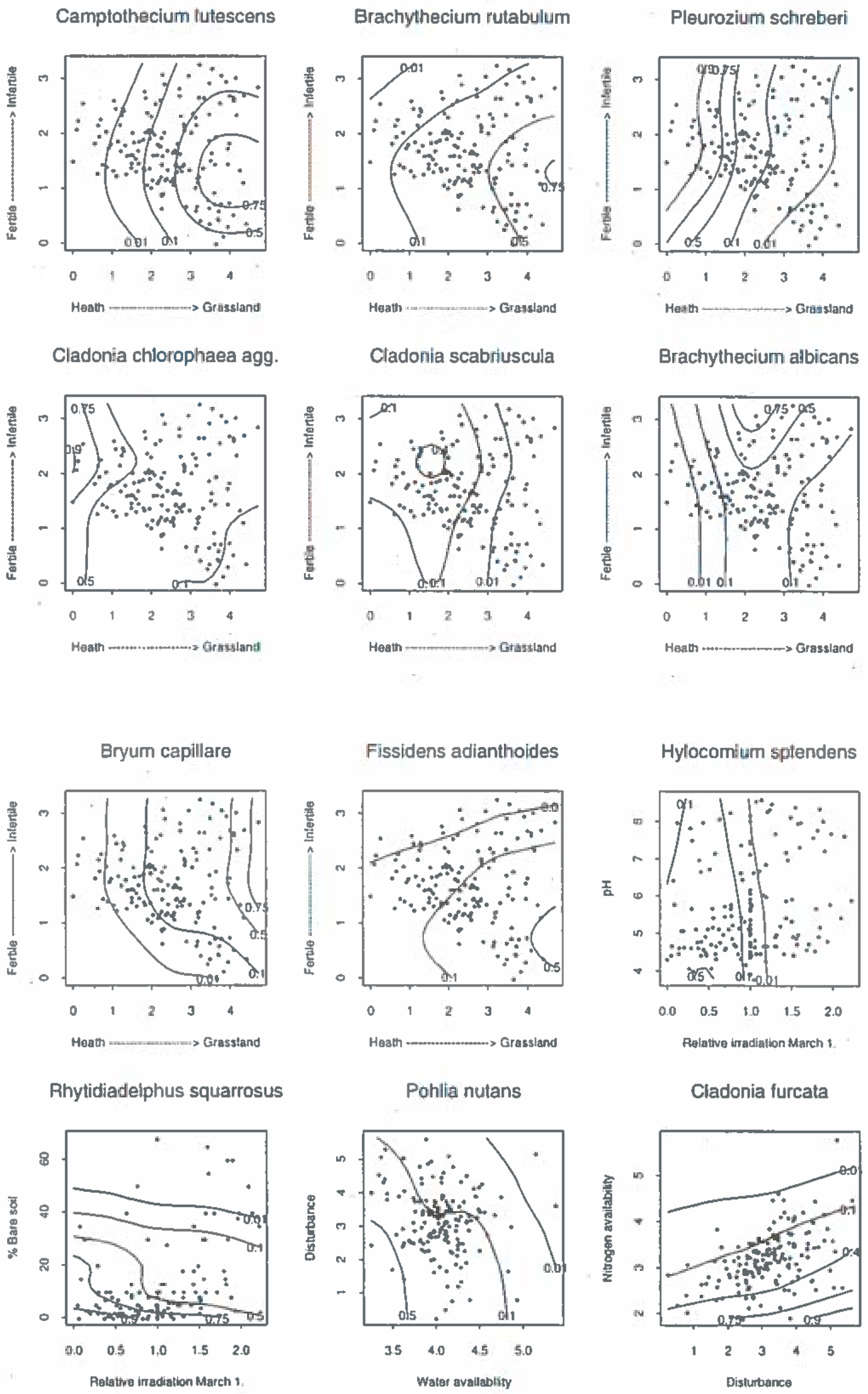


Figure 3. Contour diagrams of the 18 most frequent cryptogams of the data-set. The diagrams show the distribution modelled in terms of the two primary phanerogam ecoclines ("continentality" and "fertility"). With regards to R. squarrosus, P. nutans, H. splendens og C. furcata, the best environmental variables explained considerably more of the variation than did the phanerogam coenoclines, and they were consequently modelled in terms of these variables.

Species preferences

Figure 3 shows contour plots of the 18 most frequent cryptogamic taxa in the recent material. The contour plots were based on generalised additive models of species occurrences in terms of the first two phanerogam coenoclines, except for the few cases where the best two-terms model based on environmental variables was obviously better than the phanerogam based model.

Marked differences between the species was observed, some like *Ceratodon purpureus (Hedw.) Brid.*, *Hypnum cupressiforme Hedw.* and *Rhytidiadelphus squarrosus (Hedw.) Warnst.* behaved as generalists occurring throughout the studied grasslands, whereas species like *Camptothecium lutescens (Hedw.) B.S.G.*, *Hypnum jutlandicum Holmen et Warncke* and *Brachythecium albicans (Hedw.) B.S.G.* were restricted to a well characterised segment of the ecoplane.

Changes in cryptogam flora over time

The old and recent material are too different to be compared in their entities. Figure 4 shows how the important environmental predictors pH and irradiation varies between the recent and the old data-set, and it was decided to divide the material into 5 subsets, with reasonable representation and uniform distribution of old and new samples, and carry out comparisons mainly on these subsets (fig. 4). Apart from the four regions shown in figure 4, a fifth group was defined consisting of all samples from grasslands on limestone soils.

The 6 commonest species of each data-set (9 species in all) were selected for statistical comparisons, and supplemented with *Abietinella abietina (Hedw.) Fleisch.*, because this species was reported to decline in the Netherlands (During & Willems, 1986). All selected species are widely distributed within the sampled regions (Holmen 1959). The resulting comparison is shown in table 3. *Ceratodon purpureus* and *Brachythecium rutabulum (Hedw.) B.S.G.* were found to be more frequent in the new set, whereas *Rhytidiadelphus triquetrus (Hedw.) Warnst.* and *Abietinella abietina* were more frequent in the old data-set. Differences were also found with respect to *Fissidens adianthoides auct*, *Rhytidiadelphus squarrosus Hedw.* and *Hypnum cupressiforme Hedw.*, but these were less conspicuous.

The number of species per plot was found to be significantly higher on dry calcareous soil in the recent material, whereas a higher, although not significantly so, species number was observed on dry calcifugous soils in the old material (tab. 3). A closer look revealed that the difference in diversity found on dry calcareous soils were caused by bryophytes, whereas the difference on dry calcifugous soils were caused by lichens (and significantly so).

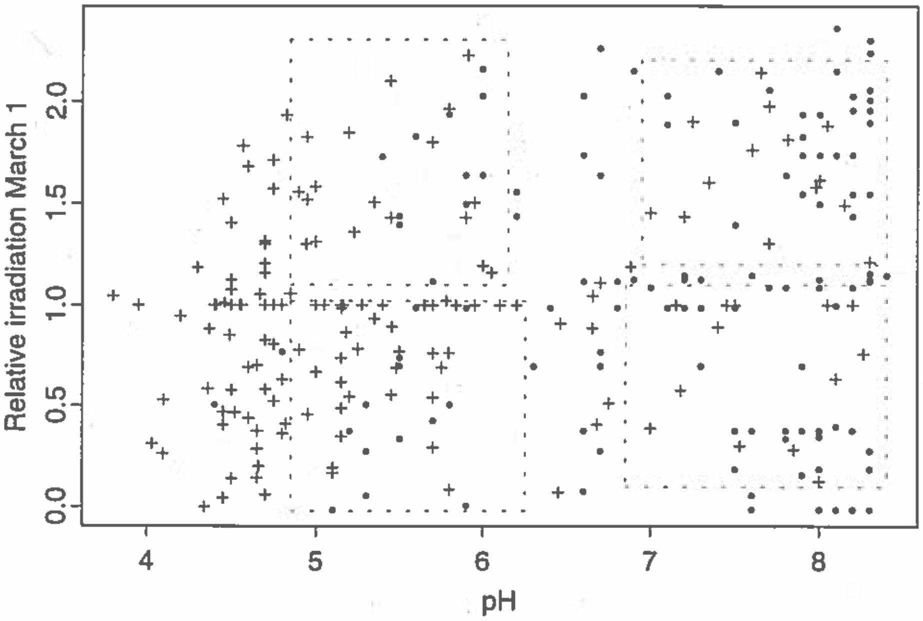


Figure 4. Scatterplot showing the distribution of recent (+) and old (•) samples with respect to pH and Relative irradiation March 1. Environmental segments within which species comparisons are carried out are indicated with broken lines

Table 3. Comparison of old and recent cryptogam data from grasslands, divided in 5 groups based on pH, topography and soil type (fig. 3). Number of samples and number of species records are given together with indication of significance of differences. T-test is used to test for differences in species numbers, and G-test for independence for differences with respect to single species records. Probability levels: *: P < 0.05, **: P < 0.01. Species and records with a declining trend are in italics whereas species with increasing trends are in bold. Non-significant differences are indicated with arrows.

	Limestone	Dry calcifugous	Humid calcifugous	Dry calcareous	Humid calcareous
Number of old/recent samples	21/7	15/18	19/38	28/14	23/13
Number of mosses	6.0/6.4	6.2/5.9	6.1/6.9	**3.5/6.9** **	4.7/5.8
Number of lichens	0.6/0.4	*4.1/1.3* **	0.6/0.8	1.1/0.9	0.3/0.3
Number of cryptogams	6.6/6.9	10.3/7.2 ↓	6.6/7.8	**4.6/7.8** *	5.0/6.1
Ceratodon purpureus	**2/4** *	6/12 ↑	1/11 ↑	**2/5** *	0/2
Rhytidiadelphus triquetrus	5/0 ↓	1/0	*10/5* **	0/1	4/0
Camptothecium lutescens	19/7	5/6	4/10	16/11 ↑	19/8
Brachythecium rutabulum	0/1	**0/7** *	1/9 ↑	**1/7** **	**4/7** *
Hypnum cupressiforme	4/1	9/13	6/24	**9/10** *	12/7
Dicranum scoparium	0/1	4/5	6/21	1/1	1/1
Fissidens adianthoides	11/3	*4/0* *	1/3	2/4	8/5
Abietinella abietina	4/1	*3/0* *	1/0	6/0 ↓	2/0
Scleropodium purum	7/5 ↑	2/9 ↑	11/28	4/2	*14/2* *
Rhytidiadelphus squarrosus	0/1	**1/8** *	13/32	0/1	7/6

Table 4 shows species found exclusively in the old or the recent data-sets (except species recorded only once). We find it worth noticing the occurrence in the old data of *Hymenostomum microstomum (Hedw.) R. Brown, Streblotrichum convolutum (Hedw.) P. Beauv., Peltigera spp.,Pterygoneurum ovatum (Hedw.) Dix., Cladonia mitis Sandst., Coelocaulon aculeatum (Schreb.) Link,* and in the new data of *Dicranella heteromalla (Hedw.) Schimp., Atrichum undulatum (Hedw.) P. Beauv., Bryum rubens Mitt., Polytrichum formosum Hedw., Dicranum polysetum*

Table 4. Species occurring exclusively in either the old or the new data-set. Only species with at least two records are included.

Grasslands 1940-50		Grasslands 1990's	
Brachythecium glareosum	2	Atrichum undulatum	6
Brachythecium velutinum	3	Bryum rubens	7
Bryum argenteum	3	Campylopus introflexus	2
Cephalozia bicuspidata	3	Campylopus pyriformis	2
Cladonia cervicornis	2	Cephaloziella divaricata	3
Cladonia mitis	4	Cladonia macilenta ssp bacillaris	4
Cladonia pleurota	2	Cladonia macilenta ssp. macilenta	4
Coelocaulon aculeatum	4	Dicranella heteromalla	10
Ditrichum flexicaule	3	Dicranum polysetum	4
Hymenostomum microstomum	15	Ephemerum serratum	3
Leptobryum pyriforme	2	Lophocolea heterophylla	2
Leptogium gelatinosum	2	Polytrichum formosum	7
Mnium stellare	2		
Mycobilimbia sabuletorum	2		
Neckera complanata	3		
Peltigera canina/membranacea	9		
Peltigera didactyla	3		
Peltigera rufescens	6		
Pterygoneurum ovalis	4		
Streblotrichum convolutum	8		

Sw. and *Cladonia macilenta Hoffm.* Many of the exclusive species can be explained by the relative representation of calcareous versus calcifugous grasslands in the two data-sets. This however does not apply to the three *Peltigera* species, *Cladonia mitis* and *Coelocaulon aculeatum* in the old data-set and *Bryum rubens (Mitt.)* in the new data-set, although the latter may well be among the unidentified Bryum species that occur in the old data-set. Furthermore, 16 collections of the recent material were pooled under the "name" Weissia/Hymenostomum /Astomun, and some of these might belong to Hymenostomum microstomum.

Discussion

In a gradient analysis based on a larger data-set from Danish grassland (Ejrnæs & Bruun subm.), the two most prominent ecoclines for phanerogam vegetation were interpreted as

1) a gradient from humid, acidic grassland to drier, calcareous grassland;
2) a gradient in productivity (from extremely dry and infertile to moderately fertile) influenced by pH and water/nutrient availability.

The generality of these phanerogam ecoclines is supported in the present study, and they are demonstrated to be important predictors for cryptogams as well. The finding, that cryptogams respond strongly to the composition of phanerogams whereas the reverse is less obvious, have at least two potential causes:

1) The lack of precision in the cryptogam data (recorded on a crude scale) creates less precise coenoclines,
2) grassland cryptogams reflect the environment less well than vascular plants, due to lower representativity of a sample (fewer species) and/or more stochastic occurrences.

It is tempting to add, that the slow growing cryptogams depend on the vegetation structure of species composition of the vascular plants, whereas plants are independent of cryptogams. Recent findings of bryophyte mediated effects on the regeneration by seed of vascular plants (van Tooren 1990) and the importance of lichens for vegetation composition (Newsham et al 1995), clearly indicates that this notion is at most half true.

Herben (1987) used PCA and small grassland data-sets for coenocline extractions, and demonstrated that substitution of vascular plants with bryophytes of equal abundance inevitably led to less explained variation. He therefore concluded that the distribution of bryophytes was determined largely by other factors than vascular plants. Our results are consistent with Herbens (1987) results, yet lead to the opposite conclusion! Cryptogams respond to the same major gradients as vascular plants in temperate grassland, but small differences in structure of relevant gradients and a more random distribution of cryptogams are likely to lead to increased noise, when cryptogams are included in gradient analysis based on vascular plants. This conclusion is consistent with the results of Cox & Larson (1993) studying bryophyte and vascular plant gradients on talus slopes in Canada. Our results are also consistent with the finding of Økland (1990) and Carleton (1990), that subordinate vegetation components, whatever taxonomic group, are problematic in a context of gradient analysis as they tend to accumulate in isolated, favourable segments of the ecoclines and behave as fugitives in the remaining gradient space. This should not, however, mislead one to denying such fugitives an important information value in community ecology. And, contrary to the situation in grassland, we would hypothesise that cryptogams were superior indicators (compared to vascular plants) of environmental gradients in forests, dunes and oligotrophic mires.

Among the single species, both generalists and specialists could be distinguished, and among the specialists some behaved as characteristic species of the dry, calcareous type of grasslands *(Camptothecium lutescens, Fissidens adianthoides, Bryum capillare, Brachythecium rutabulum)*, others of the oceanic heathlike grasslands *(Hypnum jutlandicum, Pleurozium schreberi (Brid.) Mitt., Dicranum scoparium Hedw. and Cladonia chlorophaea agg.)*, and yet some of the oligotrophic sand grasslands *(Brachythecium albicans, Cladonia scabriuscula (Del.) Leight).* and to some extent also the generalists *Ceratodon purpureus* and *Hypnum cupressiforme).*

During & Willems (1986) reported a dramatic decline in the cryptogam flora of Dutch chalk grasslands, but possible explanations were multiple: acidification and eutrophication from atmospheric deposition of nitrogen and sulphur oxides, dereliction, application of artificial fertilisers etc. In this study, comparison was made only between old, unimproved grasslands, excluding scrubs and improved grassland. Unfortunately, comparisons were not paired, and therefore, the differences in cryptogam flora can be due to both changes over time and differences related to region or sampling methods.

Nothing like the Dutch situation could be observed in the Danish material. Lichens have not disappeared and no overall decrease in species richness was found. *Camptothecium lutescens* is still very common in dry, neutral to calcareous, semi-natural grassland in Denmark. We did, however, find significant differences between the cryptogams in the old grassland material from about 1950 and the recent material. Many of the exclusive species can be explained by the relative representation of calcareous versus calcifugous grasslands in the two data-sets. This however does not apply to the three *Peltigera* species, *Cladonia mitis* and *Coelocaulon aculeatum* in the old data-set and *Bryum rubens* in the new data-set (although we suspect the latter to be among the unidentified Bryum species that occur in the old data-set).

For the following reasons, we find it worth considering the possibility of a change over the last 45 years: the diversity of lichens and the two significantly more abundant bryophytes of the old data-set indicate a soil type difference not accounted for by pH and topography. *Abietinella abietina, Fissidens adianthoides* and the exclusive *Peltigera* and *Cladonia* species all prefer mineral and not too acid soils compared to raw humus soils. The species with an increasing trend are ubiquitous species that are very common on a landscape scale, whereas the declining species are more or less confined to semi-natural or natural biotopes. *Brachythecium rutabulum* and *Ceratodon purpureus* are both known to be favoured by human activities. *Brachythecium rutabulum* thrive under relatively fertile conditions and tolerate litter accumulation (During & Willems 1979, Rincon & Grime 1989) and *Ceratodon purpureus* is quoted among the acidification tolerators in a review of Rao (1982). Indications of a decline is only found in the calcifugous grassland, hypothesised to have the smallest buffer capacity against acidification.

We would like to mention two possible causes for the observed differences.

1) Relaxed grazing regimes has resulted in a general accumulation of litter and raw humus, simultaneously with a decrease in exposed mineral soil, and
2) Acid rain has led to acidification of vegetation and topsoil.

The accumulation of litter and raw humus could be amplified by increasing productivity owing to climate changes and/or deposition of nitrogen oxides and ammonia or decreased intensity of grazing. We believe the changed grazing regimes over the last century to be the most important single factor. Landscape photographs from 1920-1950 (Worsøe 1990) clearly document that former days grazing regimes were much more intensive (including also winter grazing) resulting in abundant patches of exposed mineral soil and low open vegetation.

In addition, the tendency that uncommon species are being replaced by very common species, should lead to the consideration of a possible "mass effect" of spores from the landscapes surrounding present days semi-natural grasslands.

We also considered other causes for the observed differences, and the following should be mentioned: we suspect that the generally lower number of bryophytes found per plot in the old data-set could be explained by the late summer inventories in the old material, compared to the more convenient late spring and late autumn inventories carried out for the recent Djursland and Zealand material respectively. This could very well influence recording of some of the small acrocarps, especially ephemerals such as Ephemerum serratum. Against this speaks, that species like Streblotrichum convolutum and Hymenostomum microstomum occur several times in the old data-set.

Although not conclusive, our results suggest a decline of some cryptogamic species due to changes in grazing regimes, climate, eutrophication or acidification over the last decades. A drastic impoverishment in the cryptogam flora was not found, but it should be acknowledged that Denmark has experienced the same significant changes as the rest of NW Europe: large areas of old unimproved grasslands have been turned into productive grass fields or have been overgrown by shrubs resulting in an impoverishment of the cryptogam flora on a landscape scale.

Literature

Alstrup, V. & U. Søchting 1989. Checkliste og Status over Danmarks Laver. Nordisk Lichenologisk Forening.

Andersen, A.G., Boesen, D.F, Holmen, K., Jacobsen, N., Lewinsky, J., Mogensen, G., Rasmussen, K., Rasmussen, L. 1976. *Den danske mosflora 1. Bladmosser.* Gyldendal, Copenhagen.

Böcher, T.W. 1945. Beiträge zur Pflanzengeographie und Ökologie dänischer Vegetation. 11. Über die Waldsaum- und Graskrautgesellschaften trockner und halbtrockener Böden der Insel Seeland mit besonderer Berücksichtigung der Strandabhange und Strandebenen. *Kgl.Dan.Vidensk.Selsk., Biol. Skr.IV,* 1. 1-163.

Böcher, T.W., T.Christensen, M.S.Christiansen. 1946. Slope and Dune Vegetation of North Jutland. I. Himmerland. *Kgl.Dan.Vidensk. Selsk., Biol.Skr.IV,* 3. 1-78.

Carleton, T.J. 1990. Variation in terricolous bryophyte and macrolichen vegetation along primary gradients in Canadian boreal forests. J.Veg.Sci. 1: 585-594.

Chambers, J.M. & Hastie, T.J. (eds.) 1993. Statistical Models in S. Chapman & Hall, New York..

Cox, J. E. & Larson, D. W. 1993. Environmental relations of the bryophytic and vascular components of a talus slope plant community. J. Veg. Sci. 4: 553-560.

During, H.J. & Lloret, F. 1996. Permanent grid studies in bryophyte communities 1. Pattern and dynamics of individual species. *J. Hattori Bot. Lab.* 79: 1-41.

During, H.J. & Willems, J.H. 1986. Biol: Conserv. 36: 143-158.

During, H.J. 1979. Life strategies of bryophytes: A preliminary review. *Lindbergia* 5: 2-18.

Ejrnæs, R. & Bruun, H.H. 1995. Prediction of grassland quality for environmental management. *J. Env. Mgmt.* 43: 171-183.

Ejrnæs, R.& Bruun, H.H. subm. A gradient analysis of temperate grasslands on well-drained soils.

Ellenberg, H, Weber, H.E., Düll R.., Wirth, V., Werner, W., Paulissen, D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica vol 18.* Datenbank.

Fredskild, B. 1954. Ecological and Floristic Studies on Dry Sand Slopes in Western Sealand. *Oikos* 5: 205-235.

Gilbert, O. L. 1993. The lichens of chalk grassland. *The lichenologist* 25: 379-414.

Grime, J.P., Hodgson, J & Hunt, R. Unpubl. FIBS: *An extended version of the Electronic Comparative Plant Ecology.* NERC, University of Sheffield, 1996.

Herben, T. 1987. Bryophytes in Grassland Vegetation Sample Plots: What is their Correlation with Vascular Plants? *Folia geobot. et Phytotaxon* 22: 35-41.

Hill, M.O. DECORANA: *A FORTRAN program for detrended correspondence analysis and reciprocal averaging.* Cornell University, Ithaca, NY.

Holmen, K. (ed.) 1959. The distribution of the bryophytes in Denmark. *Botanisk Tidsskrift* 55: 77-154.

Mortensen, M.B. 1953. Urtesamfund på skrænter på Hindsholm (Summ.: Grassland Communities on the Slopes of Hindsholm). *Bot.Tidsskr.* 49: 239-259.

Mortensen, M.B. 1955. Urtesamfund på skrænter på Nord-Samsø (Summ.: Grassland Communities on Slopes in Northern Samsø). *Bot.Tidsskr.* 52: 85-112.

Muotka, T. & Virtanen, R. 1995. The stream as a habitat templet for bryophytes: species' distributions along gradients in disturbance and substratum heterogeneity. Freshwater Biology 33: 141-160.

Newsham, K.K., Watkinson, A.R., West, H.M. & Fitter, A.H. 1995. Symbiotic fungi determine plant community structure: changes in a lichen-rich community induced by fungicide application. *Functional Ecology.* 9: 442-447.

Økland, R.H. 1990. A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. III. Diversity and habitat niche relationships. Nord J. Botany 10: 191-220.

Oksanen, J. & Minchin, P. 1997. Instability of ordination results under changes in input data order: explanations and remedies. *J.Veg Sci.* 8: 447-454.

Rao D.N. 1982. Responses of Bryophytes to Air Pollution. In: Smith, A.J.E. (ed.). Bryophyte Ecology. Chapman & Hall. London.

Rincon, W. & Grime, J.P. 1989. An analysis of seasonal patterns of bryophyte growth in a natural habitat. J. Ecol. 77: 447-455.

Slack, N. G. 1982. Bryophytes in relation to ecological niche theory. J. Hattori Bot. Lab. 52: 199-217.

Smith, A. E. J. 1990. The Liverworts of Britain and Ireland. Cambridge University Press.

Sokal, R.R. & Rohlf, F.J. 1981. Biometry. 2.ed. W.H. Freeman & Company. New York.

Statistical Sciences 1995. *S-PLUS version 3.3 for Windows*. Seattle: Statistical Sciences, Inc.

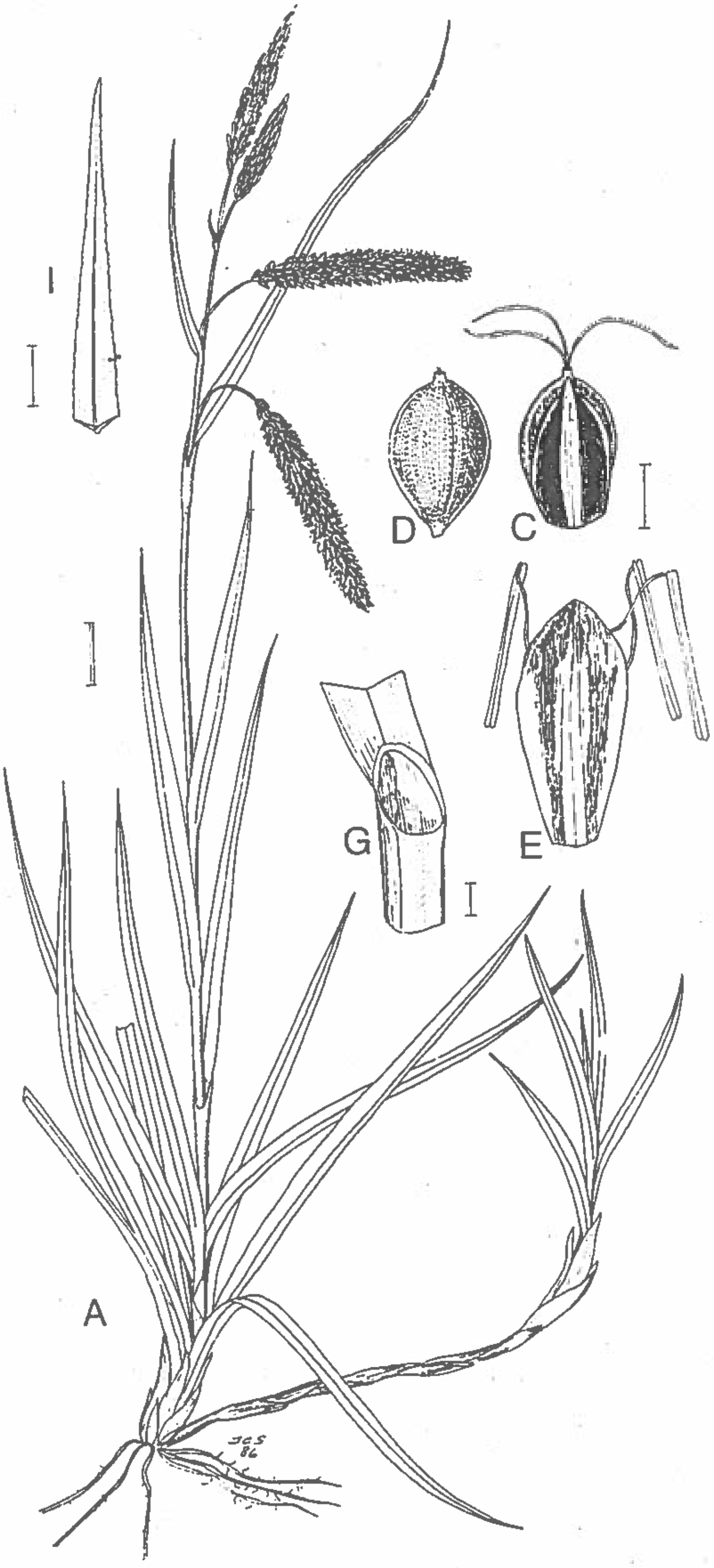
van Tooren, B. F. 1990. Effects of a bryophyte layer on the emergence of seedlings of chalk grassland species. *Acta Oecologica* 2: 155-163.

Worsøe, E. 1990 Mols Bjerge. Skippershoved, Randers.

Appendix I. Cryptogamic species found in unimproved Danish grasslands in the 1990's. Mosses first, then lichens, then hepatics. Number of occurrences as a vegetation dominant (>20% cover, app.) in parenthesis.

	East Jutland June 1997	West Zealand November 1992
Mosses		
Abietinella abietina (Hedw.) Fleisch.	1	
Amblystegium serpens (Hedw.) B.S.G.		2(1)
Anisothecium rufescens (With.) Lindb.		1
Anisothecium sp.	3	
Astomum crispum (Hedw.) Hamp.	3	
Atrichum undulatum (Hedw.) P. Beauv.	3	3
Barbula fallax Hedw.		2
Barbula sp.	1	
Barbula unguiculata Hedw.	9	
Barbula vinealis Brid. ssp. cylindrica (Tayl.) Boul.	1	
Brachythecium albicans (Hedw.) B.S.G.	28(7)	7(3)
Brachythecium rutabulum (Hedw.) B.S.G.	43(5)	9(1)
Bryoerythrophyllum recurvirostre (Hedw.) Chen	1	
Bryum capillare Hedw.	31(1)	
Bryum cf. capillare Hedw.	1	
Bryum intermedium(Brid.) Bland.		3
Bryum rubens Mitt.	1	6
Bryum sp.	5	
Calliergonella cuspidata (Hedw.) Loesk.	5(1)	1
Camptothecium lutescens (Hedw.) B.S.G.	48(24)	7
Campylium chrysophyllum (Brid.) J. Lange	5	
Campylopus introflexus (Hedw.) Brid.	2	
Campylopus pyriformis (Schultz) Brid.	2	
Ceratodon purpureus (Hedw.) Brid.	56(2)	7
Cirriphyllum piliferum(Hedw.) P. Beauv.	1	
Climacium dendroides (Hedw.) Web. et Mohr	1	
Ctenidium molluscum (Hedw.) Mitt.	6(1)	
Dicranella heteromalla (Hedw.) Schimp.	8	2
Dicranum polysetum Sw.	4	
Dicranum scoparium Hedw.	65(28)	7
Encalypta vulgaris Hedw.	1	
Entodon concinnus (De Not.) Par.	1	
Ephemerum serratum (Hedw.) Hamp.	2	1
Fissidens adianthoides auct.	19(1)	4(1)
Fissidens taxifolius Hedw.	4	
Hylocomium splendens (Hedw.) B.S.G.	17	3
Hypnum cupressiforme Hedw.	83(32)	12(3)
Hypnum jutlandicum Holmen et Warncke	29(16)	
Hypnum jutlandicum/cupressiforme	7(1)	
Mnium hornum Hedw.	2	1
Oxyrrhynchium praelongum (Hedw.) Warnst.	5	4
Oxyrrhynchium swartzii (Turn.) Warnst.	12(3)	4
Phascum cuspidatum Hedw.	14	
Plagiomnium affine (Funck) Kop.	47(3)	5(1)
Plagiomnium undulatum (Hedw.) Kop.	4	
Plagiothecium curvifolium Schlieph.		1
Plagiothecium sp.	2	
Pleuridium subulatum (Hedw.) Rabenh.	7	
Pleurozium schreberi (Brid.) Mitt.	41(22)	4(1)
Pohlia nutans (Hedw.) Lindb.	24	
Pohlia proligera (Kindb.) Arn.	1	
Polytrichum formosum Hedw.	7	
Polytrichum juniperinum Hedw.	18	
Polytrichum piliferum Hedw.	2	1
Pottia lanceolata (Hedw.) C. Muell.	3	
Pottia truncata (Hedw.) B.S.G./intermedia (Turn.) Fuernr.	7	4
Racomitrium ericoides (Hedw.) Brid.	2	
Rhodobryum roseum (Hedw.) Limpr.	7	1
Rhytidiadelphus squarrosus (Hedw.) Warnst.	77(44)	11(3)
Rhytidiadelphus triquetrus (Hedw.) Warnst.	8	1
Scleropodium purum(Hedw.) Limpr.	69(28)	8(1)
Thuidium philibertii Limpr.	4	1
Thuidium tamariscinum (Hedw.) B.S.G.	3	
Tortula ruralis (Hedw.) Gaertn., Meyer et Scherb.	14(1)	
Tortula subulata Hedw.	15(2)	
Weissia/Hymenostomum/Astomum sp.	14(1)	2
Lichens		
Cladonia arbuscula (Wallr.) Flotow	2	
Cladonia chlorophaea agg.	45(2)	
Cladonia ciliata Stirt. var. tenuis (Floerke) Ahti et Lai	9	
Cladonia cornuta (L.) Hoffm.	1	
Cladonia fimbriata (L.) Fr.	8	1
Cladonia foliacea (Huds.) Willd.	1	
Cladonia furcata (Huds.) Schrader	29(1)	4(1)
Cladonia glauca Floerke	1	
Cladonia macilenta Hoffm. ssp. bacillaris (Nyl.)	4	
Cladonia macilenta Hoffm. ssp. macilenta	4	
Cladonia pocillum (Ach.) Grognot	1	
Cladonia portentosa (Duf.) Coem.	6	
Cladonia rangiformis Hoffm.	11	
Cladonia scabriuscula (Del.) Nyl.	21	
Cladonia sp.	15	
Cladonia squamosa Hoffm.		2
Cladonia subulata (L.) Wigg.	1	
Collema tenax (Sw.) Ach.	2	
Collema cf. tenax (Sw.) Ach.	1	
Peltigera neckeri Müll. Arg.	1	
Peltigera sp.		1
Placynthiella uliginosa (Schrad.) Coppins et P. James	13(1)	
Trapeliopsis granulosa (Hoffm.) Lumbsch	2	
Hepatics		
Cephaloziella divaricata (Sm.) Schiffn.	4	
Lophocolea bidentata (L.) Dum.	7	6
Lophocolea heterophylla (Schrad.) Dum.	2	
Plagiochila porelloides (Nees) Lindenb. var. humilis	1	
Ptilidium ciliare (L.) Hampe	1	

Article V



Carex flacca Schreber

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Prediction of Grassland Quality for Environmental Management

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Fifty plots on grassland on well-drained soil were investigated for land use history and analysed for the species composition of vascular plants, macrofungi, bryophytes, lichens, hepatics and for 20 environmental variables. A DCA ordination showed an overall influence of land use history on species composition. DCA axis 1 was strongly correlated with species diversity of vascular plants. High species diversity is proposed to result from the combined action of high pH, high $CaCO_3$ content, high age of turf, grazing and absence of fertilization. A DCCA ordination lead to the proposal of 22 species as indicators of old, unameliorated grasslands in Denmark.

Keywords: history of land-use; permanent pasture; management; fertilization; DCA; DCCA; indicator species; Denmark.

1. Introduction

Grasslands are generally not considered a natural ecosystem on well-drained soil in north-west Europe (Coupland, 1993). However, Böcher (1945) and Bush (1993), among others, present evidence in favour of the hypothesis that grassland vegetation has been a continuous element in the landscape of north-west Europe since the latest glaciation, primarily occurring on slopes exposed to drought and erosion and on calcareous soils. In addition, temporary grasslands may have occurred in open places where herbivores slowed down the forest succession (Ellenberg, 1963).

The semi-natural grasslands of Europe constitute a major natural resource with an extraordinarily high species diversity (Loyd *et al.*, 1971; Willems, 1990; Kull and Zobel, 1991). However, intensive agriculture, with its use of artificial fertilizers, has changed most of the originally species-rich grasslands into highly productive swards of little conservation value (Duffey *et al.*, 1974; Londo, 1990). The deposition of nitrogenous compounds from a polluted atmosphere to grasslands has also been recognized as a threat to low-productive, species-rich grasslands (Bobbink *et al.*, 1992; Willems *et al.*, 1993).

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Only small areas remain in Europe which have been continuously grazed and not subjected to tilling or the application of fertilizers (Willems, 1990). Consequently, conservation authorities need effective tools to ensure a rapid recognition and protection of the remaining valuable grasslands.

The value of certain grassland species as indicators of old, unameliorated grasslands is pointed out by Wells *et al.* (1976), Grime *et al.* (1988) and Rodwell (1992). However, few attempts have been made to combine vegetation analysis with thorough research into history of land use.

The work presented here has two objectives: (1) to assess the influence of different management regimes on the vegetation (including plants, bryophytes and terricolous macrofungi) in some Danish grasslands; (2) to propose some indicators of old unameliorated grasslands.

2. Study area and methods

2.1. STUDY AREA

The study was carried out in the environs of Ordrup Næs, north-west Zealand on a near-shore diluvial moraine formation. All study sites lie on well-drained soil, within an area of 25 km^2. Mean annual temperature is 8 °C and mean annual precipitation is about 500 mm. Soil types vary from sand to loam (Leeper, 1964).

The vegetation found on old unameliorated grasslands of the area shows, according to the British vegetation classification (Rodwell, 1992), affinities with *Deschampsia flexuosa* (U2) or *Festuca ovina* (U1,U3) grasslands on acid soils, to *Cynosurus cristatus–Centaurea nigra* grassland (MG5) on neutral to slightly acid soils and to *Festuca ovina–Avenula pratensis* grassland (CG2) on calcareous soils, with most sample plots belonging to the MG5 type. A DCA ordination of data from 184 sites from most of Denmark (Grøntved, 1927; Böcher, 1945; Böcher *et al.*, 1946) revealed that our study covers a considerable part of the variation found in Danish grasslands (Bruun and Ejrnæs, 1993).

2.2. HISTORY OF LAND USE

The history of land use was investigated in detail by analysis of aerial photographs, farmer interviews and study of old land registrations. From this investigation, three key variables were selected and ranked separately on 5-point scales: A, age of turf, where 1 = cultivated 5 years ago, 2 = cultivated 6–15 years ago, 3 = cultivated 16–45 years ago, 4 = cultivated more than 45 years ago, 5 = not cultivated in this century (and probably never cultivated). B, fertilization, where 1 = never fertilized, 2 = not fertilized directly but part of a larger intensively fertilized pasture, 3 = fertilized once or twice during the last 40 years, 4 = fertilized a few times but with considerable amounts of NPK during the last 10 years (at least 1000 kg NPK/ha in total), 5 = high, constant level of fertilization during at least 20 years (averaging 2–300 kg NPK ha^{-1} year^{-1}). C, an estimate for the importance of grazing and trampling during the latest 10 years, combining history of land use with appearance of the vegetation, where 1 = no grazing, 2 = extensively grazed but no marked influence of the grazing animals on the vegetation, 3 = extensively grazed but marked effects on vegetation, 4 = moderately to intensively grazed with a short turf, 5 = intensively grazed and affected by trampling too.

2.3. FIELD METHODS

Eleven study sites of 5–15 ha each and with different histories of land use were selected. All sites were dominated by a grass- and herb-rich vegetation; sown grasslands were avoided. All sites but one were grazed.

In each of the sites, sample plots were placed by random numbers in previously selected areas of homogeneous vegetation and topography (judged subjectively). A total of 50 sample plots were laid out in an attempt to cover the known and visible variation concerning topography, history and vegetation.

The size of the sample plots was chosen as $6\,\mathrm{m} \times 6\,\mathrm{m}$—a size chosen because we also wanted to get representative records of fruiting terricolous macrofungi (all fungal species producing visible fruitbodies, except ectomycorrhizal, coprophilous and wood-inhabiting species). Each sample plot was divided into 16 subplots. Inside each subplot, two smaller subplots were placed systematically; one measuring $0{\cdot}25\,\mathrm{m} \times 0{\cdot}25\,\mathrm{m}$, assigned for the recording of vascular plants, and the other a circle of $20\,\mathrm{cm}^2$ for the recording of the remaining cryptogams (mainly bryophytes). In the close vicinity of each sample plot, six soil samples and four shoot/root samples were taken and subsequently pooled. The sample plots and subplots were marked permanently.

The recording was carried out in 1992. As an abundance measure, we used frequency in subplots, as recommended by Økland (1990). Vascular plants and macrofungi were recorded during 4–14 May and 15–22 July. Through August to late November the plots were visited at least fortnightly, but macrofungi were only recorded when new fruitbodies appeared. Other cryptogams were recorded by collections on 8 and 28 November with a soil sampler, followed by identification in the laboratory.

The nomenclature of vascular plants follows Moore (1982), while that of macrofungi follows Hansen and Knudsen (1992) for Agaricales, Jülich (1984) for Aphyllophorales and Dennis (1978) for Ascomycetes. The nomenclature of bryophytes follows Damsholt, Holmen and Warncke (1969), hepatics follow Grolle (1983) and lichens follow Søchting (1990).

2.4. ENVIRONMENTAL VARIABLES

Soil and root samples were taken in August, both to a depth of 10 cm.

Extractable NO_3^- and pH were analysed on fresh soil samples passed through a 2 mm sieve. pH was converted to $[H^+]$ for subsequent correlation analysis and vector fitting. NO_3^- was measured by the cadmium-reduction method on a Tecator Aquatec 5400 Flow Injection Analyzer (FIA), following extraction with 1 N KCl.

After drying soil samples at 40°C, the following analyses were carried out: PO_4^{3-} was analysed by the molybdate method (FIA as above) following extraction with water (chosen because both acid and calcareous soils were represented in the material); loss on ignition was found after placing soil samples at 600°C for 6 h; particle-size fractions were determined by passing 100 g dry soil through sieves with size of meshes 500, 250, 125 and 63 μm, with the coarsest fraction made up of the rest from the initial sieving through a mesh-size of 2 mm. Finally, a qualitative test for the presence of free $CaCO_3$ was carried out by stirring 100 g dried soil in 1 N HCl.

Root samples were washed carefully in a sieve with a size of meshes of 1 mm, a subsample of about 1/16 was thoroughly cleared for moss remains, sand particles, etc., dried at 40°C, weighed, and subsequently the N per cent was determined by pyrolytic destruction (Dumas method) in a LECO nitrogen determinator. Total root N content was calculated as N% × root-dw. Standing dead + living plant material was harvested in all plots in August on 4 × 86 cm^2, pooled, dried and weighed.

Inclination and aspect were measured in the field, and converted to mean annual potential irradiation (in per cent of that experienced by level ground) obtained with a precision of 5% (Barry and Van Wie, 1974). Inclination was also used as an independent variable. Wind exposure was estimated on a 5-point scale.

Species diversity (α-diversity) of vascular plants, bryophytes and macrofungi was calculated for each sample plot as the mean number of species per subplot.

2.5. NUMERICAL TREATMENTS

Ordination was used to perform both indirect and direct gradient analyses. CANOCO 3.12 (ter Braak, 1987–1992) was used, providing both DCA (Hill, 1979; Hill and Gauch, 1980) and DCCA (ter Braak, 1986). Detrending by segments was used as recommended by Knox (1989) and Økland (1990) and non-linear rescaling was preferred as it can be interpreted in ways of floristic turnover (Økland, 1990). We also used the possibility to substract the variation explained by a certain covariable in the DCCA. Downweighting of rare species was avoided, but otherwise standard options were used.

Rare species with only three recordings or less were omitted from further analysis as their occurrence might be markedly influenced by chance. As the basic unit for ordination is the response curves of the recorded species in relation to one or more hypothetical environmental variables, we decided also to omit species consisting of several ecotypes, among which we could not distinguish effectively in the field. This was the case for *Festuca rubra coll.* and *Poa pratensis coll.* Sample plot 33 is omitted from the ordination and placed passively in the diagram afterwards as this sample plot was exposed to a shrub clearing a few years ago.

The coenoclines of the DCA are interpreted by vectors of the environmental variables showing their direction of steepest increase. Vectors are calculated by a regression procedure (CANOCO 3.12: ter Braak, 1987–1992).

Correlations between environmental variables and between these and species diversity were tested by use of Kendall's rank correlation coefficient. A non parametric test was chosen as some variables are on an ordinal scale and others were not normally distributed. Significance of the DCCA was tested by use of a Monte Carlo permutation test against the null-hypothesis that the configuration was random given the chosen constraining variables.

3. Results

3.1. ORDINATION

The numerical properties of the basal floristic datamatrix and its derivation for use in ordination is presented in Table 1. Obviously, many species of macrofungi have been omitted from ordination. In 1992, both spring and late summer were abnormally dry in Denmark, which in part explains the low number of frequent macrofungi. As bryophytes and lichens were also sparsely represented in several sample plots, it was decided not to run ordinations on separate bryophyte or fungi datasets.

The resulting DCA ordination of 49 sample plots has eigenvalues for the three first axes of 0·423, 0·301 and 0·197. As recommended by Kenkel and Orlóci (1986), we also

TABLE 1. Numerical properties of the grassland dataset. The two columns to the right show the properties before and after modification (see text). Definitions according to Økland (1990).

Number of sample plots $= N$	50	49
Number of species $= m$	290	192
Vascular plants	153	117
Bryophytes and lichens	38	27
Fungi	99	48
Number of matrix elements $= o_t$	14·500	9·408
Number of nonzero matrix elements $= o_0$	3·202	2·020
Proportion of nonzero matrix elements $= o_0/o_t$	0·16	0·21
Vascular plants	0·21	0·24
Bryophytes and lichens	0·17	0·22
Fungi	0·08	0·15
Mean number of species per sample plot m_m	46·6	41·2
Vascular plants	31·9	28·0
Bryophytes and lichens	6·3	6·0
Fungi	8·4	7·1

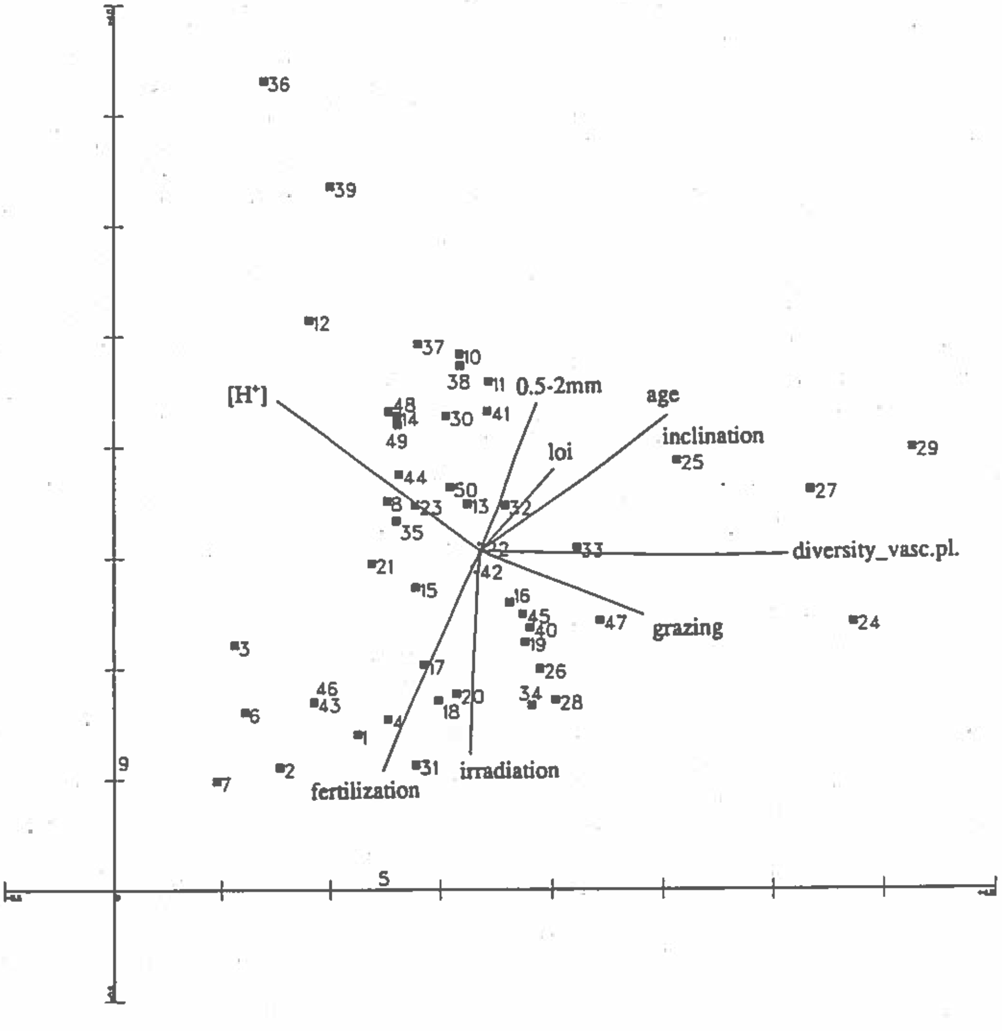

Figure 1. DCA ordination of modified dataset of 50 sample plots (No. 33 passive). Axes 1 (horizontal) and 2 (vertical). The eight most significant environmental variables including the diversity of vascular plants are depicted as vectors indicating the direction of steepest increase. The seven variables are: $[H^+]$, *coarse sand (0·5–2 mm)*, loss on ignition, *age* of turf, *inclination*, *grazing* pressure, potential *irradiation* and *fertilization*. Sample plots 24, 27,29, 33 and 47 on calcareous soil.

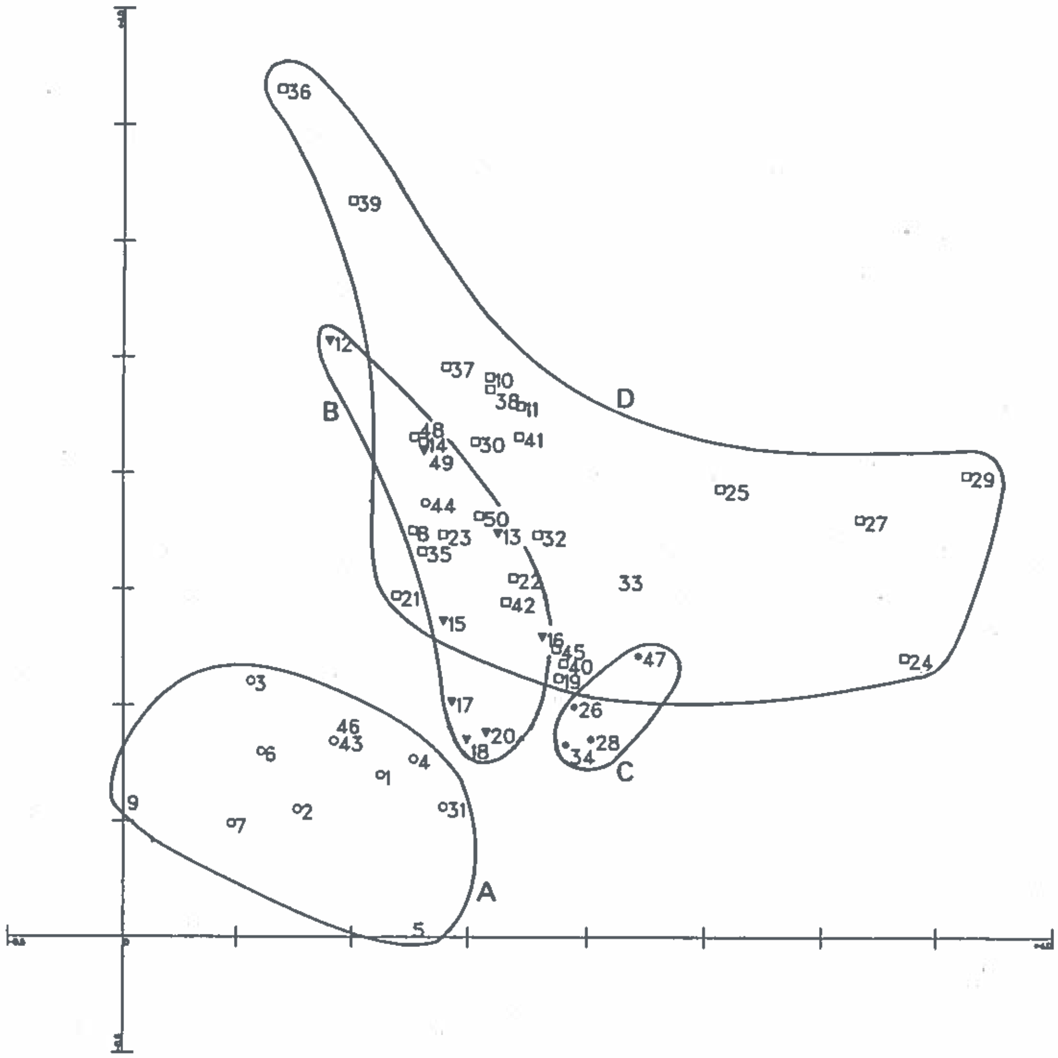

Figure 2. Classification according to history of land use onto the DCA ordination shown in Figure 1. All sample plots are grazed, except No. 35. Group *A* (circles) young oldfields (5–15 years). *B* (triangles) aged oldfields (30–50 years). *C* (asterisks) old fertilized grassland (>50 years). *D* (squares) Old unameliorated grassland (>50 years).

performed a CA on the same material to test if there was any instability in the performance of DCA (see also Oksanen, 1988). This was not the case as long as the outlying sample plot 33 only participates as passive sample in the ordination.

A rank correlation analysis was carried out between environmental variables and axes 1 and 2. The eight most significant environmental variables ($P<0{\cdot}001$) and DCA axes 1 and 2 are shown in Figure 1, with vectors showing their directions of steepest increase. A rank correlation analysis between these eight variables (Table 2) revealed a group of correlated variables, with positive correlations between *age of turf*, *loss on ignition*, *inclination* and *coarse-sand fraction*, while they all in turn show negative correlations with *fertilization. pH*, *grazing* and *irradiation* show no strong correlations to other variables.

The far strongest correlation variable to ordination coenoclines is the *species diversity of vascular plants*, which coincides with axes 1. A closer look at Table 2 reveals some possible determinants of species diversity. Strongly positively correlated are *pH*

TABLE 2. Kendall rank correlation between the seven most significant environmental variables and diversity of vascular plants. Levels of significance are indicated by ***$P<0{\cdot}001$, **$P<0{\cdot}01$, *$P<0{\cdot}05$, —ns

	Diversity of vascular plants	Coarse sand (0·5–2 mm)	Loss on ignition	H⁺ concentration	Potential irradiation	Inclination	Grazing	Fertilization
Age of turf	0·3729 **	0·4852 ***	0·6117 ***	0·0115 —	−0·2479 *	0·3935 ***	0·1215 —	−0·6222 ***
Fertilization	−0·3177 **	−0·5346 ***	−0·4160 ***	−0·0467 —	0·3202 **	−0·4834 ***	0·0508 —	
Grazing pressure	0·2648 **	−0·2723 **	0·0161 —	−0·1015 —	0·1068 —	−0·0853 —		
Inclination	0·2577 **	0·3919 ***	0·1840 —	−0·0569 —	−0·3123 **			
Pot. irradiation	0·0614 —	−0·1421 —	−0·1438 —	−0·0843 —				
[H+]	−0·3836 ***	−0·0433 —	0·0384 —					
Loss on ignition	0·2285 *	0·3829 ***						
0·5–2 mm	0·2472 *							

Figure 3 (*opposite*).

($P<0{\cdot}001$) and to a lesser degree *age of turf* and *grazing* intensity ($P<0{\cdot}01$), while fertilization shows a significant negative correlation ($P<0{\cdot}01$).

3.2. THE INFLUENCE OF HISTORY OF LAND USE

Figure 2 shows a classification of the plots according to history of land use drawn onto the DCA ordination. The four classes represent some often encountered types of land use history in Denmark: old, unameliorated grasslands; old grasslands, which have

Figure 3. DCCA ordination of 192 species, *constrained axes 1 (horizontal) and 2 (vertical). Only frequent species are shown (the 127 species recorded in at least 3 sample plots and* 15 subplots). The three constraining variables are depicted as vectors (cf. Figure 1), *the* H^+-concentration is run as covariable. The angled line demarcates an area of high age and low fertilization. The species in this area (black square) are considered potential indicators of old unameliorated grassland. Abbreviated names of species: *Achi mil, Achillea millefolium* L.; *Agro cap, Agrostis capillaris* L.; *Agro vin, Agrostis vinealis* Schreber; *Aira car, Aira caryophyllea* L.; *Aira pra, Aira praecox* L.; *Anem nem, Anemone nemorosa* L.; *Anth odo, Anthoxantum odoratum* L.; *Anth vul, Anthyllis vulneraria* L.; *Arab hir, Arabis hirsuta* (L.)Scop.; *Arme mar, Armeria maritima* (Miller)Willd.; *Arrh ela, Arrhenaterum elatius* (L.)Beauv. ex J. & C. Presl; *Aven pra, Avenula pratensis* (L.)Dumort.; *Aven pub, Avenula pubescens* (Huds.)Dumort.; *Br ho.ho, Bromus hordeaceus* L. ssp. hordeaceus; *Brac alb, Brachytecium albicans* (Hedw.)B.S.G.; *Brac rut, Brachytecium rutabulum* (Hedw.)B.S.G.; *Briz med, Briza media* L.; *Bryu rub, Bryum rubens* Mitt.; *Call vul, Calluna vulgaris* (L.)Hull; *Cama vir, Camarophyllus virgineus* (Wulf.:Fr.)Kumm.; *Camp lut, Camptothecium lutescens* (Hedw.)B.S.G.; *Camp rot, Campanula rotundifolia* L.; *Care are, Carex arenaria* L.; *Care car, Carex caryophyllea* Latourr.; *Care fla, Carex flacca* Schreber, *Ce fo.tr Cerastium fontanum* Baumg. ssp. triviale (Link)Jalas var. triviale: *Cent jac, Centaurea jacea* L.; *Cent sca, Centaurea scabiosa* L.: *Cera pur, Ceratodon purpureus* (Hedw.)Brid.; *Cera sem, Cerastium semidecandrum* L.; *Cirs aca, Cirsium acaule* Scop.; *Clad fur, Cladonia furcata* (Huds.)Schrader; *Copr fri, Coprinus friesii* Quél. ss.Lange; *Copr pli, Coprinus plicatilis* (Curt.:Fr.)Fr.; *Crin sca, Crinipellis scabella* (Alb.& Schw.:Fr.)Murr.; *Cyno cri, Cynosurus cristatus* L.; *Dact glo, Dactylis glomerata* L.; *Dant dec, Danthonia decumbens* (L.)DC.; *Dauc car, Daucus carota* L. ssp. carota; *Desc fle, Deschampsia flexuosa* (L.)Trin.; *Dicr sco, Dricranum scoparium* Hedw.; *Elym rep, Elymus repens* (L.)Gould; *Ento pap, Entoloma papillatum* (Bres.)Dennis; *Erop ver, Erophila verna* (L.)Chevall.; *Fest ovi, Festuca ovina* L.; *Fest pra, Festuca pratensis* Hudson; *Fili vul, Filipendula vulgaris* Moench; *Fiss adi, Fissidens adianthoides* Hedw.; *Gale vit, Galerina vittiformis* (Fr.)Sing.; *Gali ver, Galium verum* L.; *Gera mol, Geranium molle* L.; *Gera san, Geranium sanguineum* L.; *Hemi del, Hemimycena delectabilis* (Peck.)Sing.; *Hier pil, Hieracium pilosella* L.; *Hier umb, Hieracium umbellatum* L.; *Holc lan, Holcus lanatus* L.; *Holc mol, Holcus mollis* L.; *Hype mac, Hypericum maculatum* Crantz; *Hype per, Hypericum perforatum* L.; *Hypn cup, Hypnum cupressiforme* Hedw.; *Hypo rad, Hypochoeris radicata* L.; *Knau arv, Knautia arvensis* (L.)Coulter; *Leon aut, Leontodon autumnalis* L.; *Leon his, Leontodon hispidus* L.; *Linu cat, Linum catharticum* L.; *Loli per, Lolium perenne* L.; *Loph bid, Lophocolea bidentata* (L.)Dum.; *Lotu cor, Lotus corniculatus* L.; *Luzu cam, Luzula campestris* (L.)DC.; *Lyco liv, Lycoperdon lividum* Pers.; *Mara ore, Marasmius oreades* (Bolt.:Fr.)Fr.; *Medi lup, Medicago lupulina* L.; *Myce aet, Mycena aetitis* (Fr.)Quél.; *Myce cin, Mycena cinerella* Karst.; *Myce fil, Mycena filopes* (Bull.:Fr.)Kumm.; *Myce oli, Mycena olivaceomarginata* (Massee)Massee; *Myos str, Myosotis stricta* Link; *Omph fib, Omphalina fibula* (Bull.:Fr.)Quél.; *Omph set, Omphalina setipes* (Fr.:Fr.)Quél.; *Onon rep, Ononis repens* L.; *Oxyr pra, Oxyrrhynchium praelongum* (Hedw.)Warnst.; *Pana acu, Panaeolus acuminatus* (Schaeff.)Quél.; *Pana ate, panaeolus ater* (Lange)Kühn.& Romagn. ex M.Lge; *Ph pr.be, Phleum pratense* L. ssp. bertolonii (DC.)Bornm.; *Pimp sax, Pimpinella saxifraga* L.; *Plag aff Plagiomnium affine* (Funck)Kop.; *Plan lan, Plantago lanceolata* L.; *Pleu sch, Pleurozium schreberi* (Brid.)Mitt.; *Poly vul, Polygala vulgaris* L.; *Pote cin, Potentilla cinerea* Chaix ex Vill.; *Pote ere, Potentilla erecta* (L.)Räuschel; *Pote rep, Potentilla reptans* L.; *Pott tru, Pottia truncata* (Hedw.)B.S.G.; *Prim ver, Primula veris* L.; *Prun vul, Prunella vulgaris* L.; *Ranu acr, Ranunculus acris* L.; *Ranu bul, Ranunculus bulbosus* L.; *Rhyt squ, Rhytidiadelphus squarrosus* (Hedw.)Warnst.; *Rume ala, Rumex acetosella* L.; *Saxi gra, Saxifraga granulata* L.; *Scle pur, Scleropodium purum* (Hedw.)Limpr.; *Soli vir, Solidago virgaurea* L.; *Stel gra, Stellaria graminea* L.; *Succ pra, Succisa pratensis* Moench; *Tana vul, Tanacetum vulgare* L.; *Taralery, Taraxacum* sect. Erythrospermum Dahlst. emend H.Lindb.fil.; *Taraloff Taraxacumsect. Taraxacum; Thym pul, Thymus pulegioides* L.; *Trif arv, Trifolium arvense* L.; *Trif med, Trifolium medium* L.; *Trif pra, Trifolium pratense* L.; *Trif rep, Trifolium repens* L.; *Tuba fur, Tubaria furfuracea* (Pers.:Fr.)Gill.; *Vero arv, Veronica arvensis* L.; *Vero cha, Veronica chamaedrys* L.; *Vero off, Veronica officinalis* L.; *Viol can, Viola canina* L.; *Viol hir, Viola hirta* L. The following species with a negative score on axis 1 are omitted from the figure: *Anthriscus sylvestris* (L.)Hoffm., *Convolvolus arvensis* L., *Equisetum arvense* L., *Jasione montana* L., *Senecio jacobaea* L., *Vicia sativa* L. ssp. nigra (L.)Ehrh., *Vicia lathyroides* L.

been intensively fertilized; aged oldfields, which have been grazed continuously during at least 30 years and not subjected to intensive fertilization; and young oldfields of only 5–15 years, which have been grazed since abandonment, and have been subjected to intensive fertilization before abandonment.

Old unameliorated grasslands (D) differ floristically from the young oldfields (A). A less convincing, but still distinct, difference is seen between old grasslands which have been fertilized and those which have not (C). However, it seems that aged oldfields, which have not been subjected to intensive fertilization (B) in some cases develop a vegetation reminiscent of old unameliorated grassland. Plants threatened on a national scale were nevertheless only found around sample plots belonging to class D: *Dactylorrhiza sambucina*, *Scabiosa canescens*, *Dianthus superbus*, *Potentilla cinerea* and *Astragalus danicus* (Asbirk and Søgaard, 1991). Sample plot 44 does not fit well into the classification, but we do not attach too much importance to this, as there are some uncertainties concerning the tilling of the plot in 1981.

3.3. INDICATOR SPECIES

In order to search for indicator species of grasslands with a natural or semi-natural vegetation, a DCCA was carried out using the variables related to history of land use, i.e. *age of turf, fertilization and grazing* to constrain the ordination. The DCCA was run with *pH* as covariable as it had shown to be the strongest variable not closely correlated with land use parameters.

Figure 3 shows a biplot of the species and environmental variables on the first two axes of the DCCA. Eigenvalues of the first two axes were 0·276 and 0·118, respectively, and a Monte Carlo permutation test showed significance level of $P<0{\cdot}01$. Only species which occur in at least three sample plots and 15 subplots are shown. Furthermore, an arbitrary delimitation is made of a part of the ordination diagram that should be indicative of high age and low influence from fertilizing.

Table 3 shows those of the species that have been found in the indicator area of Figure 3. The table consists of 36 species, of which 31 are vascular plants. These are divided into three groups using available information on autecology (Hansen and Jensen, 1972; Arnolds, 1982; Hallingbäck and Holmåsen, 1985; Holst, 1987; Grime *et al*., 1988). The first group consists of seven species which elsewhere have shown to thrive also in fertilized grasslands or in young successional stages of oldfield succession. The second group consists of seven species which are less suitable as grassland indicators because they are more common in other habitats, i.e. dune, heath, meadow or wood. The last group consist of 22 species, which are proposed as indicators of old unameliorated grasslands of high conservational interest in Denmark. Five of these are mentioned by Wells *et al.* (1982) as indicators of unameliorated grasslands of more than 130 years old.

4. Discussion

The importance of management practices for the potentially species rich seminatural grasslands of north-western Europe has been elucidated by many workers (Duffey *et al*., 1974; Wells *et al*., 1976; Grime, 1990). In the present study, age of turf, fertilization and grazing turn out to be among the eight of 20 measured variables most significantly correlated with the floristic change along the first two axes of a DCA, with age of turf and fertilization ranking 2 and 3.

TABLE 3. The 36 potential indicator species from Figure 3 divided into three groups according to the literature (see text): *i* indicator species, *o* species with main occurrence in other habitats than grassland, *c* species thriving in oldfields or fertilized grassland. Species marked with an asterisk are according to Wells *et al.* (1976) indicators of grassland of at least 130 years old.

i	*Agrostis vinealis*	o	*Anemone nemorosa*
i	*Aira praecox*	o	*Cladonia furcata*
i	*Arabis hirsuta*	o	*Hieracium umbellatum*
i	*Avenula pratensis**	o	*Holcus mollis*
i	*Briza media*	o	*Hypnum cupressiforme*
i	*Camarophyllus virgineus*	o	*Lophocolea bidentata*
i	*Carex caryophyllea**	o	*Rhytidiadelphus squarrosus*
i	*Carex flacca*		
i	*Centaurea jacea*	c	*Cynosurus cristatus*
i	*Cirsium acaule*	c	*Hieracium pilosella*
i	*Danthonia decumbens*	c	*Leontodon autumnalis*
i	*Festuca ovina*	c	*Lotus corniculatus*
i	*Filipendula vulgaris**	c	*Luzula campestris*
i	*Fissidens adianthoides*	c	*Prunella vulgaris*
i	*Leontodon hispidus*	c	*Trifolium pratense*
i	*Linum catharticum*		
i	*Polygala vulgaris**		
i	*Primula veris*		
i	*Succisa pratensis**		
i	*Thymus pulegioides*		
i	*Viola canina*		
i	*Viola hirta*		

Species diversity of vascular plants was by far the most significantly correlated parameter with the first axis of the DCA. A distinct influence of land use history on diversity is proposed by our results, but other parameters such as pH seem to be involved as well.

Surprisingly, none of the attempts to measure soil fertility, e.g. root mass, root N%, total root N, shoot mass, NO_3^-, PO_4^{3-} showed strong correlations with the major coenoclines. It thus seems difficult to track the history of land use by analysing soil and plant samples. The failure of the root nitrogen variables as fertility measures could be explained by the fact that the root samples were taken following a period of summer drought. Species or ecotypes with different adaptations should be expected to translocate nutrients to the roots more or less efficiently during drought. This factor could explain the surprisingly high root N values in some low-productive plots.

Woodmansee *et al.* (1981) points to the fact that, except after episodes of drought or frost, levels of dissolved NO_3^- and PO_4^{3-} are very low in grasslands of low to moderate nutrient status. Another possible explanation, indicated by, for example, Heal and Harrison (1990), is that the measuring of pools is generally insufficient, as it is the turnover rates that are of importance to the organisms.

On account of the strong correlation between vegetation patterns and history of land use, it would be tempting to use information of site history as a guideline for conservation. Nevertheless, it is often very laborious, if not impossible, to get reliable information on site history. Furthermore, the effect of a given action, for example fertilization, is dependent on characteristics of the soil and the composition of the vegetation (Willems *et al.*, 1993). Therefore, we would rather recommend the use of vegetational criteria for conservation planning, based on knowledge of the composition and prerequisites of an undisturbed grassland vegetation. One way of doing this would be to use the indicator species concept.

Luff *et al.* (1992) used ground beetles to classify a wide range of grassland habitats. We recommend the use of plants as indicators, as they are generally easy to determine and mostly occur in numbers large enough to characterize an area of concern.

Wells (1976) and Grime *et al.* (1988) give examples of potential indicators for low-productive British grasslands. Generally, we find a good agreement with our results on Danish grasslands (Table 3), but we are still in need of a better understanding of the autecology of grassland species, especially concerning their performance in the cultural landscape.

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References

Arnolds, E. (1982). *Ecology and Coenology of Macrofungi in Grasslands and Moist Heathlands in Drenthe, the Netherlands*, Vol. 2: *Autecology and Taxonomy*. Vaduz: J. Cramer.

Asbirk, S. and Søgaard, S. (1991). *Rodliste '90. Særligt beskyttelseskrævende planter og dyr i Danmark.* Hillerød: Skov- og Naturstyrelsen.

Barry, R. G. and Van Wie, C. C. (1974). Topo- and microclimatology in alpine areas. In *Arctic and Alpine Environments* (J. D. Ives and R. G. Barry, eds). London: Methuen.

Bobbink, R., Boxman, D., Fremstad, E., Heil, G., Houdijk, A. and Roelofs, J. (1992). Critical loads for nitrogen eutrophication of terrestrial and wetland ecosystems based upon changes in vegetation and fauna. In *Critical Loads for Nitrogen* (P. Grennfelt and E. Thörnelöf, eds). Århus: Nordic Council of Ministers.

Bruun, H. H. and Ejrnæs, E. (1993). Naturtypen overdrev–vegetationen og dens forudsætninger. M.Sc. thesis. University of Copenhagen. Copenhagen: Skov- & Naturstyrelsen.

Bush, M. B. (1993). An 11 400 year paleoecological history of a British chalk grassland. *Journal of Vegetation Science* **4**, 47–66.

Böcher, T. W. (1945). Beiträge zur Pflanzengeographie und Ökologie Dänischer Vegetation, II. Über die Waldsaum- und Graskrautgesellschaften trockener und halbtrockener Böden der Insel Seeland mit besonderer berücksichtigung der Strandabhänge und Strandebenen. *Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter* **IV,1**, 1–163.

Böcher, T. W., Christensen T. and Christiansen. M. S. (1946). Slope and Dune Vegetation in North Jutland, I. Himmerland. *Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter* **IV,3**, 1–78.

Coupland, R. T. (ed.). (1993). *Natural Grasslands. Eastern Hemisphere and Resumé. Ecosystems of the world*, Vol. 8B. Amsterdam: Elsevier.

Damsholt, K., Holmen, K. and Warncke, E. (1969). A list of the Bryophytes of Denmark. *Botanisk Tidsskrift* **65**, 163–183.

Dennis, R. W. G. (1978). *British Ascomycetes.* Vaduz: J. Cramer.

Duffey, E., Morris, M. G., Sheail, J., Ward, L. K., Wells, D. A. and Wells, T. C. E. (1974). *Grassland Ecology and Wildlife Management.* London: Chapman & Hall.

Ellenberg, H. (1963). *Vegetation Mitteleuropas mit den Alpen.* Stuttgart: Eugen Ulmer. Grime, J. P. (1990). Mechanisms promoting floristic diversity in calcareous grasslands. In *Calcareous Grasslands–Ecology and Management* (S. H. Hillier, D. W. H. Walton and D. A. Wells, eds). Huntingdon: Bluntisham Books.

Grime, J. P., Hodgson. J. G. and Hunt, R. (1988). *Comparative Plant Ecology. A functional Approach to Common British Species.* London: Unwin Hyman.

Grolle, R. (1983). Hepatics of Europe including the Azores: an annotated list of species, with synonyms from the recent literature. *Journal of Bryology* **12**, 403–459.

Grøntved, J. (1927). Formationsstatistiske undersøgelser på nogle danske overdrev. *Botanisk Tidsskrift* **40**, 1–71.

Hallingbäck, T. and Holmåsen, I. (1985). *Mossor. En fälthandbok.* Stockholm: Interpublishing.

Hansen, K. and Jensen, J. (1972). The Vegetation on Roadsides in Denmark. Qualitative and Quantitative Composition. *Dansk Botanisk Arkiv* **28**(2), 21–61.

Hansen, L. and Knudsen, H. (eds). (1992). *Nordic macromycetes,* Vol. 2. *Polyporales, Boletales, Agaricales, Russulales.* Copenhagen: Nordsvamp.

Heal, O. W. and Harrison, A. F. (1990). Keynote paper: Turnover of nutrients: a technological challenge. In *Nutrient Cycling in Terrestrial Ecosystems* (A. F. Harrison, P. Ineson and O. W. Heal, eds). London: Elsevier.

Hill, M. O. (1979). *DECORANA—a Fortran Program for Detrended Correspondence Analysis and Reciprocal Averaging*. New York: Cornell University.

Hill, M. O. and Gauch, H. G. (1980). Detrended correspondence analysis: an improved ordination technique. *Vegetatio* **42**, 47–58.

Holst, J. (1987). *En Undersøgelse af Vegetation og Flora på Opgivne Torre, Sandede Landbrugsarealer på Djursland.* Miljøministeriets projektundersøgelse 1986, teknikerrapport no. 17. Copenhagen: Skov- og Naturstyrelsen.

Jülich, W. (1984). *Die Nichtblätterpilze, Gallertpilze und Bauchpilze.* Kleine Kryptogamenflora Vol. 2b/1. Stuttgart: Gustav Fischer Verlag.

Kenkel, N. C. and Orlóci, L. (1986). Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. *Ecology* **67**, 919–928.

Knox, R. G. (1989). Effects of detrending and rescaling on correspondence analysis: solution stability and accuracy. *Vegetatio* **83**, 129–136.

Kull, K. and Zobel, M. (1991). High species richness in an Estonian wooded meadow. *Journal of Vegetation Science* **2**, 711–714.

Leeper, G. W. (1964). *Introduction to Soil Science.* Melbourne: Melbourne University Press.

Londo, G. (1990). Conservation and management of semi-natural grasslands in Northwest Europe. In *Vegetation and Flora of Temperate Zones* (U. Bohn and R. Neuhäusel, eds). Haag: SPB Academic Publishing.

Loyd, P. S., Grime, J. P. and Rorison, I. H. (1971). The grassland vegetation of the Sheffield region. 1. General features. *Journal of Ecology* **59**, 863–886.

Luff, M. L., Eyre, M. D. and Rushton, S. P. (1992). Classification and prediction af grassland habitats using ground beetles (Coleoptera, Carabidae). *Journal of Environmental Management* **35**, 301–315.

Moore, D. M. (1982). *Flora Europaea Checklist and Chromosome Index.* Cambridge: Cambridge University Press.

Oksanen, J. (1988). A note on the occasional instability of detrending in correspondence analysis. *Vegetatio* **74**, 29–32.

Økland, R. H. (1990). Vegetation ecology: theory methods and applications with reference to Fennoscandia. *Sommerfeltia Suppl.* **1**.

Rodwell, J. S., ed. (1992). Grasslands and Montane Communities. *British Plant Communities,* Vol. 3. Cambridge: Cambridge University Press.

Søchting, U. (1990). Dansk Lavflora. Manuscript, University of Copenhagen, Department of Thallophytes.

ter Braak, C. J. F. (1986). Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**, 1167–1179.

ter Braak, C. J. F. (1987–1992). *CANOCO—a Fortran Program for Canonical Community Ordination by (Partial)(Detrended)(Canonical) Correspondence Analysis, Principal Components Analysis and Redundancy Analysis.* Version 3.12. Wageningen: TNO Institute of Applied Computer Science, Statistics Department.

Wells, T. C. E., Sheail, J., Ball, D. F. and Ward, L. K. (1976). Ecological studies on the Porton Ranges: Relationships between vegetation, soils and land-use history. *Journal of Ecology* **64**, 589–626.

Willems, J. H. (1990). Calcareous grasslands in continental Europe. In *Calcareous Grasslands—Ecology and Management* (S. H. Hillier, D. W. H. Walton and D. A. Wells, eds). Huntingdon: Bluntisham Books.

Willems, J. H., Peet, R. K. and Bik, L. (1993). Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. *Journal of Vegetation Science* **4**, 203–212.

Woodmansee, R. G., Vallis, I. and Mott, J. J. (1981). Grassland nitrogen. In *Terrestrial Nitrogen Cycles* (F. W. Clark and T. Roswall, eds). *Ecological Bulletins* **33**.

3. Future perspectives

The conventions of scientific writing include the ideals of precision and objectiveness. Self-criticism exerted by scientists writing scientific papers is just as hard as natural selection in the terms of Darwin, leading to fast elimination of less well fit ideas. I find this to be critical for the evolution of new original ideas, and it is therefore the intention of this chapter to serve the role of an island, where new ideas or perspectives are allowed to be presented.

First, I will focus on hypotheses and ideas that have emerged during my study, yet did not fit in the restricted discussions in the papers, and then I will set up propositions for future research in relation to these. The papers presented in the previous chapter will be referred to as [1] to [5].

3.1 Ideas and hypotheses

The first hypothesis is fairly general, yet has a large potential applicability:

Simple information about vegetation cover (trees, herbs, bare soil), pH, soil type, topography and soil moisture can be used to predict the occurrence and composition of unimproved dry grassland vegetation with satisfactory accuracy.

The interesting perspective of this hypothesis is that the predictors mentioned could potentially be obtained from available soil databases, elevation models and remote sensed data. If the model works reasonably well, then the predicted outcome can be compared to actual vegetation, and the antropogenic impact (in terms of tilling, eutrophication, reseeding, and pesticide treatment) be quantified in units of floristic turnover. The hypothesis regards an operative model working on a landscape scale, and it should therefore be subjected to validation through field sampling in contrasted landscapes and different situations.

The hypothesis is not as trivial as it seems. Generalisation in terms of vegetation type modelling has obvious advantages compared to the stochastic occurrences of single species, turning prediction into a game of chance. My study of single species responses [3] indicate that such a generalisation can be justified. Although the predictors in the hypothesis are well known to plant ecologists, the actual model relating them to vegetation is not as evident. The primary ecoclines found in the gradient analysis part of my thesis [1] could be summarised as

1) An *ecosystem ecocline* from dry, calcareous grassland with a continental flora-element to moist, leached and acidic grasslands with an oceanic flora-element.
2) A *fertility ecocline* from fertile grassland on moist calcareous moraine soils to infertile grasslands on dry eolian/marine sand.
3) A *regional ecocline* reflecting regional differences with respect to predominating geological features, precipitation and, probably, landscape history.
4) A *successional ecocline* from infertile and/or grazed grasslands with prevalence of the stress tolerant strategy to fertile, ungrazed grasslands dominated by tall, fast-growing competitors.

At least the first and second ecocline could be modelled in terms of environmental predictors [1] of which some, like pH, topography and soil type are simple and operational. The ecoclines mentioned in 2) and 4) are not surprising, and they both receive due attention in ecological literature (e.g.Grime 1979, Tilman 1988). The regional ecocline in 3) is harder to interpret in ecological terms but is probably reflecting multiple regional differences within the sampled area with respect to the geology and history of the landscape. The underlying metapopulation processes (Gilpin & Hanski 1991) is believed to bring about variation that is not readily reduced to a few major gradients. It should be considered whether the inclusion of local species pools could improve the predictions of the model without sacrificing its simplicity. The ecosystem gradient underlying the first ordination axis is hardly mentioned in contemporary vegetation studies, although it has received some attention in phytosociology (e.g. Pott 1995) and early phytogeographical studies (e.g. Sterner 1922, Böcher 1945). Despite this, it was found to be the best predictor of species composition in this study.

Secondary successions

The second idea could be seen as an elaboration of the first hypothesis:

The outcome of secondary successions on well drained soils will depend on 1) the species pool, 2) the landscape and 3) the environment.

This statement is more of a research concept than a hypothesis, but as it will appear in the next section, more specific sub-hypotheses can be deduced from the statement and subjected to testing.

In this century, the area of semi-natural grassland has diminished considerably. Reduced grazing, conversions to arable land and extensive use of fertilisers have changed the flora and vegetation of open land biotopes dramatically. Increasing concern for wildlife (including plants, insects and fungi) has resulted in a quest for opportunities to revert arable land and improved pastures to heathland and semi-natural grassland. Predictive models of open land successions could serve as a management tool securing that authorities make the right priorities.

Tilman (1988) asked: "*Why is it, for instance, that species with similar physiological, morphological and life history traits are dominant in a similar order during secondary successions in different habitats worldwide..*". Despite this encouraging statement, I believe it to be less complicated to create a static model of permanent, more or less steady state grassland (hypothesis 1), than to predict the outcome of a secondary succession. Although a general successional pattern might be deduced, the biological mechanisms determining the outcome of a succession are not trivial (Tilman 1997). A comprehensive model may be out of immediate reach, but still a quantification of the relative importance of the three involved factor-complexes of the statement would be a very important step forward.

Plant ecologists have traditionally focused on local scale ecological processes involving the interaction of species with each other and with the environment (Grime 1973, Grubb 1977, Tilman 1985, Campbell et al. 1991). Recently attention has been drawn to other processes, e.g. the role of the species pool (Taylor et al. 1990) and the importance of recruitment limitation (Tilman 1997). Zobel's (1997) approach to determining the actual species pool comes very close to my second statement (fig. 2). The species pool in my hypothesis corresponds to the *local species pool* in Zobel's figure, the landscape is the *dispersal* determinant and the environment is parallel to the *filter*. Zobel (1997) distinguishes between abiotic factors and biotic interactions, yet acknowledges that these act "in concert". This makes sense, not least because biotic interactions depend on the species present at any time, so the environment changes character during the course of succession. In this way, the sequence of species arriving to a particular biotope may play a major role for the course and speed of succession, leaving the door open for stochasticity as an important factor.

A quantification of the relative contributions of the three factor-complexes, will rely on carefully designed experiments, where the abiotic environment, the species involved and the course of species introductions can be controlled and manipulated. It will be of major interest also to quantify the importance of stochasticity, as the ratio within treatment variance and between treatment variance.

The third and last hypothesis is related to the second statement, but only regards the prediction of one vegetation parameter, namely species density. Contrary to what could be expected this specification and narrowing of the subject leads to further complications. At first sight the hypothesis might seem slightly off the track, but hopefully its relevance to my thesis will emerge from the following discussion:

α-diversity is promoted and largely determined by the favourability of the environment over time.

A clarification and elaboration of the statement is appropriate. α-diversity is used here in the sense of Whittaker (1972), describing the number of species found in an environmentally homogeneous sample. In my own investigations I used 10 samples of 0.1 m^2 as a measure of α-diversity, but the hypothesis also applies to somewhat larger scales, as long as the criterion of homogeneity and constant area is fulfilled. I include in the term *environment* both the abiotic and biotic environment as these are interdependent and hardly separable. The term *favourability* comprehends the *accessibility of essential resources*. What is essential resources will of course depend on the organisms in focus, for plants the availability of light, water

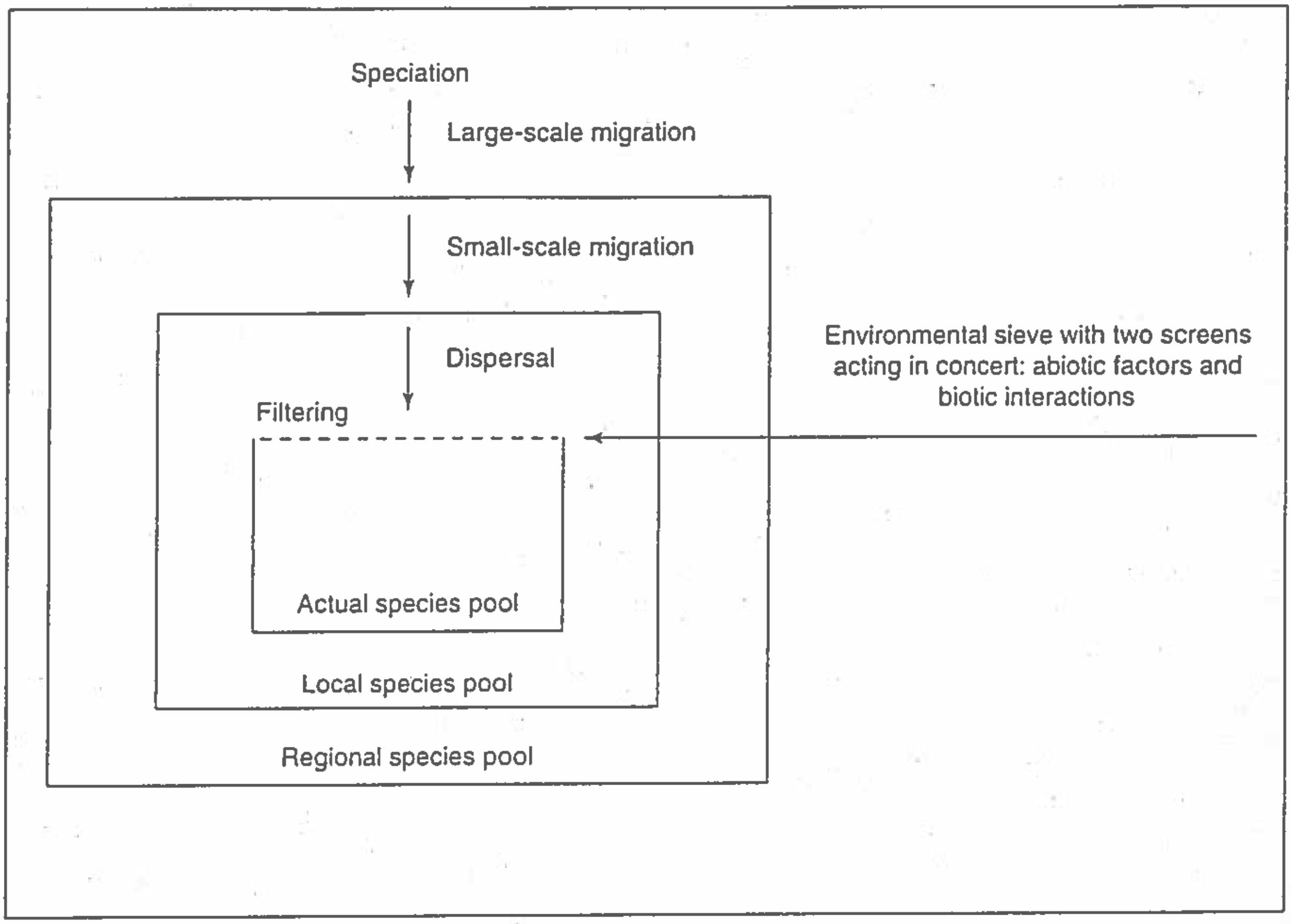

Figure 2. The role of large- and small-scale processes in determining species richness. After Zobel 1997.

and nutrients is essential; but more relevant than the total amount of resources is perhaps *a predictable and balanced supply*. In fact, favourability is direct proportional to the probability that an average plant will complete its life cycle. Major differences as regards demands exist between plants with different strategies and life forms. The demand of trees is obviously different from herbs, and bryophytes and lichens have yet other. The phrase "over time" refers to different time scales, viz evolutionary time, historical time and ecological time (Zobel 1992).

No upper limit to plant diversity

Whittaker (1972) gives a thorough discussion of diversity, and also specifically discusses environmental *favourableness* as a general predictor of diversity. Reviewing existing studies of relationships between diversity and *productivity*, Whittaker (1972: 235) concludes that: *"It is likely that, over a broad range of environments, these two dimensions are non-correlated."* Whittaker points to the importance of temperature differences along the latitudinal gradient and to the importance of time-scales relevant for historical as well as evolutionary processes. I find the following statement (Whittaker 1972: 241-242) intriguing for the study of plant species diversity: *"The time scale for this question* [α-diversity of plants] *is different from that of the steady states studied for island faunas (MacArthur & Wilson 1967, Wilson 1969)..... There are limits to the extent to which passerine birds can divide their hyperspace.....No such limitation is apparent for vascular plants, evolution of which has featured chemical coadaptation ..... and elaboration of niche difference through more narrowly specific relationships with consumers, symbionts and pollinators."* This view is supported by the work of Levin (1970) indicating, that the niche-hyperspace relevant for niche-differentiation, rather than being composed by essential resources, is composed by gradients in limiting factors, which may be both limiting resources and biotic controls such as predators or parasites.

Taylor et al. (1990) stresses the importance of the species pool as determinant of species diversity: *"....the species pool hypothesis predicts that the decrease in species density with increasing habitat fertility level in temperate regions discussed by Grime (1979, 1988a), is a consequence not of a general decrease in the intensity of competition, but of a general decrease in the size of the pool of species that are suited or adapted to increasingly specialized (i.e. more fertile) habitat conditions."*

According to Taylor et al. (1990) the number of species capable of growing in a certain place is determined primarily by the extension in time and space of a relevant ecosystem. It is argued that the Sonoran desert of North America and the Amazon rainforest are both species rich, despite high and low productivity respectively.

Fertility and diversity

The humped back model of species density in herbaceous vegetation (Grime 1973, Al-Mufti et al. 1977) predicts that maximum density is observed at intermediate weights of standing crop + litter. The biological interpretation of this relationship given in Grime (1979:p.182-186) acknowledges the impact of species pools as well as ecological interactions between vascular plants and their abiotic and biotic environment (fig. 3).

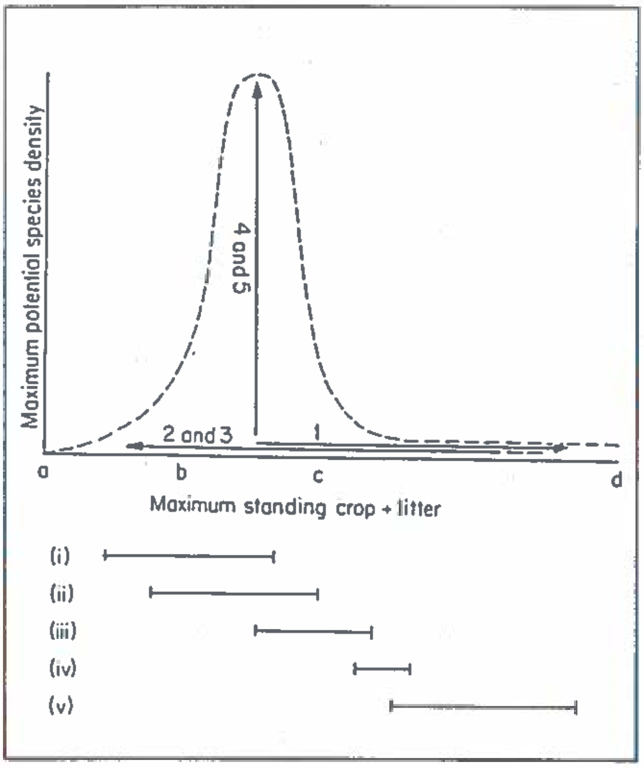

Figure 3. Model summarising the impact of five processes upon the species density in vegetation. Key to processes: 1, Dominance; 2, stress; 3, disturbance; 4, niche-differentiation; 5, ingres of suitable species or genotypes. The horizontal line describes the range of contingencies encompassed by a number of familiar herbaceous and woody vegetation types. Key to vegetation types: (i) paths, (ii) grazed rock outcrops with discontinuous soil cover, (iii) infertile pastures, (iv) fertilised pastures, (v) derelict fertile pastures. After Grime (1979: 182).

Grime (1979) also considers why the British species pool of calcareous grassland is larger than that of calcifugous grassland, and suggests that calcicoles have evolved mainly at low altitudes, where low precipitation and high temperatures promote base-rich soils. Grime further suggests that the climatic fluctuations of the semiarid grassland ecosystem produces vegetation disturbance and environmental heterogeneity, which is assumed to be conducive to speciation. An important, and somewhat overlooked, observation of Grime (1979: p.165) is that communities in the intermediate range of gradients also draw from a comparatively large pool of species, simply because they share some of the characteristics of all the more extreme environments.

The results presented in [1] indicate that species diversity is not a trivial issue. Although the diversity of vascular plants was found to be clearly related to three major ecoclines [1], the interpretation was not straight forward, admitting an influence of both evolutionary, historical and ecological processes. At one important point, the results disagree with the species pool hypothesis. A majority of the studied grassland species have Ellenberg values for nitrogen of 2 (-3). Nevertheless, the highest species density recorded along the fertility ecocline (DCA-2), correspond to a calibrated Ellenberg environment indication above 4 [unpublished calculation]. The difference appears small, but it should be remembered that we are dealing with a natural productivity gradient within relatively infertile grasslands, and that the weighted averaging used to calculate environment calibrations will tend to shorten the range of calibrated environment values compared to the range of species values. In practice, the results imply that in the most diverse grasslands, species with a relatively high nitrogen value (6-8) coexist with species indicative of infertile grasslands (2-3), and this is consistent with the model of Grime (1979).

Species pool hypothesis revisited

The species pool hypothesis is still relevant for the interpretation of the observed patterns along axis 1 and 4 [1], where diversity responses are identical with the species pool maxima with respect to the most influential gradient along the axes. Despite this coincidence, the species pool hypothesis as stated by Taylor et al. (1990) appears premature, and many questions are left unanswered. If their interpretation is correct, then an ecosystem reminding of the calcareous grasslands of NW Europe must have been more widespread than any other types reminiscent of present days plant communities. I am willing to accept that base-rich soils have predominated in the presumably drier and warmer low altitudes where speciation has taken place. But why is it, that the highest species density in today's Danish landscape is recorded in relatively fertile grasslands [1] that, when subjected to dereliction, turns into relatively species poor grasslands dominated by grasses and forbs of large stature, e.g. *Dactylis glomerata, Festuca arundinacea, Bromus erecta, Centaurea scabiosa, Lathyrus pratensis*. It is not evident that ungrazed vegetation should have been less common than grazed vegetation in evolutionary time. It is also not clear why the pool of species adapted to forested habitats is considerably smaller than that of grasslands. A tempting explanation would be that the grassland species pool draw from the steppe species pool, and that the steppe ecosystem has had a much larger distribution over time than temperate forests. Against this explanation speaks, that the vast majority of temperate grassland species in Denmark are not readily characterised as steppe species [1: fig. 7]. On the contrary, most Danish grassland plants prefer an oceanic to sub-oceanic climate. The same is true for the macromycetes, where real steppe taxa, e.g. in the genera *Geastrum, Mycenastrum, Tulostoma, Marasmius* and *Marasmiellus* are rare compared to ubiquitous genera such as *Galerina, Conocybe, Hygrocybe, Entoloma, Agaricus, Mycena* and *Clitocybe* (Bruun & Ejrnæs 1993).

The origin of species

Darwin (1859) described and interpreted the distribution of finches on the Galapagos islands. He observed that the unique species found on these islands were closely related to species of the American continent, and took this as an argument in favour of dispersal and subsequent speciation, as opposed to that times prevailing belief in the Creation. The speciation that had taken place on the island was interpreted as the result of the daily fight for survival, and the survival of the fittest (natural selection). Darwin also wondered why different, yet closely related, bird species occupied different islands, when the islands were situated relatively close to each other. Darwin's interpretation was that interspecific interactions prevented the establishment of new species on an island following chance immigrations - given that the island was already occupied by a bird with a similar niche.

Darwin's notion of the role of competitive interactions has implications for the process of speciation also. The development of different species with similar niches would probably not have occurred, in the case of one large island as opposed to many small. Or, in other words, *strong interspecific competition* can also act as a barrier to speciation, although the elimination of less well fit species is part of evolution. I would hypothesise, that also *intraspecific competition* could act as a barrier. I find it unlikely, that major genetic changes will produce perfectly adapted daughter species at once. Rather, it should be imagined, that a balanced adaptation taking into account the trade-offs imposed by a new morphology would demand both time and resources.

Punctuated equilibria

In favour of this view on speciation stands the palaeontological documentation of long periods of *stasis* followed by *abrupt appearance* of new life forms in the fossil record of evolution (Eldrege & Gould 1972). This pattern led Eldredge & Gould (1972) to deduce their theory of *punctuated equilibria*, saying that speciation occurs relatively fast, in small isolated populations, as opposed to the Darwinian belief in *phyletic gradualism* stressing the importance of the slow accumulation of very small adaptive changes over time, governed by natural selection. The theory of punctuated equilibria does not exclude natural selection as an important factor determining which species will survive in a common area, but hypothesise that the driving mechanism behind speciation must be sought elsewhere (Gould & Eldredge 1977). If the rate of speciation depends on the landscape, the population genetics, and the accessibility of unoccupied niches, then evolutionary time can not readily be quantified in absolute units. One must imagine that under favourable conditions the evolution of a species should be counted in thousands, not millions, of years, and also that this event could not have happened under a different set of conditions, no matter the time provided.

Species pools and chance

One of Gould's (1989) favourite issues is the importance of stochasticity in the history of life. Gould (1989) points to the regular occurrence of mass extinctions in the history of the earth. He mentions one of the most extensive mass extinctions occurring between the Permian and Triassic geological periods some 225 million years ago. This extinction wiped out 52 % of all families, which has been estimated to correspond to between 80 and 96 % of all species. The lucky survivors constituted the material for subsequent evolution, and in fact no new phyla and only few new classes have evolved since then.

This perspective is however much influenced by the intensively studied animal fossil record, and recent palaebotanical studies have cast doubt on the impact of the hypothesised global catastrophes on plants (Willis & Bennett 1995).

Moderate fertility is favourable

From this point I will reconsider my hypothesis, discussing its relevance on ecological, historical and evolutionary time scales respectively. There is much evidence in favour of a unimodal response of species diversity to productivity gradients (Grime 1973 & 1979, Moore & Keddy 1989, Grime 1997). The interpretation of this pattern is not agreed on, however (Grime 1979, Taylor et al. 1990, Campbell et al. 1991, Oksanen 1996). The biological reasoning embodied in plant strategy theory (Grime 1979) is coherent, and much to prefer for Oksanens "no-interaction model" (Oksanen 1996). Oksanen explains the pattern by stating that in stressed environments species density is small because plants are small and scattered, and under fertile conditions, the reason for low species density is that plant density is small due to the large plant size. But, Oksanen forgot to consider *why* the size and density of plants vary along gradients in fertility, and later studies have showed that the humped back relationship is not a sampling artefact (Rapson et al 1997, Zobel & Liira 1997).

I interpret the unimodal species response much the same way as Grime (1979), and find it to be compatible with my hypothesis: on an ecological time scale the most favourable environment is found under intermediate levels of stress. Here, neither chronic nutrient deficiency nor depletion of light and nutrient by competitors is of major importance to plants.

Inter-trophic interactions

Also interactions with other trophic levels should be considered. The importance of vertebrate grazing for diversity has long been acknowledged (Tansley & Adamson 1925), and now experimental evidence has been presented in favour of a unimodal response of the intensity of invertebrate herbivory to a primary productivity gradient (Frazer in press, Frazer & Grime in press), herbivory being constrained by resource shortage and predators at either end of the gradient.

Experiments have shown that grazing and arbuscular mycorrhiza (AM) may promote α-diversity (Grime et al. 1987) probably by reducing the intensity of interspecific interactions (Grime 1979, Moora & Zobel 1996), but this is only part of the story. The very interesting experiment of Moora & Zobel (1996) suggest that AM might both reduce suppression of small plants by a different neighbour species and amplify intraspecific competitive suppression. It is tempting to see the two processes demonstrated by Moora & Zobel from the fungus perspective: investing in small actively growing plants will pay off as a future supply of carbohydrates to the fungus, especially if it is a "new" species: contact to species with differing plant phenologies could secure a safe and continuous carbon supply to the fungus. Whatever the mechanisms behind, Moora & Zobel's experiment suggest a potential AM mediated promotion of micro-scale diversity by a weakening of interspecific relative to intraspecific interactions. Such an environment will appear favourable from a plants point of view, as establishment probability is enhanced by continuously vacant microhabitats with facilitated access to resources. The contradictory experimental evidence regarding the impact of AM on diversity reported in the review of (Zobel et al. 1997) may be due to differences in experimental set up. We know from field observations that mycorrhizal grassland communities can differ considerably in species diversity, and should therefore not expect an unambiguously positive effect of AM. It seems likely that the significance of AM will depend largely on the environmental and physiological context, i.e. on the species composition and population structure of the AM fungal community, the selection of plant species and their physiological condition and life history stages, as well as the abiotic and biotic soil environment. A recent support for this view can be found in Streitwolf-Engel et al (1997).

Migration and extinction

On a historical time scale, say following last ice age, the most important process of relevance to diversity in Danish grassland vegetation is immigration of grassland species from their refuges, and the local or national extinction of species, once arrived. Although these processes have taken place repeatedly in the course of glacials and interglacials, I will concentrate on the present interglacial, and present evidence for the hypothesis that calcareous soils have been favourable for grassland plants, and that this circumstance may have resulted in comparatively large grassland species pools in areas of abundant limestone soils.

Table 1. Open land species that have been found as macrofossils, pollen or spores in remains from late glacial to Atlantic. Species present in the current Danish flora are listed in the top and extinct species in the bottom. From Bruun & Ejrnæs (in press)..

Flora of the prehistoric open landscape of Denmark

Allium schoenoprasum
Anthyllis vulneraria
Armeria maritima
Artemisia sp.
Astragalus sp.
Botrychium lunaria
Botrychium multifidum
Calluna vulgaris
Campanula sp.
Carex sp.
Centaurea scabiosa
Diphasiastrum complanatum
Filipendula sp.
Galium sp.
Gentiana amarella
Gentiana campestris
Geranium sp.
Helianthemum sp.
Hypericum sp.
Jasione montana
Liguliflorae-type
    (Hieracium, Leontodon,
    Taraxacum)
Lotus corniculatus
Lychnis sp.
Lycopodium clavatum
Onobrychis viciifolia
Origanum vulgare
Plantago lanceolata
Plantago maritima
Plantago media
Poaceae
Potentilla erecta
Primula veris
Ranunculus sp.
Rumex acetosa
Rumex acetosella
Sanguisorba sp.
Saussurea/Carlina
Sedum sp.
Stellaria graminea
Succisa pratensis
Thalictrum sp.

Astragalus alpinus
Astragalus frigidus
Dryas octopetala
Gypsophila fastigiata
Helianthemum oelandicum
Meum athamanticum
Oxyria digyna
Pleurospermum austriacum
Polygonum viviparum
Saxifraga oppositifolia
Silene acaulis

Table 1 lists those species found as macrofossils, pollen or spores in deposits from late glacial to late atlantic, that can be interpreted as grassland taxa. The list is by no means a complete list of the postglacial flora, but it gives an impression. The flora of the open treeless landscape from 11.000-8.000 BC was apparently a mixture of typical grassland species, species belonging to present days alpine and subarctic vegetation in N Scandinavia, Scotland, the Alps and the Carpathians, as well as steppe species with a pronounced continental distribution (Bruun & Ejrnæs in press).

From preboreal to atlantic time, immigration of trees gradually changed the open steppe-tundra into a forested landscape - first a light forest composed of *Betula* and *Pinus*, then also *Corylus* and finally *Quercus*, *Tilia* and *Fraxinus*. In this period, grassland species must have retreated to refuges, where conditions have been hostile to trees. We do not know how many species survived this period and how many species became extinct, and reimmigrated following the accelerating landnam about 4000 BC. The presence of a grassland element is not easily discovered in pollen analyses (Bruun & Ejrnæs in press), but a continuous open land vegetation has been recorded from W Jutland (Odgaard 1994), Blekinge (Berglund 1966) and Britain (Bush 1993). The findings of Bush (1993) also support a hypothesis of active forest clearing (e.g. through ring-barking) by mesolithic humans, the motivation for which is proposed to have been the conversion of forest to rough pasture attractive for game animals and edible plants.

Grassland refuges

The presence of refuges for grassland plants during Boreal and Atlantic in NW Europe has been hypothesised by several authors (Sterner 1922, Böcher et al. 1946, Iversen 1954 and Pigott & Walters 1954). Sterner (1922) summarised the general hypothesis developed from phytogeographical observations, stating that the xerophilous and heliophilous herbaceous flora in a landscape untouched by humans, should be looked for on steep southerly exposed slopes or precipices (especially with calcareous soil), sandy soils in areas of low precipitation, and rocky escarpments. Figure 4 shows the density in Denmark of a group of species hypothesised to be late glacial relicts judged from their present discontinuous distribution. The

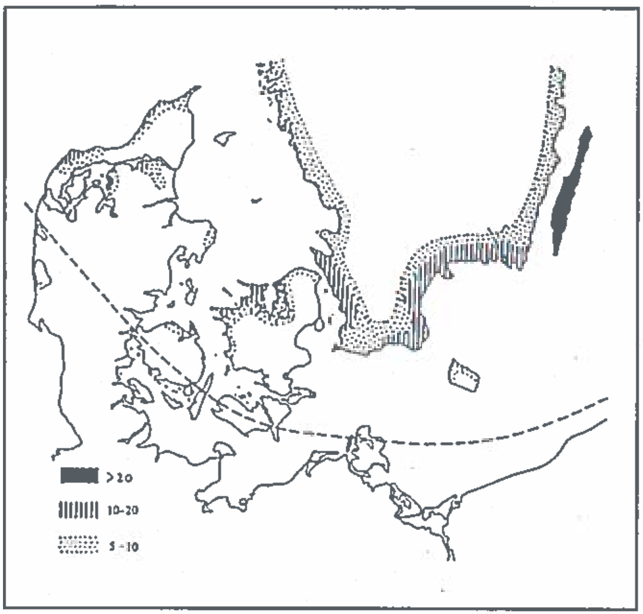

Figure 4. Refuges for late-glacial plants in Denmark and South Sweden. Density of a group of species hypothesised as late-glacial relicts by Iversen (1954, 1957) and Böcher et al. (1946). North of the broken line a land uplift has exposed slopes and marine deposits formed by the Littorina and Yoldia sea.

highest density of relicts are clearly found in landscapes with abundant calcareous soils and/or dry climate and in coastal areas influenced by erosion and land uplift. The explanation behind this pattern is not only that these conditions suit the grassland plants well, but as much that they are hostile to establishment and growth of trees (Sterner 1922, Böcher et al. 1946). Consistent with my hypothesis is the finding of extraordinarily high species diversity in Estonian alvar grasslands (Kull & Zobel 1991). Here, abundant shallow limestone soils and a rising seashore have maintained an open landscape with sparse tree cover, and the geographic position, on the continent, has been favourable, in comparison with Denmark and Sweden, for immigration processes from refuges in southern and eastern Europe. Supportive is also the observation that the distribution of calcicoles is not so limited by pH in drier climates (Etherington 1975: 268). A small scale version of this aspect can be observed in Denmark where several predominantly calciphilous vascular plant and bryophyte species show a markedly wide pH-amplitude in the precipitation poor Great Belt region, e.g. *Scabiosa columbaria, Helianthemum nummularium, Carlina vulgaris, Avenula pratensis, Filipendula vulgaris* and *Camptothecium lutescens.*

Mobile temperate grasslands

The evolutionary aspects of my hypothesis have already been discussed above. To recapture, favourability on an evolutionary time scale must include extension of the ecosystem in space and time and availability of empty niches. The numerous endemics occurring on even small islands or mountains indicate that extension of an ecosystem in time is of far greater importance than extension in space, and it even seems likely that the fragmentation of a community could be conducive to speciation. Populations in fragmented biotopes will more easily be subjected to genetic drift, and the absence, in isolated places, of many species from the regional species pool means more vacant niches.

I hypothesise that the null community (where speciation has taken place) of the temperate semi-natural grassland of north-western Europe has existed mainly in a dry temperate climate, with glacial refuges south of the Alps and in transition zones of sparse forest cover towards the steppe. Relict populations of all temperate woody taxa except *Sorbus* and *Salix* have been demonstrated to occur as relicts in southern Europe by Bennet et al. (1991), who suggest that the species survived the very dry conditions under full glacial in montane ravines. Grassland plants, being generally more tolerant of drought, might well have survived there too. It is likely that ice movements, fluctuating climate and forests contributed to fragmentation of the evolutionary environment of grassland species, and that this has been conducive rather than restrictive to speciation. Whittaker (1972) proposed that interaction with other trophic levels was a key to the understanding of the outstanding diversity encountered in tropical rainforest. Following his argumentation, I suggest that niche availability, and hence speciation, is promoted by herbivory, arbuscular mycorrhiza and probably also other endophytic fungi, and that these factors work very differently in the forest, heathland and grassland ecosystem.

What is considered a favourable environment will obviously depend on the relevant organisms, and until now I have focused almost exclusively on herbaceous vascular plants. In a study on grassland cryptogams [4], no correlation was found between cryptogam and phanerogam diversity, and not surprisingly so: grazed grassland on calcareous clay, for instance, is inferior compared to infertile sand grasslands from a *Cladonia* point of view.

Much is to be gained from a widening of the perspective to include processes on different scales (Zobel 1997), but no important insights will come from a conflict or rivalry between local scale explanations and explanations focusing on the size of the species pool (e.g. Taylor et al. 1990). It should rather be kept in mind, that the study of the expression of living organisms in a living environment remains an indispensable key to the understanding of processes working on historical and evolutionary time scales.

3.2 Survey and experiment

Hypotheses are meant to be subjected to tests aiming to reach a falsification or, what is usually harder to achieve, a verification. Two short suggestions will be made of tests of the ideas and hypotheses presented above. The first deals with a survey, relating to the first hypothesis, designed to validate a landscape scale implementation of the ecocline models in [1]. The second treats the design of an experiment aiming to test my second and third hypothesis.

Landscape scale validation

The first hypothesis calls for a carefully planned survey of open land biotopes in connection with the development of model predictions of potential land cover. A validation must have two objectives: 1) Are the model predictions reliable and 2) Is the readily available environmental information sufficiently accurate. The planning and implementation should involve the following steps:

1 One or more areas are selected, including a range of semi-natural biotopes along gradients in soil types and topography.
2. A modelled map of herbaceous plant communities on well drained soils is created within the study area on the basis of existing databases and small scale models [1] [5].
3. A survey is carried out, including sampling of vegetation, soil type, pH, estimation of water availability and investigation of land use history.
4. Model predictions are compared to vegetation types and the database information is compared to environmental measurements.

The scale chosen for sampling and prediction is crucial for the outcome of the validation of the model. A sampling unit of 10 m^2 was used in [1], but for a landscape model to be operational, larger scales are needed. A sampling scheme must also take into account that some plant communities occupy large areas whereas others are small and fragmented. Linear biotopes such as road verges, field margins, streams etc. constitute a particular challenge to sampling.

Two criteria must be met for a successful validation of the model. First the predictions of the semi-natural plant communities must be sufficiently correct, next, important biotopes should only as an exception escape the mapping process. Therefore sampling is proposed to be carried out in two tempi. First, a survey of the biotopes recognised by the modelled map should be carried out by systematic sampling within each area. Subsequently, a stratified systematic sampling of relevant unrecognised plant communities is carried out in both unmapped and mapped parts of the landscape.

The sampling method is suggested to be a modified version of Raunkiær's frequency in subplots method [1]. Assuming that most areas will be large, a subplot area of 1 m^2 is suggested, with nested circles of 0.1 m^2 and 0.001 m^2 (Böcher & Weiss Bentzon 1958). The small circles comprises a very small effort, yet result in useful estimates of shoot density. The more heterogeneous the mapped units are, the more subplots will be needed - between 10 and 25 in each biotope is believed to be sufficient. The survey will not only serve the purpose of model validation, but also be among the first landscape scale quantifications of the impact of modern agriculture on vegetation.

Synthetic succession

The objectives for the experiment outlined below is to test the second and third hypotheses presented above. The experimental concept is suggested to be a synthetic multi-species succession in replicated microcosms in an outdoor situation with experimental control over growth medium, seed rain and vegetation manipulations. The experiment will conform to a standard factorial design. Treatments are selected to represent a realistic variation with respect to features of the landscape and the environment. The species pool aspect is represented in a selection of species with reference to available autecological information. Four pairs of treatments are suggested:

A) An organic acidic soil in a humid micro-climate vs. a calcareous, mineral soil in a drier micro-climate.
B) High vs. low nutrient availability.
C) Uncut vs. repeatedly cut.
D) Sequence of species corresponding to their abundance in the cultural landscape (road verges, field margins, set asides, etc.) vs. semi-natural grassland vegetation.

The environment is represented by the treatments from A to C corresponding to the most important local scale ecoclines found in Danish grassland along DCA-axes 1, 2 and 4 [1]. Treatment D represents the landscape factor. For each of the 8 different combinations of treatment A to C, an appropriate species pool will be defined, and four to five species will be drawn from this pool. All 32-40 species will then be pooled and assigned abundance values corresponding to *the cultural landscape* and the *semi-natural grasslands* respectively. Based on these values, two contrasting sequences of species will be determined and applied to the pots as seeds or seedlings over a period of 2-3 years, with due regard to the species specific regeneration phenologies (spring vs. autumn germination)

This is the outline of the experiment. There is, however, both practical and theoretical complications related to its implementation. As seen from the cubic shape of the ecoplane of DCA1-2, variation along each of the two axes occur mainly in the middle range of the other axis. The consequence is, that an environment cannot express the extremes of axis one and two simultaneously. It is therefore suggested to restrict the difference between the treatments in A), so that a fertility gradient B) is within reach. This implies that strong acidity and severe drought should be avoided. In practice, treatment A) could involve the addition of sphagnum and lime respectively to a non-calcareous soil aiming at pH-values of 4.5 and 7 respectively. The climatic difference could be achieved by the placement of pots on either side of a 1-2 m high wall running south-west to north-east. Watering of the pots should aim at eliminating episodes of severe drought.

There are other practical challenges:

1. Germination under semi-field condition is a game of chance, and as the number of species from different species pools and their sequence of establishment is crucial for the outcome, it would be advantageous to germinate seedlings under controlled conditions of light and temperature and introduce them to the pots as seedlings. The prize for improved security, i.e. the loss of an opportunity to study treatment effects on germination, seems to be worth paying.
2. The importance of vertical light gradients in natural vegetation has long been acknowledged, and it is considered crucial to simulate this phenomenon in the pots also, e.g. by inserting a shading, and vertically adjustable cylinder in the pot periphery. This remedy will exclude the somewhat artificial possibility of plants escaping competition and cutting by growing horizontally out of the pots (pers. obs. Sheffield 1996).
3. Established plants will set seed. Regeneration within the pot should be allowed, but dispersal between pots should be minimised, in order to exclude differences due to the spatial arrangement of pots.
4. Other organisms are known to interact with plants - notably arbuscular mycorrhiza (AM), saprotrophic micro-organisms, bryophytes and soil invertebrates. Stable populations of the latter can not be sustained in the pots, whereas micro-organisms (including AM) and bryophytes should be included as a standard inoculum, in order to simulate the biological processes in a succession realistically.
5. Herbivores, including snails and slugs, should be excluded, using fences and possibly also pesticide application on pot surfaces.
6. Pot size should be kept at a minimum, yet be large enough to sustain even fast growing C-strategists. A surface area slightly above 0.1 m2 (allowing for comparison with vegetation sampled by Raunkiær's method), and a depth of 30 cm is considered to be suitable.
7. In order to estimate the stochastic within treatment variation, a reasonable replication is necessary - say 10-12 replicates per treatment, resulting in a 160-192 pot experiment.

The course of the experiment should be followed by replicated, non-destructive methods. Preferably the following parameters should be recorded twice a year, once in spring and once in autumn:

1. The spatial distribution of species in the pots (shoot number counted on a grid basis and categorised as seedlings or established plants).
2. The average size (height) of species.
3. The estimated cover (on a grid basis).
4. Vertical light gradients in the pots.
5. Nutrient depletion at the time of seedling establishment.

6. Mycorrhizal activity (e.g. bioassay using rate of seedling infection in target seedlings of an alien species harvested after a couple of weeks).
7. Seed set.

The overall null hypothesis of the experiment would be, that no differences in vegetation composition and structure could be detected between the treatments. The more intriguing alternative hypotheses that should be investigated can be summarised as:

H_1: The species composition is identical to the species pool corresponding to a particular treatment.

H_2: The vegetation is determined by the sequence of species arrivals.

H_3: Intensity of competition (depletion of light and nutrients) will vary with the environment treatments and determine the number of species capable of coexisting.

H_4: Intensity of competition interact with sequence of arrival.

H_5: The within treatment variability will be large compared to the between treatment variability.

H_6: The survival probability will increase with increasing mycorrhizal activity.

4. Nature quality

Environmental management aiming at a general protection of wildlife beyond the narrow scope of conserving rare species threatened with extinction, is a relatively new discipline. It has, however, been going on for decades (Duffey & Watt 1971), and in 1992 the Danish government passed on a legislation including a general protection of semi-natural communities such as dry grassland (Anon. 1992). However, the definition of these communities and the objectives for the management has not yet been stated clearly, and managers frequently face dilemmas regarding e.g. invasion of open areas by woody plants.

I will attempt to set up biological criteria for a well thought out nature management in Denmark, hence the title *nature quality*. I will focus on examples from grasslands and related ecosystems, but it is my ambition to suggest generally applicable principles. Nature quality is not yet an approved term of the English language (but see Klijn 1994), but related terms emphasising the quest for an assessment of values have been used extensively, e.g. *nature conservation*, *conservation value* and *habitat quality* (e.g. Margules & Usher 1981, Van Horne 1983, Rossi & Kuitunen 1996). However, neither of the commonly used terms describe the phenomenon approached here adequately: the term *conservation* appears inappropriate, Denmark being a small country where relatively few organisms and ecosystems can be regarded as threatened on a wider geographical scale (Stolze in press). In the previous chapter I emphasised the importance of species pools and the landscape, and seen in that perspective, the term *habitat* is too narrow. In fact habitat, in its original sense, refers to the abiotic environment of a specific species, and not to a multispecies community (Whittaker 1972).

Diversity and rarity

The general goal for nature protection and management in Denmark relates to the management of localities and landscapes in a sustainable way, giving priority to semi-natural communities and values related to landscape aesthetics, public recreation, scientific and educational interests (Anon. 1992). Further objectives are the promotion of public access and the reversion of arable land to valuable semi-natural communities. I will only discuss biological criteria, excluding predominantly recreational and aesthetic interests, although an agreement between these different interests seems within reach in most situations. I will take as a starting point for this treatment not only the text of the legislation (Anon. 1992), but also the motivation behind those of the paragraphs dealing particularly with the protection of wild plants and animals. Unfortunately, the motivation is not stated very clearly in the comments to the legislation, but I nevertheless dare to deduce the following underlying notions:

1. *Nature management can lead to benefits to the society, most notably of recreational, educational and scientific character.*

2. *Other organisms have a right to exist.*

Margules & Usher (1981) reviewed the criteria for the assessment of conservation values used in the literature and emphasised five criteria mentioned in more than half of the papers: *diversity, rarity, naturalness, area* and *threat of human interference*. They stressed the difficulties related to combining different, partly overlapping criteria in one common assessment, and pointed to the need for a quantitative approach.

Diversity and rarity have the advantages of being relatively easy to assess and handle, and I suspect that is the reason why red data books and biodiversity assessments have been so much in focus (Asbirk & Søgaard 1991, From & Söderman 1997). However, in the context of nature quality, rarity and diversity are no more than quantifiable properties of species and communities, that commonly but certainly not always, correlate with the intensity of human interference with ecosystems, and they are therefore less appropriate as general objectives for nature management. I will consequently leave rarity and diversity here, although I do acknowledge the significance of rarity as a criterion in the field of conservation.

Humans - in or out?

Naturalness embraces the meaning of nature quality, namely the absence of a disturbing human interference. But, naturalness is also a very vague and imprecise term, that needs careful definition. Attempts to produce definitions often invoke paradoxes, and the most conspicuous paradox in the context of *naturalness* is the ambivalence of humans towards nature.

An antagonistic relationship between humans and their environment date back to the ancient fight for survival against an environment where natural forces (cold winters, wind erosion, scrub encroachment, herbivore attacks, diseases etc.) were considered predominantly negative. Today, the conflict is less pronounced: a notion of affinity with nature has gradually taken over, and we recognise that the natural resources of the earth have been overexploited by humans for centuries, leading to an impoverishment of the environment as well as flora, funga and fauna. The emerging holistic view of humans as an integrated part of nature, is not readily consistent with the objective to restrict human activities in order to improve nature quality. I see, on the other hand, neither ecological nor obvious philosophical (Fink 1995) arguments for a separation of humans and nature.

As a consequence of these considerations, I will prefer to substitute *naturalness*, that tends to exclude humans from nature, with a term that emphasises the degree of human interference with the environment instead.

Wildness

I see two alternatives to naturalness, namely *undisturbedness* and *wildness*. *Undisturbedness* is commonly used among conservationists, but unfortunately it creates unwanted associations of virgin environments, and I therefore prefer to use *wildness*. My definition of wildness sounds:

Wildness is the extent to which a species or habitat is unaffected by historic humans. Wildness can be assessed in two dimensions. The first dimension relates to the intensity and extent of direct and indirect human interference, and the latter relates to the time a habitat or species has been left without direct interference.

First it should be stated, that although I mention both species and communities, it lies implicit in the statement, that a biotope containing several wild species is of greater importance than a single wild species. There is however wild species, especially animals, which habitat requirements always exceed the area range of semi-natural biotopes, and such species obviously deserve special attention. The positive value of habitat size, as mentioned by Margules & Usher (1981), can also be deduced from the definition above: the intensity of indirect human interference, such as the constrained exchange of species with the surrounding landscape, will decrease with the size of the habitat.

Why only involve historic humans? It is crucial to the applicability of the above definition to decide under which circumstances the interference of humans is to be considered as negative. This problem was also recognised by Margules & Usher (1981), and they defined a natural ecosystem as one in which humans, if present, are totally dependent upon and limited by their environment. Such natural human beings are not encountered in Denmark in historic time, although a high degree of self-sufficiency was a matter of life or death for many people a few centuries ago. Consequently, I will advocate in favour of measuring the intensity of human interference rather than classifying human activities as being acceptable or not.

Unaffectedness and *time* (following the relaxation of human interference) are both included in my definition of wildness. The *intensity* of interference is however considered more important than the *recovery time*, so a severely affected habitat will always be less wild than a moderately affected habitat. I consciously distinguish between direct and indirect human interference. Direct interference involves the area specifically, whereas indirect interference involves the surroundings and thereby the exchange of biota with these, and potentially also the local climate. Indirect interference is generally less severe than direct interference from the point of view of a specific area, but policy makers ought to be very concerned about the constraints imposed on valuable areas by an impoverished and rapidly changing landscape.

Effect assessment

An assessment of the intensity of human interference must also take into account the reversibility of the change brought about. Ceased breeding of a highly mobile bird due to intensive forestry should be considered less severe than the destruction of the last habitat of a low mobile ground beetle. The same considerations apply to plant communities, although the lack of knowledge regarding the reversibility of ecological processes constrain the feasibility of such evaluations.

An important decision is whether the aim is to record and quantify human interference directly, or alternatively to assess its *effect* on the ecosystem. Exact history of land use is difficult or impossible to document. The management by private land owners of permanent grassland and woodlands is poorly documented, and the memory of the land owner is only valid, in an ideal situation, one life time back. Even more decisive is that scenarios can easily be suggested where differing biotopes would react very differently to the same land use. Suppose that two contrasting grasslands, on dry sandy soils and moist calcareous clay respectively, were subjected to three years of intensive fertiliser treatment. On the moist calcareous clay, the additional nutrients would be used by potential fast-growers like *Lolium perenne, Festuca arundinacea* and *Dactylis glomerata* leading to competitive exclusion of smaller plants. Nutrients would either enter active cycles or be retained due to the large CEC of the soil. On dry sand, the limiting factor for growth would be water availability, and few or none of the species in the community would be potential fast-growers. The soil would not (unless rich in humus) retain the nutrients, and leaching would tend to re-establish the conditions in the community prior to fertiliser application. It should be stressed, that leaching does not imply that the human interference has disappeared (the nutrients probably went to the ground water or a nearby fresh water recipient), but merely that the sandy grassland in focus is less affected.

Once accepting that the severity of a certain antropogenic land use will depend upon the properties of the abiotic and biotic environment, the advantage of a quantification of *effect* rather than *action* becomes obvious. The practical challenge of an "effect-assessment" of nature quality lies in the absence of reference ecosystems without human interference, to which present day communities can be compared. First it should be noted, that there is nearly always more than one possible reference community corresponding to a particular set of abiotic conditions. The reference statement of relevance for grassland could be:

Temperate grassland, dune and heathland have had a limited distribution in the landscape due to a humid climate favouring the forest ecosystem. Prerequisites for the occurrence of open land communities are therefore conditions hostile to growth of woody plants, summarised as 1) grazing, 2) erosion, 3) drought, 4) shallow soils, 5) calcareous soils, 6) land uplift. A potentially important role is also hypothesised for open areas within forests created by wind falls, fires or prehistoric humans.

This definition has both habitat and landscape implications. One of the conditions faced by the nature management is that the indirect human interference in terms of landscape changes relative to a prehistoric landscape is so massive, that ecosystems can no longer be expected to function naturally. The landscape influence is most pronounced in successional communities where colonisation is important, and in communities depending on key organisms that are no longer there.

Aurochs and horse

This is the case for temperate grasslands, where large grazers are among the essential prerequisites. In prehistoric times *aurochs, wild horse, elk, red deer, roe deer, wild boar, beaver* and *man* are all believed to have contributed to the formation and maintenance of open areas (Bruun & Ejrnæs in press). In the current Danish landscape only *roe deer* occur in high numbers. Furthermore, the abundance, movement and distribution of *roe deer, red deer* and the introduced *fallow deer* and *wild rabbit* is determined by the structure of the cultural landscape, and human activities, especially hunting (Jeppesen 1987a, 1987b, Asferg & Jeppesen 1996). Natural grasslands may once have been a preferred feeding habitat of these herbivores, but certainly no longer.

From a landscape point of view, the prehistoric Danish landscape would have been covered in forest, with only a negligible fraction of open land. Maybe only a few percent, maybe as much as 10 percent was kept open by waterlogging, erosion, fire, forest dynamics, wild animals (especially herbivores) and prehistoric humans, but the significance of a continuous open landscape element can be seen in the high number of indigenous species confined to the open plant communities of today. It has recently, in a nation wide survey, been estimated, that approximately 10 % of current terrestrial Denmark is covered by open semi-natural communities, including bogs, salt marshes, fens and dunes (cit.). The figure for communities without noticeable human interference (cultivation, fertilisation) is probably much lower. Regarding dry grasslands, Bruun & Ejrnæs (1995) found that only 30 % of the estimated area defined as protected semi-natural grassland in a particular landscape had not been cultivated before. Only 5 % were also used for livestock grazing, the remainder being. It seems reasonable to hypothesise similar figures for open land communities in a prehistoric landscape.

The relevance for the management of these considerations is obvious: the remaining grasslands of high nature quality cover a very small area, and new semi-natural grasslands are not within immediate reach: forestry aims to maintain forests as such, arable land is too perturbed and succession along newly established roads and abandoned quarries is constrained by recruitment limitation. Consequently, the loss of grasslands due to successions caused by dereliction and scarcity of wild herbivores remain a serious threat to this community type in Denmark. Grazing by domesticated animals, although being a direct interference caused by humans, could therefore also be considered a remedial action taken to avoid the negative effect of the indirect human interference imposed on biotopes by the cultural landscape. This, of course, depends on the judgement, that livestock grazing has lesser *effect* on the community than absence of grazing, compared to a prehistoric reference grassland.

Indicators of nature quality

The usefulness of wildness as the primary criterion for a nature quality assessment will not only depend on its clarity of definition, but also on its properties as a priority tool. Can we measure and quantify wildness? The approach of Kowarik (1988) studying the assessment of conservation value of woodlands is relevant to this question. Kowarik combined properties of the forest ecosystem (e.g. tree species diversity, dead wood, structure) in a weighed index to assess the extent of human interference. I suggest a similar approach for grasslands (including heathland, dunes, fens etc.) although the indicators of interference might be different.

Figure 5 shows an attempt to classify a range of open land communities according to the two dimensions of wildness. A prerequisite for this classification is the notion that dry grasslands and dunes have been a continuous part of the Danish landscape since the late glacial. Cultivation, fertilisation and dereliction has been recognised as the most important human interference with semi-natural grasslands [5]. Consequently, an index has been proposed (table 2) for long grassland continuity and absence of tilling and fertilisation (Ejrnæs & Bruun, 1995).

In the first of my three hypotheses (chapter 3), I suggest a slightly different approach, implying a model using all species, and not only selected indicators. Such a model is believed to be more informative and robust than an index of indicator species. Furthermore, given a common agreement on the reference condition of semi-natural grasslands, the human interference, and hence reduction in nature quality, can be assessed as the euclidean distance in ordination space between the actual situation and the reference situation.

Management tools

The criteria developed here do not support any kind of habitat or landscape engineering (e.g. Haggar et al. 1991) with the purpose of promoting diversity or survival of locally rare plants. Neither do they justify the deliberate seeding, planting and releases of plants and animals in the environment with the purpose of hunting or nature quality improvement. Arguments against such activities are numerous and of both biological and aesthetical nature (Ejrnæs & Mark 1997). Grazing, and any possible relaxation of the present human interference with the landscape and the biotopes, remain the most obvious tools for a management aiming to promote nature quality.

This simplification of the management objective might appear to be the first step in a phasing out of nature management, but on the contrary: a well planned livestock grazing remains an enormous task, as many semi-natural plant communities have low priority in current agricultural practices. Even more demanding is the planning of a landscape scale relaxation of human interference respecting both human and wildlife interests.

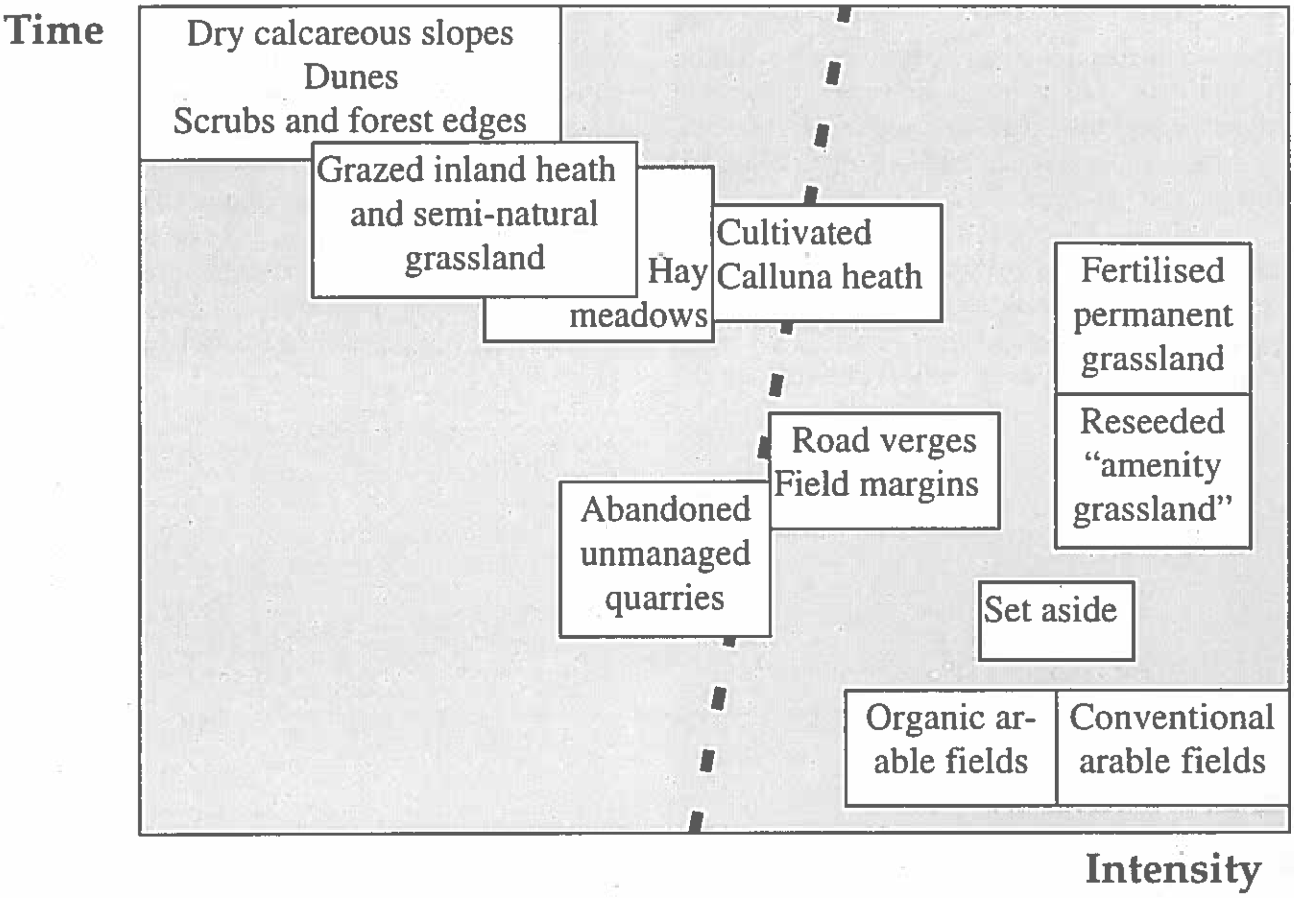

Figure 5. Time and intensity in human interference. An example showing the approximate position of different plant communities. The broken line is a tentative delimitation of areas of primary and secondary interest to the nature management. It should be acknowledged, that some of the categories occupy an array of positions, especially with respect to the time axis - for example road verges and set aside.

Table 2. Index for the identification and evaluation of semi-natural grasslands. First column contains species regarded as indicators of a high degree of human interference, and they count minus one. Second column species have been identified as typical species of semi-natural grasslands and count +1. Third and fourth column species have been identified as almost exclusive for semi-natural grasslands in Denmark and count +2. Some species are grouped, either because they often substitue each other in grasslands or owing to determination difficulties faced with vegetative or grazed plants. After Ejrnæs & Bruun 1995.

-1	+1	+2	
Poa trivialis	Calluna vulgaris	Nardus stricta	Phleum phleoides
Poa annua	Hieracium umbellatum	Anemone nemorosa	Carex pilulifera/caryophyllea/ericetorum/montana
Elymus repens	Veronica officinalis	Arnica montana	Geranium sanguineum
Lolium perenne	Carex flacca	Antennaria dioica	Helianthemum nummularium
Ranunculus repens	Centaurea jacea	Genista anglica/tinctoria	Hypochoeris maculata
Rumex obtusifolius/crispus	Festuca ovina	Potentilla erecta	Potentilla tabernamontani/collina/heptaphylla/arenaria
Cirsium arvense	Luzula campestris	Scorzonera humilis	Filipendula vulgaris
Cirsium vulgaris	Campanula rotundifolia	Vaccinium myrtillus	Pulsatilla vulgaris/pratensis
Plantago major	Dianthus deltoides	Briza media	Silene nutans
Stellaria media	Galium saxatile/sterneri	Campanula persicifolia	Lathyrus montanus
Polygonum aviculare	Lotus corniculatus	Acinos arvensis	Platanthera bifolia/clorantha
Viola arvensis/tricolor	Pimpinella saxifraga	Arabis hirsuta	Polygala vulgaris
Linaria vulgaris	Trifolium medium	Cirsium acaule	Viola hirta/canina
Chamaenerion angustifolium	Sedum acre	Linum catharticum	Succisa pratensis
	Thymus serpyllum/pulegioides	Primula veris	
		Scabiosa columbaria/canescens	
		Leontodon hispidus	
		Avenula pratensis	
		Danthonia decumbens	

There are, of course, other legitimate interests in the landscape than those outlined in this text. Some areas may be considered valuable for historical or aesthetical reasons, other owing to their optimal recreational position near urban areas.

Finally, I would like to stress, that one of the most obvious threats to the wildness of the Danish landscape is the lack of dynamics. Small and fragmented semi-natural or near natural communities is what remains of the prehistoric landscape, and in order to preserve these, the management will inevitably attempt to freeze successions. Consequently the ecotones between forest and open land will diminish and the successional transitions from grassland to forest will gradually disappear. In order to avoid this depressing perspective, the creation of one or more nature reserves large enough to sustain populations of wild grazers, should be given priority in the future.

5. Conclusion

During my PhD-study, I have been occupied with questions relating to the description and explanation of patterns in dry temperate grassland vegetation. In this thesis I have presented answers to some of these questions, other problems remain unsolved and new ideas and gaps in my knowledge have emerged. The results that I consider most important are listed below with the relevant manuscript reference given as [1]-[5].

A) The floristic variation is continuous

Despite a tradition among grassland researchers of dividing temperate grassland vegetation in mutually exclusive plant communities according to e.g. soil type (calcareous grassland, calcifugous grassland etc.), this study demonstrates that the major coenoclines are continuous [1] [2].

B) Evidence of four important ecoclines

A gradient analysis [1] reveals, that temperate grassland vegetation on well drained soil can be summarised in four ecoclines:

1. An ecosystem ecocline from dry calcareous to moist acidic grassland.
2. A fertility ecocline governed by water and nutrient availability.
3. A geographical ecocline reflecting differences among regions with respect to climate and soil types.
4. A competition ecocline determined by productivity and stability.

C) Twelve grassland types are recognised

A classification reveals 12 plant communities that, despite the absence of sharp boundaries, are well characterised in environmental and floristic terms [2].

D) Ecoclines from gradient analysis of vegetation have relevance for single species

Vegetation and single vascular plant species are shown to respond to the same gradients, justifying the gradient analysis approach to statistical modelling of plants [3].

E) Bryophytes respond to the same major gradients in temperate grassland as vascular plants [4]

F) Wildness is an important criterion for nature quality

There is a demand for models describing the vegetation dynamics on a landscape scale. But, biologists should not only provide models, but also biological criteria for their use. Wildness is defined, and suggested as the fundamental criterion for the assessment of biological values of biotopes and landscapes.

G) Gaps in my knowledge

As important as the achievements of a study is the unravelling of gaps in knowledge or inadequacy of theory. The detection of *universal* gaps demands a comprehensive knowledge of the entire field of biology, knowledge that becomes increasingly difficult to achieve, as specialisation and branching of the biological science proceeds. I will prefer, therefore, to present the gaps revealed in *my* knowledge, in the hope of course, that other researchers will find the perspective useful. Some of the gaps are treated in the previous paragraphs as hypotheses and proposals for future work, and here I will limit myself to make three points that I find relevant:

1. In the context of gradient analysis, there is a need for the development and application of practical and relatively fast field methods for assessing fertility/productivity, water availability and nutrient availability.

2. Warming (1895) prophesied the discovering of biotic mutualism in his early work on plant communities, and Whittaker (1972) pointed to the importance of biotic controls exerted on plants by members of other trofic groups. Despite this encouragement, very little is known about the interactive effect of environment, herbivores, soil biota and mycorrhiza on plant communities - and this research field remain a potential key to a better understanding of structure and processes in temperate grassland vegetation. There is an obvious need for interdisciplinary studies involving e.g. soil microbiologists, mycologists, plant pathologists, invertebrate zoologists and botanists.

3. Speciation, succession, extinction, dispersal and germination are all important processes that are likely to be influenced by stochasticity. But, how important is stochasticity, and can it be subjected to studying?

Literature

Al Mufti, M.M., Sydes, C.L., Furness, S.B., Grime, J.P. & Band, S.R. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *J. Ecol.* 65: 759-792.

Anon. 1992. Naturbeskyttelsesloven - lov nr. 9 af 3. januar 1992. Folketingsbehandling og forarbejde. Miljøministeriet, Skov- og Naturstyrelsen.

Asbirk, S. & Søgaard, 1991. Rødliste 90 - særligt beskyttelseskrævende planter og dyr i Danmark. Miljøministeriet, Skov- og Naturstyrelsen.

Asferg, T. & Jeppesen, J.L. 1996. Rådyrjagten i Danmark 1993/94. Faglig rapport fra DMU, nr. 152. Miljø- og Energiministeriet. Danmarks Miljøundersøgelser.

Austin, M.P. & Gaywood, M.J. 1994. Current problems of environmental gradients and species responses curves in relation to continuum theory. J.Veg.Sci. 5: 473-482.

Bennett, K.D., Tzedakis, P.C. & Willis, K.J. 1991. Quaternary refugia of north European trees. J. Biogeogr. 18: 103-115.

Berglund, B.E. 1966. Late-quaternary vegetation in Eastern Blekinge, South-Eastern Sweden. A pollen-analytical study II. Postglacial time. Opera Botanica 12: 1-180.

Böcher, T.W. & Weis Bentzon, M. 1958. Density determination in plant communities. *Oikos* 9:1, pp 35-56.

Böcher, T.W. 1945. Beiträge zur Pflanzengeographie und Ökologie dänischer Vegetation. 11. Über die Waldsaum- und Graskrautgesellschaften trockner und halbtrockener Böden der Insel Seeland mit besonderer Berücksichtigung der Strandabhange und Strandebenen. *Kgl.Dan. Vidensk.Selsk., Biol.Skr.IV*, 1. 1-163.

Böcher, T.W., T. Christensen, M.S. Christiansen. 1946. Slope and Dune Vegetation of North Jutland. I. Himmerland. *Kgl.Dan.Vidensk.Selsk., Biol.Skr. IV*, 3. 1-78.

Bruun H.H. & Ejrnæs, R. (eds.) in press. Overdrev - en beskyttet naturtype. Skov og Naturstyrelsen.

Bruun, H.H. & Ejrnæs, R. 1993. *Naturtypen overdrev - vegetationen og dens forudsætninger.* M.Sc. thesis, Department of Botany, University of Copenhagen.

Bruun, H.H. & Ejrnæs, R. 1995. Beskyttede overdrev under lup. Urt 1995 (1): 26-31.

Bush, M.B. 1993. An 11.400 year palaeoecological history of a British chalk grassland. J.Veg.Sci 4: 47-66.

Campbell, B.D., Grime, J.P., Mackey, J.M.L. & Jalili, A. 1991. The quest for a mechanistic understanding of resource competition in plant communities: the role of experiments. Functional Ecology 5: 241-253.

Darwin, C. 1859. The origin of the species. 1.edition. Murray, London.

Duffey, E. & Watt, A.S. (eds.) 1971. The scientific management of animal and plant communities for conservation. 11th symposium of the British Ecological Society. Blackwell, Oxford.

Ejrnæs, R. & Bruun, H.H. 1995b. Naturkvalitet på overdrev. Urt 1995 (4): 123-129.

Ejrnæs, R. & Mark, S. 1997. Den gode den onde og den uautentiske. Urt 1997 (1): 22-29.

Eldredge, N. & Gould, S.J. 1972. Punctuated Equilibria: an alternative to phyletic gradualism. In: Models in paleobiology, Schopf, T.J.M. Schopf, 82-115. Freeman, Cooper & Co.

Ellenberg, H. 1974. Zeigerwerte der Gefäßpflanzen Mitteleuropas. Scripta Geobotanica 9: 97 pp.

Etherington, J.R. 1982. Environment and Plant Ecology. Sec. ed. John Wiley & Sons, Chichester.

Fink, Hans 1995. Eftertankens naturbegreb. In: Christensen, T.M. & Larsen, S.E. (eds.). Mennesket og naturen - Essays om natursyn og naturbrug. Odense Universitetsforlag. Odense.

Fraser LH, Grime JP. Primary productivity and trophic dynamics investigated in a North Derbyshire dale. Oikos (In press).

Fraser LH. Top-down vs. bottom-up control influenced by productivity in a North Derbyshire dale. Oikos (In press).

From & Söderman 1997. Nature Monitoring Scheme - Guidelines to monitor terrestrial biodiversity in the nordic countries. Nord 1997:16. Nordic Council of Ministers. Copenhagen.

Gauch & Whittaker 1972. Coenocline simulation. Ecology 53: 446-451.

Gilpin, M. & Hanski, I. 1991. Metapopulation Dynamics: Empirical and Theoretical Investigations. Academic Press, London.

Gittins 1965. Multivariate approaches to a limestone grassland community. 1. A. Stand ordination. J. Ecol. 53: 385-401.

Gould, S.J. & Eldredge, N. 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. Paleobiology vol. 3: 115-151.

Gould, S.J. 1989. Små fisk - store fisk. Naturhistoriske eftertanker. Munksgaard, København. [translated essays from: *Ever since Darwin*, Norton 1977, *The Panda's thumb*, Norton 1980 & *Hen's teeth and Horse's toes*, Norton 1983.].

Grime, J.P. 1973. Control of species density in herbaceous vegetation. *J. Env. Mgmt.*, 1: 151-167.

Grime, J.P. 1974. Vegetation classification by reference to strategies. Nature 250: 26-31.

Grime, J.P. 1979. *Plant strategies and vegetation processes*. Chichester: Wiley.

Grime, J.P. 1997. The humped back model: a response to Oksanen. J.Ecol. 85: 97-98.

Grime, J.P., Hodgson, J & Hunt, R. 1988. *Comparative Plant Ecology*. Unwin Hyman Ltd. London.

Grime, J.P., Mackey, J.M.L., Hillier, S.H. & Read, D.J. 1987. Floristic diversity in a model system using experimental microcosms. *Nature* vol. 328: 420-422.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52: 107-145.

Haggar, R. J. Jones, D., Jones, A.T. 1991. Enhancing botanical diversity with herbicides. Brighton crop protection conference 1991 5C-2: 627-630.

Hill, M.O. 1973. Reciprocal averaging; an eigenvector method of ordination, J. Ecol. 61: 237-249.

Iversen, J. 1954. The Late-Glacial Flora of Denmark and its Relation to Climate and Soil. Danmarks Geologiske Undersøgelse, II. rk., Nr. 80. København.

Iversen, J. 1957. Istidsrelikter i Bornholms Flora, Bornholms naturhistoriske Forenings jubilæumsskrift 1957.

Jeppesen, J.L. 1987a. Impact of Human Disturbance on Home Range, Movements and Activity of Red Deer (Cervus Elaphus) in a Danish Environment. Danish Review of Game Biology 13 (2).

Jeppesen, J.L. 1987b. The Disturbing Effects of Orienteering and Hunting on Roe Deer (Capreolus capreolus). Danish Review of Game Biology 13 (3).

Keddy, P.A. 1992. Assembly and response rules: Two goals for predictive community ecology. J.Veg.Sci.: 157-164.

Klijn, F. 1994. Up to date information on nature quality for the environmental management in Flandern. In: Blust et al. (eds.) Ecosystem classification for environmental management. Klüwer Academic Publishers.

Kowarik, I. 1988. Zum menschlichen Einfluβ auf Flora und Vegetation. Landschaftentwicklung und Umweltforschung 56: 1-280. Berlin.

Kull, K. & Zobel, M. 1991. High species richness in an Estonian wooded meadow. J.Veg.Sci. 2: 715-718.

Lewin, S.A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. The American Naturalist 104: 413-423.

Lloyd, P.S., Grime J. P. & Rorison, I.H. 1971. The grassland vegetation of the Sheffield region. 1. General features. J.Ecol. 59: 863-886.

MacArthur, R.H. & Wilson, E.O. 1967. The theory of island biogeography. Princeton University Press, Princeton, 203 pp.

Margules, C. & Usher, M.B. 1981. Criteria used in assessing wildlife conservation potential: a review. Biological Conservation 21: 79-109.

Mitchley, J. & Grubb, P.J. 1986. Control of relative abundance of perennials in chalk grassland in southern England. J. Ecol. 74: 1139-1166.

Moora, M. & Zobel, M. 1996. Effect of arbuscular mycorrhiza on inter- and intraspecific competition in two grassland species. Oecologia 108: 79-84.

Moore, D.R.J. & Keddy, P.A. 1989. The relationship between species richness and standing crop in wetlands: the importance of scale. Vegetatio 79: 99-106.

Odgaard, B.V. 1994. The holocene vegetation history of northern West Jutland, Denmark. Opera Botanica 123:1-171.

Økland, R. H. 1990. Vegetation ecology: theory, methods and applications with reference to Fennoscandia. Sommerfeltia suppl. 1: 233 pp.

Oksanen, J. 1996. Is the humped relation between species richness and biomass an artefact due to plot size? J.Ecol. 84: 293-295.

Pigott, C.D. & Walters, S.M. 1954. On the interpretation of the discontinuous distribution shown by certain British species of open habitats. J. Ecol. 42: 95-117.

Pott, R. 1995. The origin of grassland plant species and grassland communities in Central Europe. Fitosociologia 29: 7-32.

Rapson, G.L. , Thompson, K. & Hodgson, J. 1997. The humped back relationship between species richness and biomass - testing its sensitivity to sample quadrat size. J. Ecol. 85: 99-100.

Raunkiær, C. 1907. Planterigets livsformer og deres betydning for geografien: 132 pp. Gyldendalske Boghandel. København. (C. Raunkiær. 1934. *The Life Forms of Plants and Statistical Plant Geography, being the collected papers of C.Raunkiær*. Oxford University Press)

Rossi, E. & Kuitunen, M. 1996. Ranking of habitats for the assessment of ecological impact in land use planning. Biological Conservation 77: 227-234.

Smith, I., Shugart, H.H., Woodward, F.I. (eds.) 1997. Plant functional types: their relevance to ecosystem properties and global change. University Press, Cambridge.

Sterner, 1922. The continental flora of South Sweden. Geografiska Annaler 4: 221-441.

Stolze, M. (ed.) In press. Gulliste 1997. [Identify species where at least 20 % of the global population is Danish].

Streit-Wolf-Engel, R., Boller, T, Wiemkin, A. & Sanders, I.R. 1997. Clonal growth traits of two *Prunella* species are determined by co-occurring arbuscular mycorrhizal fungi from a calcareous grassland. J.Ecol. 85: 181-191.

Tansley, A.G. & Adamson, R.S. 1925. Studies of the vegetation of the English Chalk grasslands of the Hampshire-Sussex border. J.Ecol. 13: 177-223.

Taylor, D., Aarssen, L, W. & Loehle, C. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. Oikos 58: 239-250

Tilman, D. 1985. The resource-Ratio hypothesis of plant succession. The American Naturalist 125: 827-852.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, New Jersey.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78: 81-92.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47: 893-901.

Warming, E. 1884. Om Skudbygning, overvintring og foryngelse. Naturhistorisk Forenings Festskrift.:1-105.

Warming, E. 1895. Plantesamfund. Grundtræk af den økologiske plantegeografi. P.G. Philipsens Forlag, København. (Oecology of Plants, Oxford 1909).

Warming, E. 1923. Økologiens Grundformer. Kgl. d. Vid. Selsk. Skr., Nat. Math. Afd. 8. Rk. IV, 2: 119-187.

Whittaker, R.H. 1967. Gradient analysis of vegetation. Biol Rev. 42: 207-264.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21: 213-251.

Willems, J. H., Peet, R.K. & Bik, L. 1993. Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. J.Veg.Sci. 4: 203-212.

Willis, K.J. & Bennett, K.D. 1995. Mass extinction, punctuated equilibrium and the fossil plant record. TREE: 10:308-309

Zobel, K. & Liira, J. 1997. A scale-independent approach to the richness vs biomass relationship in ground-layer plant communities. Oikos 80: 325-332.

Zobel, M. 1992. Plant species coexistence - the role of historical, evolutionary and ecological factors. Oikos 65: 314-320.

Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in ecology and evolution*: 266-269.

Zobel, M., Moora, M. & Haukioja, E. 1997. Plant coexistence in the interactive environment: arbuscular mycorrhiza should not be out of mind. Oikos 78:1.

Supplementary literature

Bruun, H.H. & Ejrnæs R. (eds.) In press. *Overdrev - en beskyttet naturtype*. App 150 pp. Skov- og Naturstyrelsen

Ejrnæs, R. & Bruun, H.H. 1995b. *Naturkvalitet på overdrev*. Urt 1995 (4): 123-129.

Ejrnæs, R. & Mark, S. 1997. *Den gode den onde og den uatentiske*. Urt 1997 (1): 22-29.

Bruun, H.H. & Ejrnæs, R. 1995. *Beskyttede overdrev under lup*. Urt 1995 (1): 26-31.

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