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The effects of nutrients and disturbance on dry grass-dominated vegetation

PhD thesis

Erik Aude

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Abstract:	A combination of field investigation and microcosm experiments was used to test the influence of nutrients and disturbance on the species composition and diversity of dry grassland vegetation. The Ph.D. thesis is based on four manuscripts. Two of which concern investigation of hedgerow bottom vegetation of organic- and conventional farms. The third manuscript focuses on bryophyte performance in grassland and the influence of grazing, nutrients and vascular plants. The last manuscript deals with the combined influence of varying degree of herbicide drift and varying degree of nutrients on standardised vegetation.

Keywords	Bryophytes, moss, diversity, vegetation, microcosm experiment, hedgerow, organic, nutrients, disturbance, herbicide, drift, productivity, Nitrogen, plant community, biomass, farming
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Contents

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Preface

The present thesis is the outcome of a Ph.D.-study initiated in June 2001 and terminated in January 2004. The study has been carried out in a co-operation between the Department of Physiological Ecology, Botanical Institute, University of Copenhagen and Department of Wildlife Biology and Biodiversity, National Environmental Research Institute, Kalø, of which the latter funded the study. Anders Michelsen was the supervisor at the University of Copenhagen and Knud Tybirk was the supervisor at the National Environmental Research Institute. The Danish Environmental Protection Agency (Miljøstyrelsen) and DARCOF (Danish Research Council of Organic Farming) financed parts of the study.

The study included a three-month stay in England at the Centre for Ecology and Hydrology, Merlewood, Section of Land Use.

The thesis consists of an overall introduction with presentation of the theoretical background and aims of the research followed by an overall discussion, conclusions and presentation of gaps of knowledge. Acknowledgement and statements by co-authors are hereafter presented followed by references and four papers. In chapter 3, the titles of the four papers published in, submitted to or prepared for international, peer reviewed scientific journals, are given. The papers referred to by use of the Roman numbers I-IV in the thesis.

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Erik Aude

Summary

While the development objective of my Ph.D.-study was to investigate the importance of disturbance and productivity for the shaping of dry grass-dominated plant communities, the specific objectives were to test a number of hypotheses regarding vegetation development in hedgerow vegetation and experimental vegetation in response to experimental treatments.

I combined field studies with experiments. Firstly, field vegetation data and explanatory variables were collected in organic and conventional hedgerows (Paper I and II). Secondly, an outdoor factorial microcosm experiment was carried out in order to test the influence of nutrients, defoliation and vascular plant species composition on the recruitment and diversity of bryophytes (Paper III). Finally, a full factorial experiment was established in order to test the separate and interaction effect of nutrient enrichment and herbicide disturbance on biomass, species diversity and frequency of bryophytes (Paper IV). While nutrient gradients were simulated by differential nutrient addition, disturbance took the form of herbicide application and repeated defoliation (simulated grazing).

Nutrients

Result from the mesocosm experiment showed that nutrient enrichment resulted in a significant change in soil N, conductivity and pH (Paper IV). Both experiments showed furthermore that nutrient enrichment resulted in an increase in productivity and a subsequent following negative influence on plant diversity (Paper III and IV).

In particular, nutrient enrichment resulted in litter accumulation at least at low disturbance levels, and litter amounts explained more variation in species diversity than living biomass (Paper IV).

In comparison to disturbance, nutrient enrichment explained more of the variation in species diversity (Paper III and IV). This indicates that a reduction in nutrient levels is of highest priority in the conservation and restoration of species diverse plant communities dominated by grasses.

Disturbance

Herbicide disturbance affected species diversity and litter accumulation significantly (paper IV). Herbicide disturbance moreover explained the largest part of the variation in total biomass (Paper IV). There was however a difference in the effects of disturbance on biomass and litter. Herbicide disturbance showed significantly negative impact on litter accumulation but no significant impact on living biomass (Paper IV).

The classical hypothesis of maximum species diversity at intermediate disturbance level was questioned in this study because results showed the relationship between disturbance and species diversity was highly depended on nutrient level (Paper IV).

Interactions

Statistically significant interactions were found between herbicide disturbance and nutrient enrichment according to productivity, species diversity and bryophyte abundance (Paper IV).

The interaction was for example expressed in a negative disturbance influence on species diversity at infertile conditions, whereas at intermediate nutrient levels the disturbance affect was unclear. At the highest nutrient level disturbance had a positive influence on species diversity (Paper IV).

The relationship between productivity and species diversity varied along the disturbance gradient (Paper IV).

Bryophytes

Nutrient enrichment demonstrated a negative impact on both abundance (Paper III and IV) and species diversity (Paper III) of bryophytes. High nutrient levels without disturbance resulted in the lowest species diversity and to complete bryophyte extinction in up to 50 % of sample plots (Paper III). Vascular plant biomass showed an inverse relationship to bryophyte abundance (Paper III). Litter explained a larger part of the variation in bryophyte abundance compared to living biomass (Paper IV). Nutrient enrichment level did, however, explain more of the variation in frequency of bryophytes than litter and biomass together (Paper IV).

Disturbance prevented complete bryophyte extinction (Paper III and IV), but disturbance did not fully compensate for the negative effect of nutrient enrichment. Five out of 11 acrocarp bryophytes were unable to persist/colonise at high nutrient levels even with biomass removal (Paper III).

Hedgerow

This Ph.D.-study reinforces and illustrates the problems of low habitat quality and poor dispersal abilities in the hedgerows of the Danish landscape (Paper II). An ordination of almost all Danish hedgerow vegetation sample plots (n = 687) together with relevant reference data from plant communities of the Danish landscape revealed that nutrient levels were the most important gradient in the data. Hedgerow vegetation sample plots were similar to plant communities of low naturalness (Paper II).

Organic farming

There were no differences in soil nutrient levels and structural parameters between organic and conventional hedgerows. In spite of this the species diversity were found to be significantly higher in organic hedgerows. The higher diversity resulted from higher numbers of bryophytes, weeds, ruderals, and plant species characteristic of semi natural habitats (Paper I & II).

Thus organic farming seems to support a better hedgerow habitat for some species. However, the experiment could not confirm that spray drift doses alone were responsible for the lower diversity in conventional hedgerows (Paper IV). The additional plausible explanations of a higher species diversity in organic hedgerows was: 1) A larger species pool, 2) Use of larger herbicide doses in conventional hedgerow than the tested doses, and 3) Higher rates of dispersal vectors. More research is however needed to pinpoint the mechanisms behind the higher species diversity in organic farmlands.

Conclusions

It was concluded that a successful conservation and restoration of botanical diversity in the Danish landscape requires:

1. Cessation of nutrient pollution of small biotopes and permanent grassland, e.g. by establishing "buffer zones" around fields.

2. Biomass removal is important but not enough (e.g. in road verge management) to maintain and conserve all species.

3. Conversion to organic farming will have a beneficial effect on some species.

Papers included in the thesis

I Aude, E., Tybirk, K. & Pedersen, M.B. 2003: Vegetation diversity of conventional and organic hedgerows in Denmark. - Agriculture, Ecosystems and Environment 99 (1-3): 135-147.

II Aude, E., Tybirk, K., Michelsen, A., Ejrnæs, R., Hald, A.B. & Mark, S. 2003: Conservation value of herbaceous vegetation in hedgerows – does organic farming make a difference? - Biological Conservation (in press 2003).

III Aude, E. & Ejrnæs, R. 2004: Bryophyte colonisation and persistence in experimental grassland dominated by vascular plants – accepted for publication in Oikos.

IV Aude, E. 2004: Plant species diversity and the interaction of productivity and disturbance tested by experimental grassland vegetation. - Manuscript prepared for publication in Journal of Ecology.

Table 1: Overview of included papers. The grey cells indicate subjects included in the paper. The text inside the cell clarifies the type of subject. α, β and γ refers to level of diversity, sample plot diversity, between plot diversity and ecosystem diversity, respectively.

	Paper I	Paper II	Paper III	Paper IV
Study type				
Field study	Hedgerows	Hedgerows		
Experimental study			Microcosm	Mesocosm
Response variables				
Plant species diversity	α, β and γ	α	α	α
Plant species composition				
Plant types				
Plant communities				
Biomass				
Bryophytes				
Explanatory variables				
Organic vs. conventional				
Crop type				
Soil variables				
Hedgerow structure				
Disturbance	Herbicides	Herbicides	Defoliation	Herbicide
Nutrient enrichment				
Plants species composition				

1 Introduction

1.1 Historical background

After the Weichelian glaciation, the natural vegetation of the European landscape developed into a closed forest type which also had a significant mixture of open habitats such as heathland, grassland, wetland, scrub and glades, which were maintained due to large herbivores, unproductive soils, winds and fires (Svenning 2002). However, the increasing human cultivation of the landscape that started 5000 years ago (Odgaard 1994, Bradshaw & Holmqvist 1999) had a significant impact on the natural biodiversity (e.g. McNeely et al. 1995). The conversion of natural habitats to agricultural fields has accelerated during the latest 200 years due to agricultural innovation. Within the last 40 years, deliberate habitat destruction has gradually stopped, and today the major threat to the biodiversity of many European agricultural landscapes is nutrient and pesticide pollution influencing native plant communities. Thus modern agriculture is responsible for the loss of wildlife, and its habitats all over Europe. Although relatively few species of the European fauna and flora have actually become totally extinct during the last decade, the biodiversity of the European continent has been affected by decreasing species numbers and loss of habitats in many regions. Approximately 30 % of vertebrates and 20 % of higher plant species are classified as 'threatened' at the European scale (Anon. 1997). The majority of species are directly threatened by habitat loss due to destruction, modification and fragmentation of ecosystems (Delbaere 1998). It is, however, widely accepted, with for example in the Rio Declaration (Anon. 1992), that biodiversity must be conserved, in particular through sustainable use of natural resources (Washer et al. 2000). To achieve this goal, conservation of biodiversity must be fully integrated into the agricultural sector, because this sector has great influence on the environment (Washer et al. 2000).

In this Ph.D.-thesis the focus is on plant ecology in intensively cultivated agricultural landscapes.

1.2 Vegetation processes and influence of nutrients and disturbance

One of the main assumptions in this project is that the distribution of plant species in plant communities of the landscape is non-random and continuous. Rather it is accepted that plant species are distributed according to assembly rules (e.g. Keddy 1992, Weiher & Keddy 1995, Zobel et al. 1998, Wilson 1999). Assembly rules help to explain the specific species composition of different plant communities, which is a subset of the local species pool, which is a subset of a regional species pool, which again is a subset of the global species pool. These different subsets of species pools are structured by biotic (Wilson 1999) and abiotic filters (Keddy 1992). Two of the most important factors influencing the species composition and species diversity of plant communities are accordingly: 1) Size and composition of the species pool at different levels, 2) The ability of species to reach and survive in a target community (Zobel et al. 1998).

A reduction in the size of a species pool will reduce the potential filtering processes and thereby the variation in the species composition and species diversity of plant communities. The focus in this study is the filtering processes, or more specific the abiotic and biotic vegetation processes that determine the outcome of secondary succession on dry soils. Given this research issue, I have attempted to keep the potential species pool as a constant variable. This was achieved by comparing very similar hedgerow plant communities (Paper I and II) or simply by controlling the species pool by use of experimentally sown vegetation (Paper III and IV). Another fundamental assumption in this study is that plants species have evolved different strategies to handle competition, stress and disturbance (*sensu* Grime 1977). According to Grime (1979) two of the most important filtering processes in the agricultural landscape are the site productivity and the level of disturbance. These two factors are centres of attention in this study.

1.2.1 Nutrient enrichment

There is a considerable interest in the mechanisms responsible for the reduced diversity at high nutrient levels, not only for scientific theoretical reasons, but also for the applied interest in forecasting of consequences for the conservation and restoration of plant communities (Foster & Gross 1998).

Nutrient enrichment leads to higher productivity in most grasslands if no other factors are limiting (Grime 1979). Nutrient enrichment is among the most studied factors in vegetation ecology and especially in grassland. The traditional applied motivation for studies of nutrient-vegetation relationship in grasslands has been to raise yields (e.g. Milton 1940). Some of the long-term experiments have, especially in the later years, produced valuable inputs to ecological theory (e.g. Pigott 1982, Mahaila & Hera 1994, Wilson et al. 1996, Virtanen et al. 2000).

Numerous scientists have documented the influence of nutrient enrichment on grasslands (e.g. Milton & Davies 1947, Traczyk & Kotowska 1976, Traczyk et al. 1976, Grime 1979, Bobbink 1991, Keddy et al. 1997, Kleijn et al. 1997), and also on field margins (Boatman 1994, Boatman et al. 1994, Kleijn & Snoeijing 1997). Nutrient enrichment experiments have, however, only incidentally included changes in the bryophyte flora, with Willis (1963), Bobbink (1991) and Virtanen et al. (2000) as notable exceptions.

Experimental manipulations of grassland vegetation have generally shown that species diversity decreases following an increase in productivity (e.g. Foster & Gross 1998). It may be a cumulative or interactive effect that determines the observed patterns of diversity and productivity (Waide et al. 1999). A test of cumulative or interactive effects requires controlled experiments.

1.2.2 Relationship between productivity and diversity

The relationship between productivity of biomass and species diversity has attracted much attention with the unimodal (hump-back) model (Grime 1973, Al-Mufti 1977) being the most investigated. Recently, comprehensive reviews of productivity-diversity studies found no universal pattern in the relation between productivity and species density (Grace 1999, Waide et al. 1999, Mittelbach et al. 2001). Up to 30 % of the reviewed studies found no relationship at all (Waide et al. 1999). It can be concluded that despite the general assumption about diversity reduction with high nutrient inputs, we are still far from reaching a comprehensive theory on the relationship enabling the development of tools for forecasting.

1.2.3 Disturbance

The influence of disturbance in semi-natural vegetation has also attracted scientific attention. Disturbance described as an 'extinction-causing event' (Collins et al. 1995) includes a wide range of factors that can be defined as a discontinuous, unpredictable force that kills or badly damages the biota and alters the availability of resources (Mackey & Currie 2000). These definitions are complementary to a similar disturbance definition put forward by Grime (1979): "The mechanism which limits the plant biomass by causing its partial or total destruction". The relationship between disturbance and species diversity has likewise been suggested to follow a unimodal model (Grime 1973). At sufficiently high productivity, competitive exclusion will occur at low disturbance level. At a higher disturbance level, species of high competitive ability are suppressed and conditions will be more favourable to less aggressive species. At the highest disturbance level species diversity is expected to decrease, as only species adapted to a high disturbance level will survive (Grime 1973). In vegetation studies, the impact of disturbance is typically included as a binary variable and evaluated by comparing presence or absence of: grazing (Buttenschøn & Buttenschøn 1982, Grime et al. 1987, Gough & Grace 1998, Kahmen et al. 2002, Jacquemyn et al. 2003), mowing (Kahmen et al. 2002, Jacquemyn et al. 2003, Paper III), soil disturbance by mammals (Platt 1975), burning (Glenn & Collins 1992) and herbicides (de Snoo 1999, Jutila & Grace 2002, Paper I, II and IV). Only in a few cases varying degrees of disturbance have been quantified (Turkington et al. 1993, Kleijn & Snoeijing 1997, Wilson & Tilman 2002, Paper IV). In this study two types of disturbance were included: herbicide application and defoliation (simulated grazing/mowing). These two types of disturbance treatments are not directly comparable but both fulfilled the definitions put forward by Grime (1979), Collins et al. (1995) and Mackie & Currie (2000), and being so markedly different they were found to complement each other well. The defoliation disturbance was included as a binary variable (defoliation vs. not defoliation), (Paper III). The herbicide disturbance was included as a four-levelled gradient in herbicide concentration (Paper IV). The intention was to simulate herbicide drift in doses that are experienced by the semi-natural vegetation in the field margins. The concentrations of drift doses depend primarily on wind speed and nozzle type (de Snoo & de Witt 1998). Several studies have estimated the concentration of drift doses that can easily reach 25 % of field dose at low wind speed (3-4.5 m/s) (de Snoo & de Witt 1998). The applied doses in the experiment were 0, 1, 5 and 25 % of the field dose. The field dose recommended by the production company represents 100 % dose and equals complete plant extinction. The concentrations of 100 % match 4 l ha^{-1} that equals 1440 g active ingredient per ha. The chosen herbicide, Glyphosat (Roundup™), is the most frequently used herbicide in Denmark (Anon. 2003).

Diversity studies including simultaneous gradients in disturbance and nutrient enrichment are rare, and the results point in different directions (Turkington et al. 1993, Kleijn & Snoeijing 1997, Wilson & Tilman 2002, Paper IV). At present it can therefore be concluded that little is known about the nutrient and disturbance interactions as determinants of species diversity (Jacquemyn et al. 2003).

1.3 Importance of species diversity

1.3.1 Factors influencing species diversity of dry grassland

Plant species diversity in grass-dominated plant communities is influenced by other filtering factors than disturbance and nutrient enrichment. These filtering factors are e.g. continuity (Gibson & Brown 1991), the regeneration niche (Grubb 1977), scale (Gross et al. 2000), local heterogeneity (Bates 1982) starting conditions (Rydin 1997), size of species pool (Zobel 1992, 1997, Zobel et al. 1998), dominance of invasive species (Kleijn et al. 1997) and mycorrhiza (Grime et al. 1987, Egerton-Warburton et al. 2001). In this study, attempts were made to minimise the variation in these factors.

As species diversity furthermore depends on soil variables in dry grassland communities (Grime 1979, Ejrnæs & Bruun 2000) and hedgerows (Paper I) soil texture and soil chemicals has also been examined (Paper I-IV).

1.3.2 Species diversity vs. naturalness and species composition

Evaluation of conservation value and restoration success should not focus solely on optimising species diversity. Low species diversity is characteristic in many natural oligotrophic habitats such as bogs and heathland. High species diversity as criteria is well known to be an insufficient target for conservation and restoration of ecosystems (e.g. Angermeier & Karr 1994). A number of other criteria are therefore suggested to better assess conservation value and establish meaningful targets (Margules & Usher 1981). One of the most convincing guidelines for conservation of ecosystems is naturalness (Angermeier 2000). Evaluation of naturalness needs inclusion of species composition (e.g. Ejrnæs et al. 2002). One technique that includes the use of species composition is to compare collected vegetation data with data of reference biotopes. This kind of comparison requires use of multivariate analyses and is executed in Paper II. The inclusion of species diversity as a parameter in experiments can also lead to insights into vital vegetation processes (e.g. Grime et al. 1987, Bobbink 1991, Keddy et al. 1997, Paper III and IV). High species diversity is probably also needed to reduce temporal variability in ecosystem processes in changing environments (Loreau et al. 2001). Species diversity can also be a fruitful parameter when examining real plant communities. When comparing species diversity of plant communities it is important that the communities are of equal naturalness and that the compared species diversity is 'native' to the compared communities (Paper I and II).

1.3.3 Ecosystem function

As opposed to the negative relationship between nutrient enrichment and species diversity discussed above, recent experimental studies have shown a positive, inverse relationship between species diversity and productivity (e.g. Loreau et al. 2002). These studies indicate an effect of diversity on the productivity along artificially generated gradients in species density (Naeem et al. 1994, Hector 1998, Hector et al. 1999, Tilman et al. 2001). A compilation of evidence from relatively short-termed experiments indicates that species diversity may have beneficial effects on productivity, especially in grassland ecosystems (Schläpfer & Schmid 1999). The direction of causality has been a subject of intense debate and the positive effect of species diversity on productivity is probably of relatively minor importance in most natural plant communities compared to the negative effect of nutrients on diversity (Huston et al. 2000).

Recent studies of the species diversity impact on ecosystem functioning have focussed on productivity, Grime (1998) has suggested investigating other important aspect of ecosystem functioning such as the filtering role for some subordinates.

1.4 Importance of hedgerows as habitats and dispersal corridors for grassland diversity

The general decline in habitat quality (caused by nutrient enrichment, herbicide disturbance, cessation of grazing) of most habitats in the agricultural landscape has occurred simultaneously and in parallel with major changes in the landscape constellation. The historical changes in the agricultural landscape of northern Europe have been analysed (e.g. Niels-Christiansen 1985, Agger & Brandt 1988, Ihse 1995, Kristensen 2001) and the overall impression of the landscape changes are instability, monotony and fragmentation. Habitat destruction has been found to be the most important factor causing species extinctions in the landscape (Leach & Givnish 1996). 'Hot spots' defined as nature types with high naturalness such as some types of grassland and woods are found in only a few percent of the agricultural landscape (Grime 1988, Erikstad & Jonsson 1997, Ejrnæs et al. 1998). In such highly fragmented and dynamic landscapes the importance of dispersal and recruitment becomes crucial.

It has been claimed that the impoverished biotic diversity of remaining habitat patches are strengthened by colonisation problems due to past habitat destruction, fragmentation and isolation of less common species (e.g. Hanski 1997, Eriksson & Kiviniemi 1999). The negative relation of some grassland species to isolation suggests dispersal limitations in the landscape (Bruun 2000). Although short-distance dispersal is mentioned to be of minor importance to the post-glacial distribution of species (Cain et al. 1998), a future survival of species in the few and often isolated 'hot spots' requires gene exchange. Therefore, to restore and maintain biodiversity in the isolated refuges it is important to ensure dispersal opportunities via 'stepping stones' and corridors in the agricultural landscapes. In this respect small biotopes (*sensu* Agger & Brandt 1988), such as hedgerows, road verges and field margins, are essential to facilitate dispersal and to ensure a sustainable development of the landscape. The function of hedgerows as dispersal corridors of forest species (McCollin et al. 2000, Smart et al. 2001) and as refuges of grassland species (Smart et al. 2002) has recently been described. There are also historical indications that hedgerows can function as important refuges and dispersal corridors for plants (Richards 1928, Warming 1919, Pollard et al. 1974). In Denmark, hedgerows are the most frequent linear biotope in most landscapes (Agger & Brandt 1988). I have therefore been focussing on hedgerows in my Ph.D.-project (Paper I and II).

1.5 Importance of organic farming

The impoverished development of the environment caused by innovation of the conventional agriculture may have contributed to progress of alternative farming techniques. During the last decade, the European Union has encouraged development of organic farming (Bowler & Ilbery 1999) which uses no artificial pesticide application (Lampkin 1990). In 2001, organic farming covered 6.5 % of the Danish agricultural land (Yussefi & Willer 2003). Similar development have been reported in other European countries, so today organic farming covers approximately 3 % of the European agricultural land (Yussefi & Willer 2003).

Comparison of organic and conventional arable fields has demonstrated a higher diversity of vascular plants (e.g. Hald & Reddersen 1990, Hald 1999, Rydberg & Milberg 2000, Mäder 2002, Ahnström 2002), arthropods (Feber et al. 1998, Mäder 2002), earthworms (Reganold et al. 1993) and micro-organisms (Mäder 2002) in organic fields. Whereas there are indications of a positive influence of organic agriculture on the biodiversity in fields (e.g. McNeely et al. 1995, Stolze et al. 2000, Azzez 2000), the impact on the species pool in neighbouring habitats is poorly documented in the scientific literature. Likewise, there is hardly any evidence of long-term effects of organic farming on species composition in hedgerows (Ahnström 2002). A part of my Ph.D.-project has therefore been devoted to testing whether long-term organic farming contributes to more diverse hedgerows with higher naturalness (Paper I and II).

2 Objectives of the thesis

Development objective

- To contribute to the understanding of the role of nutrient enrichment and disturbance for the assembly of plant composition and plant diversity of the agricultural landscape.

Immediate objectives

- To test and quantify the impact of management type on plant species composition and species diversity in hedge bottom vegetation (Paper I and II).
- To assess the conservation value of hedgerow vegetation in relation to different management strategies by comparison with other plant communities in the landscape (Paper II).
- To test the influence of nutrient enrichment, defoliation and vascular plant species composition on the recruitment and diversity of bryophytes (Paper III).
- To test the separate and interaction effects of nutrient enrichment and herbicide disturbance on biomass, species diversity and frequency of bryophytes in experimental grassland vegetation (Paper IV).

An overview of papers is presented in Table 1.

3 Nomenclature & terminology

3.1 Biomass

Biomass always refers to vascular plant biomass. Biomass can be divided into living biomass and litter (dead plant biomass in which plant structure is still recognisable). This means that total biomass = biomass + litter.

The term 'productivity' always refers to biomass and litter. Thus, productivity => ('results in') biomass + litter.

3.2 Number of plant species

Different terms can be used for number of plant species. Peet et al. (1983) suggested using the term 'species density' when referring to the number of species in small sample plots. In this thesis species density is called 'species diversity', because different sizes of sample plots are included, but it is similar to species richness and number of species inside a delimited area. So, the number of different plant taxa inside a delimited area = species density = number of species = species richness = (alfa) species diversity.

3.3 Hedgerows

Hedgerows have been defined in different ways (Pollard et al. 1974, Forman & Baudry 1984, Forman 1995, Barr & Gillespie 2000, Baudry et al. 2000, French & Cummins 2001). The term hedgerow is, however, often used as a common term for hedges, shelterbelts and fencerows, which are all linear landscape features with marked woody vegetation.

In this study the focus is on the herbaceous vegetation strip which is found in the area between the woody part of the hedgerow and the field, and the woody part is not dealt with in this study. So when the term hedgerow is used, it most often refers to the herbaceous zone as described above.

3.4 Identification and nomenclature of plant species

Identification of vascular plant species was based on Hansen (1993). Hubbard (1984) was, however, used for some grasses and Schou (2001) for *Hieracium* species and Schou (1993) for *Carex* species. Identification of bryophytes was based on Andersen et al. (1976) and Smith (1978). Nomenclature of vascular plants follows Hansen (1993), and bryophytes follow Andersen et al. (1976).

4 Data sources

In order to either reject or confirm the hypotheses put forward in Papers I-IV and to fulfil the objectives as stated above, data were collected in two different ways. First, data of field vegetation data and explanatory variables were collected in uniform organic and conventional hedgerows (Paper I and II). Then data obtained from a microcosm experiment (Paper III) and a mesocosm experiment (Paper IV) was used to either accept or reject the field observations.

4.1 Field data

In 2001, which was the first year of the study, the aim was to compare species diversity and species composition in organic and conventional uniform hedgerows (n = 2 x 13) on similar sandy soils within a restricted area of south-western Denmark (Paper I, Fig. 1). In 2002, the aim was to compare organic and conventional uniform hedgerows (n = 2 x 15) on more clayey soil, in northern and eastern Denmark. Data from the two years were published in paper II.

To ensure an optimal comparison of hedgerows, a number of specific criteria should be fulfilled for a hedgerow to be included, with reference to number of tree rows, age, tree species, length, soil type and neighbouring nature type. The typical hedgerow was 14 years old, had a width of 2.7 m, a height of 3-7 m and a north-south orientation. The locations of sampled hedgerows are shown in Fig. 1. Systematic placement of the sample plots and their unit size (10 m^2) followed recommendations by Økland (1990). The abundance of vascular plants and bryophytes was recorded as a frequency.

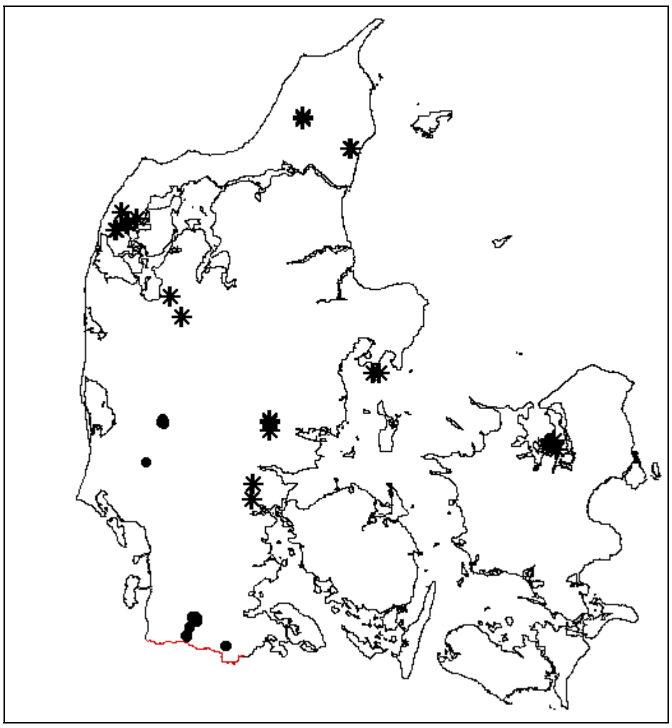

Figure 1. Locations of the investigated hedgerows in Denmark (excluding the Island of Bornholm). Circles and asterisks indicate hedgerows investigated in 2001 and 2002 respectively.

4.2 Experimental data

Observations and hypotheses based on field data from hedgerow bottoms (Papers I and II) were tested and evaluated in two different experiments: a microcosm experiment (Paper III) and a mesocosm experiment (Paper IV). Microcosm and mesocosm tests provide controlled experimental conditions. Microcosm studies are generally small and contain a few species, whereas mesocosm tests are relatively large and, contain most of or all the species in an ecosystem (Linthurst et al. 1995). Given the expenses and efforts required to establish and maintain mesocosms, microcosms are often used when only one or a few species are required for a test (Linthurst et al. 1995).

4.2.1 The microcosm experiment

To test for the influence of nutrient status, defoliation and vascular plant species composition on the recruitment and diversity of bryophytes, a multi-factorial experiment using outdoor microcosms was established in May 1998 by the co-author (Paper III). The individual microcosm consisted of a plastic container with an area of 0.1 m^2. Three treatments, each with two levels, were applied to the microcosms: 1) fertilised (17 g/m^2) vs. unfertilised (0.4 g/m^2), 2) defoliation (simulating grazing/mowing) vs. no defoliation, 3) composition of vascular plant vegetation expressed as generalist vs. specialist species (Table 2). The eight different treatment combinations were replicated four times.

Bryophyte colonisation was a spontaneous process, except that all microcosms received the same initial standardised inoculum from three different grassland types. After 3½ years, the aboveground biomass of bryophytes and vascular plants was harvested from the microcosm.

Table 2: Surviving generalist and specialist species in the microcosms.

Specialist species	**Generalist species**
Agrostis capillaris	*Dactylis glomerata*
Bromus erectus	*Elymus repens*
Centaurea scabiosa	*Festuca rubra*
Festuca ovina	*Lolium perenne*
Filipendula vulgaris	*Medicago lupulina*
Galium verum	*Plantago lanceolata*
Geranium sanguineum	*Rumex acetosa*
Hieracium pilosella	*Trifolium repens*
Lotus corniculatus	
Ranunculus bulbosus	
Taraxacum sect. Erythrospermum	
Trifolium pratense	

4.2.2 The Ebdrup mesocosm experiment

To test for the separate and interactive effects of nutrient enrichment and herbicide disturbance on biomass, species diversity and frequency of bryophytes, a full factorial experimental design was established (Paper IV). The design included four levels of herbicide disturbance (0, 1, 5 and 25 % of field dose), three levels of fertilisers (0, 2.5 and 10 g N m^{-2}) and 10 replicates. The individual mesocosm sample plot was 7 x 7 m, and all of the 120 mesocosms were situated on a former cultivated sandy field. To prevent germination of seed from the seed bank and influence of the potentially nutrient rich topsoil (Pywell et al. 2002), the soil was initially deep ploughed. The sown vegetation consisted of a stratified random selection of 30 vascular herb species of grass-dominated vegetation (Table 3). After three growth seasons the dry weight of all vascular plants species were used. Bryophyte frequency was determined as a frequency in nine circles after harvesting of vascular plants. Forty-three other taxa spontaneously established in the sample plots (Table 4)

4.3 Soil variables

Soil samples were collected from all investigated sample plots of both the field study and the mesocosm experiment. Chemical soil analyses were performed by laboratory technicians at the laboratory of Botanical Institute, University of Copenhagen. Soil texture was analysed at the Danish Institute of Agricultural Sciences in Foulum.

Table 3. Characteristics and vitalities of 31 sown species. The plant strategy follows Grime (1988) and, C, S and R refer to competitive, stress tolerant and ruderal species, respectively. Height follows Lid (1987). Seed germination is expressed as the percentage germination of 20 seeds in petri-dishes during a period of 59 days (n = 2). Emergence and establishment are expressed as percentage of sample plots with success after four months and 2½ years, respectively. The final dominance of sown species is expressed as percentage of total harvested biomass.

Species name	C	S	R	Height (cm)	Seed germination (%)	Emergence (% of plots)	Establishment (% of plots)	Final dominance (%)
Competitive species								
Artemisia vulgaris	8	0	4	70	38	43	18	0.6
Cirsium arvense	12	0	0	80	25	0	0	0
Elytrigia repens	8	0	4	70	20	7	13	<0.1
Euphorbia esula	8	2	2	40	0	0	3	<0.1
Leucanthemum vulgare	8	2	2	30	48	40	88	1.0
Tanacetum vulgare	8	0	4	80	100	95	80	8.3
Urtica dioica	12	0	0	70	40	1	2	<0.1
Stress tolerant species								
Campanula rotundifolia	0	12	0	20	90	8	19	<0.1
Festuca ovina	0	12	0	20	73	100	94	20.1
Filipendula vulgaris	0	12	0	40	55	0	0	0
Hieracium pilosella	2	8	2	15	70	72	72	0.3
Lotus corniculatus	2	8	2	15	60	96	25	0.3
Pimpinella saxifraga	0	8	4	30	23	0	1	<0.1
Solidago virgaurea	2	8	2	40	18	0	1	<0.1
Ruderal species								
Poa annua	0	0	12	15	95	95	0	0
Lapsana communis	4	0	8	40	10	26	1	<0.1
Myosotis arvensis	0	4	8	25	10	23	11	<0.1
Oenothera biennis	2	2	8	60	3	49	40	0.5
Verbascum thapsus	2	2	8	100	58	97	57	1.1
Aphanes arvensis	0	4	8	5	3	0	0	0
Lepidium campestre	2	2	8	25	3	97	43	<0.1
CSR-strategies								
Agrimonia eupatoria	6	0	6	50	0	3	8	<0.1
Agrostis capillaris	4	4	4	30	78	100	99	31.5
Convolvulus arvensis	5	2	5	50	48	6	5	<0.1
Galium verum	4	4	4	30	23	7	3	<0.1
Hypericum perforatum	4	4	4	40	85	3	33	<0.1
Hypochoeris radicata	4	4	4	30	100	98	85	0.2
Linaria vulgaris	6	0	6	40	0	75	60	0.6
Agrostis gigantea	6	0	6	80	-	-	98	35.0
Unknown CSR-value								
Centaurea cyanus				40	100	97	0	0
Lychnis viscaria				30	48	0	4	<0.1
Total								99.5

Table 4. Spontaneously established taxa in 120 sample plots of the Ebdrup mesocosms, sorted according to total frequency.

Species	Establishment after 2 year (% of plots)
Ceratodon purpureus	50
Rumex acetosella	25
Chenopodium album	23
Spergula rubra	23
Holcus lanatus	13
Viola trivialis	11
Epilobium montanum	10
Scleranthus annuus	9
Senecio sylvaticus	7
Galium sp.	6
Arnoseris minima	6
Taraxacum sp.	6
Achillea millefolium	6
Bryum sp.	6
Betula pubescens	6
Erodium cicutarium	5
Veronica arvensis	5
Polygonum aviculare	5
Lolium perenne	5
Tripleurospernum inodorum	3
Chamaenerion angustifolium	3
Galeopsis ladanum	3
Viola arvensis	3
Silene vulgaris	3
Cerastium fontanum	3
Polygonum convolvulus	3
Anthoxanthum odoratum	2
Pohlia nutans	2
Festuca rubra	2
Conyza canadensis	2
Holcus mollis	1
Quercus robur	1
Polygonum sp.	1
Polytrichum piliferum	1
Spergularia arvensis	1
Senicio viscosus	1
Polygonum lapathifolium ssp. lapathifolium	1
Funaria hygrometrica	1
Echium vulgare	1
Centaurea jacea	1
Dianthus deltoides	1
Trifolium repens	1
Viola sp.	1

5 Results and discussion

The overall relationship between nutrient enrichment and disturbance and plant species diversity of grass-dominated vegetation is presented in Figure 2.

5.1 Nutrient enrichment and vegetation

This section deals with the influence of nutrient enrichment on the vascular vegetation. The influence of nutrients on the coexistence of bryophytes and vascular plants are dealt with in a later section 'Bryophytes – a sensitive subordinate group'.

In the comparative study of organic and conventional hedgerows there were no statistical differences in soil nutrients that could explain differences in species diversity (Paper I and II). Therefore the following section focuses on Papers III and IV.

5.1.1 Nutrient addition change soil chemicals

As expected, the mesocosm experiment revealed that nutrient enrichment resulted in significant change in soil N, conductivity and pH (Paper IV). This is in agreement with other studies (Wilson & Tilman 1991, Mahaila & Hera 1994, Morecroft et al. 1994) that found nutrient additions to alter soil chemistry.

5.1.2 Nutrients reduce species diversity

The primary source of nutrient enrichment of semi-natural vegetation of the agricultural landscape is misplacement of e.g. slurry and artificial fertilisers derived from agricultural activity. The nitrogen level has been found to reach 15 g N m^{-2} in field boundary vegetation (Tsiouris & Marshall 1998). Another source of nutrients is from NH_3-deposition, which easily reaches 1.5 g N m^{-2} per year in the Danish landscape (Bak et al. 1999). However, in wood edges that has a similar vertical structure as hedgerows nitrogen deposition rates of 10 g N m^{-2} per year have been measured (Beier & Gundersen 1989). This means that hedgerow vegetation in a worse case scenario can receive 25 g N m^{-2} per year (15 + 10), which is more than twice the highest concentration used in the Ebdrup-experiment.

The nutrient enrichment concentration used in the two experiments (0, 2.5 and 10 g N m^{-2}) resulted in increased productivity and decreased species diversity (Papers III and IV). This is in agreement with the results obtained in numerous grassland studies (e.g. Willis 1963, Grime 1979, Wilson & Tilman 1991, Foster & Gross 1998, Gough et al. 2000). Nutrient enrichment has also been shown to decrease the species diversity of boundary vegetation (Kleijn & Snoeijing 1997, Kleijn & Verbeek 2000). As an exception, some studies have not detected changes in species diversity after nutrient enrichment (e.g. Morecroft et al. 1994) but this can be ascribed to the delay of vegetation response (van der Woude et al. 1994, Milchunas & Lauenroth

1995). Waide et al. (1999) emphasised the need for a mechanistic understanding of the typically observed relationship between productivity and species diversity. One of the most controversial mechanisms behind this relationship is increased (Grime 1979) or constant (Wilson & Tilman 1991) competition along a gradient of productivity (Grace 1991, Goldberg & Novoplansky 1997). Nutrient enrichment has nevertheless repeatedly been found to result in increased asymmetry of competition (e.g. Austin & Austin 1980, Keddy et al. 1997) and exclusion of subordinate species resulting in dominance by a few species with a high competitive ability (e.g. Mahmoud & Grime 1976, Grime 1979). The competitive exclusion hypothesis is, however, questioned by Stevens & Carson (1999) who suggest a more random procedure resulting in the assemblage-level thinning hypothesis. It is, however, questionable whether the assemblage-level thinning hypothesis has general validity or is restricted to a first-year succession of ruderals.

Increased litter and living biomass as a consequence of nutrient enrichment has been suggested as the critical determinants of diversity (Willis 1963, Bobbink 1991). Excessive biomass accumulation may lead to unfavourable light levels (Facelli & Pickett 1991, Tilman & Wedin 1991, Foster & Gross 1998, Jacquemyn et al. 2003) near or below the light compensation point of some species. As light is vital for phototrophic organisms, some species will go extinct if light levels drop below the light compensation point. A recent experiment found that light alone did not control species diversity and therefore rejected the light compensation hypothesis. Rather, support was found for the density hypothesis (that predicts a more random loss of species) (Rajaniemi 2002). In this study, light was however only reduced by 50 % and it is doubtful whether the new light level affected competition of the included species seriously. Another mechanism explaining the effect of nutrient induced litter accumulation is the recruitment inhibition of subordinate species (Foster & Gross 1998). Increasing amounts of litter, in particular, have also been suggested to influence plant species diversity in other ways (Pigott 1982). Results obtained in my study showed that nutrient enrichment resulted in litter accumulation at low disturbance level (Paper IV). Compared to living biomass, litter explained more of the variation in species diversity (Paper IV) and litter *per se* has been found to negatively influence some species. A high nutrient level reduces diversity by reducing the number of colonising species and/or persisting species (Paper III).

In a study by Gough et al. (1994) covering natural marsh communities biomass and litter production was found to explain only a small amount of the variation (2 %) in species diversity. In marsh communities, however, gradients in salt concentration and disturbance may be more important than natural gradients in productivity. Another explanation may be that natural productivity gradients only occasionally reach the levels experienced under artificial fertilisation regimes. Supportive to this interpretation is the finding of Ejrnæs & Bruun (2000) that the highest plant species diversity in Danish semi-natural grasslands occurs in the naturally productive grasslands on moist calcareous soils.

In my studies, nutrient enrichment explained more variation in species diversity than disturbance (Papers III and IV). This supports that a reduction or removal of nutrients should be of high priority in the conservation and restoration of grass-dominated communities. Therefore, a no-fertiliser buffer zone (Schippers & Joenje 2002) and immediate termination of nutrient enrichment of all small biotopes and permanent grassland is recommended.

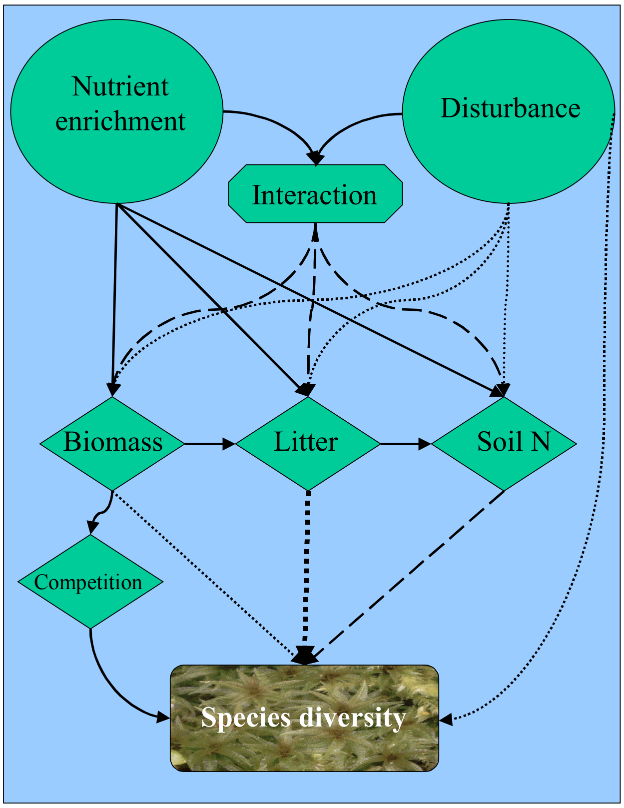

Figure 2. Nutrient enrichment-disturbance model indicating the relations found in present study. The solid lines indicate mainly positive relations, punctuated lines indicate mainly negative and intermediate punctuated lines indicate unknown or dependent relation.

5.2 Disturbance and vegetation

This section deals with the effects of disturbance on vascular vegetation. The coexistence between bryophytes and vascular plants and the specific relationship to disturbance are dealt with in the following section: "Bryophytes a sensitive subordinate group?"

Disturbance has two important functions for biological conservation in the agricultural landscape. In the small isolated "hot-spots" disturbance is often needed to prevent encroachment and maintain biodiversity. In other plant communities of the landscape that receive nutrient from the agricultural activity disturbance may compensate the critical influence of nutrients by partly prevention of competitive exclusion and recruitment inhibition.

5.2.1 Disturbance and soil variables

In my study, two types of disturbance were included: herbicide application and repeated defoliation. These two disturbance treatments are not directly comparable but both fulfilled the disturbance definitions put forward by Grime (1979), Collins et al. (1995) and Mackie & Currie (2000). Moreover, being so different they serve as a qualitative validation of the generality of disturbance effects on vegetation.

The defoliation disturbance was included as a binary variable (defoliation vs. not defoliation) and is described further below in the bryophyte section (Paper III). The herbicide disturbance was included as a four-levelled gradient in herbicide dose. Herbicide disturbance differs from e.g. grazing and mowing because plant material remains *in situ* and it is therefore more comparable to e.g. frost and drought with a loss of solutes (Grime 1977, 1979). Therefore, it was unexpected to find soil conductivity to be significantly negatively affected by herbicide application (Paper IV). Other studies reported disturbance to increase soil nutrient release (Collins et al. 1985). The most plausible explanation of lower conductivity is disturbance-related decrease in litter and a following smaller decomposition and nutrient release from dead plants (Paper IV).

5.2.2 Relationship between disturbance and species diversity

Grassland experiments (Grace 1999, Kahmen et al. 2002, Jacquemyn et al. 2003) and field observations (During & Willems 1986, Porley 1999) have proposed that some kind of disturbance is necessary to prevent a decrease in species diversity. The importance of disturbance is however debated and it has recently been concluded that disturbance is unlikely to account for more than a small amount of variation in species diversity (Mackey & Currie 2000). It is nevertheless basic biological knowledge that succession of plant communities will result in changed species composition (e.g. Gleason 1926) and species diversity. Therefore some degree of disturbance is necessary to maintain species diversity of most plant communities. I found the degree of disturbance required to maintain species diversity to be strongly dependent on the nutrient status (Paper IV).

The qualitative effect of disturbance on species diversity is in vegetation studies often presented as a hump-back, unimodal or a peaked relationship. This was originally called the 'intermediate disturbance hypothesis' that predicted maximum species diversity at intermediate disturbance (Grime 1973, Huston 1979). A part of this hypothesis has been applied almost as a convention that predicts disturbance to reduce the competitive ability of dominant species (e.g. Grime 1973, Huston 1979, Zobel 1992, Turkington et al. 1993, Jacquemyn et al. 2003).

My study, however, showed that the effect of disturbance depended on nutrient level (Fig. 3 and Paper IV). At infertile conditions only a minor peak in diversity could be observed along a disturbance gradient. My results therefore confirmed the models and a review presented by Mackey & Curie (2000), which predicted that a monotonic relationship is more common than unimodal responses. The most plausible explanation for a monotonic relationship in infertile conditions is a selective extinction without recruitment of new species.

The sensitivity to herbicide has been shown to differ between vascular plant species (Marrs et al. 1991, Marrs et al. 1993, Marrs & Frost 1997) and bryophytes (Stjernquist 1981). Small doses of herbicides have furthermore been shown to lead to extinction of some vascular species (Kleijn & Snoeijing 1997). Therefore the most plausible explanation of a negative herbicide disturbance effect on species diversity is higher extinction rates of sensitive species (Paper IV).

In fertile conditions the effect of disturbance was almost opposite to infertile conditions with a positive monotonous relationship to species diversity (Paper IV). The reason for this pattern is probably an increasing reduction of dominant species which allow recruitment of subordinate species e.g. *Chenopodium album* or persistence of established species (especially nutrient loving species not belonging to the plant community) (Paper IV).

5.2.3 Increased recruitment

Some types of disturbance (mowing, burning, herbicide and plant removal) have been shown to increase the recruitment of plant species (Eriksson & Ehrlen 1992, Eriksson & Eriksson 1997, Kiviniemi & Eriksson 1999, Jutila & Grace 2002) whereas another type of disturbance (cutting without hay removal) has been shown to decrease the recruitment of vascular species (Jutila & Grace 2002). In my study, a disturbance-related change in recruitment was dependent on nutrient level (Paper IV). High disturbance level resulted in the highest recruitment of species at high nutrient level (Paper IV). A possible explanation for this relationship is discussed in section 8.2.6.

5.2.4 Reduced biomass

Accumulation of biomass leads to unfavourable light condition, and a recent study found variations in light penetration to the soil surface to explain more than 50 % of the variation of species diversity (Jutila & Grace 2002).

Herbicide disturbance thereby became the factor explaining the largest part of the variation in total biomass (Paper IV). However, the effect of herbicide was not the same on living biomass and litter. Herbicide disturbance showed a significantly negative effect on litter accumulation (Paper IV) but no significant effect on living biomass. It was unexpected to find that litter was more influenced by disturbance than living biomass. Litter has, however, in other studies also been found to be a significant factor influencing grassland vegetation processes (e.g. Foster & Gross 1998, Jutila & Grace 2002). My interpretation of the results is that litter is an accumulation of dead plant biomass from previous years and therefore expresses a time aspect in the nutrient induced biomass increase.

5.2.5 Herbicide disturbance

Despite a vast number of herbicide studies, only a small number have investigated the effects of unintended drift of herbicide on the boundary vegetation. Field margins and non-target plants can easily receive up to 20-25% of the applied herbicide field dose (de Snoo & de Wit 1998, de Snoo 1999, Boutin et al. 2001). This may have serious impacts on the diversity and cover of non-target species (Marrs et al. 1989, 1991, Marrs & Frost 1997, Hald et al. 1994, Fletcher et al. 1996, Fischer & Milberg 1997, Jobin et al. 1997, Kleijn & Snoeijing 1997, de Snoo 1999, de Snoo & van der Poll 1999). The above-mentioned studies are in agreement with the result presented in Papers I and II, where higher species diversity was found in organic hedgerows than in conventional hedgerows (see more details in a following hedgerow section). On the other hand, some studies found that reduced herbicide drift was of minor or undetectable importance for the boundary flora (Hald 1988, Marshall 1992), which can be explained by the delayed responses of established plant communities (Pigott 1982, van der Woude et al. 1994, Milchunas & Lauenroth 1995). Some studies found no clear positive relation between number of species and absence of herbicide (Jobin et al. 1997, Kleijn & Verbek 2000, Kleijn & Snoeijing 1997, Wilson & Tilman 2002), which may help explaining the findings presented in Paper IV, i.e. that herbicide drift disturbance showed an ambiguous effect on species diversity, depending on the nutrient level.

The drift of herbicides has also been found to influence other organisms than plants (Hald et al. 1994, Haughton et al. 1999, Jobin et al. 1997, Boutin & Jobin 1998).

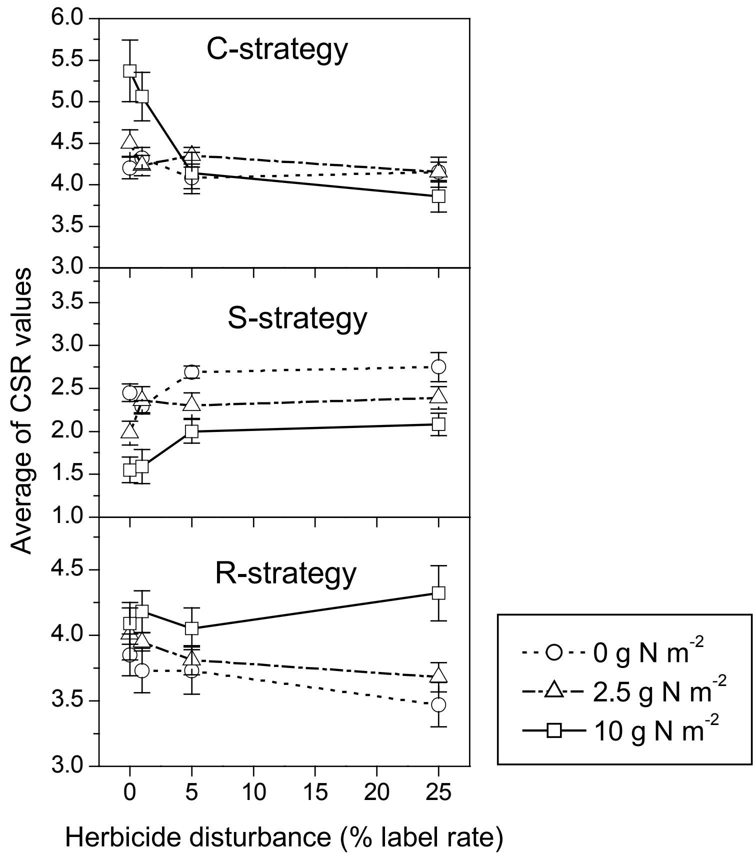

Figure 3. The change in unweighted average of C-S-R values (Grime 1979) of the Ebdrup-experimental sample plots (n = 120) with four herbicide disturbance levels and three nutrient levels.

5.2.6 **Stress vs. disturbance**

Stress is defined as 'the external constraints, which limit the rate of dry matter production of all or parts of the vegetation' (Grime 1979). Stress limits plant production to a continuously low level (Grime 1988), due to shortages of light, water and mineral nutrients or sub-optimal temperatures (Grime 1979). Stress and disturbance function in a similar way (e.g. Grime 1973, 1979) namely by reducing the dominance of competitive species. Therefore the short-term effect of a disturbance or a stress situation may influence the vegetation in a similar way. Herbicide application has naturally not contributed much to the evolution of plant species. Nevertheless, herbicides have been described as a disturbance agent (Grime 1979, Jutila & Grace 2002).

Data from the Ebdrup-experiment (Fig. 3) showed that increased herbicide disturbance resulted in an expected decreased in average C-values of sample plots. The decrease in C-values was followed by an increase in average of S-values. On the other hand, the effect on average R-values of sample plots differed between nutrient levels. At the highest nutrient levels there was an increase in R-values with increasing herbicide dose, whereas at lowest and intermediate nutrient levels R-values were decreasing (Fig. 3). As mentioned above (Section

8.2.2.) high nutrient status and high disturbance level result in recruitment of nutrient loving species (e.g. *Chenopodium album*) from outside the research area. It seems likely that it can be explained by a mass effect (Shmida & Wilson 1985, Ejrnæs & Poulsen 2001b) from the surrounding landscape. Obviously, species such as *Myosotis stricta* and *Trifolium arvense* thrive under infertile and disturbed conditions but their occurences in the landscape are more rare than *Chenopodium album* which can explain the lower recruitment of ruderals from infertile habitats in my study. More research is however needed to disclose the mechanisms.

5.3 Interactions between nutrient enrichment and disturbance

Statistically significant interactions were found between herbicide disturbance and nutrient enrichment on productivity, species diversity and bryophyte abundance (Paper IV). We found no statistically significant interaction between nutrient enrichment and disturbance in the microcosm experiment (Paper III), but more replicates would probably have shown a significant interaction ($n = 4$; p-value = 0.08; Paper III).

5.3.1 Effects on productivity

There was a marked difference in productivity between the three nutrient levels in undisturbed plots. Following a disturbance event, productivity decreased in the most fertile plots (Paper IV). At lowest nutrient level, disturbance had almost no effect on biomass (Paper IV). The most striking observation was a tendency for a lower biomass at highest nutrient and disturbance level compared to infertile conditions (Paper IV).

5.3.2 Effects on species diversity

The effect of disturbance on species diversity varied along the nutrient gradient (Paper IV). At infertile conditions disturbance had a negative influence on species diversity. At intermediate nutrient level the disturbance effect was unclear. At the highest nutrient level disturbance had a positive influence on the species diversity (Paper IV).

The relationship between productivity (litter and biomass) and species diversity varied along the disturbance gradient (Paper IV). An analysis of all data revealed no significant relation between productivity and species diversity, but when data was divided into different groups of disturbance levels significant relations appeared. The most significant (negative) relation was between litter and species diversity at low disturbance level, whereas at high disturbance level the relationship was significantly positive (Paper IV).

5.3.3 Effects on bryophytes

The frequency of bryophytes was clearly negatively influenced by nutrient enrichment at 0, 1 and 5 % disturbance level, whereas at 25% disturbance level bryophytes were favoured by nutrient enrichment.

The interaction effect on bryophyte abundance is explained by the complete change in nutrient response at highest disturbance level compared to low disturbance level.

The observed tendency towards a positive relation between nutrient status and bryophyte abundance at high disturbance level has not been described earlier for grassland. The reason may be that a high nutrient level offers a more favourable microclimate because of a faster recruitment at high disturbance (as mentioned in section 8.2.6). This is an example of the fine balance between bryophytes and vascular plants, where bryophytes in this situation benefit from the presence of vascular plants. When a low nutrient level is combined with a high disturbance, the vegetation is very sparse and there is much exposed soil. The exposed soil, which consists of pure dry sand without organic matter, is probably too unfavourable for fast recruitment and growth of bryophytes. A direct beneficial effect of nutrient on bryophytes cannot, however, be excluded, but will require further research.

5.3.4 Other studies of interaction

Although both disturbance and nutrient enrichment are well-known factors controlling species diversity, few studies have included simultaneous manipulations of the two factors. In a vegetation experiment which included a gradient in both nutrient level and herbicide disturbance, no interaction between the two parameters was found (Kleijn & Snoeijing 1997). The lacking interaction might, however, be due to the relative low number of replicates (n = 4). Another recent vegetation study (Wilson & Tilman 2002), which also included a gradient in both nutrients and tilling disturbance (0, 25, 50 and 100%), reported results that diverged from those presented in the present study. Wilson & Tilman (2002) found a significant unimodal relationship between disturbance and species richness at infertile conditions with a peak between 25 and 50 % disturbance. In contrast to them I found a very small peak in species diversity at 1 % disturbance. It is possible that the difference in disturbance intervals can explain this discrepancy.

Wilson & Tilman (2002) reported species diversity to decrease with nitrogen addition regardless of disturbance level. This is in sharp contrast to the present study where I found higher species diversity at highest disturbance level at fertile compared to infertile condition. A possible explanation of this difference could be the duration of the experiments. Wilson & Tilman (2002) presented data from eight years whereas the present study presents data from only three growing seasons and thereby presents a snapshot of the early succession. Another explanation may again be the different use of disturbance intervals.

Finally, the most interesting result of the eight-year experiment performed by Wilson & Tilman (2002) was a marked tendency of increased species diversity in undisturbed plots at the highest nutrient level. This tendency supports the findings in Papers I & II. Consequently, it cannot be excluded that the absence of herbicide disturbance in organic hedgerows actually is contributing to the higher species diversity found in organic hedgerows (Papers I & II). The study of Wilson & Tilman (2002) lasted eight years, which could explain some of the difference to present study.

On the basis of the above-mentioned and documented interactions between nutrient enrichment and disturbance it is possible to conclude that the classical 'hump-back' relationship between disturbance and species diversity should be applied with caution. The pattern of species diversity clearly depends on location within the nutrient-disturbance matrix.

5.4 Bryophytes, a sensitive subordinate group

Bryophytes are rarely included in grassland vegetation studies. In one study, they have been found to respond to almost the same variables as vascular plants in grassland (Ejrnæs & Poulsen 2001a). Another study based on a small amount of grassland sample plots and a doubtful multivariate analysis concluded, however, that bryophytes were largely responding to other factors than vascular plants (Herben 1987). Overall vascular plant diversity decreases with increasing latitudes (Grime 1979), which means a reduced national species pool (*sensu* Zobel et al. 1998). Therefore it is recommended to include bryophytes in vegetation studies at these high latitudes (Diekmann 1995).

Bryophytes are claimed to be good indicators of habitat quality and ecological functioning of habitats (Carroll et al. 2000, Hylander et al. 2002). A higher number of rare bryophytes and a higher number of bryophyte species were found in areas with lower land use intensity (Zechmeister & Moser 2001). The lack of sclerenchyma and their size makes most bryophytes extremely vulnerable to competitive exclusion by vascular plants. For this reason bryophytes may act as early indicators of environmental change. In grassy plant communities bryophytes may be considered sensitive subordinate species that coexist in a subtle balance with vascular plants. This balance is, however, spoiled when nutrient enrichment starts (Paper IV).

5.4.1 Nutrient

Nutrient enrichment was shown to have a negative impact on both abundance (Papers III and IV) and diversity (Paper III) of bryophytes. The frequency of bryophytes was approximately 100 % higher at infertile condition compared to fertile condition (mean frequency was 6.15, 5.15 and 3.07 at 0, 2.5 and 10 g N m^{-2} respectively).

High nutrient levels without disturbance led to the lowest species diversity and to complete bryophyte extinction in 50 % (Paper III) and 30 % of sample plots (Paper IV). Vascular plant biomass turned out to be inversely related to bryophyte abundance (Paper III), which has also been found in other studies (e.g. Willis 1963, Jeffrey & Pigott 1973, Bergamini et al. 2001). On the other hand, when litter was separated from biomass (Paper IV) litter explained a greater and significant part of the variation in bryophyte abundance (Paper IV). Litter has in other studies explained the decrease of subordinate vascular species (Foster & Gross 1998, Grace 1999, Gough et al. 2000).

No relationship was found between bryophyte favourability and litter in a wetland study by Bergamini et al. (2001) but was reported to be of relevance by Quene & Bakker (1988). The mechanism behind the harmful influence of litter has been mentioned earlier for vascular plants (section 8.1) and is probably similar for bryophytes. It is, however, not all studies that have found decreases in bryophyte cover to be explained by a changed competitive balance between the two plant groups as a result of nutrient enrichment of grassland (Carroll et al. 2000). This indicates a possible direct negative influence of nutrients on bryophytes. In my study, nutrient level also explained more of the variation in frequency of bryophytes than litter and biomass together (Table 5 in Paper IV). This indicated that it cannot be excluded that nutrient *per se* is responsible for some of the variation in bryophytes. This deserves further research but some of the probable mechanisms are: 1) toxic effects (Carroll et al. 2000), 2) differences in germination of spores and 3) bryophyte competition (Rydin 1997).

5.4.2 Disturbance

Decreased grazing disturbance of dry grassland during last century is suggested to be responsible for a decline in grassland bryophytes (During & Willems 1986, Porley 1999). In the present Ph.D.-study the relationship between grazing (defoliation) and bryophyte diversity is investigated in more detail. On one hand, herbicide disturbance appeared harmful to the abundance of bryophytes under infertile conditions (Paper IV). On the other hand, at high nutrient levels, disturbance resulted in a positive influence on the frequency of bryophytes. This means that disturbance can both increase and decrease bryophyte abundance depending on the nutrient level (Paper IV). Bryophyte species diversity thus clearly depends on location within the nutrient-disturbance matrix.

Disturbance has, however, been shown to prevent complete bryophyte extinction (Paper III and IV). Disturbance did, however, not fully compensate for the negative effect of fertilisation (Paper III). Fertilisation resulted in a changed species composition and 41 % of the species, primarily acrocarps, could not persist or colonise even when vascular plant biomass was reduced (Paper III). Five out of 11 acrocarps were unable to persist/colonise at high nutrient levels even with defoliation (Paper III). In fact, defoliation at high nutrient levels resulted in lower cover and fewer species of bryophytes than low nutrient levels without defoliation. This means that defoliation disturbance is not sufficient to conserve or restore grassland bryophyte species diversity in nutrient polluted grasslands. Results obtained in this Ph.D.-project therefore support the findings and the concerns for grassland bryophytes expressed by During & Willems (1986) and Ejrnæs & Poulsen (2001b). The results also emphasise the current particular threats to acrocarp bryophytes (Longton 1992) and species with limited dispersal potential. In Denmark the agricultural landscape favours pleurocarps like e.g. *Brachythecium rutabulum,* which has a relative high growth rate (Furness & Grime 1982) and high dispersal potential. High densities of pleurocarps with these traits in the agricultural landscape will be potentially invasive in semi-natural habitats due to increased spore pressure and a resulting mass effect (Ejrnæs & Poulsen 2001b).

5.4.3 Hedgerows

In only a few cases have bryophytes been included in the study of hedgerow vegetation (e.g. Richards 1928). In the comparison of organic and conventional hedgerows, there was a significantly higher species diversity of bryophytes in the organic hedgerows than in similar conventional hedgerows (Paper II). The observed difference cannot be explained by differences in nutrient levels, as measured soil variables showed consistently high and similar nutrient status in both farm types (Papers I and II). While the obvious difference in management regime is presence/absence of pesticides, especially herbicides, the Ebdrup-experiment did not confirm the hypothesis that herbicides cause decreased bryophyte diversity. In fact, high disturbance levels led to increased bryophyte abundance under fertile conditions. Some of the plausible explanations for the higher bryophyte diversity in organic hedgerows compared to conventional hedgerows may be differences in species pools, litter accumulation or simply that boundary vegetation on conventional farms experiences higher herbicide levels than the ones used in the Ebdrup-experiment. More research is needed in this area.

The Ph.D.-study has confirmed that bryophytes are sensitive indicators of changes in grassland vegetation due to eutrophication and disturbance. Bryophytes have been suggested as perfect representatives of the subordinate species group because they respond similarly to nutrient and disturbance like subordinate vascular plants. This suggestion is confirmed by a recent vegetation study in the agricultural landscape of Scotland (Wilson et al. 2003). Here they found that the abundance of bryophytes was easier to predict than that of vascular plants.

It can be concluded that to maintain and restore bryophyte diversity in the Danish landscape the following initiatives are needed:

- Firstly, the nutrient pollution of small biotopes and permanent grassland should cease.

- Secondly, biomass removal is of high priority (cuttting without biomass is not enough) and should be used to deplete habitats of excessive nutrients (e.g. in road verge management).

- Finally, conversion to organic farming will have a beneficial effect on some bryophytes, for complex reasons not fully explained by this project.

In Denmark, bryophytes make up a neglected group of organisms. Results obtained in this project emphasise the concern for bryophytes in Denmark. A red list of bryophytes has not been worked out and the national plan for future bryophyte monitoring includes only two bryophyte species, which are very rare in Denmark, but are of European interest (Anon. 1992). National monitoring of nature types in Denmark (Søgaard et al. 2003) does, however, incidentally include bryophytes as indicators. The most monitored bryophyte species in the monitoring program of nature types is nevertheless the invasive *Campylopus introflexus*, occurring in dunes and heath communities.

Bryological studies have contributed importantly to the development of the current understanding of the means by which plant community structure is regulated (Watson 1980), but there is an urgent need for bryophyte research, monitoring in the landscape and creation of a national red list.

5.5 Hedgerows as plant dispersal corridors?

Linear elements have high species diversity in proportion to their area (Skånes 1990), and linear biotopes are claimed to contribute significantly to diversity in different landscape (Framstad & Fry 1997, Bunce et al. 1999). The function of hedgerows as dispersal corridors of forest species (McCollin et al., 2000, Smart et al. 2001) and refuges of grassland species (Smart et al. 2002) has recently been described.

On the other hand, there are general indications of decreasing plant diversity in hedges due to intensification of agriculture (Bunce et al. 1994). Rare and endangered species are today normally missing in hedgerows and corridors (Forman 1995). Nutrients and herbicides have been suggested to be responsible for this negative trend in field boundary habitats (e.g. Kleijn et al. 1997, Kleijn & Veerbek 2000). High levels of nutrients close to arable fields have been suggested to favour only a few dominating plant species (e.g. Hald et al. 1994, Kleijn et al. 1997, Kleijn & Veerbek 2000). In this Ph.D.-study I have studied the effects of low habitat quality and poor dispersal opportunities for the plant diversity in the hedgerows of the Danish landscape (Paper II). A DCA-ordination of almost all Danish hedgerow vegetation plots (n = 687) together with relevant reference plant communities of the Danish landscape revealed that the most important vegetation gradient correlated with nutrient status. The hedgerow plots were placed in the most fertile end of the ordination space, together with plant communities with very low naturalness (Paper II). This impoverishment of hedgerow vegetation was supported by another analysis of Danish hedgerows (Tybirk et al. 2001). In this study Tybirk et al. (2001) report a disproportionate large numbers of competitive and ruderal species among the 30 most abundant species. This is in contrast to the national Danish plant species pool, where species adapted to infertile condition is the prevailing strategy (Ejrnæs 2000).

In Denmark, changes in species composition of plant communities in the agricultural landscape have not been monitored and it is difficult to document the intensity of change. Some evidence, such as old excursion reports, however, do indicate that hedgerow vegetation have changed considerably since the beginning of last century (Andersen 1910, Warming 1919).

Dominance by a few plant species results in reduced recruitment of most other species. Aspects of recruitment problems of grassland vascular species have been widely studied (e.g. Eriksson & Ehrlen 1992, Eriksson & Kiviniemi 1999, Kiviniemi & Eriksson 1999). Recruitment problems of bryophytes in grassland have, however, not attracted much scientific attention. Recruitment problems of native grassland plant species are dealt with in paper III with bryophytes as test organisms representing the group of subordinates.

Dispersal of plant species in modern Danish conventional hedgerows from 'hotspot' islands therefore may be expected to be very limited and probably without any importance.

5.6 Organic farming, a lifeline for plant species diversity?

No difference in soil nutrient levels between organic and conventional farms was found in this study (Papers I and II). Furthermore, the two farming systems showed no differences in structural parameters of importance for biodiversity. In spite of this, statistically significant higher species diversity was found in organic hedgerows than in conventional. The higher diversity covered more bryophytes, more weeds and ruderals, and more species from semi-natural habitats (Papers I & II).

The Ebdrup-experiment was established to either reject or accept the hypothesis that the field observations could be explained by unintended herbicide doses. The experiment, however, did not support the findings from the comparative study of organic and conventional hedgerows. In the experiment, herbicide disturbance resulted in higher species diversity at high nutrient levels as the nutrient level also found in the hedgerows.

A recent vegetation study from the agricultural landscape of Scotland supports the results from the experiments and concludes that use of herbicide was an insignificant predictor of plant diversity (Wilson et al. 2003). Other studies confirm that use of herbicides can have a positive diversity effect when applied on clonal vegetation (Pakeman & Marrs 1992, Marrs et al. 1998).

This suggests that herbicides may have a dualistic effect on species diversity of semi-natural vegetation that depends on nutrient level and properties of the vegetation. The dualistic effect of herbicide underlines the insufficiency in use of species diversity as the only parameter of an evaluation of naturalness.

In the repeated "Countryside Survey" in the UK, Bunce et al. (1999) found a significantly reduced species diversity of 14% in hedgerows during a 12-year period. That study shows an interesting similarity between species that have declined significantly and species that was found significantly more frequent in organic hedges (Tybirk et al., 2003, Paper II).

Different mechanisms may explain the disagreement between field observations and the experiment. These are described below:

5.6.1 Use of herbicides

A plausible explanation as to why the result from the experiment (Paper IV) could not support the significant difference in species diversity from Papers I & II, is that hedgerow vegetation on conventional farms occasionally receive herbicide concentrations higher than the 25 % applied in the experiment. A British survey of farmers showed that ca. 60 % of the farmers applied herbicides directly in the hedgerow bottom to control weeds (Marshall & Smith 1987 cited in Boatman 1989). Interviews with Dutch farmers likewise showed that directly spraying in field margins is a common phenomenon (de Snoo 1999). Therefore it cannot be excluded that some of the hedgerows studied may have received up to 100 % of field dose and which may have resulted in a higher extinction rate that was included in the experiment. Furthermore, as part of the standardised hedgerow establishment all conventional hedgerows received 100 % of herbicide as part of the initial hedgerow cultivation. It is highly plausible that such a herbicide application, even after 10 years, may still affect the composition of hedgerows today.

5.6.2 Use of nutrients

Another explanation is higher nutrient supply in conventional hedgerows. Even if there were no differences in measured soil nutrients, higher nutrient application cannot be excluded on conventional farms. If the vegetation has absorbed the nutrient surplus it will result in higher biomass on conventional farm leading to competitive exclusion and higher extinction rates. The method chosen to record vegetation in the hedgerows (Papers I and II) unfortunately does not give such information. Future vegetation studies in a similar comparative study should therefore include species biomass.

5.6.3 Dispersal

A great deal of differences in species diversity was due to significantly more weedy and ruderal species in organic hedgerows. Organic fields contain a higher diversity of weedy and ruderal species (Hald & Reddersen 1990, Hald, 1999; Rydberg & Milberg, 2000, Mäder et al. 2002), which can explain a higher immigration rate of these plant groups from the field to the hedgerow bottom vegetation. On the other hand, the higher diversity of semi-natural species cannot be explained in the same way as weedy species. An alternative or complementary explanation is that organic farms enclose a larger species pool, which for example can be a result of a more diverse landscape configuration e.g. with less drainage, more small biotopes, distance to natural or semi-natural habitats or higher coherence on organic farms. A Dutch study on landscape quality that include coherence as an important parameter indicated (n = 8) that organic farms had a higher landscape quality (Hendriks et al. 2000). More research on the distribution of farms is needed to confirm this as an explanation. Despite the barriers of movement encountered by many plant species in modern fragmented landscapes (Primack & Miao

1992, Wiens 2001) there is a higher probability that non-weedy species have dispersed from nearby semi-natural habitats according to classical island biogeography (MacArthur & Wilson 1967) if the distance between sources and target are smaller. Some studies indicate relations between landscape ecological features and species diversity (Dzwonko & Loster 1988, Skånes 1990, Honnay et al. 1999, Bruun 2000) and species composition (Dzwonko 1993, Dzwonko & Loster 1997, Graae 2000, Le Coeur et al. 1997, Le Coeur et al. 2002). In this study hedgerows were positioned close to each other in the same type of landscape and differences in species diversity can hardly be explained by differences in the landscape context but more detailed landscape research is needed to fully reject an influence of the spatial arrangement.

In addition it cannot be excluded that significantly higher population density of potential dispersal vectors (e.g. birds) on organic farms (e.g. Christensen et al. 1996) result in higher immigration rates of plant species in organic hedgerows.

An experiment of Wilson & Tilman (2002) with inclusion of both disturbance and nutrient enrichment found after eight year a marked tendency to increased species diversity at zero disturbance and high nutrient level. This finding indicate a support to the findings in Papers I & II. Therefore it cannot be fully excluded that absence of herbicide drift doses in organic hedgerows actually contribute to the higher species diversity in organic hedgerows (Papers I & II). A prolongation of the experiment could confirm if continuity would increase the species richness with no herbicide disturbance.

5.6.4 Soil disturbance

Another potential explanation for the higher species density in organic hedgerow could be that related to the fact that soil disturbance normally is higher in organic hedgerows. In this study, however, conventional hedgerows were associated with disturbed cereal fields whereas the organic hedgerows often had grass leys as neighbours. A differences in soil disturbance regime is therefore not likely to explain the differences in species diversity.

5.6.5 Extinction rates

Finally it is worth repeating that several studies have shown that even small drift doses of herbicide can have extinction effects on sensitive plant species (Marrs et al. 1989, Kleijn & Snoeijing 1997). More research is however needed to identify herbicide sensitivity of semi-natural species. Differences in sensitivity between plant species (Marrs et al. 1989, Kleijn & Snoeijing 1997) underline that species diversity must be accompanied by a study of species composition. A narrow focus number of species could result in a risk of ignoring extinction of sensitive species.

No use of herbicides will lower the probability of extinction of sensitive species. On the other hand the present study confirmed that the nutrient level enrichment was mainly responsible for the variation (decline) in species diversity (Papers III & IV). Papers I & II strongly indicate that organic farms also have too high nutrient levels in their small biotopes. Therefore it is strongly recommended to introduce a 'no nutrient buffer zone' (e.g. 20 m) around all organic fields as a natural part of organic farm management.

Organic farming may be considered a first, yet small, step in a more sustainable direction. More research is however needed to pinpoint the mechanisms behind the higher species diversity on organic farms and to investigate whether the difference is also significant from a conservation point of view – i.e. does organic agriculture prevent extinction of species that are threatened locally or regionally?

6 Conclusions and recommendations

My study has been devoted to an investigation of the effect of nutrients and disturbance on species assembly in grass-dominated vegetation with special focus on bryophytes. Field observations were combined with two vegetation experiments, carried out to test hypothesis derived from the field. The results that I consider most important are summarised below.

There were no differences in soil nutrient levels or structural parameters between investigated organic and conventional farm. In spite of this a statistical higher species diversity were found in organic hedgerows. The higher diversity enclosed more bryophytes, more weedy and ruderals, and more species from semi-natural habitats. Some of the species that are declining in the British agricultural landscape were however significant more abundant in Danish organic hedgerows. Absence of herbicide on organic farms was hypothesised as explaining factor. A mesocosm experiment was created to confirm or reject the hypotheses with inclusion of a nutrient and a herbicide disturbance gradient. However, this experiment could not confirm that spray drift doses alone were responsible for the lower diversity in conventional hedgerows. The additional plausible explanations of a higher species diversity in organic hedgerows is: 1) A larger species pool, 2) Use of larger herbicide doses in conventional hedgerow than the tested doses, and 3) Higher rates of dispersal vectors. Organic farming is nevertheless suggested as a first, yet small, step in a more sustainable direction.

An overall comparison of Danish hedgerow vegetation with other nature types highlighted the problems of low habitat quality and poor dispersal abilities in the hedgerows of the Danish landscape.

The experiment presented also other important results. For example nitrogen enrichment resulted in changed chemical soil properties, higher total biomass and in particular higher litter accumulation. Nutrient enrichment was in comparison to disturbance best to explain the variation in species diversity. It was moreover concluded that nutrient enrichment is most responsible for decreased plant diversity and decreased colonisation and persistence of bryophytes. This means that a removal of nutrients is of highest priority in the conservation and restoration of dry grassland plant communities.

Herbicide disturbance resulted in changed chemical soil properties and reduced litter accumulation and influence on species diversity.

Statistical significant interactions were found between herbicide disturbance and nutrient enrichment according to productivity, species diversity and bryophyte abundance. Results moreover show that the classical "humb-back" relationship between disturbance and productivity and species diversity should be applied with caution because it varied along the nutrient gradient. The pattern of species diversity clearly depends on location within the nutrient-disturbance matrix.

Results reinforce bryophytes as a sensitive indicator group of detrimental changes in the grassland vegetation. Vascular biomass was negative related to bryophyte abundance. Disturbance showed to prevent complete bryophyte extinction, disturbance did however not fully compensate for the negative effect of nutrient enrichment.

Result from the present Ph.D. project conclude that maintaining and restoring bryophyte diversity and other subordinate species in the Danish landscape require:

1. Immediately termination in nutrient enrichment of all small biotopes and permanent grassland e.g. by establishing a "no nutrient buffer zone" around all fields, including organic fields.

2. Biomass removal is important but not enough (e.g. in road verge management) to maintain and conserve all species.

3. Conversion to organic farming will have a beneficial affect on some species.

7 Future research and gaps in knowledge

The last data from the Ebdrup-experiment were collected in autumn 2003 and the last data from the soil analysis were completed in November 2003. On account of that, much data analysis can still be made on the unique set of data testing hypotheses. Further research will give vital insight into:

- Colonisation – extinction and turnover rates along the nutrient and disturbance gradients
- Differences in species composition in the disturbance-nutrient matrix with inclusion of CSR-values and plant function traits as predictor variables.
- The combined influence of nutrient and disturbance on community stability, resilience, persistence and invasiveness.
- Relationship between species composition of vegetation and species composition of invertebrates.
- The relationship between seedling establishment and final species composition along the gradient of nutrient and disturbance.
- Influence of nutrients and disturbance on plant species composition and the dependence on scale

A continuation of the Ebdrup-experiment could help to explain:

- The time factor in the colonisation – extinction and turnover rates along the nutrient and disturbance gradients
- Flowering and seed production at the plant community level and thereby ecosystem function in the disturbance-nutrient matrix.
- Whether herbicide drift doses have some indirect affect on the vegetation of e.g. via a reduction in seed dispersal vectors
- Whether the vegetation structure helps to explain increased productivity.
- Whether the auto-correlation between sample plots depends on successional stage

Further experiments should help to explain:

- Why bryophyte abundance is favoured by nutrients at high disturbance level
- Differences in sensitivity of bryophyte species to increased NH_3 deposition.
- Differences in the sensitivity of semi-natural species to herbicides

Finally, further field vegetation studies of hedgerows and road verges combined with comprehensive landscape analyses and analyses of farm management should help to explain the higher species diversity of organic farms and the role of continuity.

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Abstracts I-IV

Paper I

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Vegetation diversity of conventional and organic hedgerows in Denmark

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Abstract

Many attempts have been made to reduce the impact of modern conventional farming on the environment and semi-natural ecosystems. One of them is organic farming, known primarily for the absence of pesticides and artificial fertilisers. The objective of this study was to study and test the differences in the spontaneous vegetation of comparable hedgerows in the same area situated within organic and conventional farming systems. The hedge bottom vegetation was surveyed during August 2001 in 13 hedgerows of each farming system. Farming type had not changed on either side of the hedgerows for the lifetime of the hedges (10–14 years). Sampling was associated with a set of 16 measured environmental variables. In the two farming systems hedgerows were comparable in terms of landscape, age, soil type, nutrient status and width. A mixed analysis of variance (ANOVA) found no significant difference in measured soil and radiation variables between farming types. Farming types only differed in the use of pesticides. Significant differences between farming types in plant species diversity at alpha, beta and gamma levels were found. More species that are normal in semi-natural habitats were found on organic farms. There was an overlap in species composition between farming type, but a slightly higher species turnover on conventional farms. The ordination axes were highly correlated with calibrated Ellenberg values of fertility, light and soil moisture. Soil fertility and farming type were important factors to explain variation in species composition. Organic farming had a significantly reduced impact on hedge bottom vegetation compared to conventional farming. Higher extinction due to pesticide drift and immigration rates may be responsible for the significantly higher species diversity and different species composition in hedges on organic farms. The differences in species diversity and plant types are briefly discussed.

Keywords: Farming type; Fertility; Hedge bottom; Naturalness; Pesticide; Species diversity

Paper II

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Conservation value of the herbaceous vegetation in hedgerows – does organic farming make a difference?

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Abstract

The aim was to compare and test differences in the conservation value of hedge bottom vegetation on organic and conventional farms. The studied hedgerows (28 organic and 28 conventional) were on average 14 years old and established in the same way, except that organic hedgerows were established and managed without use of pesticides. We investigated three sample plots of 10 m^2 in all hedgerows together with a set of 13 explanatory variables. There were no differences in soil texture between hedgerow types but organic farms had higher pH and lower conductivity. Organic farms had higher total N values, which are explained by a slightly higher content of organic matter. There was highly significant interaction between farming type and neighbouring crop type according to soil phosphate concentration. Significantly more plant species were found in the organic hedgerows. The species compositions in organic hedgerows appeared significantly more similar to semi-natural communities when compared with other plant communities. We conclude that organic farming is slightly superior with regard to conservation of herbaceous diversity of hedgerows in intensively cultivated agricultural landscapes. The possible reasons for this are discussed.

Keywords: Ellenberg; Fertility; Habitat quality; Plant species diversity; Pesticide

Paper III, accepted for publication in Oikos

Bryophyte colonisation and persistence in experimental grassland dominated by vascular plants

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Abstract

A three-year multi-factorial microcosms experiment simulating dry grassland was used to test five hypotheses concerning establishment and persistence of bryophytes in grassland vegetation. The experimental treatments included fertilisation, defoliation and species composition of vascular vegetation. ANOVA-modelling showed a significant response of bryophyte species richness to fertilisation (negative) and defoliation (positive). Species composition of vascular vegetation had no effect on bryophyte richness, but a significant negative relationship was found between vascular plant biomass and species richness of bryophytes. Vascular plant dry weight above 400 g m^{-2} appeared fatal to bryophytes. At high nutrient levels, bryophytes extinction seemed to be avoided by defoliation, but defoliation did not fully compensate for the negative effect of fertilisation on bryophyte richness. At the single species level, our experiment provided new autecological insight in the responses of *Brachytecium rutabulum* and *Funaria hygrometrica*. The relationship between bryophyte richness and bryophyte cover was shown to follow the theoretical species-area relationship, suggesting that bryophyte cover may be used as indicator of habitat quality for subordinate species such as bryophytes and lichens in grassland monitoring. The implications of the results for grassland conservation are discussed.

Paper IV, prepared for publication in Journal of Ecology

Plant species diversity and the interaction of productivity and disturbance tested by experimental grassland vegetation

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Summary

1. The effects of disturbance intensity and nutrient enrichment were investigated in experimentally grassland vegetation. Three levels of nitrogen and four levels of disturbance (herbicide drift) were applied in a full factorial design with 10 replicates.
2. Thirty species were selected stratified random and sown in a seedbed where the dry sandy soil initially was deeply ploughed to avoid germination from the existing seedbank. The sown species represented different plant heights and four groups of C-S-R-strategy with one grass from each group.
3. Biomass of sown and invaded vascular species were harvested, dried and weighted after three growing seasons. Bryophyte abundance was noted as a frequency in nine circles in each of all 120 sample plots.
4. Chemical and physical soil variables were measured. Both treatments showed a significantly influence on the chemical soil variables.
5. Nutrient enrichment increased the productivity. There was however no significant difference in productivity between intermediate and high nutrient level. The study could not exclude a positive feedback effect of a higher species diversity at intermediate nutrient levels.
6. The interaction of N-enrichment and disturbance significantly influenced both species diversity, frequency of bryophytes, biomass and litter.
7. Disturbance explained biomass accumulation best whereas N-enrichment was the most important factor to explain species diversity and abundance of bryophytes.
8. The relationship between biomass and species diversity varied from a significant negative monotonic relation at low disturbance level to a unimodal effect at high disturbance level. The relationship between litter and species diversity varied from negative monotonic at low disturbance to positive monotonic at high disturbance.

Keywords: Bryophyte, chance effect, diversity, herbicide, glyphosate, mesocosm, moss, species richness.

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A combination of field investigation and microcosm experiments was used to test the influence of nutrients and disturbance on the species composition and diversity of dry grassland vegetation.

The Ph.D. thesis is based on four manuscripts. Two of which concern investigation of hedgerow bottom vegetation of organic- and conventional farms. The third manuscript focuses on bryophyte performance in grassland and the influence of grazing, nutrients and vascular plants. The last manuscript deals with the combined influence of varying degree of herbicide drift and varying degree of nutrients on standardised vegetation.

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The effects of nutrients and disturbance on dry grass-dominated vegetation