The fate of grassland species in the modern changing landscape: Effects of management on vegetation and population dynamics in road verges and pastures

Inger Auestad

Dissertation presented for the degree of Philosophiae Doctor

Natural History Museum

Faculty of Mathematics and Natural Sciences

University of Oslo

2009

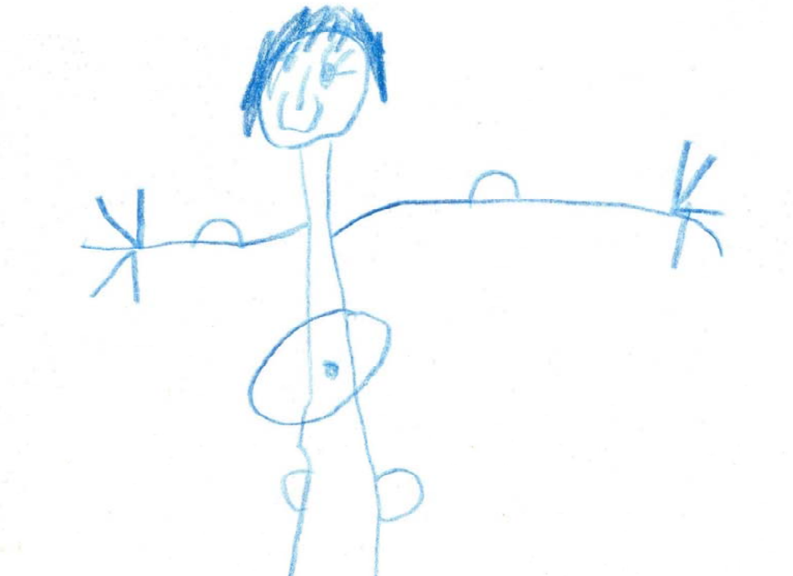
Series of dissertations submitted to the
Faculty of Mathematics and Natural Sciences, University of Oslo
Nr. 834

ISSN 1501-7710

Cover: Inger Sandved Anfinsen.
Printed in Norway: AiT e-dit AS, Oslo, 2009.

Produced in co-operation with Unipub AS.
The thesis is produced by Unipub AS merely in connection with the
thesis defence. Kindly direct all inquiries regarding the thesis to the copyright
holder or the unit which grants the doctorate.

Unipub AS is owned by
The University Foundation for Student Life (SiO)



TAKK

Først vil jeg rette en stor takk til mine veiledere Rune Halvorsen, Knut Rydgren og Ingvild Austad. Rune har alltid vært positiv og raus med sine store kunnskaper og er alltid rask til å svare! Ingvild, som dro i gang vegkant-arbeidet for 11 år siden, er utrettelig med gode ideer og entusiasme for nye og spennende problemstillinger. Knut har vært en klippe på alle nivå i arbeidet, men jeg takker særlig for feltinnsatsen i polleninfernoet i Lærdal i innledende fase av arbeidet. Kan man ønske mer av en veileder enn at han er kunnskapsrik, hjelpsom og i tillegg trivelig?

Jeg takker ellers fagmiljøet ved Avdeling for ingeniør- og naturfag, HSF, i sær Leif Hauge (som er miljøets fremste Lærdalsekspert), Eli Heiberg, Stein Joar Hegland og Liv Norunn Hamre. Sistnevnte har vært en uovertruffen kontornabo, og vårt skjebnefellesskap som stipendiater strekker seg fra LTRE og DCA til blånissevotter og ammete! Marianne Evju og Anette Edvardsen ved NHM i Oslo har vært hyggelige forbundsfeller. Tidligere kollega Ann Norderhaug takkes for vennskap og faglig støtte i tidlig fase av arbeidet med vegkanter. I tillegg vil jeg gi biologilærer Tore R. Nielsen ved Sandnes videregående skole all ros for inspirerende innføring i biologiens spennende verden en gang på seint 80-tall!

Many thanks are due to Professor Hans de Kroon at the Department of Experimental Plant Ecology, Radboud University of Nijmegen, for hosting me three months in 2007 and generously sharing his long experience in plant population biology. This has contributed greatly to my work on *Pimpinella saxifraga.* Moreover, I wish to acknowledge the staff at the lab, especially José, Josef, Heidi and Maiike for making our stay in the Netherlands an enjoyable experience for the whole family!

Statens vegvesen Region Vest og Lærdal kommune takkes for praktisk tilrettelegging av arbeidet. Jeg vil også rette en takk til grunneierne Arne H. Tønjum, Odd A. Aspevik og Lars Nese som stilte undersøkelsesområdene til disposisjon. Mange timer har blitt tilbragt på kne i vegkanter og beitemarker, men heldigvis ikke alene. Jeg takker alle som har deltatt som feltassistenter, særlig Hanne Sickel, som sporty stilte opp flere somre på rad, og dermed gjorde ellers monotone feltdager til trivelig venninnesamvær. En takk går også til Bjørg Skår, som alltid var en hyggelig vertinne i felt, og som stilte med pinneis og solparasoll under hetebølgene, og kaffi og Lærdalslefse når været var ufyselig.

Mor og far og mine nieser Elizabeth og Sunniva var pålitelige barnevakter i flere feltsesonger, noe som reduserte belastningen på hjemmefronten. Kristin og John-André har bidratt med både feltassistanse (sic!) og korrekturlesing.

De største takkene er igjen til slutt: Det er bedre å være to enn en, og du Kyrre har vært uovertruffen å være i lag med, ikke minst når jeg til tider lurte på om arbeidet hadde noen ende. Tusen takk for all støtte, og for all glede vi har delt over felles naturopplevelser. En spesiell takk går også til Sjur, som har laget tegningen av mor på feltarbeid, og til Idunn som var med i felt (i magen) sommeren 2004. Dere to har vært akkurat så tålmodige at jeg greide å bli ferdig, men også akkurat så utålmodige at jeg har fått de nødvendige pausene fra vegkantene og beitemarkene, og dermed deltatt i alt det andre som er fint i livet!

Studien er en del av det Strategiske høgskoleprogrammet *Landskapsøkologiske problemstillinger knyttet til erstatningsbiotoper: Effekten av skjøtsel og etablering på artsdiversitet i vegkanter*, finansiert av Norges forskningsråd (prosjektnr. 156325/530). Jeg har også mottatt finansiell støtte fra Høgskulen i Sogn og Fjordane.

Sogndal, desember 2008

Inger Auestad

CONTENTS

ABSTRACT

This thesis presents a study of vegetation and plant population dynamics in a local vegetation–environment context, and examines the importance of management regimes for the maintenance of grassland species.

In the modern, changing landscape, semi-natural grasslands are declining, followed by changes in species composition and a huge biodiversity loss at regional as well as international level. Moreover, the remaining grasslands often receive different management than the traditional regime. 'Novel' grasslands like road verges, on the other hand, steadily increase, and they have been suggested as refuges for declining grassland species, given appropriate management.

I surveyed the vegetation–environment relationships of aboveground vegetation and seed bank. Moreover, I studied management effects on vegetation dynamics as well as on population dynamics of *Pimpinella saxifraga*. This low-growing perennial species is considered an indicator of semi-natural grasslands.

Road verges and pastures shared many species. The aboveground vegetation varied gradually along the most important gradient; the management history, whereas other significant environmental factors did not separate the two habitats. The seed bank response to environmental factors resembled the response in aboveground vegetation, but at a coarser scale. For both aboveground vegetation and seed bank, I found that the environmental relationships depended on the scale of observation.

The ambiguous effect of management and lack of directional change in species composition indicated considerable resistance to changes in management. The vegetation's large proportion of perennial species may on one hand have contributed to fine scale dynamics, but their long life span probably slowed down the vegetation dynamics, in our study reinforced by high drought frequency acting as a resetting mechanism for succession.

The study of *P. saxifraga* population dynamics revealed that considerable management effects were buffered through life-history trade-offs. The present road verge management prevented seedling production, but the species nevertheless managed relatively well, due to the 'mosaic' management of the road verges (ranging from twice cutting via one cutting to no cutting in different distances from the road bed). This spatially fine-scaled variation in management generated a trade-off between fertility and survival, thus creating source-sink dynamics for the species. This exemplifies the unique potential of this novel ecosystem to maintain semi-natural grassland species.

LIST OF PAPERS

The thesis is based on the following papers, which will be referred to in the text by their Roman numerals. The published paper is reprinted with kind permission of the publisher.

I. Auestad, I., Rydgren, K. & Økland, R.H. (2008) Scale-dependence of vegetation-environment relationships in semi-natural grasslands. *Journal of Vegetation Science* **19**: 139-148.

II. Auestad, I. & Rydgren, K. Soil seed banks: echoes of the aboveground vegetation? Manuscript

III. Auestad, I., Rydgren, K. & Austad, I. High resistance in grassland vegetation prohibits management response. Manuscript

IV. Auestad, I., Rydgren, K. & de Kroon, H. *Pimpinella saxifraga* is maintained in road verges by mosaic management. Manuscript

INTRODUCTION

Traditional semi-natural grasslands are considered of great nature value in Norway and other European countries as they are species-rich and hold vulnerable and rare species (Garcia 1992; Norderhaug *et al.* 2000; Pykälä 2000b). Besides their aesthetic values, semi-natural grasslands also represent important cultural historical values. In southern Scandinavia, semi-natural grasslands were formed and upheld from the Iron Age (2500-1000 BP) through a specialized utilization system (Losvik 1999) which largely existed until the start of the 20th century (Birks *et al.* 1988; Berglund 1991). In general, all infields were grazed in spring, but during summer the livestock grazed in the mountains or in the outfields. This gave time for the infield grassland vegetation to recover and develop before the grass was mown in late July. Hay was dried at site before brought into the barn. The aftermath was grazed by the livestock when they returned to the farm in late summer. Only small quantities of fertilisers (manure) were added to the infield grasslands. Through time, the continuous management of mowing and grazing acted as a reset mechanism for succession (Glenn-Lewin & van der Maarel 1992) and created a low-growing, light-open vegetation characterized by high species richness at fine scales (Kull & Zobel 1991).

Since the start of the 20th century, land-use changes have reduced the area and connectivity of semi-natural grasslands considerably (Kull & Zobel 1991; Norderhaug *et al.* 2000; Poschlod & WallisDeVries 2002). Increasing exploitation of fertile farmed areas combined with the overgrowth of marginal farmland (especially during the last 50 years) have led to a huge loss or severe changes in grassland habitat quality, greatly increasing the extinction risk of species from the agricultural landscape (Brys *et al.* 2004; Kålås *et al.* 2006). The loss of semi-natural grasslands is presently considered a major threat to European biodiversity (Pykälä 2000a; Lennartsson & Oostermeijer 2001). The remaining fragments of the old semi-natural grasslands often receive modified management, e.g. hay meadows are mown to different times than previously or, more commonly, they are not mown anymore, just grazed. However, in some cases the livestock graze only in spring and autumn, as they spend the summer grazing in the mountains. Such grassland that are not presently mown but otherwise managed more or less in the traditional manner, and have been reported to be species rich, upholding a suite of vulnerable, declining grassland species considered characteristic for the traditional, semi-natural grasslands (Eriksson *et al.* 1995; Hellström *et al.* 2003; Losvik 2007). In the modern landscape these 'modified' traditional semi-natural grasslands (presently pastures) often represent the only possible basis for comparison to other grasslands, as the traditional hay meadows are about to disappear.

Although most species found in the agricultural landscape also occur in habitats kept open by natural disturbances (e.g. flood plains, rocky outcrops and scree), human efforts to control such disturbances have lately decreased naturally light-open habitats (Kålås *et al.* 2006). Moreover, the ongoing climate changes, combined with increased introductions of exotic species, impose novel ecological pressure on the semi-natural grasslands (Lau 2008). The long-term survival of species from semi-natural grasslands may depend on large-scale conservation programmes involving appropriate management. Another solution, commonly adapted in many European countries, include re-creation of semi-natural grasslands by sowing or planting native plants (Kiehl *et al.* 2006).

However, the modern landscape also comprises a type of grasslands that closely resembles the semi-natural grasslands; road verges. These landscape elements cover large areas; and rough calculations estimate that the area of Norwegian road verges exceeds 1000 km^2 (Auestad *et al.* 2000). Contrary to the semi-natural grasslands, road verges presently increase rather than decrease both in length and extent (Forman & Alexander 1998; Schaffers & Sýkora 2000; Cousins 2006). For traffic safety reasons, road verges are annually cut. They are generally well drained, and although airborne deposition of N may lead to soil N enrichment, they are generally low in nutrients. Hence, many road verges are managed in a way that resembles traditional grassland management. Road verges may be species rich as well as holding rare or endangered plant species (Hansen & Jensen 1972; Tikka *et al.* 2001; Cousins & Eriksson 2002; Saarinen *et al.* 2005) and may even represent remnants of old, semi-natural grasslands. Comparisons of species composition in road verges and nearby grasslands have, however, also shown pronounced differences in species composition (Norderhaug *et al.* 2000; Tikka *et al.* 2001; Jantunen *et al.* 2007). This raises the question of why some light-demanding grassland species may survive in road verges, whereas others do not. The question may be answered through in-depth investigations of vegetation and environmental conditions of road verges and remnants of traditional, semi-natural grasslands, followed by studies of their response to applied management regimes. Comparing patterns over various spatial scales as well as different biological levels (vegetation and populations) may reveal the potential of both habitats to hold grassland species.

Vegetation–environment relationships in aboveground vegetation

To sustainably manage semi-natural grassland ecosystems, we need to understand relationships between management regime, important environmental factors and the species composition (Chapin *et al.* 1996). Different environmental complex gradients have been suggested in the literature as major determinants of the wide variation in semi-natural grassland vegetation, ranging from management history (Kahmen *et al.* 2005), soil element concentrations (Austrheim *et al.* 1999; Norderhaug *et al.* 2000) and soil moisture conditions (Garcia 1992; Bratli & Myhre 1999) to regional-scale climatic variables (Losvik 1993; Yeo & Blackstock 2003). The inconsistency of these findings displays the high complexity of semi-natural vegetation, but may also reflect differences in grain and extent of studies, varying from small plots to entire fields (Bratli & Myhre 1999; Yeo & Blackstock 2003) and from local to international study focus.

Variation on a hierarchy of scales is typical of semi-natural grasslands where management greatly influences the vegetation-environment relationships (Austrheim *et al.* 1999; Kahmen *et al.* 2005). Semi-natural grassland vegetation has developed by modification of natural ecological gradients and addition of new management related gradients through long histories of human use, e.g. cutting or grazing or both (Pärtel & Zobel 1999; Hansson & Fogelfors 2000). A broad analysis of vegetation-environmental relationships therefore requires comparisons on different scales, based on reliable measurements of relevant environmental variables.

Vegetation–environment relationships in soil seed bank

Parallel to the variation in aboveground vegetation, there is a variation in the composition of the soil seed bank. Soil seed banks play a crucial role for the population dynamics and persistence of most flowering species (Harper 1977) and may average out the effects of environmental heterogeneity on species composition in time and space. The dynamic link between seed bank and the aboveground vegetation gives reason to expect interdependence in their spatio-temporal patterns. Species dispersal ability and seed bank persistence are moreover regarded as key traits in the survival of plants in fragmented, changing agricultural landscapes (Geertsema *et al.* 2002). Seed banks have received special interest as potential sources for reintroduction of presently rare but previously common species in the aboveground vegetation (Matus *et al.* 2003). However, as most grassland species are perennials and possess transient seed banks, their species composition often differ considerably from aboveground vegetation. Due to this lack of similarity, seed banks have usually been regarded as poor restoration tools for long-time abandoned grasslands (Milberg 1992; Bekker *et al.* 1997). Investigations of species composition in seed banks have, on the other hand, hardly ever been supplied by comparative investigations of the underlying complex gradients that structure the variation (but see Peco *et al.* 1998; Stark *et al.* 2003). Such knowledge could also contribute to the understanding of the relation between seed banks and aboveground vegetation in different grasslands, such as road verges and pastures.

Management and vegetation dynamics

Management is regarded fundamental for sustaining light-open vegetation since mowing and grazing act as a reset mechanism for succession (Glenn-Lewin & van der Maarel 1992). These measures prevent tall species from ousting smaller species and provide regeneration gaps. For road verges, annual cutting of grass has been shown to create treeless, light-open vegetation resembling traditional semi-natural grasslands (Parr & Way 1988; Schaffers *et al.* 1998; Jantunen *et al.* 2007).

The general conception is that semi-natural grasslands are best managed in correspondence with the regime under which they have evolved (Smith *et al.* 1996; Jefferson 2005; Spiegelberger *et al.* 2006). Such regimes vary widely, among the most relevant aspects for road verge management being the timing and frequency of cutting and the intensity of hay removal. The details of road verges management may, however, not readily be inferred from studies of meadows without particular appraisal. Generally, grassland vegetation responds differently to management due to large variation in e.g. climate and edaphic conditions, as well as differences in historical management regimes. Moreover, no traditional management regime exists for road verges to guide the choice of appropriate regimes. Lastly, important elements of the traditional management regimes (e.g. spring and autumn grazing) cannot be implemented in road verges for traffic safety reasons. Experimental studies of the effect of management on vegetation dynamics in such novel ecosystems are therefore needed to guide management and restoration processes (Seastedt *et al.* 2008).

Management and population dynamics

Management effects on semi-natural grassland vegetation have to a great extent been evaluated on aspects of vegetation (species composition and richness). The effects on plant population dynamics have been less focussed, especially by means of transition matrix modelling (but see Lennartsson & Oostermeijer 2001; Lehtilä *et al.* 2006; Endels *et al.* 2007; Jantunen *et al.* 2007). Studies of population dynamics allow determination of which life history traits that are most affected by treatments, and which that are most resistant. Such knowledge is essential for pinpointing the effect of the actual management regimes on declining grassland species, thereby permitting more efficiently directed management decisions (Lennartsson & Oostermeijer 2001; Brys *et al.* 2004). The umbellifer *Pimpinella saxifraga* exemplifies a suite of perennial, low-growing species adapted to the light-open environment and infertile soils of semi-natural grasslands (Wells *et al.* 1976). Transition matrix models are widely used tools for studying population dynamics (de Kroon *et al.* 2000; Caswell 2001) as they provide a link between the individual and the population that allow assessment of the influence of all vital rates of a plant on population growth rate (λ). For decomposition of variation in λ, retrospective analyses like Life table response experiments (LTRE) have proven very useful, as it identifies the management effect on specific vital rates and hence permits directed management decisions.

Main objectives

In this thesis, I investigate plant population dynamics in a vegetation–environment context to gain insight in the role of road verges and pastures (presently grazed in spring and autumn, formerly also mown in summer) for maintaining grassland species. Specifically, I address the following questions:

I Which environmental and management factors determine plant species composition in semi-natural grasslands within a local study area? Is the relation between plant species composition and explanatory factors scale-dependent?

II Does the seed bank respond to the same environmental gradients as the aboveground vegetation? Are response-patterns similar also at varying spatial grain levels?

III Can appropriate management regimes affect the vegetation dynamics of road verges and pastures and aid the maintenance of vulnerable and declining grassland species?

IV Can road verges act as refuges to vulnerable and declining grassland species like *Pimpinella saxifraga?* How are vital rates impacted by management regimes?

STUDY SITES

I chose six semi-natural grasslands, three pastures (Molde pasture, Stuvane pasture and Nese pasture) and three road verges (Molde road verge, Stuvane road verge and Nese road verge) in Lærdal, Sogn og Fjordane county, W Norway (61º04' N, 7º32'– 49' E) for all studies reported in this paper (Fig. 1). The locations were chosen to span the regional variation in grassland vegetation.

The vegetation is low-growing and species rich and hold many species considered characteristic for semi-natural hay meadows in the region (Losvik 2007). The sites were situated within an extent of ca 11 km, at altitudes from 35 to 420 m a.s.l., all faced south (from SE to SW). Areas of the pastures varied from 2.8 to 7.5 ha while the road verges comprised narrow (3 – 5 m) strips of 50 - 100 m length.

All sites were situated in the southern boreal, slightly continental region (Moen 1999), had low annual precipitation (ca. 500 mm, Førland 1993) and annual mean temperature of ca. 5.9 ºC (Aune 1993) for the normal period 1961-1990. The precipitation in the four years was relatively normal except for 2006 when rainfall in March-August equalled only 65% of the normal rainfall for the period.

The three pasture sites – Molde pasture (MP), Stuvane pasture (SP) and Nese pasture (NP) – had experienced spring and autumn grazing for centuries. MP and NP had also been mown in July until the mid eighties. Two of the road verge sites, Molde road verge (MR) and Stuvane road verge (SR), lay close to the MP and SP sites, respectively, and before road improvement in these areas (in 1950), they actually shared management with the respective pasture site. The vegetation adjacent to these verges was dry grassland. The Nese road verge (NR) was established during widening of the road in 1964 and had no former history of grazing or mowing. This verge bordered encroached grassland dominated by young *Alnus incana*. The distance between NV and NP was ca. 1 km. The traffic intensity varied from low at the MR site to high at the two other sites. Since 1990, the road verge sites have been cut annually, either by the road authorities or by Lærdal municipality.

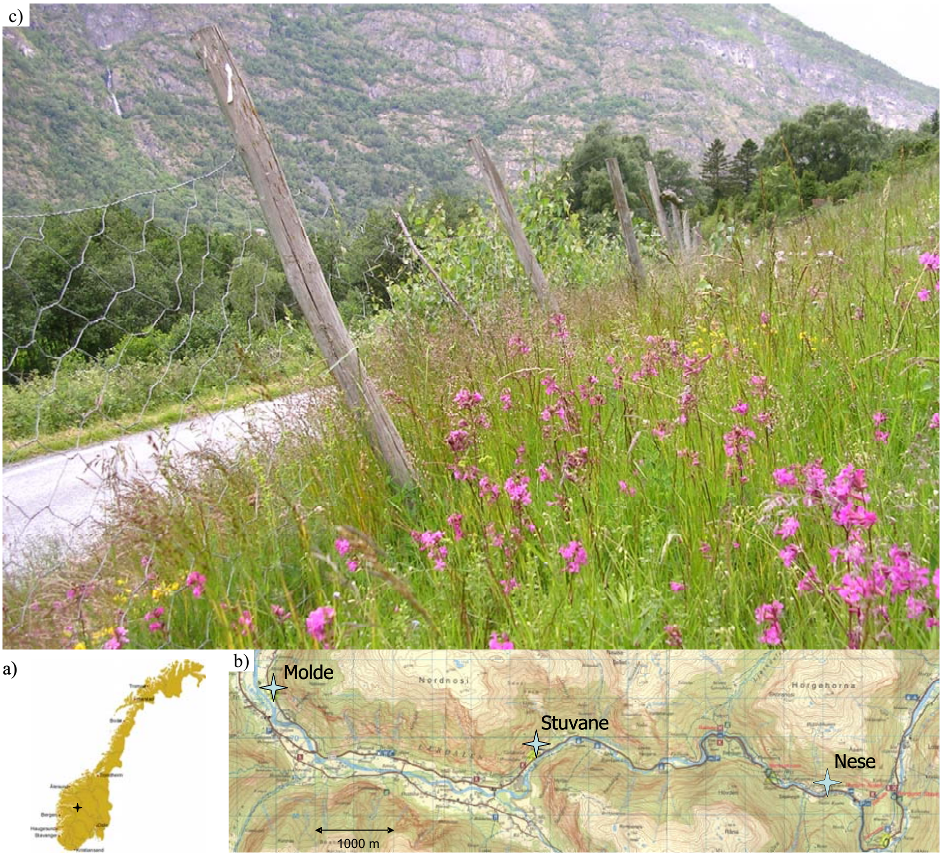


Fig. 1. Map of Norway with Lærdal indicated (black star) (a); map of Lærdal with the three locations Molde, Stuvane and Nese indicated (blue stars) (b) and the vegetation of the pasture bordering the road verge at Molde, dominated by *Lychnis viscaria* (c).

METHODS

In each of the six study sites I subjectively placed seven blocks (15 – 16 m^2 extent) to span apparent local environmental variation. Plots of 0.5 × 0.5 m were placed at random within each block, five in each road verge block and three in each grassland block. Species content of all 168 plots were analyzed in 2003 by dividing each 0.25 m^2 plot into 16 subplots of 0.0156 m^2, and using subplot shoot frequency (0 – 16) as a measure of vascular plant species abundance.

I recorded twenty-one explanatory variables in each of the 168 plots, including several soil chemical and physical variables determined in soil samples, in addition to a management index quantifying management impact over time in each of the six sites. I

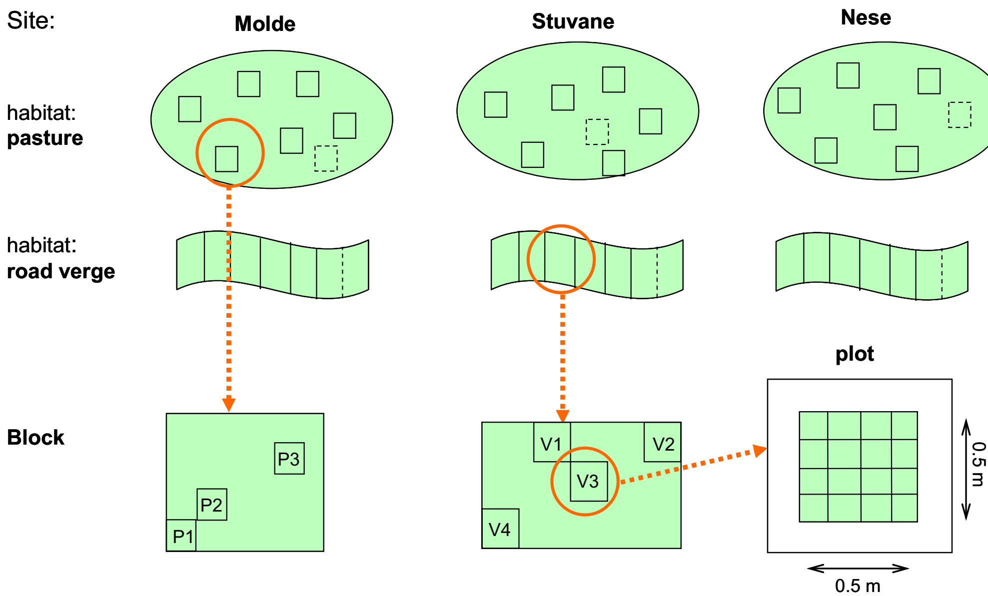


Fig. 2. **The study design with plots (0.25 m^2) nested in blocks nested in sites. One pasture site and one road verge site was situated within each of the three locations Molde, Stuvane and Nese. All pasture treatments (P1-3) were applied in each pasture block and all road verge treatments in each road verge block at each location. The treatment abbreviations are explained in Table 1.**

evaluated vegetation-environment relationships at different spatial levels by means of DCA ordination and split-plot GLM analyses.

For all further investigations, I reduced the amount of plots by excluding one block per site, giving a total of six blocks in each of the six grasslands.

Soil for seed bank studies was sampled in 2005 in two plots per pasture block and three plots per road verge block. The 108 soil samples were treated by the seedling emergence method (ter Heerdt *et al.* 1996) and the species composition was compared between the seed bank and the aboveground vegetation and related to explanatory variables at different spatial grain levels.

I applied management treatments to the pastures and road verges in a split-plot design, three treatments within each pasture block (P1-3) and four treatments within each road verge block (V1-4), thus nesting plots in blocks in sites (Fig. 2). The treatments were chosen to simulate present treatments in the two habitats, and compare them to feasible alternatives that varied mainly with respect to cutting intensity and timing (Table 1). P1 equals the present pasture treatment (spring and autumn grazing and no mowing). P2 simulates the traditional pasture treatment, including a single late cutting (August) and hay removal (by raking) in addition to spring and autumn grazing. P3 resembles P2 but the raking is tougher and more litter is removed. V1 represents present regime of outer parts of the road verges (mowing in June and August, no removal of hay). V2 is similar to V1 but includes removal of hay. V3 represents a lower frequency regime with one annual mowing (August), the hay is removed. I also included a treatment with no active management (V4).

The species composition of the plots was analyzed all years (2003-2006) in the same manner as in 2003. I evaluated the effect of management treatments on various aspects of vegetation dynamics in road verges and pastures by means of floristic dissimilarity measures and ordination analyses.

For the population dynamic study I mapped and tagged *Pimpinella saxifraga*-individuals (ramets) in plots under all four road verge treatments (V1-4) and two of the pasture treatments (P1-2). I censused the plants' survival, growth and flowering annually in 2003 – 2006 and used the data to construct projection matrices for the overall population and the eighteen site-treatment combinations. λ and elasticities were calculated for all vital rates in all populations. Finally, I decomposed the site-and treatment related variation in λ by performing two-ways LTRE's using the vital rates as model components to evaluate the effect of management on population dynamics of *Pimpinella saxifraga* in road verges and pastures.

Table 1. Details of the management treatments applied in *Study III*. *Study IV* comprises the treatments V1-V4 and P1-P2.

Habitat		Cutting time	Hay removal	Spring+ autumn grazing	# plots per year	Comments
Road verges	V1	Jun + Aug	no	no	18	Simulate present 'outer verge' management
	V2	Jun + Aug	normal	no	17*	Like V1+ removal of hay
	V3	Aug	normal	no	18	Lower frequency management
	V4	-	no	no	17(13*)	No management
Pastures	P1	-	no	yes	18	Present management
	P2	Aug	normal	yes	18	Simulate traditional meadow management
	P3	Aug	hard	yes	18	Like P2 + hard raking

*Note that due to misplaced management, the number of plots under treatment V2 and V4 was 17 in years 2003-2005 and (respectively) 17 and 13 in 2006.

RESULTS

Vegetation–environmental relationships in aboveground vegetation (Study I)

Road verges and pastures shared many species, but the main variation in grassland vegetation related to management history, and thus the two habitats were slightly separated along the main gradient. Soil moisture conditions were related to vegetation variation on block scale, whereas element concentrations in the soil were significantly related to variation in species composition on all spatial scales. Road verges and pastures did not differ with respect to any of these factors. The results moreover showed that vegetation-environment relationships are dependent on the scale of observation.

Vegetation–environmental relationships in soil seed banks (Study II)

The seed bank responded in parallel to the aboveground vegetation to the explanatory variables. Both management regime, local climatic and soil chemical variables impacted on the vegetation variation, but whereas the aboveground vegetation responded on all grain levels, the seed bank related mainly at site level. At finer grains, the association between the seed bank and the aboveground vegetation was generally poor. However, this difference did not invalidate the overall resemblance in response patterns.

Management and vegetation dynamics (Study III)

Various aspects of vegetation dynamics responded differently to the imposed management treatments. Whereas species richness and vegetation height and litter thickness changed differently in response to treatment, overall vegetation change and turnover rates varied over time but not between treatments. No evidence of directional vegetation dynamics along underlying environmental gradients were found, rather the vegetation appeared relatively resistant to changes in management regime.

Management and population dynamics (Study IV)

The present management regime of pastures gave a slightly higher λ than present road verge management regime as the two annual cuttings in road verges prevented seedling production. However, *P. saxifraga* exhibited various examples of life-history trade-offs between fertility and survival in response to management regimes. Moreover, the road verge populations demonstrated spatially dependent dynamics. Their linear structure enabled zonal variation in management regimes, which in turn created a source-sink situation that probably increase the plant's overall fitness. *P. saxifraga* appeared to be rather resistant to abandonment, probably partly due to its ability to germinate despite litter accumulation. Compared to the management effects, other conditions (e.g. edaphic, climatic and management history) impacted the population growth rate strongly and modified or even overruled the effect of applied management regimes.

DISCUSSION AND CONCLUSIONS

This thesis elucidates crucial aspects of the importance of road verges and pastures to declining grassland species. The detailed investigations of vegetation–environmental relationships in aboveground vegetation and soil seed bank provided a useful basis for a multi-level comparison of management effects, both at vegetation and population levels. The project will provide the Road authorities with information that might enable them to implement environmentally adequate management regimes to species-rich road verges.

The examination of vegetation–environmental relationships at local scale revealed that the choice of analysis methods had great bearings on the conclusions (*Study I*, *II*). Implementation of split-plot GLM in search for relations between vegetation patterns and environmental variables enabled simultaneous investigation of several spatial scales. Management history related significantly to aboveground vegetation at coarse (site) scale, whereas edaphic and local climatic factors showed significant relation at finer (block and plot) scale (*Study I*, Table 1). Thus, new light was thrown on the diverging conclusions on the nature of vegetation–environment relations found in literature (Vandvik & Birks 2002; Yeo & Blackstock 2003; Kahmen *et al.* 2005), and on the debate over suitable plot sizes for analyses of grassland vegetation (Chytrý & Otýpková 2003; Otýpková & Chytrý 2006). Plot size should reflect the scale at which environmental variables vary. In line with Økland (2007), I recommend the use of small plots in a nested design, followed by a multi-scale approach that explicitly addresses the potential pseudoreplication of such data (*Study I*).

Investigation of the soil seed banks of the two habitats revealed that, despite modest similarities between the seed bank and the aboveground vegetation, the two compartments responded similarly to environmental variables (*Study II*). Also in this study the importance of scale is demonstrated as the seed bank (in contrast to the aboveground vegetation) relates to the environmental variables mainly at coarse (site) scale. The seed bank should not be expected to contribute considerably to the maintenance of the aboveground species composition, as many of the perennial species common in the vegetation have a transient seed bank (Thompson *et al.* 1997). They rather depend on clonal organs for propagation, although many of them are slow re-colonizers (Lindborg & Eriksson 2004).

The pastures held many species regarded as characteristic (Losvik 2007) for regional, species-rich semi-natural grasslands. Although they shared a considerable amount of species with the road verges, the two habitats were separated along the main vegetational gradient, which in turn was shown to reflect management history (*Study I*). Hence, road verges and pastures differed mainly with respect to management, whereas other significantly related variables such as soil moisture and element concentrations in soil did not separate the two habitats (*Study I*, Fig. 2a). I therefore conclude, in line with Tikka *et al.* (2000), that road verge habitats have the potential to hold species characteristic for semi-natural grasslands, given appropriate management and sufficient propagule supply. As the multi-scaled analysis enabled comparison of scale-specific variables, I argue that the potential of road verges to hold species-rich grassland vegetation has great validity.

The study of population dynamics of *Pimpinella saxifaga* gave novel insights in the life history of a perennial, low-growing species adapted to the light-open, infertile semi-natural grasslands, and confirmed that changes in management influence vital rates such as fertility, growth and survival (*Study IV*). However, the net effects of management on λ were generally modest (*Study I*V, Fig. 2), as the species buffered negative influence on one life history trait by investing more in another trait, and vice versa. Hence, individuals deprived of seed set possibilities had higher survival (*Study IV*, Fig. 3a). Buffering of variation to λ generally reduces a species' extinction risk (Morris *et al.* 2008) and in long-lived grassland species, perennial organs like the tap root of *P. saxifraga* ensures high resistance to management changes. The buffering capacity of the numerous perennial grassland species is also bound to contribute to the slow vegetation dynamics response to management changes observed in the road verges and pastures (*Study III*). Moreover, as response at the vegetation level reflects many species' responses, we may expect a broad range of responses depending on the various species' life history traits, not necessarily producing a directional, detectable response along underlying gradients. Thus, I found no support for the supposition that appropriate management may induce directional vegetation dynamics along important, management history related gradients (*Study III*, Fig. 5), thereby making the road verges more similar to the pastures. This does not necessarily contradict the high importance of management history to species composition demonstrated in *Study I*. The management experiment in *Study III* ran for only four years, whereas the management index (MI) in *Study I* reflected 70 year's management regime. Rather, the results demonstrate the importance of long time continuity of management for maintenance of semi-natural grassland vegetation (Fischer & Wipf 2002).

The generally arid conditions of the area combined with random drought events also contribute to the slow vegetation dynamics as succession processes are halted and low-growing species are allowed to colonize gaps (Buckland *et al.* 1997; Bartha *et al.* 2003; Bennie *et al.* 2006). The temporal, climatic variation however seemed to increase the non-directional vegetation dynamics as reflected in species similarity between years (*Study III*). As the population dynamics study did not include variation between years, this aspect remains unexplored in the analysis of variation in λ for *P. saxifraga.* The species' exceptionally high drought tolerance (Buckland *et al.* 1997) may however be expected to mediate the drought effect on population dynamics.

In opposition to the modest effect of management on vegetation dynamics and population dynamics, *Study IV* indicated that considerable variation between sites (in particular the pastures) affected the λ of *P. saxifraga*. Moreover, the pastures were well separated along the gradient in soil moisture and nutrients (*Study I*) in a manner that indicated that dry and poor site conditions gave lower site-specific λ. Our study thus confirms relations between demographic performance and environmental factors (Colling & Matthies 2006; Maschinski *et al.* 2006), and furthermore indicated that environmental conditions may overrule the effect of the present treatments. This underlines the importance of carrying out population studies in multiple sites (Menges 2000), and moreover interpret the results in a vegetation–environment context.

Management implications

This study provided insight into fundamental aspects of grassland vegetation by addressing the dynamics of the aboveground vegetation as well as of populations of a selected grassland species, both interpreted in the context of vegetation–environment patterns in aboveground vegetation and seed banks. The results allow drawing important conclusions regarding the effect of management in pastures and road verges.

The study confirms the importance of traditional management for the maintenance of the variety of species considered characteristic for semi-natural grasslands, as the pastures on average held a larger number of such species than the road verges (*Study I*, *III*). Whereas *Study I* showed that the abiotic conditions may be favourable for maintaining grassland species in road verges, *Study III* indicated that developing semi-natural grassland vegetation may be very time-consuming. Moreover, the discrepancy between the large importance of management history to species composition (*Study I*) and the moderate impact of management to vegetation dynamics (*Study III*) supported the notion that semi-natural grassland vegetation is better maintained by upholding more or less traditional management in existing grasslands, than by grassland restoration or re-creation (Myklestad & Sætersdal 2004). The slow vegetation dynamics require thorough monitoring over extended periods to ensure that the target vegetation actually is maintained by the implemented management regime. My study thus underlines that continued maintenance of the remains of semi-natural grasslands is crucial for protecting the vulnerable species and vegetation related to these habitats.

Templates for appropriate road verge management regimes have generally been sought in cutting regimes for hay meadows, resulting in regimes consisting of one or two cuttings per summer. As shown in *Study IV*, such regimes may be detrimental to the fecundity of grassland species like *P. saxifraga*. I therefore suggest experimental testing of the effect of cutting grass in road verges at times of the year corresponding to the traditional spring and autumn grazing. My results indicate that the spring and autumn grazing of the studied pastures (formerly hay meadows) can maintain a considerable number of vulnerable grassland species (*Study I*).

However, road verges are not hay meadows, neither are they pastures. As discussed by Seastedt *et al.* (2008), novel ecosystems (such as road verges) are composed by new combinations of species under new abiotic conditions. Therefore, traditional management regimes may not be appropriate templates; rather, there is a need for developing novel regimes that enhance desirable system components. The linear form of the road verges allows a fine-scale mosaic application of different management regimes. I argue that this probably created a source-sink situation (Eriksson 1996) for plants in the studied road verges. Individuals growing in the zones that received survival-lowering management (no cutting) produced seeds that compensated the lack of seeds in the zones where the management of two cuttings prevented normal fertility (*Study IV*). This is an example of the unique potential of the novel road verge ecosystems to maintain characteristic semi-natural grassland species.

ACKNOWLEDGEMENTS

I thank Knut Rydgren, Ingvild Austad, Liv Norunn Hamre and Stein Joar Hegland for helpful comments on this manuscript.

REFERENCES

Auestad, I., Norderhaug, A., Hamre, L. N. & Austad, I. (2000) *Vegkanten - variert og verdifull*. Høgskulen i Sogn og Fjordane, Sogndal.

Aune, B. (1993) Temperaturnormaler, normalperiode 1961-1990. *Det Norske meterologiske institutt Rapport Klima* **1993:** 1-63.

Austrheim, G., Olsson, E. G. A. & Grøntvedt, E. (1999) Land-use impact on plant communities in semi-natural sub-alpine grasslands of Budalen, central Norway. *Biological Conservation* **87:** 369-379.

Bartha, S., Meiners, S. J., Pickett, S. T. A. & Cadenasso, M. L. (2003) Plant colonization windows in a mesic old field succession. *Applied Vegetation Science* **6:** 205-212.

Bekker, R. M., Verweij, G. L., Smith, R. E. N., Reine, R., Bakker, J. P. & Schneider, S. (1997) Soil seed banks in European grasslands: does land use affect regeneration perspectives? *Journal of Applied Ecology* **34:** 1293-1310.

Bennie, J., Hill, M. O., Baxter, R. & Huntley, B. (2006) Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *Journal of Ecology* **94:** 355-368.

Berglund, B. E. (1991) The cultural landscape during 6000 years. *Ecological Bulletin* **41**.

Birks, H. H., Birks, H. J. B., Kaland, P. E. & Moe, D. (1988) *The cultural landscape: past, present and future*. Cambridge University Press, Cambridge.

Bratli, H. & Myhre, A. (1999) Vegetation-environment relationships of old hay meadows at Sverveli, Telemark, S Norway. *Nordic Journal of Botany* **19:** 455-471.

Brys, R., Jacquemyn, H., Endels, P., de Blust, G. & Hermy, M. (2004) The effects of grassland management on plant performance and demography in the perennial herb *Primula veris*. *Journal of Applied Ecology* **41:** 1080-1091.

Buckland, S. M., Grime, J. P., Hodgson, J. G. & Thompson, K. (1997) A comparison of plant responses to the extreme drought of 1995 in northern England. *Journal of Ecology* **85:** 875-882.

Caswell, H. (2001) *Matrix population models: construction, analysis, and interpretation, 2nd ed*. Sinuauer, Sunderland, Mass.

Chapin, F. S. I., Torn, M. S. & Tateno, M. (1996) Principles of ecosystem sustainability. *American Naturalist* **148:** 1016-1037.

Chytrý, M. & Otýpková, Z. (2003) Plot sizes used for phytosociological sampling of European vegetation. *Journal of Vegetation Science* **14:** 563-570.

Colling, G. & Matthies, D. (2006) Effects of habitat deterioration on population dynamics and extinction risk of an endangered, long-lived perennial herb (*Scorzonera humilis*). *Journal of Ecology* **94:** 959-972.

Cousins, S. A. O. (2006) Plant species richness in midfield islets and road verges - the effect of landscape fragmentation. *Biological Conservation* **127:** 500-509.

Cousins, S. A. O. & Eriksson, O. (2002) The influence of management history and habitat on plant species richness in a rural hemiboreal landscape, Sweden. *Landscape Ecology* **17:** 517-529.

de Kroon, H., van Groenendael, J. & Ehrlén, J. (2000) Elasticities: a review of methods and model limitations. *Ecology* **81:** 607-618.

Endels, P., Jacquemyn, H., Brys, R. & Hermy, R. (2007) Reinstatement of traditional mowing regimes counteracts population senescence in the rare perennial *Primula vulgaris*. *Applied Vegetation Science* **10:** 351-360.

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

Eriksson, Å., Eriksson, O. & Berglund, H. (1995) Species abundance patterns of plants in Swedish semi-natural pastures. *Ecography* **18:** 310-317.

Fischer, M. & Wipf, S. (2002) Effect of low-intensity grazing on the species-rich vegetation of traditionally mown subalpine meadows. *Biological Conservation* **104:** 1-11.

Forman, R. T. T. & Alexander, L. E. (1998) Roads and their major ecological effects. *Annual Review of Ecology and Systematics* **29:** 207-231.

Førland, E. J. (1993) Nedbørsnormaler, normalperiode 1961-1990. *Det Norske meterologiske institutt Rapport Klima*: 1-63.

Garcia, A. (1992) Conserving the species-rich meadows of Europe. *Agriculture, Ecosystems and Environment* **40:** 219-232.

Geertsema, W., Opdam, P. & Kropff, M. J. (2002) Plant strategies and agricultural landscapes: survival in spatially and temporally fragmented habitat. *Landscape Ecology* **17:** 263-279.

Glenn-Lewin, D. C. & van der Maarel, E. (1992) Pattern and processes of vegetation dynamics. *Plant succession. Theory and predictions* (eds. D. C. Glenn-Lewin, R. K. Peet & T. T. Veblen), pp. 11-59. Chapman & Hall, London.

Hansen, K. & Jensen, J. P. (1972) The vegetation on road sides in Denmark. *Dansk Botanisk Arkiv* **28:** 1-61.

Hansson, M. & Fogelfors, H. (2000) Management of a semi-natural grassland; results from a 15-year-old experiment in southern Sweden. *Journal of Vegetation Science* **11:** 31-38.

Harper, J. L. (1977) *Population biology of plants*. Academic Press, London.

Hellström, K., Huhta, A.-P., Rautio, P., Tuomi, J., Oksanen, J. & Laine, K. (2003) Use of sheep grazing in the restoration of semi-natural meadows in northern Finland. *Applied Vegetation Science* **6:** 45-52.

Jantunen, J., Saarinen, K., Valtonen, A. & Saarnio, S. (2007) Flowering and seed production success along roads with different mowing regimes. *Applied Vegetation Science* **10:** 285-292.

Jefferson, R. G. (2005) The conservation management of upland hay meadows in Britain: a review. *Grass and Forage Science* **60:** 322-331.

Kahmen, A., Perner, J., Audorff, V., Weisser, W. & Buchmann, N. (2005) Effects of plant diversity, community composition and environmental parameters on productivity in montane European grasslands. *Oecologia* **142:** 606-615.

Kiehl, K., Thormann, A. & Pfadenhauer, J. (2006) Evaluation of initial restoration measures during the restoration of calcareous grasslands on former arable fields. *Restoration Ecology* **14:** 148-156.

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

Kålås, J. A., Viken, Å. & Bakken, T. (2006) *Norsk rødliste 2006 - 2006 Norwegian red list*. Artsdatabanken, Trondheim.

Lau, J. A. (2008) Beyond the ecological: Biological invasions alter natural selection on a native plant species. *Ecology* **89:** 1023-1031.

Lehtilä, K., Syrjanen, K., Leimu, R., García, M. B. & Ehrlén, J. (2006) Habitat change and demography of *Primula veris*: identification of management targets. *Conservation Biology* **20:** 833-843.

Lennartsson, T. & Oostermeijer, J. G. B. (2001) Demographic variation and population viability in *Gentianella campestris:* effects of grassland management and environmental stochasticity. *Journal of Ecology* **89:** 451-463.

Lindborg, R. & Eriksson, O. (2004) Effects of restoration on plant species richness and composition in Scandinavian semi-natural grasslands. *Restoration Ecology* **12:** 318-326.

Losvik, M. H. (1993) Hay meadow communities in western Norway and relations between vegetation and environmental factors. *Nordic Journal of Botany* **13:** 195-206.

Losvik, M. H. (1999) Stimulation of seed germination in an abandoned hay meadow. *Applied Vegetation Science* **2:** 251-256.

Losvik, M. H. (2007) Regional species pools of hay meadows: a case study. *Applied Vegetation Science* **10:** 239-248.

Maschinski, J., Baggs, J. E., Quintana-Ascencio, P. E. & Menges, E. S. (2006) Using population viability analysis to predict the effects of climate change on the extinction risk of an endangered limestone endemic shrub, Arizona cliffrose. *Conservation Biology* **20:** 218-228.

Matus, G., Verhagen, R., Bekker, R. M. & Grootjans, A. P. (2003) Restoration of the *Cirsio dissecti-Molinietum* in The Netherlands: can we rely on soil seed banks? *Applied Vegetation Science* **6:** 73-84.

Menges, E. S. (2000) Population viability analyses in plants: challenges and opportunities. *Trends in Ecology and Evolution* **15:** 51-55.

Milberg, P. (1992) Seed bank in a 35-year-old experiment with different treatments of a semi-natural grassland. *Acta Oecologica-International Journal of Ecology* **13:** 743-752.

Moen, A. (1999) *National atlas of Norway: vegetation*. Norwegian Mapping Authority, Hønefoss.

Morris, W. F., Pfister, C. A., Tuljapurkar, S., Harridas, C. V., Boggs, C. L., Boyce, M. S., Bruna, E. M., Church, D. R., Coulson, T., Doak, D. F., Forsyth, S., Gaillard, J.-M., Horvitz, C. C., Kalisz, S., Kendall, B. E., Knight, T. M., Lee, C. T. & Menges, E. S.

(2008) Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* **89:** 19-25.

Myklestad, Å. & Sætersdal, M. (2004) The importance of traditional meadow management techniques for conservation of vascular plant species richness in Norway. *Biological Conservation* **118:** 133-139.

Norderhaug, A., Ihse, M. & Pedersen, O. (2000) Biotope patterns and abundance of meadow plant species in a Norwegian rural landscape. *Landscape Ecology* **15:** 201-218.

Otýpková, Z. & Chytrý, M. (2006) Effects of plot size on the ordination of vegetation samples. *Journal of Vegetation Science* **17:** 465-472.

Parr, T. W. & Way, J. M. (1988) Management of roadside vegetation: the long-term effects of cutting. *Journal of Applied Ecology* **25:** 1073-1087.

Peco, B., Ortega, M. & Levassor, C. (1998) Similarity between seed bank and vegetation in Mediterranean grassland: a predictive model. *Journal of Vegetation Science* **9:** 815-828.

Poschlod, P. & WallisDeVries, M. F. (2002) The historical and socioeconomic perspective of calcareous grasslands - lessons from the distant and recent past. *Biological Conservation* **104:** 361-376.

Pykälä, J. (2000a) Mitigating human effects on european biodiversity through traditional animal husbandry. *Conservation Biology* **14:** 705-712.

Pykälä, J. (2000b) Mitigating human effects on European biodiversity through traditional animal husbandry. *Conservation Biology* **14:** 705-712.

Pärtel, M. & Zobel, M. (1999) Small-scale plant species richness in calcareous grassland determined by the species pool, community age and shoot density. *Ecography* **22:** 153-159.

Schaffers, A. P. & Sýkora, K. V. (2000) Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *Journal of Vegetation Science* **11:** 225-244.

Schaffers, A. P., Vesseur, M. C. & Sykora, K. V. (1998) Effects of delayed hay removal on the nutrient balance of roadside plant communities. *Journal of Applied Ecology* **35:** 349-364.

Seastedt, T. R., Hobbs, R. J. & Suding, K. N. (2008) Management of novel ecosystems: are novel approaches required? *Frontiers in Ecology and the Environment* **6:** 547-553.

Smith, R. S., Buckingham, H., Bullard, M. J., Shiel, R. S. & Younger, A. (1996) The conservation management of mesotrophic (meadow) grassland in northern England. 1. Effects of grazing, cutting date and fertilizer on the vegetation of a traditionally managed sward. *Grass and Forage Science* **51:** 278-291.

Spiegelberger, T., Matthies, D., Müller-Schärer, H. & Schaffner, U. (2006) Scale-dependent effects of land use on plant species richness of mountain grassland in the European Alps. *Ecography* **29:** 541-548.

Stark, K. E., Lundholm, J. T. & Larson, D. W. (2003) Relationships between seed banks and spatial heterogeneity of North American alvar vegetation. *Journal of Vegetation Science* **14:** 205-212.

Saarinen, K., Valtonen, A., Jantunen, J. & Saarnio, S. (2005) Butterflies and diurnal moths along road verges: does road type affect diversity and abundance? *Biological Conservation* **123:** 403-412.

ter Heerdt, G. N. J., Verweij, G. L., Bekker, R. M. & Bakker, J. P. (1996) An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology* **10:** 144-151.

Thompson, K., Bakker, J. P. & Bekker, R. M. (1997) *Soil seed banks of North-West Europe: methodology, density and longevity*. Cambridge Univ. Press, Cambridge.

Tikka, P. M., Högmander, H. & Koski, P. S. (2001) Road and railway verges serve as dispersal corridors for grassland plants. *Landscape Ecology* **16:** 659-666.

Tikka, P. M., Koski, P. S., Kivelä, R. A. & Kuitunen, M. T. (2000) Can grassland plant communities be preserved on road and railway verges? *Applied Vegetation Science* **3:** 25-32.

Vandvik, V. & Birks, H. J. B. (2002) Partitioning floristic variance in Norwegian upland grasslands into within-site and between-site components: are the patterns determined by environment or by land-use? *Plant Ecology* **162:** 233-245.

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

Yeo, M. J. M. & Blackstock, T. H. (2003) A vegetation analysis of the pastoral landscapes of upland Wales, UK. *Journal of Vegetation Science* **13:** 803-816.

Økland, R. H. (2007) Wise use of statistical tools in ecological field studies. *Folia Geobotanica* **42:** 123-140.