Structure and dynamics of alvar vegetation on Öland and some related dry grasslands

- Dedicated to Ejvind Rosén on his 65th birthday -

Edited by Eddy van der Maarel

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Contents

Left above: Eje Rosén, 'promotion day' Uppsala university, June 1982, with laurel-wreath; after obtaining his Ph.D. degree at Uppsala University, June 1982.

Left below: Eje enjoying coffee on Gettlinge alvar, June 1989 (photo: Renate Huber);

Right above: Lunch pause on the alvar, June 1994; but Eje (left) busy with an identification; further (left to right) Graciela Rusch, Camilla Wessberg, Dai Xiao-bing; Cecilia Dupré, Martin Sykes, Mikael Lönn & Eddy van der Maarel;

Right middle: Eje Rosén taking photographs of 1-m² permanent plots on the alvar, June 1994;

Right below: Eje Rosén in typical position during a course for students from Groningen University and Universität Oldenburg, May 2006 (photo: Roos Veeneklaas).

Ejvind Rosén 65 years

Eddy van der Maarel[1*] & Jan P. Bakker[1,2]

[1]Community and Conservation Ecology Group, Groningen University, P.O. Box 14, NL-9750 AA Haren, The Netherlands; [2]E-mail j.p.bakker@rug.nl
*Corresponding author; E-mail eddy.arteco@planet.nl

Ejvind Gösta Rosén, Eje for his many friends, young and old, was born in Gävle, the capital town of the County of Gävleborgs län, north of Uppsala, an old coastal town along the Baltic. Eje studied Biology at Uppsala University and became a Ph.D. student at the Department of Plant Ecology, then called Department of Ecological Botany (Växtbiologiska institutionen). His doctoral thesis dealt with the dynamics of the limestone vegetation of the Great Alvar, especially in relation to sheep grazing. His supervisor was docent Dr. Erik Sjögren, who knew the island from his childhood and whose father, a well-known painter, had portrayed the scenery of the Great Alvar in many paintings and etches. Sjögren, who continued a much longer tradition of ecological research on Öland – which started with the lichen research of G. Einar Du Rietz, had studied the deciduous woodlands on Öland and stimulated Rosén to study the open landscape.

After his PhD studies Eje continued with research on Öland, for which he obtained the 'docent' degree in 1988, comparable to the German habilitation degree, a qualification for a professorship.

Inspired by Eje's work, the first author who had joined the Uppsala department in the early 1980s, decided to build a research group on the fascinating dynamics of the limestone grasslands; the group also included Martin Sykes, then post-doc, now professor in Lund, who is one of the authors to this volume. When our colleague Robert K. Peet from Chapel Hill, NC, US suggested cooperation in a transcontinental study of species-rich grasslands in relation to productivity and dynamics, we decided to extend our project and from 1984 onwards Eje was instrumental in selecting suitable study sites and maintaining them, in identifying the species and in putting our findings in the broader perspective of the historical development of the Alvar landscape in relation to livestock grazing.

Parallel to our common project on fine-scale dynamics Eje continued and newly established permanent plot research on scrub encroachment (notably *Juniperus communis*) under reduction or temporary absence of grazing, and on the population dynamics of rare vascular species known for their irregular occurrence on the alvar, e.g. *Ranunculus illyricus*.

Eje used to make long seasons of field work on the island; he lived at the Ecological Research Station of Uppsala University (which has practically ceased to exist as such, despite the many efforts of Eje and others). He usually arrived in April and stayed usually until late autumn, interrupted by short visits to Uppsala and excursions elsewhere. His family spent summer holidays and shorter periods on Öland, but Eje was separated from them for most of the very long season.

The willingness of Eje to help colleagues and students with their projects was proverbial. He used to visit their research sites and give advice on the setup of descriptions and experiments. He was similarly helpful to other guests at the Station and he often gave slide shows on the alvar vegetation and its rarities.

During the 1990s two new developments occurred in the career of Eje Rosén. First the Department of Plant Ecology extended the existing ecological field course to an international event where the second author (who spent a sabbatical leave at Uppsala University) participated with students from the University of Groningen, The Netherlands, and later also students from the University of Marburg, Germany, under Prof. Peter Poschlod, and from Lund under Prof. Honor Prentice joined the course. Honor had started her Swedish career as a postdoc in Uppsala where she developed genecology with particular interest in typical alvar species; after she became a professor in Lund she continued research and teaching and she contributes with a paper in this volume.

Following our interest in the historical development of the landscape in relation to ups and downs in the agricultural management of the alvar, and possibilities for restoration after bush encroachment, the Groningen department introduced seed bank analysis in the course, and also in new research projects. A paper in this volume is one of the outcomes.

The ecology course was a highlight for many years because the students (often 25 - 30) combined intensive listening to lectures with field work and close contacts with the teachers, including Eje.

A second development was the shift of emphasis from

ecology of the alvar to management. This was stimulated by a EU funded LIFE project (1996-1999), which examined the effects of grazing and scrub clearance. Valuable information was obtained for the large-scale restoration and management programme supported by the European Union agri-environment schemes. Eje with his wide knowledge of grazing and its impact on the landscape was the obvious person to get involved in research and management plans. Many visitors and students were shown around at new experimental sites.

One of the major outcomes of this new development, to which Eje has greatly contributed, was the recognition of the agricultural landscape of southern Öland as a World Heritage. The description and justification presented by UNESCO includes: "Human beings have lived here for some five thousand years and adapted their way of life to the physical constraints of the island. As a consequence, the landscape is unique, with abundant evidence of continuous human settlement from prehistoric times to the present day." "The landscape of Southern Öland takes its contemporary form from its long cultural history, adapting to the physical constraints of the geology and topography. Södra Öland is an outstanding example of human settlement, making the optimum use of diverse landscape types on a single island."

The added list of publications witnesses Eje Rosén's achievements in ecology and nature management and his cooperation with many colleagues.

Finally we wish to confirm what many friends already know: Eje's intensive social network, particularly as an active member of the Swedish scout movement and, last not least, of 'Växtbio', his beloved institute where his friendship and helpfulness are legendary. Hundreds of colleagues will remember his splendid slide performance during the annual Christmas party at the institute which he has presented since the 1970s.

We hope that this volume will give Eje a similar pleasure as so many of his colleagues and friends have enjoyed for so many years in their cooperation with Eje.

Major publications on the dynamics and management of dry grasslands on Öland (co-)authored by Ejvind Rosén

Rosén, E. & Sjögren, E. 1973. Sheep grazing and changes of vegetation on the limestone heath of Öland. — Zoon (Uppsala) Suppl. 1: 137-151.

Rosén, E. 1980. Plant cover regeneration in a mechanically disturbed limestone heath on Öland, Sweden. — Acta Phytogeogr. Suec. 68: 123-130

Rosén, E. 1982. Vegetation development and sheep grazing in limestone grassland of south Öland, Sweden. — Acta Phytogeogr. Suec. 72: 1-104.

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

Prentice, H.C., Rosén, E., Moberg, R. & Sjögren, E. 1988. The dry alvar grasslands of Öland: ecological amplitudes of plant species in relation to vegetation composition. — Acta Phytogeogr. Suec. 76: 21-46.

Rejmánek, M. & Rosén, E. 1988. The effects of colonizing shrubs (Juniperus communis and Potentilla fruticosa) on species richness in the grasslands of Stora Alvaret, Öland. — Acta Phytogeogr. Suec. 76: 67-72.

Rosén, E. 1988. Shrub expansion in alvar grasslands on Öland. — Acta Phytogeogr. Suec. 76: 87-100.

Rosén, E. 1988. Development and seedling establishment within a Juniperus communis stand on Öland, Sweden. — Acta Bot. Neerl. 37: 193-201.

Rosén, E. & Sjögren, E. 1988. Plant cover in alvar junipers on Öland. Distribution features correlated to shrub size and shape. — Acta Phytogeogr. Suec. 76: 101-112.

Zobel, K., Zobel, M. & Rosén, E. 1994. An experimental test of diversity maintenance mechanisms, by a species removal experiment in a species-rich wooded meadow. - Folia Geobot. Phytotax. 29: 433-437.

Rosén, E. 1995. Periodic droughts and long-term dynamics of alvar grassland vegetation on Öland, Sweden. — Folia Geobot. Phytotax. 30: 131-140.

Bakker, J.P., Bakker, E.S., Rosén, E., Bekker, R.M. & Verweij, G.L. 1996. The soil seed bank composition along a gradient from dry alvar grassland to Juniperus scrubland. — J. Veg. Sci. 7: 165-176.

Zobel, M., Suurkask, M., Rosén, E. & Pärtel, M. 1996. The dynamics of species richness in an experimentally restored calcareous grassland. — J. Veg. Sci. 7: 203-210

Bakker, J.P., Bakker, E.S., Rosén, E. & Verweij, G.L. 1997. The soil seed bank of undisturbed and disturbed limestone grassland. — Z. Ökol. Nat.schutz 6: 9-18.

Pärtel, M., Kalamees, R., Zobel, M. & Rosén, E. 1998. Restoration of species-rich limestone grassland communities from overgrown land: the importance of propagule availability. — Ecol. Engineer. 10: 275-286.

Pärtel, M., Kalamees, R., Zobel, M. & Rosén, E. 1999. Alvar grasslands in Estonia: variation in species composition and community structure. — J. Veg. Sci. 10: 561-570.

Rosén, E. & Borgegård, S.-O. 1999. The open cultural landscape. — Acta Phytogeogr. Suec. 84: 113-134.

Prentice, H.C., Lönn, M., Lager, H., Rosén, E. & van der Maarel, E. 2000. Changes in allozyme frequencies in Festuca ovina populations after a 9-year nutrient/water experiment. — J. Ecol. 88: 331-347.

Rosén, E. & van der Maarel, E. 2000. Restoration of alvar vegetation on Öland, Sweden. — Appl. Veg. Sci. 3: 65-72.

Mitlacher, K., Poschlod, P., Rosén, E. & Bakker, J.P. 2002. Restoration of wooded meadows: a comparative analysis along a chronosequence on Öland (Sweden). — Appl. Veg. Sci. 5: 63-73.

Rosén, E. & Bakker, J.P. 2005. Effects of agri-environment schemes on scrub clearance, livestock grazing and plant diversity in a low-intensity farming system on Öland, Sweden. — Basic Appl. Ecol. 6: 195-204.

Rosén, E. 2006. Alvar vegetation of Öland – changes, monitoring and restoration. — Proc. R. Irish Acad. 106B: 387-399.

Structure and dynamics of alvar vegetation on Öland and some related dry grasslands: Introduction

Eddy van der Maarel

Community and Conservation Ecology Group, Groningen University, Postbus 14, NL-9750 AA Haren, The Netherlands; [2]E-mail j.p.bakker@biol.rug.nl
E-mail eddy.arteco@planet.nl

Historical notes

This volume contains contributions on the structure and dynamics of dry grassland, mostly on Öland, and particularly on the huge limestone area known as Stora Alvaret, the Great Alvar. Since the early 1980s alvar ecology has been a major research object of Växtbiologiska institutionen, the Institute of Ecological Botany (now Department of Plant Ecology) of Uppsala University. This research was certainly triggered by the doctoral dissertation of Ejvind Rosén (1982) as van der Maarel & Bakker (2007) point out in the first paper in this volume. However, ecological research on Öland has a much longer tradition. Not only the bryological-ecological studies in the decideous forests of Öland by Rosén's supervisor Erik Sjögren (1961, 1964) mentioned in the preceding paper, but also the study by Rosén & Sjögren (1973) can be mentioned as a precursor. In retrospect, the latter paper, dealing with changes of the alvar vegetation in relation to sheep grazing, was in fact the starting point for all the later dynamical-ecological work.

This study had its predecessors as well, and the Uppsala Institute has played a major part in the history of ecological research on Öland, as Sjögren (1988b) introduced in his opening paper in an earlier Special Volume on Öland (Sjögren 1988a). In particular the detailed phytosociological study of the Great Alvar by Nils Albertson (1950) has been a source of information until the present day. Albertson (1946) prepared his doctoral thesis at the Uppsala department on flora, vegetation and environment of Kinnekulle, a largely calcareous table mountain rising above the undulated landscape south of Lake Vänern. This area is very similar to Öland in substrate and vegetation and is often called an alvar area. Albertson's professor was G. Einar Du Rietz, who himself (Du Rietz 1923) published a much earlier account on the plant communities of the Great Alvar, in particular the Helianthemum oelandicum association, which had been described earlier in Uppsala dissertations by Hemmendorf (1897) and Witte (1906). From the same time dates the monograph by Gösta Grevillius (1896) who made a then novel study of the special growth forms of plants on the peculiar alvar substrate. Much further back in the history of Uppsala research on Öland, Sjögren (1988b) traced a study by Göran Wahlenberg (1821) on observations on Öland's nature. Wahlenberg was the last professor of both botany and medicine; after him the chair was split into botany and medicine and towards the end of that century ecological botany was recognized as a separate chair. From Wahlenberg to Carl Linnaeus is not a big step and so we end at the very beginning of Öland's ecology through the natural history of Öland reported by Linnaeus in his book Ölandic and Gotlandic Journey 1741 (Linnaeus 1745).

Linnaeus mentioned over 300 plant species for the island and described briefly their morphology and habitat conditions. Surprisingly many typical alvar species are well characterized, most of them with at least in part the Latin name as we know it nowadays. One of the most interesting cases is *Cistus oelandicus*, observed in large populations, on the open alvar which according to the description must be *Helianthemum oelandicum* – which is confirmed by the London Natural History Museum in its 'Linnean typification project' (see the website of this museum). From this habitat are also mentioned *Festuca ovina* and crustaceous lichens, exactly as the situation is today. Other spectucalar alvar species, e.g. *Globularia* ('rare in Europe') and *Potentilla fruticosa* are mentioned as well.

The well-known '*Avenetum*' with its remarkable richness was not recognized as a vegetation of its own but *Avena pratensis* and *Veronica spicata* and many orchid species are reported all right.

Phytosociology

Following the old research line from Du Rietz (1923), Albertson (1950) to Krahulec et al. (1986), it is logical to start the six papers following in this special volume with the paper by Swante Löbel & Jürgen Dengler (2007), who studied the dry grassland vegetation on southern Öland in much greater detail than earlier while they included areas outside the Great Alvar. Albertson's study was also very detailed, but in his approach which followed the old 'Uppsala school', very small sample plots of 0.25 m^2 were used, which is insufficient to get a realistic description of the composition of taller vegetation. Albertson himself explained that his quadrats were too small, but in his view sufficient for the low moss- and lichen dominated open alvar vegetation. Krahulec et al. (1986) used the Braun-Blanquet approach, with larger plots and more and representatively chosen sample plots. They covered only part of the variation on the Great Alvar with ca. 60 relevés and additional soil analyses. These were numerically classified and ordinated which resulted in the distinction of four community types.

In the same way Löbel & Dengler made more than 450 relevés completed by microtopography and soil analyses and were able to distinguish no less than 15 associations or equivalent units which they assigned to three major syntaxa, the subclasses *Koelerio-Corynephorenea* and *Sedo-Scleranthenea* (already treated in earlier separate studies: Dengler & Löbel 2006; Dengler et al. 2006) and the class *Festuco-Brometea*. Whereas the first category comprises impoverished variants of widely distributed syntaxa, all *Sedo-Scleranthenea* and *Festuco-Brometea* communities lack direct counterparts in central Europe. The alvar communities proved to be floristically well separated from the others. All species endemic to Öland, Öland + Gotland and Öland + some more geographically and ecologically related areas, find their place in the new syntaxonomical system, most of them as association-characteristic species. According to their ordination results soil depth and moisture content were the main factors differentiating the three main community groups.

Species richness

Löbel & Dengler also followed another line of research, that of species richness on very small plots within several alvar plant communities. Such studies had been started on Öland in 1985 by Ejvind Rosén & Eddy van der Maarel (van der Maarel 1988; Rejmánek & Rosén 1988) and were included in an international research project on species diversity on different scales in species-rich communities in relation to soil nutrient status (Peet et al. 1990; Sykes et al. 1994). In these studies it was discovered that

in the *Veronica spicata-Avenula pratensis* community fine-scale species richness (on plots of 10 to 100 cm^2) was very high and moreover did the species composition on these small plots change considerably from year to year. This high within-community species mobility was interpreted with the help of the carousel model which suggested that most of the species would move around in the community and would reach virtually all microplots in the long run (van der Maarel & Sykes 1993).

Löbel & Dengler analysed species richness in nested plots of 10 sizes from 1 cm^2 up to 9 m^2, within and around the phytosociological sample plots. They found similar high species numbers on small plot sizes as van der Maarel & Sykes (1993) did, for instance a maximum of 25 species on 0.01 m^2. Their results for the standard size of the sample plots, 4 m^2, were higher than comparable figures for the *Avenetum* obtained so far. The highest values were found in the *Gypsophila fastigiata-Globularia vulgaris* association with 80 taxa. This is one of the highest values known in the world.

Löbel & Dengler (2007) mention harsh and variable conditions, small plant sizes and a large local species pool as possible causes of fine-scale species richness. From earlier work in the *Avenetum* including fertilization and irrigation experiments we know that a low nutrient status and irregularly occurring summer droughts, and the resulting low stature of vascular plants and abundance of mosses and lichens, are important prerequisites for species richness (Huber 1994, 1999). The continuous creation of small gaps through small-scale disturbances, notably herbivore trampling and dung deposition, has been demonstrated as another important factor (Rusch & van der Maarel 1992; Rusch & Fernández-Palacios 1995; Dai 2000).

Species richness is also the main topic of the next paper in this volume by Aveliina Helm, Pille Urbas & Meelis Pärtel. This contribution continues the cooperation between the Uppsala and Tartu plant ecology departments on the topic of alvar ecology, concentrated in the beginning on the concept of species pool (species reservoir as I prefer to call it). Based on own as well as other papers (notably Eriksson 1993) the concept was further established and differentiated into regional, local and community species pool (Pärtel et al. 1996; Zobel 1997; Zobel et al. 1998). Also the idea of filtering was elaborated: the community pool is a selection of the larger pool around the local community mainly based on habitat preferences. The determination of the regional species pool for alvar communities was elaborated by Dupré (2002) by selecting species with (1) similar Ellenberg indicator values as the species in the target community and (2) a similar phytosociological position. Helm et al., comparing species richness and species characteristics of dry alvar grassland communities on the islands of Saaremaa (Estonia) and Öland (Sweden), considered that so-called

core species in the species pool – with a high frequency of occurrence in the data set – would behave different from the low-frequency satellite species. There were no significant differences in the sizes of the community species pool and a-diversity between the two regions. There was a strikingly similar number of core species, while the number of satellite species was much higher for Saaremaa. Per site, there were significantly more satellite species in Saaremaa than on Öland. Average potential height of plants was significantly larger on Estonian alvars indicating better soil conditions there. This is also expressed in the higher demand for soil moisture and lower demand for light of species from Saaremaa alvars. Core and satellite species had similar differences in their environmental demands in both regions: satellite species preferred higher soil nutrient content and more soil moisture than core species.

Species turnover and mobility

The high species turnover and species mobility within the community as related to continuous gap formation in alvar grasslands as suggested by van der Maarel & Sykes (1993, 1997) was elaborated in various studies by Graciela Rusch (Rusch 1992; Rusch & van der Maarel 1992; Rusch & Fernández-Palacios 1995) and Renate Huber (1994, 1999). Rusch indicated especially the need of small gaps for regeneration from seed in the *Avenetum*. Huber studied species turnover in very small to small plots in relation to changes in environmental conditions. In the third paper in this volume, Huber & van der Maarel (2007) repeat the set-up of the experiments and quantify turnover measures. Nutrient and water supply, light availability and removal of biomass were manipulated in an alvar dry grassland on Öland from 1990 to 1993 in order to investigate how these factors influence species richness and year-to-year turnover at fine scales. Turnover was broken down into disappearance ('extinction') and appearance ('immigration') of vascular plant species and was measured at different spatial scales in plots ranging from 4 cm^2 to 0.25 m^2.

For most treatments, turnover was highest at the finest scale, both measured as absolute and relative numbers. Turnover rate increased at all scales when the treatment implied such a change in the environment, where application of fertilizer was combined with shading. In these cases, disappearance of species largely exceeded appearance in a predictable manner, and resulted in species-poor assemblages at all scales. In plots treated with either fertilizer or shade, there were large differences in the direction of the turnover (i.e. whether immigration or extinction dominated) between years, apparently depending on the weather conditions in the respective year. After drought spells total turnover was also

high for such treatments, whereas plots regularly receiving additional water had rather similar turnover rates during the whole experiment.

In the starting paper on small-scale species dynamics van der Maarel & Sykes (1993) approached the year-to-year changes in various ways. The following contribution to the volume by Kathrin Studer & David Newbery (2007) refers to a geographically different but still quite similar *Mesobrometum* calcareous grassland in the Swiss Jura and fits very well in this volume. In this case the community dynamics were investigated in 25 1-m^2 plots where 50 0.01-m^2 subplots per plot were recorded over 6 years. Data are presented for 53 non-woody species and the variables were spatial frequency, temporal frequency, frequency fluctuation, turnover, and cumulative frequency (each species), and cumulative species richness (all species).

Spectra for all species and all variables were different for the two investigated spatial scales (0.01 m^2 and 1 m^2). The comparison with other investigations of similar grasslands showed that the behaviour of some species is specific for this type of vegetation in general (e.g. *Achillea millefolium, Arrhenatherum elatius, Bromus erectus*), but most species behaved in a stand-specific way, i.e. they may play another (similar or completely different) role in another grassland stand. Six spatio-temporal patterns were defined across species. One conclusion is that in order to understand community dynamics, not only the dynamics of mobility, but also of frequency fluctuations and spatial distribution of the species are fundamental.

Studer & Newbery also present a typology of species mobility types after comparing the systems of Herben et al. (1993) and van der Maarel (1996).

Dynamic ecology and management

Although management aspects have been part of the alvar ecology projects from the beginning (e.g. Rosén & Sjögren 1973; Rosén 1980), during the 1980s both the knowledge of the ecological basis of alvar management and the need for management and restoration increased. Under reference to the preceding tribute to Eje Rosén (van der Maarel & Bakker 2007) the experience, imagination and openness to new developments of Eje has been seminal in the development of alvar management. Important management aspects include:

1. Adaptation of grazing pressure in order to obtain optimal diversity of alvar grasslands in relation to (a) overgrazing and resulting reduction of biomass and diversity (e.g. Rosén 1982; Titlyanova et al. 1988), and (b) reduced grazing resulting in encroachment of *Juniperus* and *Potentilla fruticosa* (e.g. Rosén 1988a, Rejmánek & Rosén 1988).

2. Restoration of alvar grasslands through clearance of *Juniperus* scrub and subsequent re-introduction of grazing (e.g. Rosén 1988b), in which the availability of propagules has become a key issue (e.g. Pärtel et al. 1998) which is a matter of seedbank availability (e.g. Bakker et al. 1997) and of dispersal (e.g. Mitlacher et al. 2002).

3. Integration of alvar grasslands in a wider frame-work of ancient agricultural landscapes (the 'open cultural landscape' of Rosén & Borgegård 2002) (e.g. Poschlod & WallisDeVries 2002; Rosén & Bakker 2005).

The final two papers in this volume deal with features of the third aspect. In the contribution of Jan P. Bakker, Ejvind Rosén & Karin Steg (2007) the starting point is that alvar grasslands have formed and locally still form a mosaic with (low-productive) agricultural fields and that in the course of history fields were often abandoned. The question is which alvar species would return spontaneously on these fields and in which speed. In the past, arable fields were established locally on the alvar at the northern side of the Great Alvar near an abandoned village. For this purpose a series of arable fields was selected forming a chronosequence from still cultivated, ca. 20 years abandoned, ca. 50 years abandoned, and never cultivated. Species of man-influenced habitats gradually disappeared from the former arable fields, but a few persisted after 50 years. A group of alvar species had re-established after 20 years, but others did not re-establish even after 50 years of abandonment, although those species are present in the local species pool.

The final paper by Honor C. Prentice, B. Olle Jonsson, Martin T. Sykes, Margareta Ihse & Merit Kindström (2007) deals with fragmented grasslands in an area around a village at the northern edge of the Great Alvar. These grasslands have a different history and position in the landscape. The site will provide an arena for future investigations of the relationships between present-day species diversity and gene diversity and the spatial properties of the present and past landscapes. The interest is on the occurrence of individual vascular plant species in relation to grassland continuity and previous land use, and the dominant gradients of soil moisture and eutrophication. This part of the work is based on an earlier study by Bengtsson et al. (1988). Gen diversity has already been shown to be an interesting topic as far as alvar species are concerned (Prentice et al. 2000). Because relationships between grassland age and plant community composition are confounded by local grassland eutrophication, it appeared to be difficult to use the present grassland data set to draw conclusions about the extent to which the distributions of individual species reflect a long history of continuous grassland management or an absence of eutrophication.

Retrospect and perspective

In these various contributions most of the actual themes in the plant community research of dry grasslands have been touched upon. In addition just two out of several lines of research will be added. No contribution dealt specifically with the topic of species traits, characteristics of plant species which can be used in addition to the quantification of habitat requirements in order to understand the dynamic behaviour of alvar species. In the papers in this volume attention was largely restricted to growth form and Ellenberg indication values. Nevertheless the topic of species traits has formed an intrinsic part of alvar research starting with van der Maarel (1988) and continuing with Dupré & Diekmann (2001) and Dupré & Ehrlén (2002). In the latter paper deciduous woodlands on Öland were included. Indeed, ideas on small-scale species dynamics and species traits have also been investigated in woodlands, in particular by Camilla Wessberg (Dupré et al. 2002), which resulted among other things in the confirmation of the significance of the species pool hypothesis.

Another extension remained within the domain of alvar grasslands but focussed on the role of bryophytes in the development of 'pattern and process in the plant community' (Watt 1947; van der Maarel 1996). Manuela Zamfir studied at different scales the relation between bryophytes and vascular plants in community dynamics (Zamfir et al. 1999) and the role of species interactions (Zamfir & Goldberg 2000).

All in all the dry grasslands and more generally the alvar vegetation of Öland has inspired many ecologists to work on the island and to combine field work in this unique environment with all kinds of theoretical studies. For more than 100 years Uppsala University has been a centre for this work. The old Plant Biology Institute, made a world-known institute by professors Rutger Sernander and G. Einar Du Rietz has ceased to exist as such and the Ecological Research Station on Öland, founded by the entomology professor Bertil Kullenberg and approaching its 50th anniversary is no longer a centre of research, even if it is still a basis for field courses and field studies. Nevertheless, more publications from the old Uppsala team on the work in the 1990s and 2000s are in preparation. Meanwhile Lund University has taken over a more active role in community research on Öland.

In conclusion, not only our ecosystems but also our research and research organizations are in a continuous process of dynamics. Institutes arise and disappear, researchers retire, but research will always continue.

References

Albertson, N. 1946. Österplana hed. Ett alvarområde på Kinnekulle (Österplana hed. Ein Alvargebiet auf dem Kinnekulle). — Acta Phytogeogr. Suec. 20. [In Swedish with German summary.]

Albertson, N. 1950. Das grosse südliche Alvar der Insel Öland. Eine pflanzensoziologische Übersicht. — Sven. Bot. Tidskr. 44: 269-331.

Bakker, J.P., Bakker, E.S., Rosén, E. & Verweij, G.L. 1997. The soil seed bank of undisturbed and disturbed limestone grassland. — Z. Ökol. Nat.schutz 6: 9-18.

Bakker, J.P., Rosén, E. & Steg, K. 2007. Re-establishment of alvar plant species in abandoned arable fields on Öland. — Acta Phytogeogr. Suec. 88: 71-80 (this volume).

Bengtsson, K., Prentice, H.C., Rosén, E., Moberg, R. & Sjögren, E. 1988. The dry alvar grasslands of Öland: ecological amplitudes of plant species in relation to vegetation composition. — Acta Phytogeogr. Suec. 76: 21-46.

Dai, Xiaobing. 2000. Impact of cattle dung deposition on the distribution pattern of plant species in an alvar limestone grassland — J. Veg. Sci. 11: 715-724.

Dengler, J. & Löbel, S. 2006. The basiphilous dry grasslands of shallow, skeletal soils (Alysso-Sedetalia) on the island of Öland (Sweden), in the context of North and Central Europe. — Phytocoenologia 36: 343-391.

Dengler, J., Löbel, S. & Boch, S. 2006. Dry grassland communities of shallow, skeletal soils (Sedo-Scleranthenea) in northern Europe. — Tuexenia 26: 159-190.

Du Rietz, G.E. 1923. Studien über die Helianthemum oelandicum-Assoziation auf Öland. — Sven. Bot. Tidskr. 17: 435-446.

Dupré, C. 2000. How to determine a regional species pool: a study in two Swedish regions. — Oikos 89: 128-136.

Dupré, C. & Diekmann, M. 1998. Prediction of occurrence of vascular plants in deciduous forests of South Sweden by means of Ellenberg indicator values. — Appl. Veg. Sci. 1: 139-150.

Dupré, C. & Diekmann, M. 2001. Differences in species richness and life-history traits between grazed and abandoned grasslands in southern Sweden. — Ecography 24: 275-286.

Dupré, C. & Ehrlén, J. 2002. Habitat configuration, species traits and plant distributions. — J. Ecol. 90: 796-805.

Dupré, C., Wessberg, C. & Diekmann, M. 2002. Species richness in deciduous forests: Effects of species pools and environmental variables. — J. Veg. Sci. 13: 505-516.

Eriksson, O. 1993. The species-pool hypothesis and plant community diversity. Oikos 68: 371-374.

Grevillius, A.Y. 1896. Morphologisch-anatomische Studien über die xerophile Phanerogamenvegetation der Insel Öland. — Bot. Jahrb. 23: 24-108.

Helm, A., Urbas, P. & Pärtel, M. 2007. Plant diversity and species characteristics of alvar grasslands in Estonia and Sweden. Acta Phytogeogr. Suec. 88: 33-42 (this volume).

Hemmendorf, E. 1897. Om Ölands vegetation. Några utvecklingshistoriska bidrag. — Doctoral Dissertation Uppsala University, Uppsala, SE.

Herben, T., Krahulec, F., Hadincová, V. & Kovářová M. 1993. Small-scale spatial dynamics of plant species in a grassland community over six years. — J. Veg. Sci. 4: 171-178.

Huber, R. 1994. Changes in plant species richness in a calcareous grassland following changes in environmental conditions. — Folia Geobot. Phytotax. 29: 469-482.

Huber, R. 1999. Patterns of species richness in a limestone grassland under different treatments in relation to spatial scale. — Appl. Veg. Sci. 2: 257-266.

Huber, R. & van der Maarel, E. 2007. Plant species turnover in an alvar limestone grassland under different environmental conditions and at different scales. — Acta Phytogeogr. Suec. 88: 43-54 (this volume).

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

Linnaeus, C. 1745. Ölandska och Gotländska resa förrättad 1741. — Edited by Carl-Otto von Sydow and published by Wahlström & Widstrand, Stockholm, 390 pp.

Löbel, S. & Dengler, J. 2007. Dry grassland communities on southern Öland: phytosociology, ecology, and diversity. — Acta Phytogeogr. Suec. 88: 13-32 (this volume).

Mitlacher, K., Poschlod, P., Rosén, E. & Bakker, J.P. 2002. Restoration of wooded meadows - a comparative analysis along a chronosequence on Öland (Sweden). — Appl. Veg. Sci. 5: 63-73.

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

Pärtel, M., Kalamees, R., Zobel, M. & Rosén, E. 1998. Restoration of species-rich limestone grassland communities from overgrown land: the importance of propagule availability. — Ecol. Engineer. 10: 275-286.

Peet, R.K., van der Maarel, E., Rosén, E., Willems, J., Norquist, C. & Walker, J. 1990. Mechanisms of coexistence in species-rich grasslands. — Bull. Ecol. Soc. Am. 71: 283.

Poschlod, P. & WallisDeVries, M.F. 2002. The historical and socioeconomic pespective of calcareous grasslands – lessons from the distant and recent past. — Biol. Conserv. 104: 361-376.

Prentice, H.C., Lönn, M., Lager, H., Rosén, E. & van der Maarel, E. 2000. Changes in allozyme frequencies in Festuca ovina populations after a 9-year nutrient/water experiment. — J. Ecol. 88: 331-347.

Prentice, H.C., Jonsson, B.O., Sykes, M.T., Ihse, M. & Kindström, M. 2007. Fragmented grasslands on the Baltic island of Öland: Plant community composition and land-use history. — Acta Phytogeogr. Suec. 88: 81-92 (this volume).

Rejmánek, M. & Rosén, E. 1988. The effects of colonizing shrubs (Juniperus communis and Potentilla fruticosa) on species richness in the grasslands of Stora Alvaret, Öland. — Acta Phytogeogr. Suec. 76: 67-72.

Rosén, E. 1980. Plant cover regeneration in a mechanically disturbed limestone heath on Öland, Sweden. — Acta Phytogeogr. Suec. 68: 123-130.

Rosén, E. 1982. Vegetation development and sheep grazing in limestone grassland of south Öland, Sweden. — Acta Phytogeogr. Suec. 72: 1-104.

Rosén, E. 1988a. Shrub expansion in alvar grasslands on Öland. — Acta Phytogeogr. Suec. 76: 87-100.

Rosén, E. 1988b. Development and seedling establishment within a Juniperus communis stand on Öland, Sweden. — Acta Bot. Neerl. 37: 193-201.

Rosén, E. & Bakker, J.P. 2005. Effects of agri-environment schemes on scrub clearance, livestock grazing and plant diversity in a low-intensity farming system on Öland, Sweden. — Basic Appl. Ecol. 6: 195-204.

Rosén, E. & Borgegård, S.-O. 1999. The open cultural landscape. — Acta Phytogeogr. Suec. 84: 113-134.

Rosén, E. & Sjögren, E. 1973. Sheep grazing and changes of vegetation on the limestone heath of Öland. — Zoon (Uppsala) Suppl. 1: 137-151.

Rosén, E. & van der Maarel, E. 2000. Restoration of alvar vegetation on Öland, Sweden. — Appl. Veg. Sci. 3: 65-72.

Rusch, G. 1992. Spatial pattern of seedling recruitment at two different scales in a limestone grassland. — Oikos 65: 433-442.

Rusch, G. & Fernández-Palacios, J.M. 1995: The influence of spatial heterogeneity on regeneration by seed in a limestone grassland. — J. Veg. Sci. 6: 417-426.

Rusch, G. & van der Maarel, E. 1992. Species turnover and seedling recruitment in limestone grasslands. — Oikos 63: 139-146.

Sjögren, E. 1961. Epiphytische Moosvegetation in Laubwäldern der Insel Öland (Schweden). — Acta Phytogeogr. Suec. 44: 1-149.

Sjögren, E. 1964. Epilithische und epigäische Moosvegetation in Laubwäldern der Insel Öland (Schweden). — Acta Phytogeogr. Suec. 48: 1-184.

Sjögren, E. (ed.) 1988a. Plant cover on the limestone Alvar of Öland: Ecology – Sociology – Taxonomy. — Acta Phytogeogr. Suec. 76: 1 - 156.

Sjögren, E. 1988b. Studies of vegetation on Öland – changes and development during a century. — Acta Phytogeogr. Suec. 76: 5-8.

Studer-Ehrensberger, K. & Newbery, D.M. 2007. Species mobility and frequency dynamics in a Swiss limestone grassland. Acta Phytogeogr. Suec. 88: 55-70 (this volume).

Sykes, M.T., van der Maarel, E., Peet, R.K. & Willems, J.H. 1994. High species mobility in species-rich plant communities: an intercontinental comparison. — Folia Geobot. Phytotax. 29: 439-448.

Titlyanova, A., Rusch, G. & van der Maarel, E. 1988. Biomass structure of limestone grasslands on Öland in relation to grazing intensity. — Acta Phytogeogr. Suec. 76: 125-134.

van der Maarel, E. 1988. Floristic diversity and guild structure in the grasslands of Ölands Stora Alvar. — Acta Phytogeogr. Suec. 76: 53-65.

van der Maarel, E. 1996. Pattern and processes in the plant community: fifty years after A.S. Watt. — J. Veg. Sci. 7: 19-28.

van der Maarel, E. & Bakker, J.P. 2007. Ejvind Rosén 65 years. — Acta Phytogeogr. Suec. 88: 5-6 (this volume).

van der Maarel, E. & Sykes, M.T. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. — J. Veg. Sci. 4: 179-188.

van der Maarel, E. & Sykes, M.T. 1997. Rates of small-scale species mobility in alvar limestone grassland. — J. Veg. Sci. 8: 199-208.

Wahlenberg, G. 1821. Ytterligare anmärkningar om Ölands natur. — K. Sven. Vetensk. Akad. Handl. 1821: 305-319/

Watt, A.S. 1947. Pattern and process in the plant community. — J. Ecol. 35: 1-22.

Witte, H. 1906. Till de svenska alfvarväxternas ekologi. — Doctoral Dissertation, Uppsala University, Uppsala.

Zamfir, M. & Goldberg, D.E. 2000. The effect of initial density on interactions between bryophytes at individual and community level. — J. Ecol. 88: 243-255.

Zamfir, M., Dai, X. & van der Maarel, E. 1999. Bryophytes, lichens and phanerogams in an alvar grassland: relationships at different scales and contributions to plant community pattern. — Ecography 22: 40-52.

Zobel, M. 1997. The relative role of species pools in determining plant species richness – an alternative explanation for species coexistence? — Trends Ecol. Evol. 12: 266-269.

Zobel, M., van der Maarel, E. & Dupré, C. 1998. Species pool: the concept, its determination and significance for community restoration. — Appl. Veg. Sci. 1: 55-66.

Dry grassland communities on southern Öland: phytosociology, ecology, and diversity

Swantje Löbel[1][*] & Jürgen Dengler[2]

[1]Department of Plant Ecology, Evolutionary Biology Centre, Uppsala University, Villavägen 14, SE-752 36 Uppsala, Sweden; [2]Institute of Ecology and Environmental Chemistry, Leuphana University Lüneburg, Scharnhorststraße 1, DE-21335 Lüneburg, Germany; Present address: Plant Systematics, Biocentre Klein Flottbek & Botanical Garden, University of Hamburg, Ohnhorststraße 18, DE-22609 Hamburg, Germany; E-mail dengler@botanik.uni-hamburg.de; Corresponding author: E-mail swantje.lobel@ebc.uu.se

Abstract

We studied dry grassland vegetation on southern Öland, both within and outside the Great Alvar, using the Braun-Blanquet approach. We were able to distinguish 15 associations or equivalent units belonging to three major syntaxa. Dry grasslands on sandy soils (class *Koelerio-Corynephoretea*; subclass *Koelerio-Corynephorenea*) occurred along the east and west coasts. Weathered rock and outcrop communities (class *Koelerio-Corynephoretea*; subclass *Sedo-Scleranthenea*) inhabited shallow skeletal soils, mainly on the Great Alvar. Semi-dry basiphilous grasslands of the class *Festuco-Brometea* occurred on moraine soils, which were the least extreme in terms of soil moisture and nutrient availability. Whereas the first category comprises impoverished variants of widely distributed syntaxa, all *Sedo-Scleranthenea* and *Festuco-Brometea* communities lack direct counterparts in central Europe. The alvar communities proved to be floristically well separated from the others. Species density on 4 m^2 was highest in the *Sedo-Scleranthenea* (that of the *Gypsophilo fastigiatae-Globularietum vulgaris* with 80 taxa being one of the highest known), intermediate in the *Festuco-Brometea*, and lowest in the *Koelerio-Corynephorenea*. Harsh and variable conditions, small plant sizes, and a large local species pool are considered possible causes.

Keywords: Alvar; Biodiversity; Environmental condition; *Festuco-Brometea*; *Koelerio-Corynephorenea*; *Sedo-Scleranthenea*; Species richness; Syntaxonomy

Nomenclature: Vascular plants: Tutin et al. (1968-1993); *Allium schoenoprasum* var. *alvarense* and *Silene uniflora* ssp. *petraea*: Jonsell & Karlsson (2004); Mosses: Hill et al. (2006); Liverworts: Grolle & Long (2000); Lichens: Santesson et al. (2004).

Introduction

Since the first visit of Carl von Linné in 1741, Öland has been known for its unique vegetation and outstanding flora. Four vascular plant species (*Artemisia oelandica*, *Festuca oelandica*, *Galium oelandicum* and *Hieracium ×dichotomum*) and several infraspecific taxa (e.g. *Allium schoenoprasum* var. *alvarense*, *Crepis tectorum* ssp. *pumila*, *Helianthemum oelandicum* ssp. *oelandicum*, *Silene uniflora* ssp. *petraea*) are considered endemic to Öland or Öland and Gotland (Rosén 1982; Jonsell & Karlsson 2004). However, Dengler & Boch (2007) found three of these taxa also on alvar sites of the island of Saaremaa, Estonia. Further plant species reach the limits of their geographic range, or occur as outliers on Öland (e.g. Rosén & Borgegård 1999). In central Europe, many of the species of this latter category characterise different dry grassland syntaxa, and one wonders whether these communities also occur on Öland.

Studies aiming to classify dry grassland communities in northern Europe are rare, and their results controversial (e.g. Braun-Blanquet 1963; Hallberg 1971; Westhoff et al. 1983; Krahulec et al. 1986; Dierßen 1996; Dengler & Löbel 2006; Dengler et al. 2006a, b). In northern Europe, generally few attempts have been made to develop supra-regional, hierarchical classifications of vegetation types (cf. Lawesson et al. 1997). One usually relies on informal classifications that are not backed up by vegetation tables (e.g. Påhlsson 1999).

Like many other Scandinavian vegetation types, dry grasslands proved to be difficult to assign to higher units of the phytosociological system. Many diagnostic species are missing in northern Europe, whilst at the same time character species different syntaxa frequently occur together (e.g. Diekmann 1995, 1997). The poor characterisation of Nordic vegetation types and the lack of a formal classification cause problems since the EU legislation (e.g. the Habitats directive) is largely based on phytosociological units.

On Öland, dry grassland communities have mainly been studied and described from the Great Alvar, especially by Albertson (1950), Krahulec et al. (1986), and Bengtsson et al. (1988). Krahulec et al. (1986) provided the first modern and comprehensive classification of dry grassland types of the Great Alvar (except the open moss and *Sedum* communities). They distinguished four associations and discussed their position in the phytosociological system but refrained from validly describing these new units. Knowledge about dry grasslands outside of the Great Alvar is limited (e.g. Ammar 1978). However, species distribution maps (Sterner & Lundquist 1986) suggest that some of the alvar communities and other dry grassland types may also occur in other parts of the island. Very little was known about dry grasslands on sandy soils (subclass *Koelerio-Corynephorenea*), even though these are quite interesting from a phytogeographical point of view.

We studied the dry grassland vegetation in the northern part of southern Öland, including dry grasslands on sandy soils (*Koelerio-Corynephorenea*), weathered rock and outcrop communities (*Sedo-Scleranthenea*) and basiphilous grasslands (*Festuco-Brometea*). In the central part of the study area, where the Great Alvar is located, the limestone bedrock is only partly covered by a thin layer of quaternary deposits. Lime-poor moraine soils interchange with residual soils of varying thickness originating from the limestone bedrock. Shallow, weathered soils also occur in the smaller alvar areas on the east coast. Along the Western Landridge, soils are characterised by coarse gravel originating from ancient shorelines. Glacifluvial deposits form sandy soils along the west coast and in the northeastern part of the study area (Sterner & Lundquist 1986).

The aims of our study are (1) to characterise and compare all dry grasslands types that occur within the study area, both floristically and ecologically, (2) to assign them to units of the phytosociological system and to discuss their differentiation on Öland and in comparison with other regions, and (3) to document and discuss their differences in species richness patterns.

Methods

Vegetation sampling

During spring and summer 2001, we made 469 phytosociological relevés of dry grassland vegetation in the northern part of southern Öland. The villages Färjestaden and N Möckleby mark the northern, and Mörbylånga and Alby the southern border of our investigation area (see Fig. 1, below). Dry grassland areas were identified using topographical, geological and species distributions maps (Sterner & Lundquist 1986). Within the areas, sample plots were subjectively chosen according to homogeneity criteria. We tried to select sample plots that represent the local variation of community types.

Sample plots were 4 m² in size throughout; this size is a compromise between the usually very small plots (1 m² or less) used by many Nordic scientists (e.g. Albertson 1946, 1950) and the sizes suggested for dry grasslands in phytosociological textbooks (e.g. Dierßen 1990). Uniform plot sizes are important for the determination and comparison of many characteristics of communities, e.g. species richness, constancy values and thus fidelity of species (e.g. Dengler 2003; Dengler et al. in press).

All vascular plant, bryophyte, and lichen species (with the exception of epilithic crustose lichens) were identified in the field, or if necessary taken into the laboratory. Abundance was estimated according to the Braun-Blanquet cover-abundance scale in the modified version of Wilmanns (1998). This scale closely resembles that of van der Maarel (2005) but draws the limit between 2a and 2b at 15% instead of 12.5%. All relevés and their precise position data are available in Löbel (2002).

Additionally, species-area analyses were carried out in 31 representative stands representing the five associations on the Great Alvar to be described below. We used a nested-plot design and arranged the subsequent plot sizes (0.0001 m², 0.004 m², 0.009 m², 0.0025 m², 0.01 m², 0.04 m², 0.09 m², 0.25 m², 1 m², 4 m², and 9 m²) in a spiral so that the smallest plot was situated in the centre of the largest. All plants 'rooted' in the respective plots were recorded (grid-point system of Williamson 2003).

Structural and soil parameters

For each plot, several environmental and structural parameters were recorded. Soil depth (cm), micro-topography (cm), cover of bare rocks (%) as well as total and group-specific cover of vegetation (%) were determined in the field. We took a mixed soil sample of the uppermost layer (0-10 cm) at different points of each plot. The samples were dried at 105 °C. For each sample, the soil pH was measured with a pH electrode (WTW). In 130 soil samples, we also determined the content of organic matter (mass %) as loss at ignition (905 °C) corrected for calciumcarbonate.

Mean moisture-values (F-values) according to Ellenberg et al. (1991) were calculated for each relevé, weighting species by the mean coverage (%) that corresponds to their respective cover-abundance value.

Phytosociological classification

The phytosociological classification was undertaken according to the consistent application of the Braun-Blanquet approach proposed by Dengler (2003; see also Dengler et al. 2005). Important aspects of this approach are the objective definition of character and differential species,

and the possibility to describe one 'central syntaxon' within each syntaxon of superior rank. The central syntaxon is characterised by the diagnostic species of the syntaxonomic level(s) above, although it may have insufficient or no character species of its own. The validity of character species is limited to the distribution range of the next higher syntaxon (see also Bergmeier et al. 1990).

We mainly follow the classification scheme of dry grassland types proposed by Dengler (2004a, b), which is based on the evaluation of vegetation data from large parts of Europe. For the basiphilous rock and outcrop communities we adopt the results of our own supraregional study (Dengler & Löbel 2006; Dengler et al. 2006a). The nomenclature of the syntaxa follows the International Code of Phytosociological Nomenclature (Weber et al. 2000).

Ordination

Ordinations were undertaken using Detrended Correspondence Analysis (DCA, Hill & Gauch 1980) with detrending by segments. Three different floristic datasets were ordinated: (1) all species, (2) vascular plants only, and (3) cryptogams only. In addition, we analysed relevés assigned to the three different dry grassland (sub-)classes separately. We used mean species cover (%) in the analyses. Neither down-weighting of rare species nor transformation was applied. Ordinations were performed using the program CANOCO 4.51 (ter Braak & Šmilauer 2002), and ordination plots were created with CANOCO Draw 4.1 (ter Braak & Šmilauer 2002).

Results

Phytosociological classification and floristic characterisation

Table 1 lists the 15 plant communities distinguished, their valid names and their assignment to higher syntaxonomic units. For details of the nomenclature and synonyms, see Dengler et al. (2003, 2006), Dengler (2004a, b) and Dengler & Löbel (2006). In the text, we do not mention author citations of these syntaxa. In Table 1, the associations are also linked to the units of the Nordic vegetation classification (Påhlsson 1999).

In the synoptic table (see App. 1), we present species constancy values for all associations and for the three different dry grassland (sub-)classes. Character and differential species are indicated by shading. Fig. 1 shows the distribution of stands assigned to the various communities.

Plates 1, 2, and 3 show typical representatives of the main groups: *Koelerio-Corynephorenea*, *Sedo-Scleranthenea* and *Festuco-Brometea*.

Differentiation of the dry grassland (sub-)classes

The diagram of the ordination of all relevés of the first two DCA axes (Fig. 2) reveals a clear floristic distinction between the relevés of the three main groups, *Koelerio-Corynephorenea*, *Sedo-Scleranthenea*, and *Festuco-Brometea*. Separate DCA analyses of vascular plants and
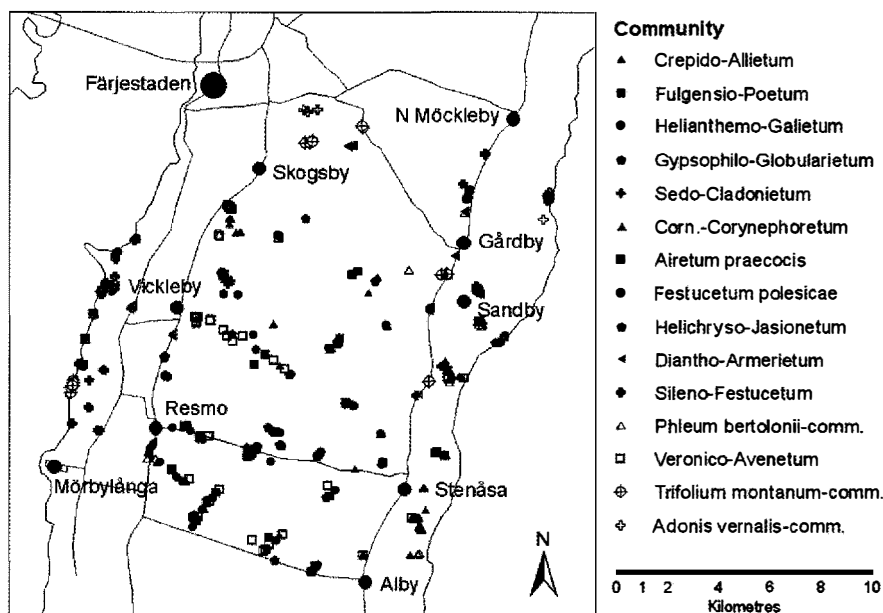
Fig. 1. Investigation area with locations of all sample plots. Dry grasslands on sandy soils (*Koelerio-Corynephorenea*) are restricted to the coastal areas; the *Sileno-Festucetum* also occurs on the Western Landridge. All weathered rock and outcrop communities (*Sedo-Scleranthenea*) except the *Sedo-Cladonietum* only occur in the alvar areas. The *Phleum bertolonii-Saxifraga granulata* community occurs in the smaller alvar areas along the east coast, whereas the *Veronico-Avenetum* is restricted to quaternary deposits on the Great Alvar. The other semi-dry basiphilous grassland communities (*Festuco-Brometea*) occur in the central parts of the island.

Table 1. Syntaxonomical classification of the dry grassland communities of southern Öland. The corresponding units in the Nordic vegetation classification of Påhlsson (1999) are given in square brackets. Since this source lacks vegetation tables, the assignments are based on the verbal descriptions only.

Class: *Koelerio-Corynephoretea* Klika in Klika & Novák 1941
    Subclass: *Koelerio-Corynephorenea* (Klika in Klika & Novák 1941) Dengler in Dengler et al. 2003
        Order: *Corynephoretalia canescentis* Klika 1934 (central order)
        Alliance: *Corynephorion canescentis* Klika 1931
            A1 – *Corniculario aculeatae-Corynephoretum canescentis* Steffen 1931 nom. invers. propos. [5.5.3.1a – *Agrostis vinealis-Corynephorus canescens*-variant]
        Order: *Thero-Airetalia* Rivas Goday 1964
        Alliance: *Thero-Airion* Tx. ex Oberd. 1957
            A2 – *Carici arenariae-Airetum praecocis* Westhoff et al. 1962 nom. invers. propos. (central association) [5.3.1.1c – *Aira praecox-Sedum anglicum*-variant]
        Order: *Trifolio arvensis-Festucetalia ovinae* Moravec 1967
        Alliance: *Armerion elongatae* Pötsch 1962
            A3 – *Diantho deltoidis-Armerietum elongatae* Krausch ex Pötsch 1962 nom. cons. propos. [5.2.1.3 – *Festuca ovina-Pleurozium schreberi*-type; 5.4.1.2a – *Festuca ovina-Armeria maritima*-variant; 5.5.3.1 – *Agrostis vinealis-Rumex tenuifolius*-type]
            A4 – *Sileno otitae-Festucetum brevipilae* Libbert 1933 corr. Kratzert & Dengler 1999 nom. invers. propos. (central association) [5.4.1.2 – *Festuca ovina-Lychnis viscaria*-type; 5.4.1.7c – *Avenula pratensis-Festuca stricta*-variant]
        Order: *Sedo acris-Festucetalia* Tx. 1951 nom. invers. propos.
        Alliance: *Koelerion glaucae* Volk 1931
            A5 – *Helichryso arenarii-Jasionetum litoralis* Libbert 1940 (central association) [5.5.3.1a – *Agrostis vinealis-Corynephorus canescens*-variant]
            A6 – *Festucetum polesicae* Regel 1928 [5.5.3.2 – *Koeleria glauca*-type]
    Subclass: *Sedo-Scleranthenea* (Br.-Bl. 1955) Dengler in Dengler et al. 2003
        Order: *Alysso alyssoidis-Sedetalia* Moravec 1967
        Alliance: *Tortello tortuosae-Sedion albi* Hallberg ex Dengler & Löbel 2006
        Suballiance: *Tortello tortuosae-Sedenion albi* (Hallberg ex Dengler & Löbel 2006) Dengler & Löbel 2006 (central suballiance)
            B1 – *Cladonio symphycarpiae-Sedetum albi* Tx. 1951 nom. invers. propos. (central association) [5.3.2.1 – *Sedum album-Tortella* spp.-type]
        Suballiance: *Tortello rigentis-Helianthemenion oelandici* Dengler & Löbel 2006
            B2 – *Crepido pumilae-Allietum alvarensis* Krahulec et al. ex Dengler & Löbel 2006 [5.3.2.1 – *Sedum album-Tortella* spp.-type]
            B3 – *Fulgensio bracteatae-Poetum alpinae* (Albertson 1950) Dengler & Löbel 2006 [5.3.2.1 – *Sedum album-Tortella* spp.-type]
            B4 – *Helianthemo oelandici-Galietum oelandici* Krahulec et al. ex Dengler & Löbel 2006 (central association) [5.3.2.2 – *Festuca ovina-Tortella* spp.-type]
            B5 – *Gypsophilo fastigiatae-Globularietum vulgaris* Krahulec et al. ex Dengler & Löbel 2006 [5.3.2.2 – *Festuca ovina-Tortella* spp.-type]
Class: *Festuco-Brometea* Br.-Bl. & Tx. ex Klika & Hadač 1944
        Order: *Brachypodietalia pinnati* Korneck 1974
        Alliance: *Filipendulo vulgaris-Helictotrichion pratensis* Dengler & Löbel in Dengler et al. 2003 (central alliance)
            C1 – *Phleum bertolonii-Saxifraga granulata* community [5.4.1.2 – *Festuca ovina-Lychnis viscaria*-type; 5.4.1.7 – *Avenula pratensis-Fragaria viridis-Filipendula vulgaris*-type]
            C2 – *Veronico spicatae-Avenetum* Krahulec et al. 1986 nom. inval. [5.4.1.7b – *Avenula pratensis-Veronica spicata*-variant]
            C3 – *Trifolium montanum-Medicago falcata* community [5.4.1.7 – *Avenula pratensis-Fragaria viridis-Filipendula vulgaris*-type]
            C4 – *Adonis vernalis-Ononis arvensis* community [5.4.1.7 – *Avenula pratensis-Fragaria viridis-Filipendula vulgaris*-type]

cryptogams (not shown) gave very similar results. The Pearson correlation coefficients of sample scores on the first and second axes were high and significant at $P < 0.05$ ($r_1 = 0.862$ and $r_2 = -0.686$).

Species differentiating the *Koelerio-Corynephorenea* from both the *Sedo-Scleranthenea* and the *Festuco-Brometea* are mainly species confined to sandy, unstable soils such as *Corynephorus canescens, Carex arenaria, Jasione montana* and the slightly acidophilous mosses *Ceratodon purpureus* and *Brachythecium albicans*. Other species, e.g. *Thymus serpyllum* ssp. *serpyllum, Festuca ovina*, and *Cladonia rangiformis*, which in central Europe are restricted to the *Koelerio-Corynephorenea* (e.g. Berg et al. 2001, 2004), show a wide amplitude on Öland, and occur in all three major syntaxa of dry grasslands. The same is true for some typical *Festuco-Brometea* taxa, e.g. *Abietinella abietina*.

Sedo-Scleranthenea communities on Öland are characterised by several acrocarpous bryophytes, especially *Tortella* spp., *Encalypta* spp., *Didymodon* spp., and *Ditrichum flexicaule* as well as several epilithic lichens. Characteristic vascular plants are *Sedum album* and several small therophytes, e.g. *Arenaria serpyllifolia, Erophila verna, Hornungia petraea*, and *Saxifraga tridactylites*. Similarly confined to weathered rock and outcrop communities are the assumed island (Baltic) endemics *Helianthemum oelandicum* ssp. *oelandicum, Allium schoenoprasum* var. *alvarense, Festuca oelandica* and *Crepis tectorum* ssp. *pumila*.

The *Festuco-Brometea* communities are characterised by many mesophilous species. Typical taxa are *Filipendula vulgaris, Veronica spicata, Helianthemum nummularium,* and *Asperula tinctoria*. Many *Festuco-Brometea* character species, however, also occur in the *Sedo-Scleranthenea*, e.g. *Anthyllis vulneraria, Medicago lupulina*, and *Homalothecium lutescens*.
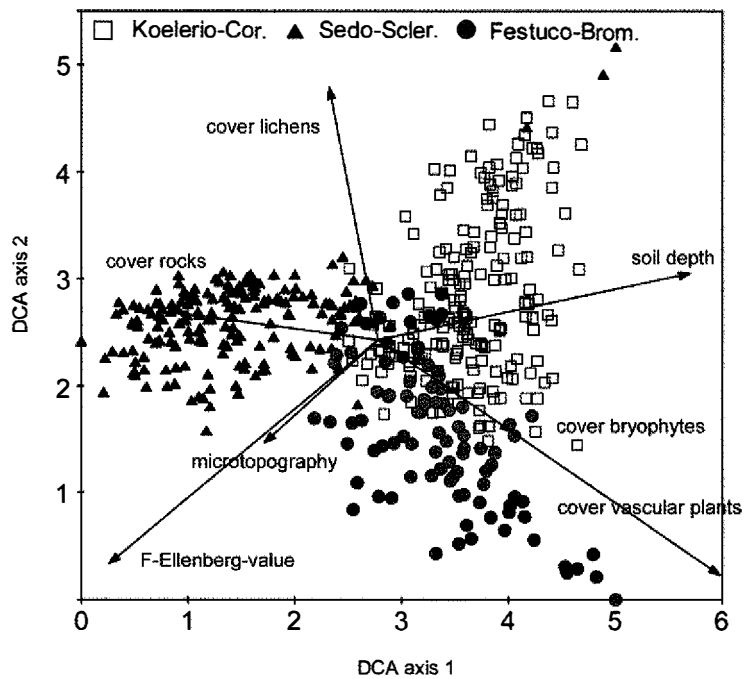
Fig. 2. Ordination diagram with axes 1 and 2 of Detrended Correspondence Analysis; eigenvalues: 0.608 and 0.442. Floristic relationships between dry grassland communities belonging to the *Koelerio-Corynephorenea*, *Sedo-Scleranthenea*, and *Festuco-Brometea* are revealed. In addition, correlations of the DCA axes with important environmental and structural variables are indicated.

Dry grasslands on sandy soils: *Koelerio-Corynephorenea*

In the study area, *Koelerio-Corynephorenea* communities occur exclusively on sandy soils outside the Great Alvar. Even though some 'Öland specialities' can be found in these stands, the communities all fit well in widely-distributed associations. We distinguish six such associations (Fig. 3).

The few relevés of the *Corniculario aculeatae-Corynephoretum canescentis* are only poorly characterised. *Corynephorus canescens* dominates the field layer, but the ground layer is poorly developed. The *Carici arenariae-Airetum praecocis* is characterised by *Aira praecox* and differentiated towards other associations by *Polytrichum*

juniperinum. Floristically, the community connects the *Cornicularie aculeatae-Corynephoretum canescentis* and the communities of the *Armerion elongatae*. The associations of the latter alliance are characterised by *Peltigera canina*, and differentiated by *Trifolium campestre*, *Festuca brevipila*, and *Allium vineale*. The *Diantho deltoidis-Armerietum elongatae* includes the characteristic *Dianthus deltoides* and *Armeria maritima* ssp. *elongata*. The *Sileno otitae-Festucetum brevipilae* (Plate 1, p. 19) is mainly negatively characterised, but is differentiated by a high number of basiphilous species. The communities of the *Koelerion glaucae* are characterised by a rather strong continental element and a rich fruticose lichen flora. The *Festucetum polesicae* contains the character species *Koeleria glauca*
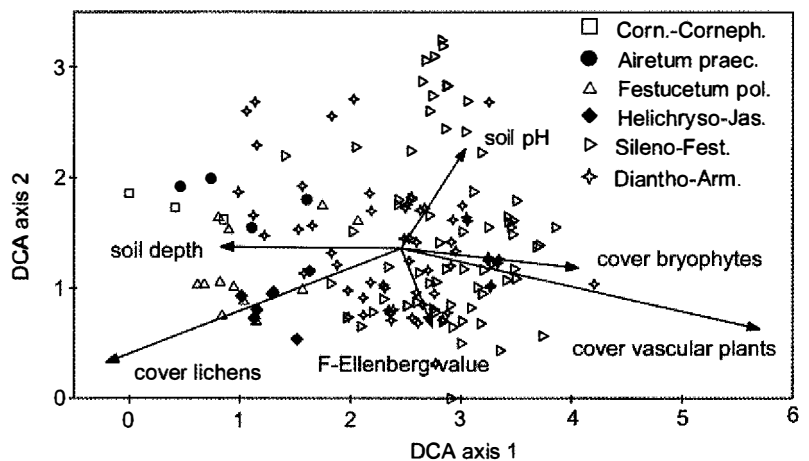
Fig. 3. Ordination diagram with axes 1 and 2 of Detrended Correspondence Analysis of the *Koelerio-Corynephorenea* relevés; eigenvalues: 0.471 and 0.350. Floristic relationships between the dry grassland communities in this subclass are revealed. In addition, correlations of the DCA axes with important environmental and structural variables are indicated.
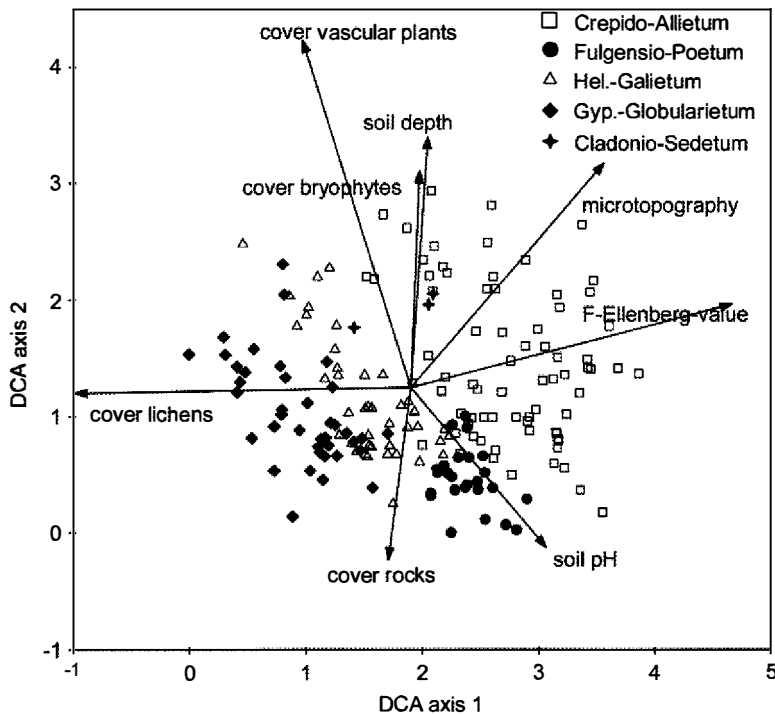
Fig. 4. Ordination diagram with axes 1 and 2 of Detrended Correspondence Analysis of the *Sedo-Scleranthenea*; eigenvalues: 0.431 and 0.322. Floristic relationships between the dry grassland communities of this subclass are revealed. In addition, correlations of the DCA axes with important environmental and structural variables are indicated.

and *Festuca polesica*. The *Helichryso arenarii-Jasionetum litoralis* has no species that characterise it specifically, but it is separated from the *Festucetum polesicae* by the occurrence of several mesophilous species, e.g. *Festuca rubra*.

Weathered rock and outcrop communities: Sedo-Scleranthenea

We distinguish five associations belonging to the *Sedo-Scleranthenea* (Fig. 4) (for details see Dengler & Löbel 2006; Dengler et al. 2006a).

The *Crepido pumilae-Allietum alvarensis* is characterised by *Crepis tectorum* ssp. *pumila* and the continental *Artemisia rupestris*. The field layer is often dominated by the graminoids *Agrostis stolonifera*, *Festuca ovina*, and *Festuca oelandica*. Several taxa indicating loamy soils such as *Prunella vulgaris*, *Sagina nodosa*, and *Leontodon autumnalis* as well as some rich fen mosses characterise this association. The *Fulgensio bracteatae-Poetum alpinae* is characterised by its rich cryptogam flora, especially the crustose lichen species *Fulgensia bracteata*, *F. fulgens*, *Mycobilimbia lurida*, and *Toninia sedifolia*. *Sedum album* is the dominating vascular species; in addition, several
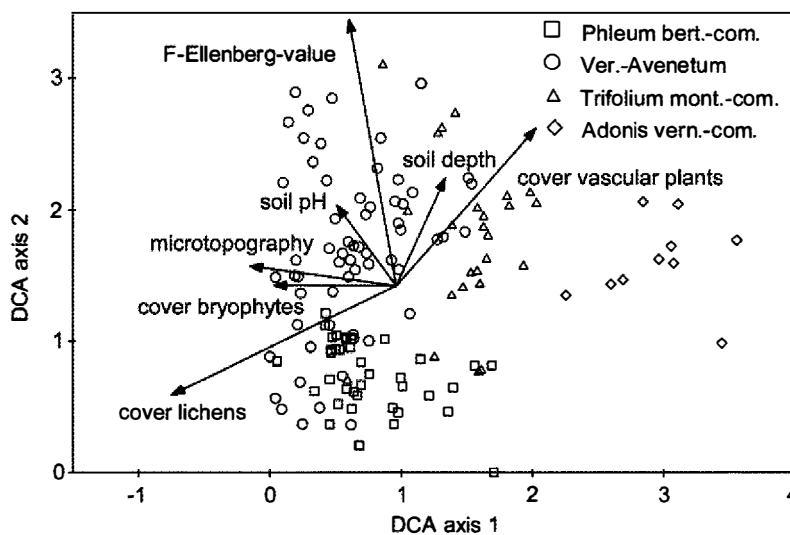
Fig. 5. Ordination diagram with axes 1 and 2 of Detrended Correspondence Analysis of the *Festuco-Brometea* relevés; eigenvalues: 0.482 and 0.353. Floristic relationships between the dry grassland communities of this class are revealed. In addition, correlations of the DCA axes with important environmental and structural variables are indicated.

Plate 1. *Silenootitae-Festucetum brevipilae* (class *Koelerio-Corynephoretea*; subclass: *Koelerio-Corynephorenea*) at the Western Landridge with *Festuca trachy-phylla*, *Sedum acre*, and *Plantago lanceolata* (photo: J. Dengler, June 2001).

Plate 2. *Helianthemo oelandici-Galietum oelandici* (class *Koelerio-Corynephoretea*; subclass: *Sedo-Scleranthenea*) on the Great Alvar with *Helianthemum oelandicum* ssp. *oelandicum*, *Sedum album*, *Allium schoenoprasum* var. *alvarense*, *Cerastium pumilum*, *Erophila verna*, and the lichen species *Thamnolia vermicularis* (photo: J. Dengler, June 1994).

Plate 3. *Veronica spicatae-Avenetum* (class: *Festuco-Brometea*) on the Great Alvar with *Filipendula vulgaris*, *Avenula pratensis*, *Festuca ovina*, *Asperula tinctoria*, and *Dianthus deltoides* (photo: J. Dengler, June 2001).

small therophytes colonise the moss cushions. *Poa alpina* separates this community from the others.

Amongst the flowering plants of the *Helianthemo oelandici-Galietum oelandici* (Plate 2, p. 19), *Helianthemum oelandicum* ssp. *oelandicum* and *Thymus serpyllum* ssp. *serpyllum* predominate. They also occur in the following community. Floristically, this central association is poorly defined, and *Galium oelandicum* and *Sisymbrium supinum* are the only characteristic species. The ground layer contains several fruticose lichens shared with the *Gypsophilo fastigiatae-Globularietum vulgaris*. This last association is characterised by *Globularia vulgaris* and *Gypsophila fastigiata*, which have their major distribution ranges in southwestern and eastern central Europe, respectively. Other typical southeastern European plants are *Vincetoxicum hirundinaria*, *Melica ciliata,* and *Oxytropis campestris*. Species indicating moist soil conditions are missing; *Agrostis stolonifera* is replaced by *Agrostis gigantea*. Finally, the *Cladonio symphycarpiae-Sedetum albi* lacks most of the typical alvar bryophyte and lichen species, but contains more acidophilous taxa, e.g. *Racomitrium canescens* and *Potentilla argentea* agg.

Semi-dry basiphilous grasslands: Festuco-Brometea

We distinguish four locally well-characterised communities (Fig. 5). Since it is unclear at present which of these will prove to be well-defined associations in the supraregional context, we treat them as informal units and we refrain from validating the *Veronico spicatae-Avenetum* (Plate 3, p. 19), which has been given a provisional name by Krahulec et al. (1986). Work on a synthesising study

aiming to resolve these problems in a supraregional context (Sweden, Norway, Finland, Denmark, N Germany, N Poland, Lithuania, Latvia, Estonia, NW Russia) is in preparation (see also Dengler et al. 2006b).

The syntaxonomical position of the *Phleum bertolonii-Saxifraga granulata* community is problematic since the community shows a mixture of elements from the classes *Molinio-Arrhenatheretea* Tx. 1937, *Koelerio-Corynephoretea* and *Festuco-Brometea*, although the last are most pronounced. Amongst the flowering plants *Filipendula vulgaris*, *Ranunculus bulbosus*, and *Saxifraga granulata* predominate. In depressions, relatively tall-growing grasses such as *Phleum pratense* ssp. *bertolonii*, *Anthoxanthum odoratum*, and *Avenula pubescens* ssp. *pubescens* dominate, whereas on hummocks, *Koelerio-Corynephoretea* taxa can be numerous.

The *Veronico spicatae-Avenetum* is characterised by the Öland endemic *Artemisia oelandica*, the orchids *Orchis mascula* and *O. morio* and the southeastern *Prunella grandiflora*. Other frequently occurring flowering plants are *Helianthemum nummularium* ssp. *nummularium*, *Filipendula vulgaris,* and *Veronica spicata*. The ground layer is much better developed than in the following communities. Some acidophilous species serve to differentiate the association, e.g. *Danthonia decumbens* and *Antennaria dioica*. The floristic composition varies much, and two subtypes each with two variants can be distinguished (Löbel 2002).

The *Trifolium montanum-Medicago falcata* community is characterised by *Trifolium montanum*, and differentiated by many slightly ruderal taxa, which are absent on the Great Alvar but frequently occur along roadsides, e.g. *Medicago*

Table 2. Site conditions and vegetation structure of the dry grassland communities of southern Öland. Mean values and standard deviations (in brackets) are presented. Note that soil organic matter was measured only in a subset of 130 plots, whereas all other data represent all 469 relevés of this study.

	Cover total (%)	Cover field layer (%)	Cover ground layer (%)	Cover bare rocks (%)	Soil organic matter (%)	Soil depth (cm)	Micro-topo-graphy (cm)	Soil pH (H$_2$O)	F-value Ellenberg
A – Koelerio-Corynephorenea									
A1 – *Corniculario-Corynephoretum*	37 (6)	35 (6)	2 (3)	0.0 (0.0)	1.2 (0.3)	51.7 (14.4)	0.0 (0.0)	5.0 (0.8)	2.2 (0.2)
A2 – *Carici-Airetum*	78 (6)	55 (6)	48 (3)	0.0 (0.0)	1.3 (0.0)	35.6 (17.1)	0.0 (0.0)	4.9 (0.3)	2.6 (0.3)
A3 – *Diantho-Armerietum*	92 (11)	83 (15)	43 (20)	0.0 (0.0)	7.7 (7.4)	23.2 (16.2)	0.4 (0.0)	4.6 (0.2)	3.2 (0.1)
A4 – *Sileno-Festucetum*	91 (11)	77 (14)	50 (24)	0.8 (0.0)	6.8 (4.0)	30.0 (17.3)	0.5 (1.3)	5.8 (1.0)	2.9 (0.5)
A5 – *Helichryso-Jasionetum*	75 (19)	54 (10)	50 (25)	0.0 (0.0)	3.4 (3.5)	34.3 (14.8)	0.0 (0.0)	6.0 (0.8)	2.8 (0.5)
A6 – *Festucetum polesicae*	79 (13)	56 (10)	51 (27)	0.0 (0.0)	1.4 (0.3)	50.4 (12.7)	0.0 (0.0)	5.3 (0.8)	2.8 (0.4)
B – Sedo-Scleranthenea									
B1 – *Cladonio-Sedetum*	80 (30)	55 (15)	55 (37)	9.3 (9.3)	14.7 (10.5)	5.5 (4.0)	0.0 (0.0)	7.2 (0.5)	2.6 (0.5)
B2 – *Crepido-Allietum*	68 (21)	57 (20)	32 (23)	3.9 (10.5)	17.3 (6.2)	7.1 (3.9)	5.2 (5.6)	7.4 (0.6)	4.5 (0.9)
B3 – *Fulgensio-Poetum*	43 (18)	18 (13)	35 (17)	28.4 (26.5)	20.8 (6.9)	2.4 (1.3)	1.6 (2.1)	7.4 (0.4)	3.3 (0.4)
B4 – *Helianthemo-Galietum*	68 (18)	52 (17)	38 (21)	4.6 (6.5)	13.6 (8.0)	5.7 (2.9)	0.5 (1.5)	7.4 (0.5)	3.6 (0.7)
B5 – *Gypsophilo-Globularietum*	78 (13)	60 (13)	52 (17)	8.1 (10.6)	22.7 (5.1)	5.1 (2.9)	0.3 (1.2)	7.2 (0.5)	3.5 (0.5)
C – Festuco-Brometea									
C1 – *Phleum bertolonii-Saxifraga granulata* comm.	96 (7)	83 (12)	52 (21)	0.5 (1.8)	12.0 (6.8)	18.9 (13.4)	5.6 (6.7)	5.9 (0.7)	3.1 (0.5)
C2 – *Veronico-Avenetum*	96 (5)	85 (12)	55 (19)	0.6 (1.9)	16.8 (6.3)	20.6 (13.3)	2.3 (5.4)	5.8 (0.8)	3.6 (1.1)
C3 – *Trifolium montanum-Medicago falcata* comm.	97 (11)	94 (11)	39 (15)	0.6 (1.9)	10.8 (3.4)	29.2 (19.6)	2.3 (5.4)	6.1 (1.0)	3.4 (1.0)
C4 – *Adonis vernalis-Ononis arvensis* comm.	89 (11)	89 (11)	15 (15)	3.2 (6.3)	11.6 (4.9)	19.5 (4.7)	0.5 (1.6)	6.0 (0.3)	3.5 (0.3)

sativa ssp. *falcata* and *Centaurea scabiosa*. *Knautia arvensis*, *Fragaria viridis*, and *Primula veris* are shared with the next community. Two subtypes are distinguished; the first is characterised by *Trifolium montanum*, the latter by *Carex caryophyllea* and *Potentilla cinerea*.

The *Adonis vernalis-Ononis arvensis* community forms a distinct group in the ordination diagram. *Adonis vernalis*, *Ononis arvensis*, and *Polygala comosa* may serve to characterise this community, at least locally.

Site conditions

The first ordination axis separating the *Sedo-Scleranthenea* from the *Festuco-Brometea* and *Koelerio-Corynephorenea* could be interpreted as mainly representing a gradient in soil depth (Fig. 2). The soil depth was negatively correlated with the soil pH and the cover of bare rocks. The second ordination axis was positively correlated with the Ellenberg F-value, and thus may indicate a gradient in soil moisture. Table 2 gives the mean values of the measured environmental and structural variables for all communities.

Dry grasslands on sandy soils

Among the *Koelerio-Corynephorenea*, the *Cornicularia aculeatae-Corynephoretum canescentis* inhabits the most extreme sites in terms of water and nutrient availability. The sandy soils are very poor in organic matter. On steep slopes, the sites are fairly unstable. The *Carici arenariae-Airetum praecocis* is slightly more mesophilous. Sites are usually affected by mechanical disturbance, especially on tracks used by walkers and cyclists. The *Helichryso arenarii-Jasionetum litoralis* occurs on soils with considerably higher pH values with a mean of pH 6.0. The soil pH measured for the *Festucetum polesicae* is surprisingly low (mean: pH 5.3). The communities of the *Armerion elongatae* grow at the least extreme sites in terms of soil moisture; in addition, the organic matter content is comparatively high here (Table 2). Soils of the *Diantho deltoidis-Armerietum elongatae* are more acid than those of the *Sileno otitae-Festucetum brevipilae* (Table 2). Sites of both associations are often grazed by cows or unused, but in the latter case, some anthropogenic disturbance occurs, especially in recreation areas. The *Sileno otitae-Festucetum brevipilae* often occurs on southern or western slopes with a distinctly warmer microclimate. These sites are partly mown.

Weathered rock and outcrop communities

Within the *Sedo-Scleranthenea*, the floristic differentiation of communities can be at least partly explained by differences in soil moisture and soil depth (Table 2, Fig. 4). The soil pH is high in all alvar communities, but decreases slightly with increasing content of organic matter

(*Gypsophilo fastigiatae-Globularietum vulgaris*).

The *Crepido pumilae-Allietum alvarensis* grows at the wettest sites on loamy soils, which are poorly drained and affected by frost action, which sometimes leads to polygon structures and an often significant microtopography. The *Helianthemo oelandici-Galietum oelandici* grows in considerably drier places, which, however, still are regularly inundated in winter. The *Gypsophilo fastigiatae-Globularietum vulgaris* occurs on well-drained sites, especially in karst areas. Sites of this community are often situated close to *Juniperus communis* shrubs with a southern aspect, which leads to an especially warm microclimate. Ecologically, the sites of the *Fulgensio bracteatae-Poetum alpinae* are clearly distinguished from the other alvar communities by extremely shallow soils and a much higher coverage of bare rocks (mean: 28.4%; Table 2). This community is the first to colonise solid bedrock and gravel. In the initial stage, single moss cushions develop; during succession, fine soil rich in organic matter accumulates and the moss cushions increase in size. Later during succession, the community may be replaced by the *Helianthemo oelandici-Galietum oelandici*. However, due to wind- and water erosion as well as trampling animals, the community may persist over quite long periods.

Semi-dry basiphilous grasslands

The *Veronico spicatae-Avenetum* inhabits a broad range of both soil moisture and soil pH. The two subtypes indicate differences in soil moisture; within each subtype, it is possible to distinguish a variant occurring on more acidic and one on more base-rich soils. Sites are extensively grazed by cows, sheep, and/or horses. The floristic differences between the *Veronico spicatae-Avenetum* and the *Phleum bertolonii-Saxifraga granulata* community may be partly due to differences in the disturbance regime. Sites of the latter community are more intensively grazed, mainly by cows. Trampling animals together with rather poor drainage lead to an extreme microtopography with height differences up to 30 cm. Arising hummocks may also be caused in part by ant activities. Sites of the *Trifolium montanum-Medicago falcata* community are not or only rarely used, being either mown or grazed by cows. Sites often have a southern aspect at the margin of scrubs or forests, or they lie in larger forest gaps. The same is true for the *Adonis vernalis-Ononis arvensis* community, whose soils have a higher loam content. Sites are lightly grazed by cows, and many are visited by tourists.

Species richness

The studied dry grassland communities differed in species richness (Fig. 6), with species numbers ranging from 7 up to 80 per 4 m^2 plot. The mean species density was highest in *Sedo-Scleranthenea* communities, followed by
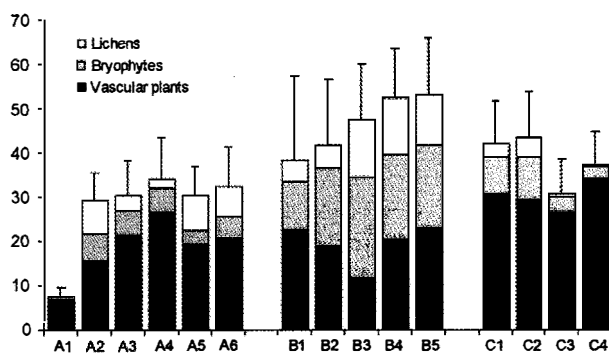
Fig. 6. Means of total and group-specific species richness on 4 m² for the dry grassland communities studied (see Table 2 for community codes). In addition, the standard deviation of the total plant species richness values is indicated. The three groups of columns correspond to the three major syntaxa, viz. from left to right *Koelerio-Corynephorenea*, *Sedo-Scleranthenea*, and *Festuco-Brometea*.

those in the *Festuco-Brometea*, and lowest in the *Koelerio-Corynephorenea*. Mean species density on 4 m² was at its maximum in the *Gypsophilo fastigiatae-Globularietum vulgaris* (53.4 species) and at its minimum in the *Corniculario aculeatae-Corynephoretum canescentis* (8.0 species). The *Crepido pumilae-Allietum alvarensis* had the lowest number of species among the alvar *Sedo-Scleranthenea* communities, with a mean of 42.1 species. Among the *Koelerio-Corynephorenea*, the *Sileno otitae-Festucetum brevipilae* showed the highest species-richness (34.5 species). With a mean of 43.9 species per 4 m², the *Veronico spicatae-Avenetum* was the most species-rich community of the Ölandic *Festuco-Brometea*.

The mean contribution of bryophytes and lichens to the total species richness at 4 m² varied between 8% and 75%. For all *Sedo-Scleranthenea* communities the number of bryophytes and lichens species exceeded on average that of vascular plants. The maximum richness values found on average for the three taxonomic groups on 4 m², were 49 vascular plants (*Veronico spicatae-Avenetum*), 40 bryophytes (*Fulgensio bracteatae-Poetum alpinae*), and 24 lichens (*Gypsophilo fastigiatae-Globularietum vulgaris*).

In the species-area analyses, we found maximum values of 4 species on 0.0001 m², 6 species on 0.0004 m², 11 species on 0.0009 m², 15 species on 0.0025 m², 25 species on 0.01 m², 33 species on 0.04 m², 43 species on 0.09 m², 54 species on 0.25 m², 63 species on 1 m², 77 species on 4 m², and 81 species on 9 m². The richest plots of the smaller sizes mostly belonged to the *Crepido pumilae-Allietum alvarensis*, those with the larger sizes mostly to the *Gypsophilo fastigiatae-Globularietum vulgaris*.

Discussion

Phytosociological classification

Even though some characteristic species of superior syntaxonomical ranks, e.g. classes and subclasses, are missing or lose their indicator value on Öland, our data showed that the three (sub-)classes are still floristically well-separated (see App. 1). Similarly, Krahulec et al. (1986) and Bengtsson et al. (1988) found a clear distinction between *Sedo-Scleranthenea* and *Festuco-Brometea* communities in their numerical analyses (they did not include *Koelerio-Corynephorenea* communities). As the *Sedo-Scleranthenea* and the *Koelerio-Corynephorenea* have both considerable numbers of specific character species, e.g. *Cerastium semidecandrum* and *Cladonia furcata* for the *Koelerio-Corynephorenea*; *Sedum album* and *Peltigera rufescens* for the *Sedo-Scleranthenea*, and of joint character species, e.g. *Sedum acre*, *Ceratodon purpureus*, *Syntrichia ruralis* var. *ruraliformis*, the concept of one class with two subclasses reflects the situation on Öland well (see App. 1). This approach had been proposed by Dengler (2001, 2003, 2004a and in Dengler et al. 2003) based on the analysis of a comprehensive dataset from large parts of Europe. It reconciles the two alternative classifications of other authors, who either distinguish these units on class level (e.g. Schaminée et al. 1996; Rivas-Martínez 2002) or accept one class with three or more orders (e.g. Mucina & Kolbek 1993; Pott 1995), which does not reflect the fact that these orders fall into two floristically and ecologically distinct groups.

The communities of the Great Alvar proved to be floristically very distinct from the others. Most associations accepted in our classification are either (largely) restricted to alvar sites or to non-alvar sites (see Fig. 1). This may be explained by differences in site conditions and history (i.e. centuries or even millennia continuity of at least semi-open conditions on the Great Alvar).

Dry grasslands on sandy soils

Within the *Koelerio-Corynephorenea*, no distinctive Fennoscandian syntaxa seem to exist. On Öland, the suboceanic *Corynephoretalia canescentis* reach the northeastern limit of their range (Dierßen 1996). We observed a few stands of *Corynephorus*-dominated pioneer grasslands, which could be assigned to the central association *Corniculario aculeatae-Corynephoretum canescentis*. However, compared with records of this association from other regions these are remarkably poor in cryptogams, especially lichens. This may be because the association inhabits only slightly acidic soils on Öland, whereas lichen-rich stands of the association are usually best developed as a long-lasting successional stage on more acidic soils (Dengler 2004a). The oceanic order *Thero-Airetalia* also reaches Öland, but

only with one fragmentary association.

The communities of the *Trifolio arvensis-Festucetalia ovinae* show the most northerly distribution within the subclass (e.g. Dierßen 1996). They are represented with two associations of the subcontinental alliance *Armerion elongatae*. Both are common within the study area, and cover huge areas.

The *Sedo acris-Festucetalia* have their main distribution in the subcontinental and continental parts of temperate Europe (Dengler 2001) and reach their northwestern limit on the island (Dierßen 1996). On Öland, we found typical stands of the *Festucetum polesicae*. This vegetation type has been reported from several regions and typically occurs adjacent to the southern Baltic Sea (e.g. Böcher 1947; Andersson 1950; Olsson 1974; Dolnik 2003; Dengler 2004a; Boch & Dengler 2006). Stands on the southern Swedish mainland, however, showed distinctly higher soil pH values than those that we observed on Öland. Records from Gotland (Westhoff et al. 1983) are floristically impoverished and lack *Koeleria glauca*.

Weathered rock and outcrop communities

Our comparison of *Sedo-Scleranthenea* communities from the whole of northern Europe with those of central Europe (Dengler & Löbel 2006; Dengler et al. 2006a) showed a clear distinction between the Nordic and central European basiphilous rock and outcrop communities (*Alysso alyssoidis-Sedetalia*). Therefore, we proposed a Nordic alliance *Tortello tortuosae-Sedion albi*, to be placed within the *Alysso alyssoidis-Sedetalia* and opposed to the central European *Alysso alyssoidis-Sedion* Oberd. & T. Müller in T. Müller 1961, comprising all Nordic communities on shallow, base-rich, skeletal soils (for details, see Dengler & Löbel 2006; Dengler et al. 2006a).

Since we found a close relationship between the Ölandic relevés from outside the Great Alvar and those reported from the Swedish mainland (Hallberg 1971), we suggested to assign them to the same association, called *Cladonio symphycarpiae-Sedetum albi*. Due to the high number of shared species, we further suggested the discrimination between the alvar communities and the other Nordic communities as two suballiances, *Tortello rigentis-Helianthemenion oelandici* and *Tortello tortuosae-Sedenion albi*, respectively (Dengler & Löbel 2006; Dengler et al. 2006a).

With our classification of the alvar communities of shallow, skeletal soils we could largely confirm the units provisionally proposed by Krahulec et al. (1986), and we thus validated their names (Dengler & Löbel 2006). An exception is the differentiation of the *Fulgensio bracteatae-Poetum alpinae* from the *Crepido pumilae-Allietum alvarensis*, which, however, could be attributed to the fact that such stands were only covered to a minor extent by Krahulec et al. (1986). Albertson's (1950) *Sedum album-*

Tortella tortuosa-community is mostly identical with the *Fulgensio bracteatae-Poetum alpinae*.

The *Crepido pumilae-Allietum alvarensis* probably occurs in all extreme alvar areas of hemiboreal Europe (Dengler et al. 2006a). For example, Pärtel et al. (1999) mention alvar stands from Estonia heavily affected by frost action in which *Artemisia rupestris* is quite common, which are placed in this association by Boch & Dengler (2006) and Dengler et al. (2006a). Albertson (1946) described a periodically inundated *Tortella-Schistidium*-subassociation of his 'Festucetum tortellosum' from a small alvar area on the Swedish mainland (Kinnekulle, Västergötland) which also may be included. The *Fulgensio bracteatae-Poetum alpinae* may similarly occur in the other Nordic alvar areas (Dengler et al. 2006a). For example, Albertson's (1946) 'Sedetum tortellosum' may be assigned to this association. Krahulec et al. (1986) considered the *Helianthemo oelandici-Galietum oelandici* as endemic to Öland. However, since we classified this community as a central association of the suballiance, we suggest that it also occurs in the other alvar regions, though lacking the name-giving species (Dengler et al. 2006a). The *Gypsophilo fastigiatae-Globularietum vulgaris* is probably endemic to Öland and Gotland (Dengler et al. 2006a). We found one relevé originating from Stora Karlsö (Westhoff et al. 1983), a small island near Gotland's coast, which may belong to this association. However, more data from Gotland are needed.

Semi-dry basiphilous grasslands

Semi-dry basiphilous grasslands (order *Brachypodietalia pinnati*, class *Festuco-Brometea*) in northern Europe widely lack characteristic species of the south-western and south-eastern alliances *Bromion erecti* W. Koch 1926 and *Cirsio-Brachypodion pinnati* Hadač & Klika in Klika & Hadač 1944, respectively, but are differentiated by a high number of mesophilous species (e.g. Löbel 2002; Dengler 2003; Dengler et al. 2003, 2006a). Therefore, a northern central alliance *Filipendulo vulgaris-Helictotrichion pratensis*, as put forward by Dengler & Löbel (in Dengler et al. 2003), seems logical, resolving most classification problems of the Ölandic *Festuco-Brometea* communities (e.g. Braun-Blanquet 1963; Krahulec et al. 1986).

The *Veronico spicatae-Avenetum* has been provisionally described by Krahulec et al. (1986). We confirmed it as a very distinct community of the alvar vegetation. Our data also support the authors' differentiation between a xerophilous and hygrophilous subtype of this community. These largely correspond to Albertson's (1950) 'Festucetum alvarense rhacomitriosum' and his 'Avenetum alvarense', respectively. *Veronica spicata*, from which the community takes its name, however, cannot serve to define the association since it also frequently occurs in the other *Festuco-Brometea* communities as well as in the *Sileno*

otitae-Festucetum brevipilae and the *Festucetum polesicae*. There are hints that the *Veronico spicatae-Avenetum* also occurs in alvar areas on Gotland (N. Ingerpuu unpubl.). However, in these relevés the characteristic Ölandic species are missing, but differential species such as *Thymus serpyllum*, *Antennaria dioica* and *Danthonia decumbens* do regularly occur. Whether the *Phleum bertolonii-Saxifraga granulata* community represents a legitimate association remains unclear. It may alternatively be considered as a subtype of the *Veronico spicatae-Avenetum*. The *Trifolium montanum-Medicago falcata* community and the *Adonis vernalis-Ononis arvensis* community are floristically well differentiated. We do not describe these communities formally here, but there are some indications that the former is widely distributed and occurs on the Swedish mainland (Hallberg 1971; Albertson 1946), Gotland and Estonia (N. Ingerpuu unpubl. data). The *Fragario-Helichtrotrichetum* described by Hallberg (1971) from Bohuslän, is closely related to the *Potentilla cinerea*-subtype of our *Trifolium montanum-Medicago falcata* community. The *Trifolium montanum*-rich subtype shows some similarities to the 'Avenetum' described by Albertson (1946) from Västergötland, especially his *Inula salicina*-consociation. Species such as *Adonis vernalis*, *Trifolium montanum*, *Polygala comosa*, *Ononis arvensis*, and *Medicago falcata* show some affinities to the alliance *Cirsio-Brachypodion pinnati*, which is distributed in the subcontinental parts of central Europe. However, a comprehensive supraregional study would be needed to decide upon the position of the *Trifolium montanum-Medicago falcata* and the *Adonis vernalis-Ononis arvensis* community in the syntaxonomic system (see Dengler et al. 2006b). In addition, the position of the *Brachypodietalia pinnati* communities rich in *Avenula pratensis* and *Filipendula vulgaris* from Russia (Znamenskiy et al. 2006), Estonia (Pärtel et al. 1999; Boch & Dengler 2006), and Latvia (Rūsina 2007) needs to be clarified since they are floristically somewhat floristically intermediate between the *Veronico spicatae-Avenetum* and the *Trifolium montanum-Medicago falcata* community of Öland.

Species richness

With the species densities recorded, the studied plant communities are among the most species-rich vegetation types on small spatial scales (0.0001-10 m²) documented so far. The richness values of the Ölandic dry grassland communities are significantly higher than those of the corresponding communities in central Europe (Dengler 2005), although central European dry grasslands already belong to the most diverse communities of that region (Hobohm 1998). This difference is particularly pronounced in the communities of base-rich, shallow, skeletal soils (*Alysso alyssoidis-Sedetalia*). In this order, the Öland stands are approximately twice as rich as their central European

counterparts on 4 m² are (Dengler & Löbel 2006). Although this increase is most pronounced in bryophytes and lichens, even the densities of vascular plants are significantly higher on Öland (Dengler & Löbel 2006).

If total plant species richness is considered, few other plant communities worldwide reach or exceed the maximum values achieved in stands of the *Tortello rigentis-Helianthemenion oelandici* on alvar sites in Öland (and similarly on Saaremaa, Estonia, cf. Dengler et al. 2006a). Comparable are lichen-rich, basiphilous grassland and heath communities of Greenland (class *Carici rupestris-Kobresietea bellardii* Ohba 1974) with documented densities of up to 70 on 0.16 m² and 85 on 4 m² (Lünterbusch & Daniëls 2004; Sieg et al. 2006). Also some types of semi-dry basiphilous grassland (*Brachypodietalia pinnati*) are very rich. Extreme vascular plant densities (non-vascular plants are not included in the available publications but play a minor role in these communities) within stands of this order are documented from a wooded meadow on the Estonian mainland (up to 25 on 0.01 m², 42 on 0.04 m², and 76 on 1 m²; Pärtel et al. 2005), from the *Brachypodio pinnati-Molinietum arundinaceae* Klika 1939 of Czechia (up to 67 on 1 m², 88 on 4 m²; Klimeš et al. 2001), and from meadow steppes in Russia (up to 80 on 1 m², Doniță et al. 2003). Finally, Cantero et al. (1999) found up to 89 vascular plants on 1 m² in mountain pastures of Argentina.

What can explain the higher small-scale species densities in Ölandic (or more generally speaking, hemiboreal) dry grasslands compared to their phytosociological counterparts in central Europe? According to the species-pool hypothesis, the small-scale species richness of a particular ecological community is determined by the size of the local species pool, which is positively correlated to the regional species pool for this community type, whose size in turn reflects historical past processes of speciation and migration (e.g. Zobel 1992; Zobel et al. 1998). Several studies have shown that small-scale species densities are positively correlated with local and regional species pools (e.g. Pärtel et al. 1996; Pärtel & Zobel 1999; Dupré et al. 2002). When, however, species richness patterns in dry grasslands of, say, southern Sweden and Germany are compared, the results do not fit in this pattern.

Although the regional species pool for dry grasslands is undoubtedly much higher for vascular plants in Germany than in southern Sweden (most dry grassland plants of Sweden occur also in Germany but not *vice versa*) and seems to be quite similar in both regions in the case of bryophytes and lichens (due to the usually large distribution ranges of most cryptogams), the small-scale species densities nevertheless behave conversely (Dengler 2005; Dengler & Löbel 2006). This does not mean that the species-pool hypothesis is wrong but only that the effect of the different species-pool sizes here is overruled by other factors. Dengler & Löbel (2006) suggested two potential

reasons. First, interspecific competition, which is generally assumed to reduce species richness (e.g. Grime 1979; Grace 1999), could be lower in northern Europe due to a lower productivity of the stands of the same vegetation type caused by shorter vegetation period, harsher climate, and less fertile soils. In an experiment, Huber (1994) showed that competitive exclusion is practically irrelevant in the *Veronico spicatae-Avenetum*, even when the stands are either sufficiently fertilized or irrigated. Second, a 'sampling effect' might contribute to the results in so far as average plant size in Nordic dry grasslands is usually smaller than in central European ones (both individuals of the same species grow lower and small-sized taxa such as cryptogams contribute more to the total richness in northern Europe). If the plants are smaller, more individuals fit on the same area, and these more individuals simply by chance may represent more different species.

Moving from continental to regional patterns of species densities, first the differences between the three major syntaxa catch the eye. The increasing species densities from *Koelerio-Corynephorenea* over *Festuco-Brometea* towards *Sedo-Scleranthenea* nicely correspond to an increase in soil pH (Table 2). When Löbel et al. (2006) applied multiple regression models to the relevés of the present study, soil pH turned out to be the single most important factor determining species densities. This relationship was linearly increasing for total richness, bryophytes, and lichens, and unimodal for vascular plants with a maximum at about pH = 6. This is consistent with analyses throughout southern Sweden (Tyler 1996), in northern Germany (Schuster & Diekmann 2003) and in Czechia (Chytrý et al. 2003), where either monotonously increasing or unimodal relationships with maxima mainly between pH = 5 and 7 were found for dry grasslands. It is widely accepted that the reason for the positive relationship between pH and small-scale species density, which is dominating in temperate and boreal regions worldwide (Pärtel 2002), lies in the predominance of calciphilous species in these regions, and this in turn can be attributed to speciation centres and glacial refugia with dominant base-rich bedrocks (Pärtel 2002; Ewald 2003).

Second, the diversity patterns within the three subclasses may be partly explained by the intermediate disturbance hypothesis (Connell 1975), according to which both too high disturbance and too low disturbance reduce species densities (e.g. Grace 1999). The fact that we found the lowest species densities of the *Koelerio-Corynephorenea* communities in the *Corniculario aculeatae-Corynephoretum canescentis*, and of the *Sedo-Scleranthenea* in the *Crepido pumilae-Allietum alvarensis*, fits well in this hypothesis, as these two associations inhabit the most disturbed sites of the respective subclass. The *Corniculario aculeatae-Corynephoretum canescentis* on southern Öland was found on active coastal cliffs and on sites heavily disturbed by cattle trampling, whereas the *Crepido pumilae-Allietum alvarensis* grows on those alvar sites that are most heavily

exposed to cryoturbation. Within the *Festuco-Brometea*, on the other hand, the two communities of the grazed alvar sites (*Veronico spicatae-Avenetum*, *Phleum bertolonii-Saxifraga granulata* community) have significantly higher species densities than those usually growing on either abandoned or mown sites (*Trifolio montanum-Medicago falcata* community, *Adonis vernalis-Ononis arvensis* community), which could be attributed to competitive exclusion due to too low levels of disturbance. Dupré & Diekmann (2001) found similar trends for different grassland types in southern Sweden.

The specifically high species densities in the communities of the Great Alvar and the adjacent smaller alvar areas seem to be at least partly attributable to a large local species pool, which comprises nearly all basiphilous dry grassland species of the regional species pool in southern Sweden. It is well-known that the Great Alvar has a long history of centuries if not millennia of at least semi-open habitats (e.g. Königsson 1968; Rosén 1982; Sterner & Lundquist 1986) and this site continuity together with the large size may have contributed to the accumulation of a huge local species pool through migration and in the case of the endemics even through speciation. This line of reasoning is supported by Pärtel & Zobel (1999) who showed for the Estonian west coast that species density of alvar communities is positively correlated with the elevation above sea level, with the latter being a surrogate for the time since the emerging from the sea. Additionally, Helm et al. (2006) demonstrated for alvar grasslands on the island of Saaremaa that extension and connectivity of grassland habitats in the past play a crucial role in determining the present-day species densities.

For the richest communities in the present study, those of the *Sedo-Scleranthenea*, also spatio-temporal niche-separation may have contributed to the extraordinary species densities (see Dengler & Löbel 2006). The sites of this subclass often have a distinct microtopography caused by cryoturbation and/or cattle trampling leading to a high small-scale heterogeneity. This combined with the high temporal variability of the environmental conditions at these sites with very shallow soils (water logging or even flooding in winter, severe drought in summer) probably enables the co-existence of a large number of taxa that normally would not grow at the same sites (e.g. *Agrostis stolonifera* with *Sedum album*). On the one hand, the multitude of spatio-temporal micro-niches on the alvar sites provides suitable habitats for species with very divergent ecological requirements; on the other hand, the high spatio-temporal heterogeneity prevents any one species from playing off its competitive superiority. This assumption is supported by Lundholm & Larson (2003), who in a Canadian alvar site found that small-scale species densities are highly positively correlated to the within-plot variability of soil depth and microtopography as well as the number of microsite types. Additionally, van der Maarel & Sykes

(1993) demonstrated for the *Veronico spicatae-Avenetum* that even without niche separation of the adult plants high numbers of different species can co-exist when they mostly are annuals or short-lived perennials and differ in their requirements for (re-)establishment (carousel model).

Acknowledgements

References

Albertson, N. 1946. Österplana hed – ett alvaromåde på Kinnekulle. — Svenska Växtgeografiska Sällskapet, Uppsala, 267 pp. [In Swedish, with German summary.]

Albertson, N. 1950. Der grosse südliche Alvar der Insel Öland – Eine pflanzensoziologische Übersicht. — Sven. Bot. Tidskr. 44: 270-331 + 4 plates.

Ammar, M.Y. 1978. Vegetation and local environment on shore ridges at Vickleby, Öland, Sweden. An analysis. — Acta Phytogeogr. Suec. 64: 1-94.

Andersson, O. 1950. The Scanian sand vegetation – a survey. — Bot. Not. 1950: 145-172.

Bengtsson, K., Prentice, H. C., Rosén, E., Moberg, R. & Sjögren, E. 1988. The dry alvar grasslands of Öland: ecological amplitudes of plant species in relation to vegetation composition. In: Sjögren, E. (ed.) Plant cover on the limestone Alvar of Öland – Ecology – Sociology – Taxonomy. — Acta Phytogeogr. Suec. 76: 21-46.

Berg, C., Dengler, J. & Abdank, A. (eds.) 2001. Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung – Tabellenband. — Weissdorn, Jena, 341 pp.

Berg, C., Dengler, J., Abdank, A. & Isermann, M. (eds.) 2004. Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung – Textband — Weissdorn, Jena, 606 pp. [With English summary.]

Bergmeier, E., Härdtle, W., Mierwald, U., Nowak, B. & Peppler, C. 1990. Vorschläge zur syntaxonomischen Arbeitsweise in der Pflanzensoziologie. — Kiel. Not. Pflanzenkd. Schleswig-Holstein Hamb. 20: 92-110.

Boch, S. & Dengler, J. 2006. Floristische und ökologische Charakterisierung sowie Phytodiversität der Trockenrasen auf der Insel Saaremaa (Estland). In: Bültmann, H., Fartmann, T. & Hasse, T. (eds.) Trockenrasen auf unterschiedlichen Betrachtungsebenen – Berichte einer Tagung vom 26.–28. August in Münster. — Arb. Inst. Landschaftsökol. Münster 15: 55-71.

Böcher, T.W. 1947. *Festuca polesica* Zapal., its chromosome number and occurrence in Denmark. — Bot. Not. 1947: 353-360.

Braun-Blanquet, J. 1963. Das *Helianthemo-Globularion*, ein neuer Verband der baltischen Steppenvegetation. — Veröff. Geobot. Inst. Eidg. Tech. Hochsch. Stift. Rübel 37: 27-38.

Cantero, J.J., Pärtel, M. & Zobel, M. 1999. Is species richness dependent on the neighbouring stands? An analysis of the community patterns of central Argentina. — Oikos 87: 346-354.

Chytrý, M., Tichý, L. & Roleček, J. 2003. Local and regional patterns of species richness in central European vegetation types along the pH/calcium gradient. — Folia Geobot. 38: 429-442.

Connell, J.H. 1975. Some mechanisms producing structure in natural communities: A model and evidence from field experiments. In: Cody, M. L. & Diamond, J. (eds.) Ecology and evolution of communities. — Harvard University Press, Cambridge, MA, pp. 460-490.

Dengler, J. 2001. Erstellung und Interpretation synchorologischer Karten am Beispiel der Klasse *Koelerio-Corynephoretea*. — Ber. R.-Tüxen-Ges. 13: 223-228.

Dengler, J. 2003. Entwicklung und Bewertung neuer Ansätze in der Pflanzensoziologie unter besonderer Berücksichtigung der Vegetationsklassifikation. – Arch. Naturwiss. Diss. 14: 1-297. — Galunder, Nümbrecht. [With English summary.]

Dengler, J. 2004a. Klasse: *Koelerio-Corynephoretea* Klika in Klika & V. Novák 1941 – Sandtrockenrasen und Felsgrusfluren von der submeridionalen bis zur borealen Zone. In: Berg, C., Dengler, J., Abdank, A. & Isermann, M. (eds.) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung – Textband, pp. 301-326. — Weissdorn, Jena.

Dengler, J. 2004b. Klasse: *Festuco-Brometea* Br.-Bl. & Tx. ex Klika & Hadač 1944 – Basiphile Magerrasen und Steppen im Bereich der submeridionalen und temperaten Zone. In: Berg, C., Dengler, J., Abdank, A. & Isermann, M. (eds.) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung – Textband, pp. 327-335. — Weissdorn, Jena.

Dengler, J. 2005. Zwischen Estland und Portugal – Gemeinsamkeiten und Unterschiede der Phytodiversitätsmuster europäischer Trockenrasen. — Tuexenia 25: 387-405.

Dengler, J. & Boch, S. 2007. Taxonomy, ecology, and distribution of six remarkable plant taxa (*Spermatophyta*, *Bryophyta*, and *Lichenes*) of the Estonian dry grassland flora. — Phyton (Horn) 47: 47-71.

Dengler, J. & Löbel, S. 2006. The basiphilous dry grasslands of shallow, skeletal soils (*Alysso-Sedetalia*) on the island of Öland (Sweden), in the context of North and Central Europe.' — Phytocoenologia 36: 343-391.

Dengler, J., Berg, C., Eisenberg, M., Isermann, M., Jansen, F., Koska, I., Löbel, S., Manthey, M., Päzolt, J., Spangenberg, A., Timmermann, T. & Wollert, H. 2003. New descriptions and typifications of syntaxa within the project 'Plant communities of Mecklenburg-Vorpommern and their vulnerability' – Part I. — Feddes Repert. 114: 587-631.

Dengler, J., Berg, C. & Jansen, F. 2005. New ideas for modern

phytosociological monographs. — Ann. Bot. (Roma) N. S. 5: 193-210.

Dengler, J., Löbel, S. & Boch, S. 2006a. Dry grassland communities of shallow, skeletal soils (*Sedo-Scleranthenea*) in northern Europe. — Tuexenia 26: 159-190 + 6 tables.

Dengler, J., Rūsina, S., Boch, S., Bruun, H.H., Diekmann, M., Dierßen, K., Dolnik, C., Dupré, C., Golub, V.B., Grytnes, J.A., Helm, A., Ingerpuu, N., Löbel, S., Pärtel, M., Rašomavičius, V., Tyler, G., Znamenskiy, S.R. & Zobel, M. 2006b. Working group on dry grasslands in the Nordic and Baltic region – Outline of the project and first results for the class *Festuco-Brometea*. — Ann. Bot. (Roma) N.S. 6: 1-28.

Dengler, J., Chytrý, M. & Ewald, J. In press. Phytosociology. In: Jørgensen, S. E. (ed.) Encyclopedia of Ecology. — Elsevier, Oxford.

Diekmann, M. 1995. Delimitation of syntaxa in northern Europe – A case study. — Ann. Bot. (Roma) 53: 65-79.

Diekmann, M. 1997. The differentiation of alliances in South Sweden. — Folia Geobot. Phytotaxon. 32: 193-205.

Dierßen, K. 1990. Einführung in die Pflanzensoziologie (Vegetationskunde). — Wissenschaftliche Buchgesellschaft, Darmstadt, 241 pp.

Dierßen, K. 1996. Vegetation Nordeuropas. — Ulmer, Stuttgart, 838 pp.

Dolnik, C. 2003. Artenzahl-Areal-Beziehungen von Wald- und Offenlandgesellschaften – Ein Beitrag zur Erfassung der botanischen Artenvielfalt unter besonderer Berücksichtigung der Flechten und Moose am Beispiel des Nationalparks Kurischen Nehrung (Russland). — Mitt. Arbeitsgem. Geobot. Schleswig-Holstein Hamb. 62: 1-183. [with English summary.]

Doniţă, N., Karamyševa, Z.V., Borhidi, A. & Bohn, U. 2003. Waldsteppen (Wiesensteppen im Wechsel mit sommergrünen Laubwäldern und Trockenrasen im Wechsel mit Trockengebüschen). In: Bohn, U., Gollub, G., Hettwer, C., Neuhäuslová, Z., Schlüter, H. & Weber, H. (eds.) Karte der natürlichen Vegetation Europas – Maßstab 1 : 2 500 000 – Erläuterungstext: pp. 426-444. — Bundesamt für Naturschutz, Bonn.

Dupré, C. & Diekmann, M. 2001. Differences in species richness and life-history traits between grazed and abandoned grasslands in southern Sweden. — Ecography 24: 275-286.

Dupré, C., Wessberg, C. & Diekmann, M. 2002. Species richness in decidous forests: Effects of species pools and environmental variables. — J. Veg. Sci. 13: 505-516.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. — Scripta Geobot. 18: 1-248.

Ewald, J. 2003. The calcareous riddle: Why are there so many calciphilous species in the Central European flora? — Folia Geobot. 38: 357-366.

Grace, J.B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. — Perspectives Plant Ecol. Evol. Syst. 2: 1-28.

Grime, J.P. 1979. Plant strategies and vegetation processes. — Wiley, Chichester, 222 pp.

Grolle, R. & Long, D.G. 2000. An annotated check-list of the *Hepaticae* and *Anthocerotatae* of Europe and Macaronesia. — J. Bryol. 22: 103-140.

Hallberg, H.P. 1971. Vegetation auf den Schalenablagerungen in

Bohuslän, Schweden. — Acta Phytogeogr. Suec. 56: 1-136 + supplement.

Helm, A., Hanski, I. & Pärtel, M. 2006. Slow response of plant species richness to habitat loss and fragmentation. — Ecol. Lett. 9: 72–77.

Hill, M.O. & Gauch, H.G. 1980. Detrended correspondence analysis: An improved ordination technique. — Vegetatio 42: 47-58.

Hill, M.O., Bell, N., Bruggeman-Nannenga, M.A., Brugués, M., Cano, M.J., Enroth, J., Flatberg, K.K., Frahm, J.-P., Gallego, M.T., Garilleti, R., Guerra, J., Hedenäs, L., Hoyoak, D.T., Hyvönen, J., Ignatov, M.S., Lara, F., Mazimpaka, V., Muñoz, J. & Söderström, L. 2006. An annotated ckecklist of the mosses of Europe and Macaronesia. — J. Bryol. 28: 198-267.

Hobohm, C. 1998. Pflanzensoziologie und die Erforschung der Artenvielfalt – Überarbeitete und erweiterte Fassung der an der Universität Lüneburg eingereichten und angenommenen Habilitationsschrift. Arch. Naturwiss. Diss. 5: 1-231. — Galunder, Wiehl.

Huber, R. 1994. Changes in plant species richness in a calcareous grassland following changes in environmental conditions. — Folia Geobot. Phytotax. 29: 469-482.

Jonsell, B. & Karlsson, T. 2004. Endemic vascular plants in Norden. In: Jonsell, B. (ed.) Flora Nordica – General Volume, pp. 139-159. — Royal Swedish Academy of Sciences, Stockholm.

Klimeš, L., Danák, M., Hájek, M., Jongepierová, I. & Kučera, T. 2001. Scale-dependent biases in species counts in a grassland. — J. Veg. Sci. 12: 699-704.

Königsson, L.-K. 1968. The Holocene history of the Great Alvar of Öland. — Acta Phytogeogr. Suec. 55: 1-172 + supplement.

Krahulec, F., Rosén, E. & van der Maarel, E. 1986. Preliminary classification and ecology of dry grassland communities on Ölands Stora Alvar (Sweden). — Nord. J. Bot. 6: 797-809.

Lawesson, J.E., Diekmann, M., Eilertsen, O., Fosaa, A.M. & Heikkilä, H. 1997. The Nordic Vegetation Survey – concepts and perspectives. — J. Veg. Sci. 8: 455-458.

Löbel, S. 2002. Trockenrasen auf Öland: Syntaxonomie – Ökologie – Biodiversität. — Diploma thesis, Inst. für Ökologie und Umweltchemie, Univ. Lüneburg, 178 + XIV pp. + 4 tables. [Available at the university library of Lüneburg.]

Löbel, S., Dengler, J. & Hobohm, C. 2006. Species richness of vascular plants, bryophytes and lichens in dry grasslands: The effects of environment, landscape structure and competition. — Folia Geobot. 41: 377-393.

Lundholm, J.T. & Larson, D.W. 2003. Relationships between spatial environmental heterogeneity and plant species diversity on a limestone pavement. — Ecography 26: 715-722.

Lünterbusch, C.H. & Daniëls, F.J.A. 2004. Phytosociological aspects of *Dryas integrifolia* vegetation on moist-wet soil in Northwest Greenland. — Phytocoenologia 34: 241-270.

Mucina, L. & Kolbek, J. 1993. *Koelerio-Corynephoretea*. In: Mucina, L., Grabherr, G. & Ellmauer, T. (eds.) Die Pflanzengesellschaften Österreichs Teil I: Anthropogene Vegetation, pp. 493-521. — Fischer, Jena.

Olsson, H. 1974. Studies on South Swedish sand vegetation. — Acta Phytogeogr. Suec. 60: 1-170.

Påhlsson, L. (ed.) 1999. Markanvändningsformer och vegetationstyper i nordiska odlingslandskap. – TemaNord 555:

1-301. — Nordisk Ministerråd, København. [In Swedish, with English summary.]

Pärtel, M. 2002. Local plant diversity patterns and evolutionary history at the regional scale. — Ecology 83: 2361-2366.

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

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

Pärtel, M., Kalamees, R., Zobel, M. & Rosén, E. 1999. Alvar grasslands in Estonia: variation in species composition and community structure. — J. Veg. Sci. 10: 561-570.

Pärtel, M., Bruun, H.H. & Sammul, M. 2005. Biodiversity in temperate European grasslands: origin and conservation. In: Lillak, R., Viiralt, R., Linke, A. & Geherman, V. (eds.) Integrating efficient grassland farming and biodiversity – Proceedings of the 13th International Occasional Symposium of the European Grassland Federation, Tartu, Estonia, 29–31 August 2005, pp. 1-14. — Estonian Grassland Society, Tartu.

Pott, R. 1995. Die Pflanzengesellschaften Deutschlands. 2nd. ed. — Ulmer, Stuttgart, 622 pp.

Rivas-Martínez, S. 2002. High syntaxa of Spain and Portugal and their characteristic species. In: Rivas-Martinez, S., Díaz, T.E., Fernández-González, F., Izco, J., Loidi, J., Lousã, M. & Penas, A. (eds.) Vascular plant communities of Spain and Portugal. Addenda to the syntaxonomical checklist of 2001. — Itinera Geobot. 15: 434-696.

Rosén, E. 1982. Vegetation development and sheep grazing in limestone grasslands of south Öland, Sweden. — Acta Phytogeogr. Suec. 72: 1-108.

Rosén, E. & Borgegård, S.-O. 1999. The open cultural landscape. In: Rydin, H., Snoeijs, P. & Diekmann, M. (eds.) Swedish plant geography – Dedicated to Eddy van der Maarel on his 65th birthday. — Acta Phytogeogr. Suec. 84: 113–134.

Rūsina, S. 2007. Diversity and contact communities of mesophytic and xerophytic grasslands in Latvia. — Latv. Veg. (Rīga) 12: 1-366. [In Latvian, with English summary.]

Santesson, R., Moberg, R., Nordin, A., Tønsberg, T. & Vitikainen, O. 2004. Lichen-forming and lichenicolous fungi of Fennoscandia. — Museum of Evolution, Uppsala, 359 pp.

Schaminée, J.H.J., Stortelder, A.H.F. & Weeda, E.J. (eds.) 1996. De Vegetatie van Nederland – Deel 3. Plantengemeenschappen van graslanden, zomen en droge heiden — Opulus, Uppsala, 360 pp. [In Dutch.]

Schuster, B. & Diekmann, M. 2003. Changes in species density along the soil pH gradient – evidence from german plant communities. — Folia Geobot. 38: 367-379.

Sieg, B., Drees, B. & Daniëls, F.J.A. 2006. Vegetation and altitudinal zonation in continental West Greenland. — Medd. Grønland Biosci. 57: 1-93.

Sterner, R. & Lundqvist, Å. 1986. Ölands kärlväxtflora, 2nd. ed. — Förlagstjänsten, Stockholm, 400 pp. [In Swedish, with English summary.]

ter Braak, C.J.F. & Šmilauer, P. 2002. CANOCO Reference manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination (version 4.5). — Microcomputer Power, Ithaca, NY, 500 pp.

Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) 1968. Flora Europaea – Vol. 2: *Rosaceae* to *Umbelliferae.* — Cambridge University Press, Cambridge, XXVII + 455 pp. + 5 maps.

Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) 1972. Flora Europaea – Vol. 3: *Diapensiaceae* to *Myoporaceae.* — Cambridge University Press, Cambridge, XXIX + 370 pp. + 5 maps.

Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) 1976. Flora Europaea – Vol. 4: *Plantaginaceae* to *Compositae* (and *Rubiaceae*). — Cambridge University Press, Cambridge, XXIX + 505 pp. + 5 maps.

Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) 1980. Flora Europaea – Vol. 5: *Alismataceae* to *Orchidaceae* (*Monocotyledones*). — Cambridge University Press, Cambridge, XXXVI + 452 pp. + 5 maps.

Tutin, T.G., Burges, N.A., Chater, A.O., Edmondson, J.R., Heywood, V.H., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) 1993. Flora Europaea – Vol. 1: *Psilotaceae* to *Platanaceae.* 2nd. ed. — Cambridge University Press, Cambridge, 2nd ed., XLVI + 581 pp.

Tyler, G. 1996. Soil chemistry and plant distibutions in rock habitats of southern Sweden. — Nord. J. Bot. 16: 609-635.

van der Maarel, E. 2005. Vegetation ecology – an overview. In: Maarel, E. van der (ed.) Vegetation ecology, pp. 1–51. — Blackwell Publishing, Oxford.

van der Maarel, E. & Sykes, M.T. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. — J. Veg. Sci. 4: 179-188.

Weber, H. E., Moravec, J. & Theurillat, J.-P. 2000. International Code of Phytosociological Nomenclature. 3rd. ed. — J. Veg. Sci. 11: 739-768.

Westhoff, V., Schaminée, J. & Sýkora, K.V. 1983. Aufzeichungen zur Vegetation der schwedischen Inseln Öland, Gotland und Stora Karlsö. — Tuexenia 3: 179-198.

Williamson, M. 2003. Species-area relationships at small scales in continuum vegetation. — J. Ecol. 91: 904-907.

Wilmanns, O. 1998. Ökologische Pflanzensoziologie, 6th ed. — Quelle & Meyer, Wiesbaden, 405 pp.

Znamenskiy, S., Helm, A. & Pärtel, M. 2006. Threatened alvar grasslands in NW Russia and their relationship to alvars in Estonia. — Biodiv. Conserv. 15: 1797-1809.

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

Zobel, M., van der Maarel, E. & Dupré, C. 1998. Species pool: the concept, its determination and significance for community restoration. — Appl. Veg. Sci. 1: 55-66.

App. 1. Synoptic table of the dry grassland communities on southern Öland. Taxa are labelled as vascular plants (V), bryophytes (B), lichens (L), and 'algae' (A). Percentage constancy values are given per taxon and per asscociations. Columns based on less than 10 relevés (and therefore less reliable) are printed in italics. The columns to the left refer to all relevés and to the three major syntaxa. In the first case, constancy was calculated based on individual relevés, whereas for in the columns A to C mean constancy values of the included associations are given. The diagnostic value of the taxa is indicated by shading and frames and refers to the situation in southern Öland.

■ = character taxon   ▢ = differential taxon
▨ = transgressive character taxon on the superior hierarchical level   ⋯ = negatively differentiating taxon within a 'species block'

Class / Subclass / Order, alliance, or suballiance / Association	Group	All relevés (mean rel.)	Subcl. A (mean ass.)	Subcl. B (mean ass.)	Class C (mean ass.)	A.a A1	A.b A2	A.c A3	A.c A4	A.d A5	A.d A6	B.a1 B1	B.a2 B2	B.a2 B3	B.a2 B4	B.a2 B5	C.a C1	C.a C2	C.a C3	C.a C4
Number of relevés or associations		469	6 ass.	5 ass.	4 ass.	3	4	60	66	7	12	3	74	25	41	39	39	61	25	10
Mean number of plant taxa (total)		41	27	47	39	8	29	30	34	30	33	39	43	48	53	54	42	44	31	37
Mean number of vascular plants		24	19	19	31	7,3	16	22	27	20	21	23	19	12	20	23	31	30	27	34
Mean number of bryophytes		11	4,3	18	6,0	0,7	6,3	5,5	5,5	2,9	5,1	11	18	23	19	19	8,1	9,7	3,4	2,8
Mean number of lichens		5,5	4,5	9,4	2,1	0,0	7,3	2,8	2,0	7,9	6,9	5,0	5,1	13	13	11	3,2	4,4	0,6	0,2

Class Koelerio-Corynephoretea

	Taxon	T	All	A	B	C	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
C	Sedum acre	V	46			22												64	16	8	.
	Ceratodon purpureus	B	25			11												33	3	8	.
	Syntrichia ruralis var. ruraliformis	B	31			9												26	5	4	.
	Cetraria aculeata	L	21			4												5	10	.	.
	Artemisia campestris ssp. campestris	V	31			10												15	5	20	.
	Cladonia foliacea	L	19			5												5	13	.	.
	Androsace septentrionalis	V	4			1												5	.	.	.
D	Cetraria islandica	V	28	39	36	11		25	5	23	100	83		9	16	66	90	10	30	4	.

Subclass A – Koelerio-Corynephorenea

	Taxon	T	All	A	B	C	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
C	Cerastium semidecandrum	V	22		10	11							33	3	.	15	.	31	8	4	.
	Cladonia furcata	L	30		14	24							33	5	4	20	10	44	41	12	.
	Corynephorus canescens	V	5		.	.							.	.	.	.	.	.	.	.	.
	Jasione montana	V	9		.	1							.	.	.	.	.	3	.	.	.
	Rumex acetosella	V	22		6	8							.	23	.	5	.	21	7	4	.
	Brachythecium albicans	B	25		8	8							33	.	4	5	.	15	5	12	.
	Carex arenaria	V	8		.	2							.	.	.	.	.	8	.	.	.
	Scleranthus perennis	V	8		1	4							.	.	.	5	.	8	8	.	.
	Trifolium arvense	V	10		.	6							.	.	.	.	.	.	3	12	10
	Cladonia fimbriata	L	8		4	5							.	.	4	10	5	3	16	.	.
	Scleranthus annuus ssp. polycarpos	V	6		0	3							.	.	.	2	.	10	2	.	.
D	Hypochoeris radicata	V	10	44	0	1	67	75	38	17	14	50		1				5	.	.	.
	Hieracium umbellatum	V	8	42	.	1	33	75	23	6	29	83						3	2	.	.
	Cladonia arbuscula	L	16	30	6	15	.	25	17	12	43	83		3	.	10	18	18	36	4	.

Order A.b – Thero-Airetalia

	Taxon	T	All	A	B	C	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
C	Aira praecox	V	4	21	.	.	.		18	5								.	.	.	.
	Polytrichum juniperinum	B	8	19	0	5	.	37	3							2		8	8	4	.

Order A.c - Trifolio arvensis-Festucetalia ovinae

	Taxon	T	All	A	B	C	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
C	Trifolium campestre	V	19	18	8	16	.			14	8		33	9	.	.	.	31	11	20	.
	Dianthus deltoides	V	18	25	2	16	.	25		29	17			4	4	.		36	13	16	.
	Peltigera canina	L	8	12	7	4	.	25					33	1	.	2	.	5	2	8	.
D	Rhytidiadelphus squarrosus	B	16	15	.	22	.	.	60	21	.	8						31	11	18	30
	Campanula rotundifolia	V	26	21	17	25	.	.	33	38	29	25		7	4	32	41	8	34	56	.
	Silene nutans	V	13	14	5	9	.	.	43	24	14			.		10	15	5	2	28	.
	Allium vineale	V	15	14	12	19	.	25	23	33	.		33	1	.	10	15	21	3	40	10

Alliance Armerion elongatae

	Taxon	T	All	A	B	C	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
C	Festuca trachyphylla	V	0	13	1	2	.	25						3				3	.	4	.
D	Potentilla argentea agg.	V	16	19	24	17	.	25	35	38	14	.	100	5	.	10	3	31	2	4	30

Association A3 – Diantho deltoidis-Armerietum elongatae

	Taxon	T	All	A	B	C	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
C	Armeria maritima ssp. elongata	V	10		.	4												3	.	12	.

Order A.d – Sedo acris-Festucetalia

	Taxon	T	All	A	B	C	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
C	Carex ligerica	V	3		.	1												3	.	.	.
	Veronica verna	V	1	7	.	.												.	.	.	.

Alliance Koelerion glaucae

	Taxon	T	All	A	B	C	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
D	Cetraria ericetorum ssp. ericetorum	L	16	30	21	7	.	25	10	3	86	58		1	4	46	54	8	15	.	.
	Flavocetraria nivalis	L	9	18	16	1	.	.	.	2	71	33		.	.	29	49	.	2	.	.

Association A5 – Helichryso arenarii-Jasionetum litoralis

	Taxon	T	All	A	B	C	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
D	Festuca rubra ssp. rubra	V	8	19	8	8	.	25	7	9	71	.	33	8	.	.	.	18	13	.	.
	Flavocetraria cucullata	L	7	10	10	3	.	.	.	.	57	.		1	4	17	28	3	10	.	.
	Racomitrium canescens	B	10	15	19	10	.	25	5	8	43	8	67	4	8	7	10	18	20	.	.

Association A6 – Festucetum polesicae

	Taxon	T	All	A	B	C	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
C	Koeleria glauca	V	3	15	.	1	.	.	.	.	3	14		.	.	.	.	3	.	.	.
	Festuca polesica	V	1	10																	
D	Cladonia gracilis ssp. gracilis	L	10	12	8	9	.	.	.	2	5	14	50	.	.	24	18	5	31	.	.
	Cladonia ciliata	L	14	17	6	15	.	25	12	8	14	42		.	4	.	15	13	21	36	4	.

Subclass B – Sedo-Scleranthenea

	Taxon	T	All	A	B	C	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
C	Sedum album	V	35	5		3	.	.	2	12	.	17						5	8	.	.
	Erophila verna	V	30	18		19	.	50	20	20	.	17						59	15	.	.
	Peltigera rufescens	L	16	3		8	.	.	.	15	.	.						31	.	.	.
	Bryum elegans	B	15	.		3												.	13	.	.
	Bryum caespiticium	B	13	1		6	.	.	.	3	3	.						3	20	.	.
	Peltigera didactyla	L	6	1		1	.	.	.	2	2	.						3	.	.	.

Order B.a – Alysso alyssoidis-Sedetalia

	Taxon	T	All	A	B	C	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
C	Acinos arvensis	V	34	5	55	19	.	.	.	20	.	8						46	21	8	.
	Arenaria serpyllifolia ssp. serpyllifolia	V	33	15	54	23	.	.	22	45	.	25						67	13	12	.
	Tortella inclinata var. inclinata	B	21	.	49	2												3	3	.	.
	Cladonia symphycarpia	L	20	.	48																
	Cerastium pumilum	V	21	4	48	12	.	.	.	.	.	25						41	7	.	.
	Saxifraga tridactylites	V	18	4	47	5	.	.	.	2	12	8						15	5	.	.
	Hornungia petraea	V	15	2	40	2	.	.	.	.	11	.						8	.	.	.
	Psora decipiens	L	11	.	27	1												.	2	.	.

Alliance Tortello tortuosae-Sedion albi

	Taxon	T	All	A	B	C	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
C	Ditrichum flexicaule	B	37	1	75	11	.	.	.	.	6	.						21	18	4	.
	Cladonia pocillum	L	14	1	35	1	.	.	.	.	3	.						5	.	.	.
	Encalypta rhaptocarpa	B	7	1	20	1	.	.	.	.	3	.						.	3	.	.
	Bacidia bagliettoana	L	5	.	11																
D	Tortella tortuosa	B	34	0	77	3	.	.	.	.	2	.	33	77	100	88	87	3	7	.	.
	Barbula convoluta	B	30	1	57	9	.	.	2	6	.	.	33	69	56	63	62	15	20	.	.
	Bryum capillare	B	18	10	30	8	.	25	8	9	.	17	.	15	48	37	49	21	5	4	.
	Bryoerythrophyllum recurvirostrum	B	13	1	26	3	.	.	.	.	5	.	.	20	48	29	31	8	5	.	.
	Leptogium lichenoides	L	9	.	21	2							.	16	60	22	8	.	7	.	.

					Koelerio-Corynephoretea											C - Festuco-Brometea			
Class / Subclass / Order, alliance, or suballiance / Association (or equivalent unit)	Group	All relevés (mean rel.)	Subcl. A (mean ass.)	Subcl. B (mean ass.)	Class C (mean ass.)	A - Koelerio-Corynephorenea						B - Sedo-Scleranthenea					C.a			
						A.a	A.b	A.c		A.d		B.a1	B.a2							
						A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
Number of relevés or associations		469	6 ass.	5 ass.	4 ass.	3	4	60	66	7	12	3	74	25	41	39	39	61	25	10
Suballiance B.a2 – Tortello rigentis-Helianthemenion oelandici																				
C Cladonia subrangiformis	V	25	8	47	10		25	3	5	14							21	20		
Encalypta vulgaris	B	22	1	43	5					5							10	8		
Allium schoenoprasum var. alvarense	V	19		36	3												3	7		
Helianthemum oelandicum ssp. oelandicum	V	19	0	36	7					2							3	23		
Trichostomum crispulum	B	18		36	3													11		
Distichium capillaceum	B	18	0	41	3					2		33					5	8		
Tortella rigens	B	16		32	1													5		
Didymodon ferrugineus	B	14		33	4							33					3	11		
Didymodon rigidulus	B	11		25	1													5		
Athalamia hyalina	B	10		25	3							33					3	7		
Festuca oelandica	V	9		22								33								
Gymnostomum aeruginosum	B	7		13	2													7		
Leptogium schraderi	L	6		13	1													3		
Silene uniflora ssp. petraea	V	1		4																
Hieracium x dichotomum	V	1	0	2						2										
D Didymodon fallax	B	24	1	54	5				2	2		33	51	76	63	46	8	11		
Weissia brachycarpa	B	23	1	42	6					3			47	52	49	64	8	15		
Agrostis stolonifera	V	26		42	6								97	44	56	13	13	10		
Pseudocalliergon turgescens	B	21		42	6							33	62	56	41	18	8	15		
Pleuridium acuminatum	B	16		32	3								35	60	41	26		10		
Campyliadelphus chrysophyllus	B	22	0	31	11					2			55	20	46	33	8	30	4	
Grimmia pulvinata	B	10	1	23	1					8			4	28	27	54			4	
Myurella julacea	B	12		22	4								34	32	22	21	5	10		
Collema tenax	L	8		17	1								19	32	24	10		5		
Ctenidium molluscum	B	11		17	5								27	24	24	10	3	15		
Pseudocrossidium hornschuchianum	B	7	0	17	1					2			12	36	27	10		2		
D Associations B2 and B3 (against B4 and B5)																				
Nostoc sp.	A	13		32								33	49	56	15	5				
Association B2 – Crepido pumilae-Allietum alvarensis																				
C Crepis tectorum ssp. pumila	V	14		23	1										2	5	3	2		
Artemisia rupestris	V	4		5	1											5		3		
D Prunella vulgaris	V	19		25	17							33	72	4	12	3	13	33		20
Sagina nodosa	V	13		17	5								58	20	5		8	10		
Leontodon autumnalis	V	9	2	13						14			42	12	7	5				
Scorpidium cossonii	B	7		9									36		7	3				
Calliergonella cuspidata	B	8		6	6								30		2	8	8	16		
Eucladium verticillatum	B	7		12	1								26	12	12	8		5		
Association B3 – Fulgensio bracteatae-Poetum alpinae																				
C Fulgensia bracteata	L	13		32	1													2		
Toninia sedifolia	L	9		25																
Syntrichia calcicola	B	10	1	31	1				2	2		33						3		
Mycobilimbia lurida	L	10		25	1													5		
Schistidium atrofuscum	B	8		19	1												3	2		
Fulgensia fulgens	L	4		11														2		
Tortella inclinata var. densa	B	6		14	1													2		
Ceratodon conicus	B	3		9	1													2		
Leptogium gelatinosum	L	3		7	1								8		2			2		
Squamarina cartilaginea	L	1		3									1							
Squamarina lentigera	L	1		4											2					
D Poa alpina	V	8	0	27	1					2		33	14	76	7	3	3	2		
Collema cristatum	L	7		19	1								9	76		8		3		
Collema crispum	L	8		20	1								14	56	20	8		2		
Bryum argenteum	B	6	1	15	1				3	2			4	48	10	13		2		
Schistidium apocarpum	B	6	1	14	1					3			15	40	7	8				4
D Associations B2 and B3 (against B4 and B5)																				
Hieracium pilosella	V	40	30	25	50		25	48	52	14	42		18	4	46	59	18	51	60	70
Potentilla tabernaemontani	V	39	21	27	44			25	56	43			8	12	51	62	49	72	44	10
Thamnolia vermicularis var. subuliformis	L	10		26										20	49	59				
Cephaloziella divaricata	B	16	10	25	6		25	7			25		19	4	49	51	15	7		
Taraxacum erythrospermum agg.	V	32	17	39	32			13	44	14	33	67	20	8	46	54	59	34	4	30
Scapania calcicola	B	9		18	1								9	8	34	41		3		
Hypogymnia physodes	L	11	11	16	6			7		57			1	4	37	38		13	12	
Sedum rupestre	V	17	6	20	22				2	14	17	33	8		29	28	31	56		
Association B4 – Helianthemo oelandici-Galietum oelandici																				
C Galium oelandicum	V	7	1	11	2			2	2				9			5		7		
Sisymbrium supinum	V	3		5																
Association B5 – Gypsophilo fastigiatae-Globularietum vulgaris																				
C Globularia vulgaris	V	7		15	1										2			3		
Gypsophila fastigiata	V	6		15										8	7			2		
Cladonia convoluta	L	3		7	1													2		
D Vincetoxicum hirundinaria ssp. hirundinaria	V	7		15	1								1		12	64		2		
Rhytidium rugosum	B	12		1	9								8	8	17	51	8	26		
Melica ciliata	V	4		9	1										10	36	3			
Oxytropis campestris ssp. campestris	V	10	6	13	9				21	14		33			2	31	5	21	8	
Arabis hirsuta var. glaberrima	V	8	1	9	8			2	3				4	4	7	28	5	16	12	
Agrostis gigantea ssp. gigantea	V	4		8	1								3	4	7	26	3			
Class Festuco-Brometea																				
C Homalothecium lutescens	B	46	13	44				7	55		17	67	36	24	44	51				
Veronica spicata ssp. spicata	V	35	19	10				22	42	14	33		26		10	13				
Helianthemum nummularium ssp. numm.	V	19	8	3					41		8		1		2	10				
Asperula tinctoria	V	20	2	13					6		8		1		17	49				
Medicago sativa ssp. falcata	V	17	13	3				8	55		17		1		7	8				
Potentilla cinerea	V	15	10	6				5	27		25		1		15	13				
Arabis hirsuta var. hirsuta	V	16	4	14				5	17			33	22		5	8				
Scabiosa columbaria	V	6	2	3						11					2	15				
D Fragaria viridis ssp. viridis	V	13	3	2	47			2	18						5	3		34	52	100
Hypericum perforatum	V	20	18	7	36		50	25	32				5	4	12	13	13	41	28	60
Order C.a – Brachypodietalia pinnati																				
C Avenula pratensis ssp. pratensis	V	44	20	22				28	70	14	8	33	7		20	49				
Filipendula vulgaris	V	35	3	21				3	17				19	4	32	49				
Ranunculus bulbosus	V	30	13	9				12	48		17		22		15	10				
Briza media ssp. media	V	15	1	1	52				3				3							

Class / Subclass / Order, alliance, or suballiance / Ass ciati n (or equivalent unit)	Group	All relevés (mean rel.)	Subcl. A (mean ass.)	Subcl. B (mean ass.)	Class C (mean ass.)	A1	A2	A3	A4	A5	A6	B1	B2	B3	B4	B5	C1	C2	C3	C4
Number of relevés or associations		469	5 ass.	5 ass.	4 ass.	3	4	60	66	7	12	3	74	25	41	39	39	61	25	10
Lotus corniculatus	V	21	8	14	49	.	.	15	9	.	25	33	30	.	5	3	■	■	■	■
Carex caryophyllea	V	13	5	1	■	.	.	8	21	.	.	.	1	.	.	5				
Cirsium acaule ssp. acaule	V	13	1	10		.	.	.	3	.	.	.	9	.	22	18				
Achillea millefolium ssp. millefolium (D)	V	43	31	13	70	.	.	80	64	43	.	33	23	.	7	.	64	57	80	80
Avenula pubescens ssp. pubescens	V	15	6	7	33	.	.	25	11	.	.	33	1	.	.	3	18	36	56	20
Cerastium fontanum ssp. vulgare	V	31	15	12	33	.	.	33	44	14	.	.	30	4	12	15	44	66	12	10
Poa pratensis	V	18	13	8	32	.	.	38	39	.	.	33	7	.	2	.	31	8	20	70
Plagiomnium affine	B	17	8	1	31	.	.	20	27	.	.	.	.	.	.	3	33	43	28	20
Trifolium pratense	V	7	3	1	28	.	.	2	.	14	.	.	5	.	.	.	3	20	28	60
Trifolium repens ssp. repens	V	16	11	10	25	.	.	18	20	29	.	33	16	.	.	.	38	15	16	30

Alliance – Filipendulo vulgaris-Helictotrichion pratensis

Galium boreale (D)	V	12	1	5	29	.	.	3	5	.	.	.	1	.	5	21	18	28	60	10
Sesleria caerulea	V	10	.	2	25	.	.	.	.	.	.	.	1	.	5	3	5	54	32	10
Hylocomium splendens	B	9	3	1	21	.	.	7	.	.	8	.	4	.	.	.	10	43	12	20

D Association C1 and C2 (against C3 and C4)

Dicranum scoparium	B	33	13	18	41	.	25	35	11	.	8	.	16	.	34	38	64	90	8	.
Stellaria graminea	V	16	11	1	20	.	.	23	32	.	8	.	5	.	2	.	49	23	8	.

Association C1 – Phleum bertolonii-Saxifraga granulata community

Saxifraga granulata (C)	V	13	7	3	26	.	25	7	11	.	.	.	14	.	2	.	■	11	4	10
Phleum pratense ssp. bertolonii	V	11	3	13	15	.	.	2	5	.	8	33	23	4	5	.	.	13	.	.
Veronica arvensis (D)	V	13	9	8	19	.	.	15	24	.	17	33	7	.	.	.	54	7	4	10
Myosotis ramosissima ssp. ramosissima	V	7	1	2	13	.	.	3	5	.	.	.	8	.	.	.	46	5	.	.
Myosotis stricta	V	7	2	8	13	.	.	2	.	.	8	33	8	.	.	.	44	8	.	.
Rhinanthus minor	V	10	6	3	18	.	25	13	.	.	.	.	14	.	2	.	44	16	.	10
Climacium dendroides	B	10	6	9	10	.	.	18	15	.	.	33	11	.	.	.	28	10	.	.

Association C2 – Veronico spicatae-Avenetum

Prunella grandiflora ssp. grandiflora (C)	V	5	.	1	■	.	.	.	.	.	.	.	.	.	2	3	.	■	8	.
Orchis mascula ssp. mascula	V	4	.	1	8	.	.	.	.	.	.	.	.	.	2	3	3	4	.	.
Orchis morio ssp. morio	V	3	.	1	6	.	.	.	.	.	.	.	.	.	2	3	5	.	.	.
Artemisia oelandica	V	1	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex flacca ssp. flacca (D)	V	12	.	9	20	.	.	.	.	.	.	.	11	.	17	15	.	49	12	20
Danthonia decumbens	V	6	1	.	13	.	.	3	.	.	.	.	.	.	.	.	.	43	8	.
Antennaria dioica	V	6	.	2	10	.	.	.	.	.	.	.	1	.	5	3	3	36	.	.

D Association C3 and C4 (against C1 and C2)

Knautia arvensis	V	9	6	.	38	.	.	13	12	.	8	.	.	.	.	.	.	.	60	90
Primula veris ssp. veris	V	4	0	.	25	.	.	.	2	.	.	.	.	.	.	.	.	8	32	60

Association C3 – Trifolium montanum-Medicago falcata community

Pimpinella saxifraga (C)	V	7	7	1	15	.	.	15	11	.	17	.	.	.	.	3	3	■	.	10
Trifolium montanum	V	3	0	.	11	.	.	.	2	.	.	.	.	.	.	.	.	■	.	.
Carex ericetorum (D)	V	14	6	6	25	.	.	7	9	14	8	.	1	.	.	28	3	44	52	.
Centaurea scabiosa	V	7	6	4	9	.	.	3	24	.	8	.	.	4	5	10	.	2	32	.

Association C4 – Adonis vernalis-Ononis arvensis community

Adonis vernalis (C)	V	2	.	.	■	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygala comosa	V	5	2	4	■	.	.	.	11	.	.	.	.	.	.	18	■	.	.	■
Ononis arvensis	V	1	.	.		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dactylis glomerata (D)	V	9	5	2	30	.	.	8	23	.	.	.	.	.	2	8	3	3	12	100
Agrimonia eupatoria ssp. eupatoria	V	2	.	.	23	.	.	.	.	.	.	.	.	.	.	.	.	2	.	90
Leucanthemum vulgare	V	2	0	.	23	.	.	.	2	.	.	.	.	.	.	.	.	2	.	90
Veronica chamaedrys ssp. chamaedrys	V	6	7	.	24	.	.	15	5	14	8	.	.	.	.	.	15	2	8	70
Clinopodium vulgare ssp. vulgare	V	1	.	.	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	50
Festuca pratensis ssp. pratensis	V	1	.	.	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	50

D Festuco-Brometea and Koelerio-Corynephorenea (against Sedo-Scleranthenea)

Anthoxanthum odoratum	V	31	32	8	53	.	50	32	20	57	33	.	9	.	22	10	85	67	28	30
Pulsatilla pratensis ssp. pratensis	V	28	55	6	27	33	.	47	58	100	92	.	.	.	7	21	18	21	46	10
Agrostis capillaris	V	25	32	2	23	.	25	73	38	14	42	.	3	.	.	8	23	26	32	10
Luzula campestris	V	25	23	.	53	.	25	37	30	29	17	.	.	.	.	.	49	56	36	70
Phleum phleoides	V	24	28	3	31	.	.	22	67	29	50	.	4	.	5	5	33	20	60	10

D Festuco-Brometea and Sedo-Scleranthenea (against Koelerio-Corynephorenea)

Anthyllis vulneraria ssp. vulneraria	V	39	16	40	49	.	25	7	27	29	8	33	34	4	41	87	69	66	32	30
Abietinella abietina	B	37	14	40	39	.	.	13	56	.	17	67	41	32	27	31	56	51	40	10
Medicago lupulina	V	36	8	59	48	.	.	8	38	.	.	100	30	40	63	62	69	25	28	70
Fissidens dubius	B	32	1	43	20	.	.	.	3	.	.	.	72	4	68	72	21	39	20	.
Linum catharticum	V	30	.	34	37	.	.	.	.	.	.	.	68	12	54	36	13	66	8	60
Taraxacum officinale agg.	V	27	13	30	37	.	.	18	27	14	17	33	24	8	34	51	44	21	12	70

Other species (with more than 10 % constancy in the whole data set)

Festuca ovina	V	82	77	78	79	100	75	82	73	57	75	67	76	56	100	92	92	97	68	60
Galium verum ssp. verum	V	68	65	45	87	.	50	83	91	100	67	67	32	12	46	69	90	80	88	90
Hypnum cupressiforme var. lacunosum	B	68	48	79	54	.	50	60	53	57	67	67	51	88	90	97	74	90	52	.
Plantago lanceolata	V	58	41	37	88	33	25	73	85	29	.	100	38	.	29	18	87	87	88	90
Thymus serpyllum ssp. serpyllum	V	52	43	60	38	.	25	28	38	100	67	33	38	52	90	87	38	79	36	.
Cladonia rangiformis	L	50	44	51	38	.	50	48	33	57	75	33	34	28	76	85	77	59	16	.
Bromus hordeaceus ssp. hordeaceus	V	38	48	46	38	33	50	35	52	57	58	100	30	60	37	5	90	16	16	30
Cladonia pyxidata agg.	L	24	27	26	23	.	100	27	15	.	17	33	16	.	32	49	38	33	.	.
Poa compressa	V	14	3	18	15	.	.	8	9	.	.	33	23	4	17	13	23	23	12	.
Euphrasia stricta	V	12	4	14	3	.	.	5	12	.	8	.	30	4	17	18	.	7	4	.
Potentilla x subarenaria	V	10	9	2	16	.	.	3	21	14	17	.	.	.	7	5	15	15	32	.

A1 = *Corniculario aculeatae-Corynephoretum canescentis*
A2 = *Carici arenariae-Airetum praecocis*
A4 = *Sileno otitae-Festucetum brevipilae*
B1 = *Cladonio symphycarpiae-Sedetum albi*

Plant diversity and species characteristics of alvar grasslands in Estonia and Sweden

Aveliina Helm, *Pille Urbas & Meelis Pärtel*

Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, Tartu EE-51005, Estonia;
E-mail pille.urbas@ut.ee; E-mail meelis.partel@ut.ee
* Corresponding author; E-mail aveliina.helm@ut.ee

Abstract

We compared species richness and species characteristics of dry alvar grassland communities on the islands of Saaremaa (Estonia) and Öland (Sweden). In addition we distinguished the species with contrasting abundance in alvars – core and satellite species – and compared their characteristics in both countries. Altogether we included 37 alvar sites from Saaremaa and 21 alvar sites from Öland. There were no significant differences in the sizes of community species pool and α-diversity between the two regions. There was a strikingly similar number of core species: 34 on Saaremaa and 35 on Öland, while the number of satellite species was 170 for Saaremaa and 91 for Öland. Per site, there were significantly more satellite species in Saaremaa than in Öland. Average potential height of plants was significantly greater on Estonian alvars indicating better soil conditions there. This is also expressed in the higher demand for soil moisture and lower demand for light of species from Saaremaa alvars.

Core and satellite species had similar differences in their environmental demands in both regions: satellite species preferred higher soil nutrient content and more soil moisture than core species. In summary, there are remarkable similarities in the species number between two regions, but the differences in species characteristics indicate that conservation knowledge from one region cannot be directly applied to protect alvars in another region.

Keywords: Calcareous grassland; Core species; Öland; Saaremaa; Satellite species; Species richness.

Nomenclature: Mossberg & Stenberg (2003).

Introduction

Alvar grasslands are dry calcareous grassland communities on shallow soil (< 20 cm) on Ordovician or Silurian limestone (Rosén 1982; Pärtel et al. 1999). Alvars have limited distribution in the world due to the lack of exposure of limestone parent material. These grasslands occur only scattered on the Swedish mainland, on the islands of Öland, Gotland, the Estonian islands of Saaremaa, Hiiumaa and Muhu, on coastal parts of the Estonian mainland (Rosén 1982; Pärtel et al. 1999) and in NW Russia, on the Izhora plateau near St. Petersburg (Znamenskiy et al. 2006). Similar communities on limestone bedrock and partly overlapping species composition have also been described from Canada and from some other parts of Europe (Belcher et al. 1992; Catling & Brownell 1995; Dengler et al. 2006; Dengler & Löbel 2006).

Alvar soils are rendzic leptosols, with a humus horizon lying directly on the limestone (Reintam 1995). Soil conditions are variable and soil heterogeneity is related to the amount of woody species in the grassland (Pärtel & Helm 2007). Alvars are characterised by high species richness both on the community level and on finer scales (van der Maarel 1988; Sjögren 1988; Pärtel et al. 1996). There are several explanations for the causes of high biodiversity on calcareous grasslands (Huber & van der Maarel 2007). First, many species prefer to grow in calcareous soils (Pärtel et al. 1996). Pärtel (2002) showed that the large regional species pool of calcareous communities is caused by the presence of evolutionary centres on calcareous areas. Secondly, the high species richness in semi-natural communities is the result of long-lasting and continuous management (Cousins & Eriksson 2002; Prentice et al. 2007) and the current number of species on alvars is determined by the management history and human population density as far back as 1000 years ago (Pärtel et al. 2007).

Alvars are semi-natural communities and due to the cessation of traditional management e.g. grazing and mowing, alvars overgrow with shrubs and trees (Pärtel et al. 1999;

Rosén & van der Maarel 2000; Bakker et al. 2007).

Pictures of grazed and abandoned alvars on Öland have often been published and are also found in papers in this volume. For comparison two pictures from Saaremaa are added here (Figs. 1 and 2).

Due to habitat loss and fragmentation, the area of alvars in Estonia has declined from ca. 50 000 ha in the 1930s to only 10 000 ha in 2000 (Kukk & Sammul 2006). In Sweden, the area of alvars has declined as well (Ekstam & Forshed

2002). Due to the general validity of the species-area relationship $S = A^z$, this kind of loss should be reflected in the decreased species number compared to the period before fragmentation. However, the slow intrinsic dynamics and long life-cycles of many grassland plants may create remnant populations and remnant communities in the modern landscape (Eriksson 1996) so that species richness may be maintained for some time. Helm et al. (2006) found that current species richness in Saaremaa alvars is not described

Fig. 1. Alvar grassland on western Saaremaa on deep soil grazed by sheep.

Fig. 2. Abandoned alvar grassland on eastern Saarema on deep soil; *Juniperus communis* is encroaching.

by current area and current connectivity of grasslands, but by historical area and connectivity, i.e. the landscape structure before fragmentation. This indicates the existence of an 'extinction debt' (Tilman et al. 1994; Hanski 2000, 2005). As species richness ultimately depends on area and connectivity future extinctions are inevitable.

Alvars are well studied, both in Sweden (Albertson 1950; Pettersson 1965; Rosén 1982; Krahulec et al. 1986; Rejmánek & Rosén 1992; Rosén & van der Maarel 2000; Ekstam & Forshed 2002; Rosén 2006; Dengler & Löbel 2006; Löbel & Dengler 2007) and in Estonia (Vilberg 1927; Laasimer 1946, 1975; Zobel 1987; Zobel & Kont 1992; Pärtel & Zobel 1995, 1999; Pärtel et al. 1999, 2007), but a rigorous comparison of species richness between the two regions is still missing.

Species richness, however, is a very general measure. We have shown previously that species with different regional abundances have different effects on small-scale diversity: species which are represented in most of the habitat patches of a studied community (core species) have influence on the α-diversity and species which are represented in only few patches (satellite species) have influence on the β-diversity (Pärtel et al. 2001). Thus, core and satellite species richness should be compared separately. Species regional abundance (belonging to core or satellite group) is most likely defined by species characteristics. In order to understand the variability in species diversity, we must study which kind of species form the actual community.

The first aim of this study was to compare the species richness and species characteristics of dry alvar grassland communities in Saaremaa and in Öland. The second aim was to distinguish the species with contrasting abundance in alvars – core and satellite species – and to compare their characteristics in both countries.

Material and Methods

We carried out our studies on alvars in two regions of the Baltic Sea: the Estonian islands of Saaremaa and Muhu and the Swedish island of Öland. Saaremaa and Muhu are situated west of the Estonian mainland (ca. 58° N, 22-23° E) with a total area of 2900 km². Öland is situated east of the South-Swedish mainland (ca. 56-57° N, 16-17° E) with an area of 1342 km². Saaremaa and Muhu are very close to each other and they can be studied together (afterwards we use the terms Saaremaa or Estonia). Both regions have a mild maritime climate with a mean precipitation of 500-600 mm per year on Saaremaa (Raukas 1995) and 400-500 mm per year on Öland (Rosén 1982). The coldest month is February with a mean temperature of –1 to –2 °C on Öland and –2.5 to –4.5 °C on Saaremaa. The summers are warm with a mean temperature in July of 16-17 °C both on

Saaremaa and Öland.

Altogether we studied 58 alvar grasslands, 37 sites on Saaremaa and Muhu, and 21 sites on Öland. These grasslands belong to the dry alvar type (*Avenetum* and *Festucetum* types; cf. Albertson 1950; Pärtel et al. 1999). Fieldwork was carried out in June and July of 1992-1994, 1996, 1998 and 1999. We recorded the size of the community's vascular plant species pool for each site (ca. 50 m × 50 m) and the small-scale species richness on 5-15 plots of 1 m × 1 m (α-diversity).

Within the overall species lists we separated between core and satellite species (Hanski 1982; Pärtel et al. 2001) on the basis of the frequency of occurrence in the two sets of sites. Core species are defined as species occurring in at least 75% of the study sites in the respective regions; satellite species are defined as occurring in less than 25% of the sites.

For comparing the species composition of alvar communities of the two regions and for comparing core and satellite species, we distinguished several species characteristics: (1) mean potential plant height, showing the potential to compete for light (Mossberg et al. 1992; Leht 1999); (2) Ellenberg indicator values for light, soil moisture, nutrient content and reaction according to Ellenberg et al. (1991). Ellenberg indicator values indicate the optimal habitat conditions for particular species.

We used the Mann-Whitney *U*-test to compare the size of community species pool and α-diversity between two regions and to evaluate the characteristics of core and satellite species.

Results

Altogether we registered 263 vascular plant species from the 37 dry alvar sites in Saaremaa and 185 species from the 21 Öland alvar sites. There were 131 species in common between the two species groups. Fig. 3 shows the frequency distribution of species occurrences on (a) Saaremaa-Muhu and (b) Öland. Most of the species occur in less than 25% of the sites and thus belong to the satellite species group. On Saaremaa, 170 out of 263 species, or 65% were satellite species, on Öland 91 out of 185 or 50% were satellite species, which is considerably less than on Saaremaa. The core species were almost equal in number with 34 on Saaremaa and 35 on Öland, but the proportion on Öland was higher: 19% against 13%. There were 16 core species in common between the two regions and 38 common satellite species (App. 1).

Five Estonian core species were satellite species in Sweden: *Leucanthemum vulgare, Pimpinella saxifraga, Pinus sylvestris, Senecio jacobaea, Trifolium montanum*, while eight Swedish core species were satellite species
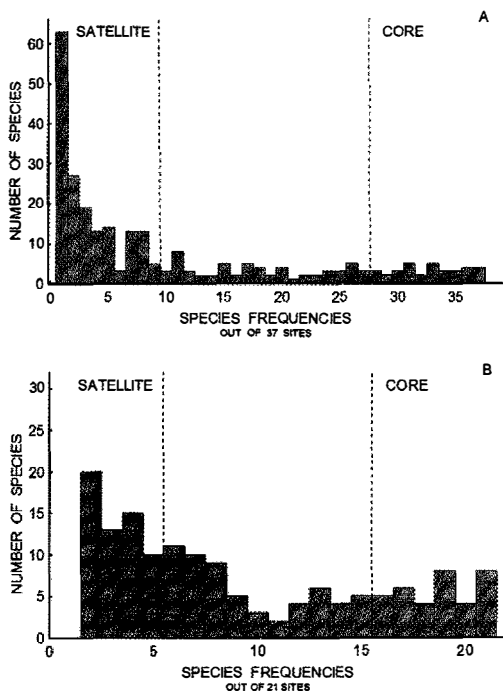
Fig 3. Frequency distribution of species over (**a**) 37 alvar sites on Saaremaa-Muhu and (**b**) 21 alvar sites on Öland. The 25% and 75% boundaries are indicated to show the amount of satellite species and core species.
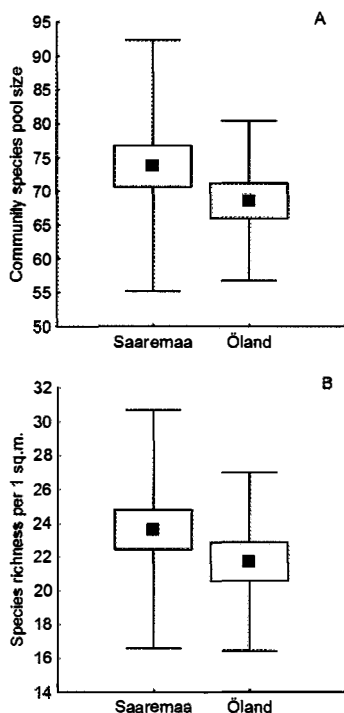
Fig 4. Mean values of (**a**) community species pool and (**b**) α-diversity per site for Saaremaa-Muhu and Öland. Box and whiskers represent SE and SD of the mean, respectively. There are no significant differences according to the Mann-Whitney U-test.

in Estonia: *Agrostis gigantea, Allium schoenoprasum, Bromus hordeaceus, Cerastium semidecandrum, Crepis tectorum, Erophila verna, Hornungia petraea, Sagina nodosa.* This is remarkable because most of these species are common in the two floras.

The size of the community species pool and the small-scale species diversity did not differ between the two regions (Fig. 4a, b). Average number of core spe-
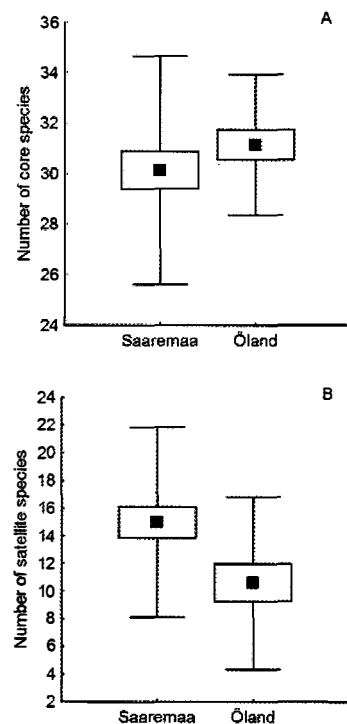
Fig 5. Mean number of (**a**) core species and (**b**) satellite species per site in alvars of Saaremaa-Muhu and Öland. Box and whiskers represent standard error and standard deviation of mean respectively. There are no significant differences between the number of core species, but according to the Mann-Whitney U-test there are more satellite species in Saaremaa ($U = 236$, $P = 0.014$).
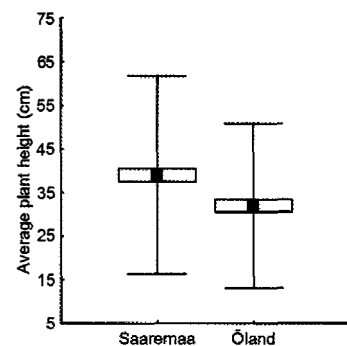
Fig 6. Mean potential height of species on alvars of Saaremaa-Muhu and Öland. Box and whiskers represent SE and SD of mean. The Mann-Whitney U-test shows significantly greater plant height in Saaremaa: $U = 16396$, $P = 0.001$.

cies per site showed no significant difference between the regions (Fig. 5a), but there were significantly larger numbers of satellite species per site on Saaremaa and Muhu alvars than on Öland (Fig. 5b).

The Mann-Whitney *U*-test indicated that the mean potential plant height was significantly greater on Estonian alvars (Fig. 6). According to the Ellenberg indicator values species from Estonian alvars had a significantly higher demand for moisture and lower demand for light as compared to species from Öland (Table 1).

In Estonian alvars, core and satellite species did not differ in mean potential height (Fig. 7a), while the Swedish core species had significantly lower mean potential height compared to satellite species (Fig. 7b). Both in Estonia (Table 2) and in Sweden (Table 3) core species preferred lower soil fertility. In addition, core species preferred drier soil in Estonia, all other demands for environmental conditions were similar between the two species groups in both countries.
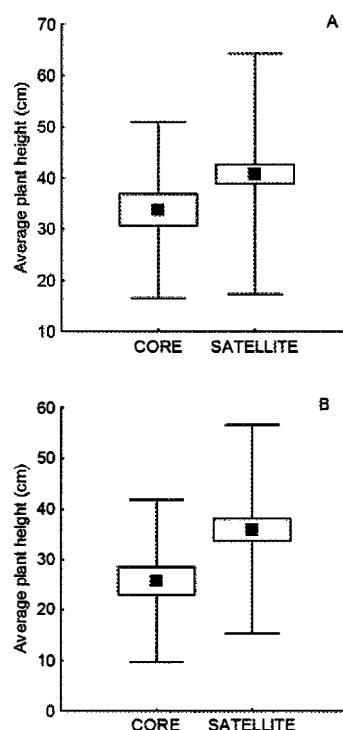
Fig 7. Mean potential height of core and satellite species on Saaremaa-Muhu (**a**) and Öland (**b**). Box and whiskers represent SE and SE of the mean. According to the Mann-Whitney *U*-test, core and satellite species differ in height only on Öland ($U = 1018$, $P = 0.012$).

Table 1. Mean Ellenberg indicator values (± SD) for alvar grasslands on Saaremaa and Öland. Mann-Whitney test: *U*- and *P*-values. Significant *P*-values are indicated in bold.

	Saaremaa	Öland	*U*	*P*
Light	6.9 ± 1.3	7.3 ± 1.0	16250.0	**0.010**
Soil moisture	4.6 ± 1.7	4.2 ± 1.6	12830.5	**0.020**
Soil nutrient content	3.5 ± 1.8	3.3 ± 1.9	734.5	0.140
Soil reaction	6.8 ± 1.6	6.4 ± 1.9	8705.5	0.180

Table 2. Mean Ellenberg indicator values (± SD) of core and satellite species for alvar grasslands on Saaremaa. Mann-Whitney test: *U*- and *P*-values. Significant *P*-values are indicated in bold.

	Core species	Satellite species	*U*	*P*
Light	7.1 ± 0.9	7.4 ± 7.9	2119	0.654
Soil moisture	4.0 ± 1.3	4.8 ± 1.7	1231	**0.026**
Soil nutrient content	2.6 ± 1.4	3.7 ± 1.9	1169.5	**0.004**
Soil reaction	6.9 ± 1.6	6.7 ± 1.7	912.0	0.234

Table 3. Mean Ellenberg indicator values (± SD) of core and satellite species for alvar grasslands on Öland. Mann-Whitney test: *U*- and *P*-values. Significant *P*-values are indicated in bold.

	Core species	Satellite species	*U*	*P*
Light	7.5 ± 0,9	7.2 ± 1.0	1134	0.149
Soil moisture	3.8 ± 1.6	4.4 ± 1.7	728.5	0.067
Soil nutrient content	2.8 ± 1.7	3.7 ± 2.0	746.5	**0.044**
Soil reaction	7.1 ± 1.4	6.5 ± 2.0	603.5	0.346

Discussion

The frequency distributions of species occurrences in the sites show a clear predominance of low-frequent species (Fig. 3a, b) forming a reversed J-shape distribution. Pärtel et al. (2001) found a U-shaped distribution when considering the species data from 16 Estonian alvars which were previously numerically classified as the *Avenetum* community type (Pärtel et al. 1999). The discrepancy between the two studies may be caused by the more complex type of communities in the current paper as bimodality is expected in the case of homogeneous species composition between sites.

It is probable that the differences in climate, geology and habitat configuration have resulted in different regional species pools for Öland and for Saaremaa. Öland is located more south than Saaremaa and due to its narrow shape the winters are milder. The area of alvar grassland is much larger on Öland and the distribution of alvars is different. In Saaremaa, alvars are small and quite equally scattered, while on Öland alvars occur mainly in the southern part of the island forming one large area called the Great Alvar (*Stora Alvaret*). Öland is geologically older; most of it emerged from the sea ca. 10 000 BP (Svensson 1989). Most of Saaremaa's calcareous areas arose from the sea 7500-4000 BP (Poska & Saarse 2002).

Though Öland is expected to have a larger regional species pool, there were no significant differences in the sizes of community species pool and α-diversity between the two regions (Fig. 4a, b). This result can be explained by the almost identical core species list in both regions. Glenn & Collins (1990) and Pärtel et al. (2001) confirmed that small-scale (α-) diversity is mainly determined by the number of locally more abundant core species while satellite species are responsible for the variation between sites and also within the site. There were no significant differences between the number of core species between alvar sites of Saaremaa and Öland (Fig. 5a), but Estonian alvars had significantly higher numbers of satellite species per area (Fig. 5b). As alvars in Saaremaa are generally smaller and more scattered than alvars on Öland, the higher number of satellite species may be caused by the edge effect. For example, Helm et al. (2006) found that the number of non-specialist (satellite) plant species in alvars of Saaremaa is negatively related to the current area since a large perimeter to area ratio supports the species present in the surrounding habitats to disperse to an alvar.

Mean potential height of the plant species involved was significantly greater on Estonian alvars (Fig. 6). This can be explained by the higher proportion of deeper and moister soils on Saaremaa, whereas most of the Öland alvars have very shallow soil. Comparison of species by Ellenberg indicator values showed the same pattern: species in Estonian alvars had a higher demand for moisture but a lower demand for light than species in Swedish alvars (Table 1). Satellite species preferred higher soil nutrient contents in both regions and, in Estonia, more soil moisture than core species (Tables 2, 3). On Öland, core species were also significantly lower on average than satellite species (Fig. 7). According to these results, core species are better adapted to survive the harsh environmental conditions of alvars and drought and low nutrient availability are tolerated better.

Alvars harbour unique, species-rich and vulnerable communities, which have high cultural and aesthetic value. For proper conservation management it is necessary to carefully study the processes that have been responsible for creating the variation in species composition and species richness of these communities. Although the species richness did not differ between Saaremaa and Öland, neither on the community level nor on finer scales, there were differences in the number of satellite species and in the species characteristics. This does not allow us to directly transfer management knowledge from one region to another without more profound studies.

Acknowledgements

References

Albertson, N. 1950. Das grosse südliche Alvar der Insel Öland: Eine pflanzensoziologische Übersicht. — Sven. Bot. Tidskr. 44: 269-331.

Bakker, J.P., Rosén, E. & Steg, K. 2007. Re-establishment of alvar plant species in abandoned arable fields on Öland. — Acta Phytogeogr. Suec. 88: 71-80 (this volume).

Belcher, J.W., Keddy, P.A. & Catling, P.M. 1992. Alvar vegetation in Canada: a multivariate description at two scales. — Can. J. Bot. 70: 1279-1291.

Catling, P.M. & Brownell, V.R. 1995. A review of the alvars of the great lakes region: distribution, floristic composition, biogeography and protection. — Can. Field Nat. 109: 143-171.

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 Ecol. 17: 517-529.

Dengler, J. & Löbel, S. 2006. The basiphilous dry grasslands of shallow, skeletal soils (Alysso-Sedetalia) on the island of Öland (Sweden), in the context of North and Central Europe. — Phytocoenologia 36: 343-391.

Dengler, J., Löbel, S. & Boch, S. 2006. Dry grassland communities of shallow, skeletal soils (Sedo-Scleranthenea) in northern Europe.— Tuexenia 26: 159-190.

Ekstam, U. & Forshed, N. 2002. Svenska alvarmarker – historia och ekologi. — Naturvårdsverkets serie Skötsel av naturtyper. Naturvårdsverket förlag, Stockholm.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. — Scripta Geobot. 18: 1-248.

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

Gaston, K.J., Blackburn, T.M., Greenwoods, J.J.D., Gregory, R.D., Quinn, R.M. & Lawton, J.H. 2000. Abundance-occupancy relationships. — J. Appl. Ecol. 37: 39-59.

Glenn, S.M. & Collins, S.L. 1993. Experimental analysis of patch dynamics in tallgrass prairie plant communities. — J. Veg. Sci. 4: 157-162.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. — Oikos 38: 210-221.

Hanski, I. 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. — Ann. Zool. Fenn. 37: 271-280.

Hanski, I. 2005. The shrinking world: ecological consequences of habitat loss. — International Ecology Institute, Oldendorf/Luhe.

Helm, A., Hanski, I. & Pärtel, M. 2006. Slow response of plant species richness to habitat loss and fragmentation. — Ecol. Lett. 9: 72-77.

Huber, R. & van der Maarel, E. 2007. Plant species turnover in an alvar limestone grassland under different environmental conditions and at different scales. — Acta Phytogeogr. Suec. 88: 33-42 (this volume).

Krahulec, F., Rosén, E. & van der Maarel, E. 1986. Preliminary classification and ecology of dry grassland communities on Ölands Stora Alvar (Sweden). — Nord. J. Bot. 6: 797-809.

Kukk, T. & Sammul, M. 2006. Loodusdirektiivi poollooduslikud kooslused ja nende pindala Eestis. — ELUS Aastaraamat 84: 114-155.

Laasimer, L. 1946. Loometsa ökoloogiast. — ENSV TRÜ Toimetised, Bioloogia 2: 1–83.

Laasimer, L. 1975. Eesti lood ja loometsad, nende kaitse. In: Renno, O. (ed.) Eesti loodusharulduste kaitseks, pp. 90-101. — Valgus, Tallinn.

Leht, M. (ed.) 1999. Eesti taimede määraja. — Eesti Loodusfoto, Tartu, EE.

Löbel, S. & Dengler, J. 2007. Dry grassland communities on southern Öland: phytosociology, ecology, and diversity. — Acta Phytogeogr. Suec. 88:13-32 (this volume).

Mossberg, B. & Stenberg, L. 2003. Den nya nordiska floran. — Wahlström & Widstrand, Stockholm.

Pärtel, M. 2002. Local plant diversity patterns and evolutionary history at the regional scale. — Ecology 83: 2361-2366.

Pärtel, M. & Helm, A. 2007. Invasion of woody species into temperate grasslands: Relationship with abiotic and biotic soil resource heterogeneity. — J. Veg. Sci. 18: 63-70.

Pärtel, M. & Zobel, M. 1995. Small-scale dynamics and species richness in successional alvar plant communities. — Ecography 18: 83-90.

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

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

Pärtel, M., Kalamees, R., Zobel, M. & Rosén, E. 1999. Alvar grasslands in Estonia: variation in species composition and community structure. — J. Veg. Sci. 10: 561-570.

Pärtel, M., Moora, M. & Zobel, M. 2001. Variation in species richness within and between calcareous (alvar) grassland stands: the role of core and satellite species. — Plant Ecol. 157: 203-211.

Pärtel, M., Helm, A., Reitalu, T., Liira, J. & Zobel, M. 2007. Grassland diversity related to the Late Iron Age human population density. — J. Ecol. 95: 574-582.

Petterson, B. 1965. Gotland and Öland. Two limestone islands compared. — Acta Phytogeogr. Suec. 50: 131-140.

Poska, A. & Saarse, L. 2002. Vegetation development and introduction of agriculture to Saaremaa Island, Estonia: the human response to shore displacement. — Holocene 12: 555-568.

Prentice, H.C. Jonsson, B.O., Sykes, M.T., Ihse, M. & Kindström, M. 2007. Fragmented grasslands on the Baltic island of Öland: Plant community composition and land-use history. — Acta Phytogeogr. Suec. 88: 91-20 (this volume).

Raukas, A. (ed.) 1995. Eesti. Loodus. — Valgus, Eesti Entsüklopeediakirjastus, Tallinn.

Raunkiær, C. 1934. The life forms of plants and statistical plant geography. — Oxford University Press, Oxford.

Reintam, L. 1995. Soils in Estonia. In: Kuldkepp, P. (ed.) Soil and fertilization. pp. 122–131. — Estonian Agricultural University, Tartu.

Rejmánek, M. & Rosén, E. 1992. Influence of colonizing shrubs on species-area relationships in alvar plant communities. — J. Veg. Sci. 3: 625-630.

Rosén, E. 1982. Vegetation development and sheep grazing in limestone grasslands of south Öland, Sweden. — Acta Phytogeogr. Suec. 72: 1-104.

Rosén, E. 2006. Alvar vegetation of Öland – changes, monitoring and restoration. — Proc. R. Irish Acad. 106B: 387-399.

Rosén, E. & van der Maarel, E. 2000. Restoration of alvar vegetation on Öland, Sweden. — Appl. Veg. Sci. 3: 65-72.

Svensson, N.O. 1989. Late Weichselian and early Holocene shore displacement in the central Baltic, based on stratigraphical and morphological records from eastern Småland and Gotland, Sweden. — Lundqua thesis, Lund.

Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. 1994. Habitat destruction and the extinction debt. — Nature 371: 65-66.

van der Maarel, E. 1988. Floristic diversity and guild structure in the grasslands of Öland's Stora Alvar. — Acta Phytogeogr. Suec. 76: 53-66.

Vilberg, G. 1927. Loost ja lootaimkattest Ida-Harjumaal. — Eesti Loodusuurijate Seltsi Aruanded 34: 1-131.

Znamenskiy, S., Helm, A. & Pärtel, M. 2006. Threatened alvar grasslands in NW Russia and their relationship to alvars in Estonia. — Biodivers. Conserv. 15: 1797-1809.

Zobel, M. 1987. The classification of Estonian alvars and their plant communities. In: Laasimer, L. (ed.) The plant cover of the Estonian SSR. Flora, vegetation and ecology, pp. 28-45. — Valgus, Tallinn.

Zobel, M. & Kont, A. 1992. Formation and succession of alvar communities in the Baltic land uplift area. — Nord. J. Bot. 12: 249-256.

App. 1. Species lists for the alvars on Saaremaa/Muhu = S and Öland = Ö. Percentage of species occurrence in studied stands. Index [c] refers to core species, index [s] to satellite species.

	S	Ö
Acer platanoides	30	0
Achillea millefolium	97 [c]	90 [c]
Acinos arvensis	49	95 [c]
Aegopodium podagraria	3 [s]	0
Agrimonia eupatoria	30	0
Agrostis capillaris	8 [s]	14 [s]
Agrostis gigantea	3 [s]	76 [c]
Agrostis stolonifera	70	81 [c]
Agrostis vinealis	16 [s]	57
Alchemilla vulgaris	65	14 [s]
Allium oleraceum	5 [s]	0
Allium schoenoprasum	3 [s]	81 [c]
Allium vineale	3 [s]	29
Anagallis arvensis	0	24 [s]
Androsace septentrionalis	3 [s]	10 [s]
Anemone sylvestris	11 [s]	0
Angelica sylvestris	3 [s]	0
Antennaria dioica	95 [c]	33
Anthemis tinctoria	22 [s]	0
Anthericum ramosum	0	5 [s]
Anthoxanthum odoratum	14 [s]	43
Anthriscus sylvestris	11 [s]	0
Anthyllis vulneraria	97 [c]	90 [c]
Aquilegia vulgaris	3 [s]	0
Arabis hirsuta	70	90 [c]
Arctostaphylos uva-ursi	3 [s]	0
Arenaria serpyllifolia	27	100 [c]
Arrhenatherum elatius	11 [s]	0
Artemisia absinthium	5 [s]	5 [s]
Artemisia campestris	49	71
Artemisia oelandica	0	14 [s]
Artemisia rupestris	41	57
Artemisia vulgaris	5 [s]	0
Asperula tinctoria	89 [c]	90 [c]
Asplenium ruta-muraria	8 [s]	10 [s]
Asplenium trichomanes	8 [s]	0
Astragalus danicus	22 [s]	0
Astragalus glycophyllos	8 [s]	0
Bellis perennis	0	24 [s]
Berberis vulgaris	32	0
Betula pendula	19 [s]	5 [s]
Botrychium lunaria	5 [s]	0
Brachypodium pinnatum	30	0
Briza media	89 [c]	33
Bromus hordeaceus	3 [s]	100 [c]
Bromus inermis	3 [s]	0
Calamagrostis epigeios	3 [s]	0
Calluna vulgaris	3 [s]	10 [s]
Campanula glomerata	59	0
Campanula persicifolia	46	10 [s]
Campanula rotundifolia	70	43
Cardamine pratensis	3 [s]	0
Carex caryophyllea	84 [c]	38
Carex digitata	3 [s]	0
Carex elata	3 [s]	0
Carex ericetorum	5 [s]	43
Carex flacca	84 [c]	76 [c]
Carex hirta	5 [s]	0
Carex montana	3 [s]	0
Carex ornithopoda	51	0
Carex panicea	5 [s]	14 [s]
Carex spicata	3 [s]	0
Carex tomentosa	38	0
Carlina vulgaris	73	14 [s]
Carum carvi	3 [s]	0
Centaurea jacea	86 [c]	71
Centaurea scabiosa	41	5 [s]
Centaurium erythraea	3 [s]	0
Centaurium pulchellum	3 [s]	0
Cephalanthera longifolia	3 [s]	0
Cerastium fontanum	46	67
Cerastium pumilum ssp. *glutinosum*	0	19 [s]
Cerastium semidecandrum	22 [s]	90 [c]

	S	Ö
Chaenorhinum minus	0	5 [s]
Cirsium acaule	92 [c]	76 [c]
Cirsium arvense	5 [s]	5 [s]
Cirsium vulgare	19 [s]	14 [s]
Clinopodium vulgare	3 [s]	0
Convallaria majalis	65	0
Convolvulus arvensis	8 [s]	29
Corylus avellana	19 [s]	0
Cotoneaster scandinavicus	0	5 [s]
Cotoneaster spec.	5 [s]	0
Crataegus monogyna	5 [s]	0
Crataegus rosaeformis	0	5 [s]
Crepis praemorsa	22 [s]	19 [s]
Crepis tectorum	22 [s]	86 [c]
Cynosurus cristatus	3 [s]	10 [s]
Cypripedium calceolus	3 [s]	0
Dactylis glomerata	46	0
Dactylorhiza incarnata	5 [s]	0
Dactylorhiza sambucina	0	5 [s]
Danthonia decumbens	14 [s]	10 [s]
Daucus carota	16 [s]	10 [s]
Deschampsia caespitosa	5 [s]	0
Dianthus deltoides	3 [s]	38
Draba incana	0	29
Echium vulgare	24 [s]	38
Elymus repens	0	5 [s]
Epipactis atrorubens	3 [s]	0
Epipactis helleborine	3 [s]	0
Epipactis palustre	5 [s]	0
Equisetum palustre	3 [s]	0
Erigeron acer	14 [s]	5 [s]
Erodium cicutarum	3 [s]	29
Erophila verna	19 [s]	86 [c]
Euphrasia officinalis	19 [s]	0
Euphrasia stricta	0	62
Festuca oelandica	0	52
Festuca ovina	97 [c]	100 [c]
Festuca pratensis	8 [s]	0
Festuca rubra	62	5 [s]
Filipendula vulgaris	95 [c]	100 [c]
Fragaria vesca	59	29
Fragaria viridis	68	33
Frangula alnus	68	0
Fraxinus excelsior	24 [s]	0
Fumana procumbens	0	5 [s]
Galium album	35	0
Galium aparine	0	5 [s]
Galium boreale	89 [c]	95 [c]
Galium mollugo	3 [s]	0
Galium uliginosum	8 [s]	0
Galium verum	100 [c]	100 [c]
Gentiana cruciata	5 [s]	0
Gentianella amarella	3 [s]	0
Geranium columbinum	0	14 [s]
Geranium dissectum	0	10 [s]
Geranium molle	0	33
Geranium pusillum	0	5 [s]
Geranium robertianum	3 [s]	14 [s]
Geranium sanguineum	19 [s]	48
Geum rivale	14 [s]	5 [s]
Geum urbanum	3 [s]	5 [s]
Globularia vulgaris	0	14 [s]
Goodyera repens	3 [s]	0
Gymnadenia conopsea	54	10 [s]
Gypsophila fastigiata	0	19 [s]
Helianthemum nummularium	27	29
Helianthemum oelandicum	0	81 [c]
Helictotrichon pratense	100 [c]	67
Helictotrichon pubescens	22 [s]	29
Hepatica nobilis	24 [s]	0
Heracleum sibiricum	3 [s]	0
Herminium monorchis	8 [s]	0
Herniaria glabra	0	33

	S	Ö
Hieracium umbellatum	8 [s]	5 [s]
Hornungia petraea	11 [s]	76 [c]
Hypericum maculatum	5 [s]	5 [s]
Hypericum perforatum	89 [c]	29
Hypochaeris maculata	14 [s]	0
Inula salicina	73	0
Juncus articulatus	0	14 [s]
Juniperus communis	100 [c]	100 [c]
Knautia arvensis	46	0
Lathyrus pratensis	11 [s]	5 [s]
Leontodon autumnalis	14 [s]	62
Leontodon hispidus	49	0
Leucanthemum vulgare	84 [c]	5 [s]
Libanotis intermedia	8 [s]	0
Linaria vulgaris	8 [s]	24 [s]
Linum catharcticum	97 [c]	86 [c]
Listera ovata	30	0
Lithospermum officinale	0	10 [s]
Lonicera xylosteum	46	0
Lotus corniculatus	86 [c]	67
Luzula campestris	32	38
Luzula multiflora	5 [s]	0
Luzula pilosa	3 [s]	0
Maianthemum bifolium	8 [s]	0
Malus domestica	5 [s]	0
Malus sylvestris	11 [s]	0
Medicago falcata	8 [s]	38
Medicago lupulina	81 [c]	76 [c]
Medicago sativa	0	5 [s]
Melampyrum arvense	3 [s]	0
Melampyrum cristatum	3 [s]	0
Melampyrum nemorosum	3 [s]	0
Melampyrum pratense	3 [s]	0
Melica nutans	5 [s]	0
Melilotus albus	5 [s]	0
Mentha arvensis	0	5 [s]
Menyanthes trifoliata	3 [s]	0
Molinia caerulea	24 [s]	0
Myosotis arvensis	0	24 [s]
Myosotis stricta	3 [s]	67
Ononis arvensis	8 [s]	0
Ononis repens	5 [s]	0
Ophrys insectifera	22 [s]	10 [s]
Orchis mascula	11 [s]	38
Orchis militaris	41	5 [s]
Orchis morio	5 [s]	0
Orchis ustulata	14 [s]	33
Origanum vulgare	14 [s]	0
Oxytropis campestris	0	38
Oxytropis pilosa	3 [s]	0
Padus avium	22 [s]	0
Paris quadrifolia	11 [s]	0
Phleum phleoides	14 [s]	38
Phleum pratense	8 [s]	0
Phleum pratense ssp. *bertolonii*	3 [s]	48
Picea abies	11 [s]	0
Pilosella officinarum	95 [c]	62
Pilosella praealtum	5 [s]	43
Pimpinella major	3 [s]	0
Pimpinella saxifraga	92 [c]	5 [s]
Pinus sylvestris	84 [c]	5 [s]
Plantago lanceolata	92 [c]	90 [c]
Plantago major	5 [s]	0
Plantago maritima	24 [s]	33
Plantago media	76 [c]	0
Platanthera bifolia	3 [s]	0
Platanthera chlorantha	30	19 [s]
Poa alpina	0	62
Poa angustifolia	54	38
Poa bulbosa	0	24 [s]
Poa compressa	62	81 [c]
Poa pratensis	5 [s]	0
Polygala amarella	70	19 [s]

App. 1, cont.

	S	Ö		S	Ö		S	Ö
Polygala comosa	22 s	0	*Rumex acetosa*	19 s	24 s	*Thymus serpyllum*	100 c	100 c
Polygala vulgaris	3 s	19 s	*Rumex acetosella*	0	57	*Tragopogon pratensis*	3 s	0
Polygonatum multiflorum	11 s	0	*Rumex crispus*	3 s	0	*Trifolium arvense*	3 s	19 s
Polygonatum odoratum	30	0	*Sagina nodosa*	19 s	81 c	*Trifolium campestre*	0	81 c
Potentilla anserina	14 s	0	*Saxifraga granulata*	8 s	48	*Trifolium medium*	8 s	0
Potentilla argentea	0	33	*Saxifraga tridactylites*	14 s	19 s	*Trifolium montanum*	78 c	10 s
Potentilla erecta	19 s	5 s	*Scabiosa columbaria*	3 s	14 s	*Trifolium pratense*	65	24 s
Potentilla fruticosa	0	24 s	*Scleranthus perennis*	0	5 s	*Trifolium repens*	19 s	19 s
Potentilla neumanniana	76 c	100 c	*Scorzonera humilis*	19 s	0	*Trifolium striatum*	0	33
Potentilla reptans	43	0	*Sedum acre*	54	95 c	*Tussilago farfara*	5 s	0
Primula farinosa	5 s	0	*Sedum album*	30	86 c	*Valeriana officinalis*	11 s	0
Primula veris	70	10 s	*Sedum rupestre*	0	71	*Valerianella locusta*	0	29
Prunella grandiflora	0	71	*Selinum carvifolia*	3 s	0	*Veronica arvensis*	0	62
Prunella vulgaris	68	71	*Senecio jacobaea*	81 c	5 s	*Veronica chamaedrys*	22 s	10 s
Prunus spinosa	0	52	*Senecio vulgaris*	11 s	0	*Veronica officinalis*	41	19 s
Pulsatilla pratensis	14 s	19 s	*Sesleria caerulea*	89 c	57	*Veronica spicata*	54	90 c
Quercus robur	14 s	0	*Silene nutans*	32	19 s	*Veronica teucrium*	22 s	0
Ranunculus acris	8 s	5 s	*Silene vulgaris*	14 s	19 s	*Viburnum opulus*	35	0
Ranunculus bulbosus	41	90 c	*Sisymbrium supinum*	0	14 s	*Vicia angustifolia*	0	19 s
Ranunculus illyricus	0	10 s	*Solidago virgaurea*	84 c	0	*Vicia cracca*	57	14 s
Ranunculus polyanthemos	49	0	*Sonchus asper*	0	10 s	*Vicia hirsuta*	0	29
Rhamnus catharcticus	73	0	*Sorbus aucuparia*	81 c	0	*Vicia lathyroides*	0	5 s
Rhinanthus minor	3 s	5 s	*Sorbus intermedia*	38	10 s	*Vicia sepium*	3 s	0
Rhinanthus serotinus	0	29	*Stellaria graminea*	8 s	33	*Vicia tetrasperma*	3 s	5 s
Ribes alpinum	51	0	*Succisa pratensis*	19 s	10 s	*Vincetoxicum hirundinaria*	3 s	24 s
Ribes uva-crispa	3 s	0	*Swida sanguinea*	27	0	*Viola arvensis*	0	19 s
Rosa canina	0	43	*Tanacetum vulgare*	3 s	0	*Viola canina*	0	10 s
Rosa majalis	16 s	0	*Taraxacum officinale*	76 c	95 c	*Viola collina*	5 s	0
Rosa mollis	11 s	0	*Tetragonolobus maritimum*	3 s	0	*Viola hirta*	22 s	10 s
Rosa spec.	19 s	0	*Thalictrum aquilegifolium*	3 s	0	*Viola mirabilis*	3 s	0
Rosa vosagiaca	22 s	0	*Thalictrum flavum*	5 s	0	*Viola rupestris*	78 c	0
Rubus caesius	30	0	*Thalictrum simplex*	3 s	0	*Viola tricolor*	0	62
Rubus saxatilis	43	0	*Thlaspi arvense*	0	24 s			

Plant species turnover in an alvar grassland under different environmental conditions and at different scales

Renate Huber[1]* & Eddy van der Maarel[2]

[1]*Department of Ecology and Evolution, Uppsala University, SE-75236 Uppsala, Sweden;*
[2]*Community and Conservation Ecology Group, University of Groningen, P.O. Box 14, NL-9750 AA Haren, The Netherlands;*
* *Corresponding author; E-mail renate.huber@theducation.se*

Abstract

Nutrient and water supply, light availability and removal of biomass were manipulated in a limestone grassland community on the Swedish island of Öland from 1990 to 1993 in order to investigate how these factors influence species richness and year-to-year turnover at fine scales. Turnover, broken down into disappearance ('extinction') and appearance ('immigration') of vascular plant species, was measured at different spatial scales in plots ranging from 4 cm^2 to 0.25 m^2.

For most treatments, turnover was highest at the finest scale, both measured as absolute and relative numbers. Turnover rate increased at all scales when the treatment implied such a change in the environment, where application of fertilizer was combined with shading. In these cases, disappearance of species largely exceeded appearance in a predictable manner, and resulted in species-poor assemblages at all scales. In plots treated with either fertilizer or shade, there were large differences in the direction of the turnover (i.e. whether immigration or extinction dominated) between years, apparently depending on the weather conditions in the respective year. After drought spells total turnover was also high for such treatments, whereas plots regularly receiving additional water supplies had rather similar turnover rates during the whole experiment.

Keywords: Competition; Disturbance; Diversity; Grazing; Irrigation, Light conditions; Öland; Species richness.

Nomenclature: Tutin et al. (1964-1980)

Introduction

Studies on species turnover originate in the Theory of Island Biogeography by MacArthur & Wilson (1967) who regarded species richness in a certain area as the result of a dynamic equilibrium between extinction and immigration of species. They developed the concepts of turnover and turnover rate as the outcome of extinction and immigration per time unit. These can be regarded as a combination of key processes in the dynamics of plant communities, not only in the course of succession (Gibson & Brown 1991), but also as internal dynamics in a stable community where the current diversity of a certain species assemblage is maintained (van der Maarel 1996).

Studies of species turnover, originally concerned with islands (MacArthur & Wilson 1967; Nilsson & Nilsson 1982, 1983, 1985), can be extended to experimentally treated mainland sites (e.g. Gibson & Brown 1991; Glenn & Collins 1992). Recently, studies in grasslands have indicated the importance of species turnover for the maintenance of plant species richness found in these communities, especially at fine scales (e.g. Glenn & Collins 1993; Herben et al. 1993; van der Maarel & Sykes 1993, 1997; Huber 1994, 1999). Van der Maarel & Sykes (1993) introduced the 'carousel model', describing fine-scale species mobility in short, open alvar limestone grassland. One implication of this model is that species disappear and appear from any patch in the community in an apparently random manner. As measures for the appearance aspect of this mobility were used (1) cumulative species number, i.e. the number of species in a given subplot plus all new species observed in the subsequent recordings; (2) cumulative species frequency, i.e. the number of plots occupied at least once during a series of recordings.

In this kind of grassland, we are dealing with fine-scale movements: species can easily move into and out of very small plots without immigrating from further away, or without going locally extinct. Furthermore, only the presence and absence of above-ground organs is considered, which mainly result from germination of locally available

seed, resprouting from below-ground organs, and from local dieback. Therefore, we should preferably use disappearance for extinction and appearance for immigration as more suitable terms.

Species turnover, taken as the sum of species disappearances and appearances, can be influenced in several ways, e.g. composition of, and conditions in, the seed bank, the structure and frequency of gaps, competitive relationships between established plants, and other environmental conditions (e.g. Gibson & Brown 1991; Rusch & van der Maarel 1992), notably weather fluctuations (Grubb 1988; Dai 1998). In the present contribution we address two main questions:

1. How do changes in the availability of nutrients, water, and light, as well as removal of biomass, affect species turnover? According to Grime (1979) and Tilman (1982, 1988) extinction rates should increase with higher nutrient availability as a result of stronger competition. On the other hand, Tilman (1993) observed a temporary increase in immigration rates following nutrient addition, caused by germination of nitrogen-dependent seed bank species. Higher rates of immigration can also be caused by vegetative expansion of nutrient-demanding species. Tilman also claimed that a subsequent reduction in richness is possible, which is not only caused by higher rates of extinction, but also by lower rates of immigration. Such a decrease in the immigration rate and hence richness can be caused by the development of a denser and higher sward: tall species dominate and the light intensity near the ground is reduced. This, for instance, makes it difficult for seedlings to establish and/or survive. Considering the normally nutrient-poor conditions of alvar grassland, fertilization could be expected to have a strong effect. On the other hand, productivity is also limited by irregular water availability. Therefore, extra regular supply with water could be expected to influence turnover rates.

Effects of light reduction on species diversity have not often been studied in a systematic way, but through the simulation of a higher sward, richness may be reduced. The only study which is known to us concerns an increasing of the light regime (Eek & Zobel 1997). Concerning grazing, there are different findings, in some cases an increased turnover was obtained (cf. Gibson & Brown 1991), in other studies turnover was lower in grazed than in ungrazed patches (e.g. Milberg & Hansson 1994).

2. Does turnover rate, i.e. the degree of disappearance and appearance vary with different scales of observation and in different years? In order to maintain an equilibrium state at a given spatial scale, disappearances and appearances must be equal. In general, populations on large plots should be more stable and their turnover rates lower (Robinson & Quinn 1988). When equilibrium conditions are negatively influenced through experimental changes, it can be assumed that the rate of disappearance increases more at fine scales, where species which are present with

only few specimens, vanish more easily (Nilsson & Nilsson 1982). With larger areas and larger population sizes, species would be able to remain present with at least some individuals, but there would also be a possibility for appearances because a larger area provides a greater chance for seedling establishment or vegetative dispersal from the surrounding area.

Material and Methods

Study area

The study was carried out between 1989 and 1994 at Gettlinge (56°23' N, 16°27' E) on the 'Great Alvar' on the Baltic island of Öland, southeastern Sweden. The alvar is a vast limestone plateau with grassland, including the species-rich plant community *Veronico-Avenetum* (Krahulec et al. 1986) occurring at sites with relatively deep soils (10 - 30 cm). Species richness is very high, especially at a fine scale – with maxima of ca. 40 species on 1 m², 33 on 0.25 m², 25 on 0.01 m², and 15 on 0.001 m² (van der Maarel & Sykes 1993).

Sheep, cattle and horses have grazed the alvar for a long time, probably for more than 2000 yr. The experimental site is lightly grazed by cattle and a few horses, but grazing was interrupted during the summer period for the time of the experiments. Mean annual rainfall is 430 mm (1965 to 1980; Rosén 1982); frequently occurring summer droughts cause heavy damage and die-back of the vegetation, leading to subsequent drastic changes in species composition (Rosén 1982; van der Maarel 1996).

During the period of observation, the amount of rainfall over the growing season fluctuated strongly (Huber 1994). While rainfall was evenly distributed during the growing season of 1990, the early summer of 1991 was extremely wet. In 1989 and 1992, two longer drought periods of 6 and 10 weeks, respectively, occurred. The start of the growing season in 1993 was also very dry. Therefore extra water was supplied to all plots in order to avoid drought damage in non-irrigated plots and to be able to finish the experimental part of the study (cf. Huber 1994).

Experimental design and sampling

Experimental plots were established within five blocks of 1.5 m × 7.5 m, situated near to each other: maximum distance between plots was ca. 20 m (Figs. 1 - 3). Each block consisted of 20 plots (thus, $n = 100$) in two rows with 20-cm buffer zones between neighbouring plots. This layout was chosen for practical reasons. These plots were sampled at three nested spatial scales, ranging from 50 cm × 50 cm (large), with a central sub-plot of 10 cm × 10 cm (medium) to 2 cm × 2 cm (small, 25 cells in a contiguous grid on the 10 cm × 10 cm sub-plot).

Fig. 1. Layout of the experiments on Gettlinge Alvar; one of the blocks is shown with 50 cm × 50 cm in two rows separated by a buffer zone (photo: R. Huber).

Fig. 2. One of the blocks with the shading net upright. Two more blocks are visible in the distance (photo: R. Huber).

Fig. 3. Block with shading device and microclimatic instruments (not discussed in this paper) in the foreground. The effect of the serious summer drought in 1992 is clear (photo: R. Huber).

Table 1. Combinations of treatments and their abbreviations.

C	=	No treatment (including no grazing)
F	=	Fertilization
S	=	Shading
W	=	Irrigation
G	=	Simulated grazing
FS	=	Fertilization + shading
SG	=	Shading + simulated grazing
FW	=	Fertilization + irrigation
FWG	=	Fertilization + irrigation + simulated grazing
FWS	=	Fertilization + irrigation + shading

Table 2. Annual nutrient supply to the F, FS, FW, FWG and FWS plots.

Element	Addition (g/m2)	Chemical compounds
N	13.3	NO_3NH_4
P	5.9	KH_2PO_4
K	14.8	KCl, KH_2PO_4
Ca	4.0	$CaCl_2$
Mg	3.3	$MgSO_4*7H_2O$
Zn	0.8	$ZnSO_4*7H_2O$
Mn	0.8	$MnSO_4*H_2O$
Cu	0.3	$CuSO_4*5H_2O$
Fe	0.3	$FeSO_4*7H_2O$
B	0.03	$Na2B_4O*7H_2O$
Mo	0.008	$Na_2MoO_4*2H_2O$

From May 1990 until June 1993 the plots were treated with 10 different combinations of nutrients and/or water, reduced light availability and changed grazing conditions in a randomized split-plot design with shading as split factor. Each factor was applied separately, and in combination (of maximally three treatments) with 10 replicates for each treatment (See Table 1 for combinations of treatments and abbreviations).

A liquid fertilizer solution (NPK and micronutrients; see Table 2 for amounts) was given four times during the growing season. The irrigation treatment consisted of the addition of water equivalent to 80 mm rainfall per month from May to August – applied twice a week in equal doses of 10 mm. This extra yearly supply of 320 mm largely exceeded 173 mm, the mean for the growing season (Rosén 1982).

A green shading net, as used in horticulture, clamped on a wooden frame, was put over the shaded plots during the whole year; this reduced photosynthetically active radiation (PAR) to ca. 30% of full light (Fig. 2). The northern sides of the frames were only closed by a wire net to avoid exclusion of pollinators and to allow pollen and diaspores to pass, but to prevent grazers from approaching the plots. Grazing was simulated by clipping the vegetation with scissors once a year in September, to 2 cm above ground level – this to mimic the height of the surrounding naturally grazed vegetation. As a matter of fact, this treatment (G) can be considered to be closest to the baseline conditions of this system, whereas the control C was rather a 'non-treatment' without any grazing. We checked for differences in effect between these two treatments. Since significant differences were hardly found, and the clipping did not

entirely mimic natural grazing conditions, we considered treatment C as an appropriate measure of 'natural' conditions, i.e. without human interference. This makes C to our 'null model', comprising the 'normal' turnover of the system.

Actually, several null models have been proposed in relation to the carousel model (van der Maarel & Sykes 1997; Palmer & Rusch 2001), and it is still unclear (1) which random configuration of species occurrences to adopt for such a null model, and (2) to which of the treatments a null model should be related. Presence/absence of above-ground organs, rooted, as well as non-rooted parts, was recorded at all scales in June of the years 1989 to 1993. In June 1994, one year after termination of the experiment, the 50 cm × 50 cm plots were re-sampled (it was not possible to sample the subplots, since their markings had been removed at the end of the treatments).

Turnover indices

In addition to the determination of absolute numbers of appearing and disappearing species, turnover calculations were based on the following measurements of the disappearance rate v_{dis} and the appearance rate v_{app} between two consecutive recordings at times t_i and t_{i+1}:

$$v_{dis} = \frac{\text{No. of species disappearing between } t_i \text{ and } t_{i+1} * 100}{\text{Cumulative no. of species at } t_i \text{ and } t_{i+1}} \quad (1)$$

$$v_{app} = \frac{\text{No. of species newly appearing at } t_{i+1} * 100}{\text{Cumulative no. of species at } t_i \text{ and } t_{i+1}} \quad (2)$$

Disappearance and appearance rates as direct measures of release and occupation of space (cf. Palmer & Rusch 2001) were calculated separately in order to disentangle the processes determining possible changes of species richness as a response to the experimental manipulations. The cumulative species number was calculated as the number of species recorded at t_i plus the number of newly occurring species at t_i+1. The turnover rate can simply be taken as the sum of these two values. Calculations were carried out for the transitions 1 (1989-1990), 2 (1990-1991), 3 (1991-1992) and 4 (1992-1993) for small and medium plot sizes: for the large plot size a fifth transition (1993-1994) was included. For the small plots (2 cm × 2 cm) mean values over 25 cells (i.e. the grid) were calculated first. Several other indices of species turnover are available but there seems to be no clear preference for any of them (Nilsson & Nilsson 1982; Gibson & Brown 1991; Kellner 1993; Milberg & Hansson 1994; Pärtel & Zobel 1995). In most indices all species in two consecutive recordings are considered, i.e. species occurring in both recordings are counted twice. In contrast, our equations (1) and (2), are based on the cumulative number of species. This is conform to the study by van der Maarel & Sykes (1993) at the same site.

Statistical methods

Absolute numbers of disappearing and appearing species and total turnover were calculated as mean values over the four experimental years. Differences between treatments were tested with the Tukey test, $p < 0.05$. The percentage data on disappearance and appearance rate were arcsine-transformed to improve the fit to a normal distribution and to reduce heteroscedasticity (Zar 1984). The material was first examined with ANOVA (balanced design in Minitab 11), followed by an F-test; all possible interactions were included in the model in order to detect overall heterogeneity in the material (App. 1). Since a strong year-to-year influence was found, subsequent analyses (procedure GLM in Minitab 11) were carried out for each year separately; technically the covariates were used as dummy variables for F, S, W, and G (Zar 1984). Two- and three-factor treat-

ments included all possible combinations (e.g. treatment FW implied that the value of the covariates F, W, and FW was set to 1, for treatment FWS covariates F, W, S, FS, FW, and FWS were set to 1).

Results

Differences between blocks and plot sizes

Significant differences between the five experimental blocks were only found in a few cases, in the small plots for the transition from year 1 to 2, and (weakly) year 2 to 3, and in the large plots from year 2 to 3 (Table 3). This block effect re-appeared in the 50 cm $\times$ 50 cm plots in the year after termination of the experiment, indicating that experimental effects dominated over site heterogeneity as

Table 3. Between-year appearance and disappearance rates for (**a**) 1989 to 1994 large plots (50 cm $\times$ 50 cm), from 1989 to 1993 (June samples) (**b**) medium plots (10 cm $\times$ 10 cm), (**c**) small plots (2 cm $\times$ 2 cm). Bold values refer to treatments with a significant response in the regression analysis ($p < 0.05$), italics to values close to significance. (app1/dis1= appearance/disappearance rate from 1989 to 1990, app2/dis2 = appearance/disappearance rate from 1990 to 1991, app3/dis3 = appearance/disappearance rate from 1991 to 1992, app4/dis4 = appearance/disappearance rate from 1992 to 1993, app5/dis5 = appearance/disappearance rate from 1993 to 1994).

a. 50 cm $\times$ 50 cm

Block	$v_{app}1$	$v_{dis}1$	$v_{app}2$ *	$v_{dis}2$ ***	$v_{app}3$	$v_{dis}3$	$v_{app}4$	$v_{dis}4$	$v_{app}5$ **	$v_{dis}5$
C	12.7	2.9	7.4	1.5	3.4	8.3	8.3	5.6	7.3	3.0
F	18.2	2.3	**3.9**	**5.1**	2.8	11.2	8.3	5.5	**13.0**	5.6
S	**20.7**	2.2	**3.8**	**5.2**	2.1	10.5	8.4	3.1	7.5	**7.2**
W	12.8	2.6	**3.6**	3.7	4.3	**3.2**	*4.0*	3.2	**3.0**	5.0
G	15.4	2.4	*4.4*	3.9	3.0	6.6	9.7	5.1	5.4	4.8
FS	**16.7**	2.3	2.6	9.8	2.3	17.3	4.5	7.5	19.6	5.3
SG	17.6	3.0	**6.2**	4.1	3.3	6.2	7.0	3.9	4.4	5.8
FW	16.5	1.5	**5.2**	4.8	3.1	9.5	4.8	4.3	11.0	4.1
FWG	21.4	1.7	5.6	4.2	2.7	7.6	7.1	3.1	4.5	5.5
FWS	17.7	1.9	3.3	17.2	3.9	16.4	**9.4**	5.7	15.1	3.5

b. 10 cm $\times$ 10 cm

Block	$v_{app}1$	$v_{dis}1$	$v_{app}2$	$v_{dis}2$	$v_{app}3$	$v_{dis}3$	$v_{app}4$	$v_{dis}4$		
C	15.0	7.0	17.4	3.8	4.2	19.2	10.4	14.8		
F	18.8	5.0	13.4	**11.6**	7.3	24.7	12.6	14.1		
S	19.3	5.8	**5.9**	**10.2**	6.1	19.7	12.4	10.0		
W	19.6	8.3	14.3	5.3	8.4	13.1	10.7	9.7		
G	17.3	7.1	11.2	6.6	4.9	12.1	9.4	8.1		
FS	20.6	6.4	4.0	37.2	5.8	34.1	13.2	**26.8**		
SG	22.4	8.7	**12.4**	10.2	10.9	17.2	12.3	7.3		
FW	18.9	6.3	7.5	16.8	6.0	17.6	19.6	7.6		
FWG	23.1	3.4	**12.9**	**9.5**	6.2	12.2	10.4	4.7		
FWS	21.2	6.9	5.4	33.4	**10.1**	33.1	17.2	16.2		

c 2 cm $\times$ 2 cm

Block	***	***	*							
C	36.7	19.6	33.1	12.7	11.4	36.6	25.5	21.0		
F	33.9	19.0	28.1	20.9	17.0	42.5	31.6	22.0		
S	33.3	17.0	26.7	23.4	16.7	36.6	29.1	23.5		
W	32.4	16.4	27.7	16.4	20.3	23.4	21.7	21.4		
G	33.6	18.5	27.3	15.4	13.9	31.7	22.4	16.3		
FS	34.9	18.3	19.9	39.8	15.6	52.3	29.6	30.7		
SG	35.7	15.9	22.5	23.4	17.8	26.5	23.9	15.2		
FW	42.3	16.5	23.4	26.6	20.1	32.4	32.0	20.3		
FWG	38.0	16.0	30.8	21.1	22.3	23.6	23.4	19.0		
FWS	39.0	18.6	19.2	43.6	21.6	43.2	28.5	31.9		
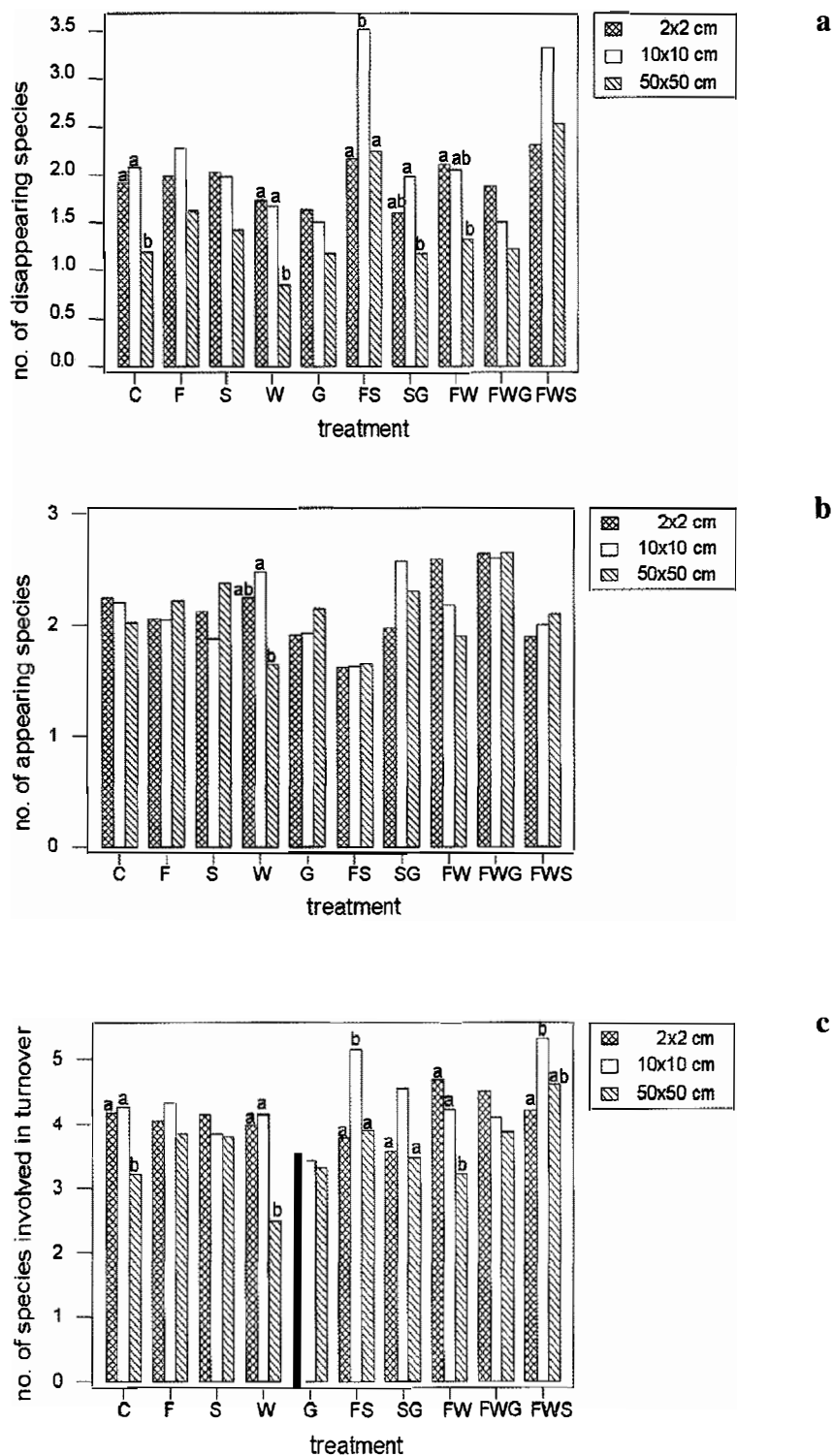
Fig. 4a. Mean number of disappearing species involved in the year-to-year turnover (1990/1991, 1991/1992, 1992/1993) on quadrats of different sizes (2 cm × 2 cm, 10 cm × 10 cm and 50 cm × 50 cm) under the different treatments (see Table 1 for abbreviations). **b.** Mean number of appearing species; **c.** Mean total number of species involved in the turnover (disappearing + appearing species). Tukey test; $P < 0.05$. Different letters indicate significant differences between plot sizes per treatment.

long as the experiment went on.

Generally, the number of disappearing species was lowest in the large plots, and in five treatments the difference towards the medium plots was significant (Fig. 4a). More species disappeared in plots treated with moisture and shade, and particularly in these treatments disappearance is significantly largest in the medium plots and not in the smallest ones. Regarding appearance the pattern was less clear, and differences were mostly insignificant: for some treatments the number of appearing species was largest in the small plots, but in others (e.g. F, G and FWS) the number of appearances was higher in the large plots (Fig. 4b). The turnover figures, combining disappearances and appearances, largely follow the disappearance pattern (Fig. 4c).

Turnover rates decreased with increasing scale (Table 3), and among the treatments, differences were much more pronounced in the small plots than in the large plots. In the small plots both disappearance and appearance rates are typically between 20 and 30% with extremes 11.4% and 52.3%, in medium plots 10 - 20% (3.4 - 37.2%) and in large plots 3 - 10 % (1.5 - 21.4%). For turnover rates (being the sum of disappearance and appearance rates) the extremes are 30.2 - 67.9% for small, 25.1 - 41.2% for medium and 7.3 - 24.9% for large plots. The lower number of species present in the smaller plots (Fig. 4, Table 3) explains, of course, the large relative values.

During the first one or two transitions the disappearance rate was much higher than the appearance rate, for all plot sizes and all treatments, particularly F-treatments.

Differences between treatments and years

Transition 1: 1989-1990
At all scales and for most treatments the appearance rate was much higher than the disappearance rate. This means that the species richness increased. This trend is reversed in the later years, particularly in the treatments FS and FWS, which leads to a strong decrease in species richness here as already described by Huber (1994).

Transition 2: 1990-1991
Application of fertilizer or shade without simulated grazing, significantly increased the rate of disappearance; especially when F and S were applied together, the disappearance rate was high (treatments FS and FWS). Moreover, S reduced the appearance rate significantly at all scales, while a significant effect for F was found only in the large plots. In the medium and small plots, FWG both resulted in a higher than expected appearance rate, as well as lower than expected disappearance rate.

Transition 3: 1991-1992
High rates of disappearance in almost all treatments are characteristic for this transition, although they are significantly lower than the control for treatment W in large and small plots. Treatments F, S and W, at the medium scale, had somewhat higher (though insignificant) appearance rates than C and so had FWS, but this was significantly lower than expected from the single-factor treatments. The same pattern occurred in the smallest plots, where F, S, and W had significantly higher appearance rates than C, but FS significantly lower than expected.

Transition 4: 1992-1993
Appearance rates were much higher than in the previous transition at all scales and for almost all treatments and reflect the re-colonization of the plots after the drought spell in 1992 (Table 3): significantly higher for FWS, but (nearly significantly) lower for W at the large scale. In this transition, the disappearance rates for many treatments were quite closer to appearance values compared with the first transition, despite the fact that both were characterized by recovery after severe drought spells.

Transition 5: 1993-1994
This sampling was carried out one year after termination of the experiment in order to follow up the dynamics of the system after cessation of the treatments. Significantly higher appearance rates were found for the former treatment F (Table 3). A strong re-colonization occurred also in other treatments earlier subjected to fertilization (especially FS and FWS), whereas S had a significantly higher disappearance rate. The rate of appearance was significantly lower in the formerly irrigated plots.

Discussion

Recently, traditional theories stating that high nutrient levels or high productivity lead to low species richness have been frequently questioned (e.g. Waide et al. 1999). The results from this study support this view. Most of the applied treatments which included fertilisation, resulted in only temporal reductions of the number of species.

We could not find a predictable pattern, the contrasting responses in the different years can only be explained in connection with the shifting climatic conditions which the community is exposed to (cf. Herben et al. 2003). Our results support earlier investigations that, at least in dry grasslands, productivity is not limited by nutrients, but by the availability of water (Walter 1939; Huston 1994).

In growing seasons with sufficient rainfall, competitively strong species could mobilize resources very fast and gain advantage (e.g. *Poa angustifolia*), but suffered on the other hand during periods of harsh environmental conditions. Interspecific competition is modified by weather conditions, and competitive rankings can change, triggered by the comparatively small differences in size between species (Herben et al. 2003). The frequent alternation between wet and dry seasons, a distinct feature in alvar

grasslands, is an important driving force for the mainte- nance of species richness (Chesson & Huntly 1997). The fast recovery after drought spells with a different species assemblage indicates both the presence and importance of below-ground storage organs. Typical alvar species are able to regain rapidly the open space, which becomes available during drought spells, when water-demanding competitors have difficulties to survive.

The regular extra supply of water, but without addi- tion of nutrients (treatment W) resulted in relatively low turnover rates throughout the experiment. This is partly explained by the uniform environmental conditions which this treatment creates (cf. Holland 1978). It demonstrates that drought is a major mortality factor, resulting in spe- cies turnover. Anyhow, species richness remained still high, since the turf remained short due to the shortage of nutrients.

Since treatment F resulted in significantly high disap- pearance under wet conditions (transition 2), one could expect low appearance and high disappearance rates for treatment FW throughout the experiment due to the regular water supply. Moreover, biomass was highest of all treatments (almost 800 g.m^{-2}; Huber 1994). Neverthe- less, species richness was only occasionally lower (Huber 1994) and turnover did not significantly differ from the control throughout the experiment. Willems & Bik (1998) observed similar patterns in a limestone grassland in The Netherlands, which they explained with the small-scale pattern of the vegetation, and the small-scale resource heterogeneity, which allows a higher species density than expected only based on productivity. There could be other explanations for our observations: 1. The comparatively low height of the turf (11-17 cm) in this treatment, still preventing competition for light. 2. The possibility of some litter removal by winter storms or by small grazers, keeping the turf slightly open. 3. The frequency of water addition, especially during the drought of 1992. Novopl- ansky & Goldberg (2001) found that infrequent water pulses favoured slow-growing species from low-productive environments. 4. The duration of the experiment might have been too short; under a long perspective treatment FW might result in stronger and more persistent rates of disappearance. 5. Willems & Bik (1998) observed very low seed numbers in a large abandoned experimental plot. The relatively small size of our experimental plots (0.25 m^2) still allowed for temporal mass effects from the surroundings.

Treatment FWG, though including high nutrient levels and water supply, generally had the most positive effect on the maintenance of a species-rich sward. In certain years this combined treatment had an effect different from that of the single factors. In transition 2, S, W, and G reduced appearance rates, whereas FWG, the combination of fac- tors, did not have this effect. Tilman (1993) found increased richness in high-nitrogen treatments in an old-field experi-

ment in Minnesota, which he explained as the result of a higher germination rate of nitrogen-dependent seed bank species. In the present study, the yearly clipping of living biomass and litter removal in the FWG-plots regularly opened the turf. This enabled the nitrogen-demanding annual *Cerastium semidecandrum* to invade the plots in large numbers, as well as low-growing perennials to survive (pers. obs.). Repeated disturbance through clip- ping delayed a possible saturation of space as expected under nutrient-rich conditions (Lavorel et al. 1994), and a species-rich turf could be maintained.

Treatments FS and FWS, which combined a high level of nutrients with reduced availability of light, were the only cases where the climatic forces could not dominate over the experimental changes. Fertilization had a positive, though only transient effect in the start of the experiment (cf. Tilman 1993). The addition of nutrients gave some species a strong advantage to grow fast into the small gaps, which were numerous after the drought spell in 1989. This resulted in a dense, but still species-rich sward (Fig. 1). Later on fast-growing species were favored, and very soon space became limited and further establishment or persistence of species was difficult (cf. Lavorel et al. 1994), which is indicated by increasing disappearance rates.

Responses to treatments FS and FWS, and changes in species richness, were persistent and directional, as reported earlier (Huber 1994); the disappearance rate was high and the appearance rate was low.

A very tall (25 - 30 cm) turf with relatively large gaps at the ground developed in FS and FWS plots due to the fact that most low-growing species disappeared during the course of time (Fig. 2). However, colonization of these gaps was comparatively difficult because of shelter from the shade netting, as well as the dense and tall sward of fast-growing species, especially grasses, and litter. This caused a homogeneous, very low, unfavourable light regime at ground level (cf. Mitchley & Willems 1995; Willems & van Nieuwstadt 1996). Regeneration by seed, which is of great importance in this grassland (Rusch & van der Maarel 1992), was almost impossible under these conditions (Huber unpubl.; Tilman 1993). The irregular pattern of highest disappearance in the medium-sized plots (Fig. 4a) can be explained by (1) a high degree of disap- pearing species in these treatments, and (2) the fact that the total number of species present in the smaller plots is much lower from the beginning.

Under conditions of simulated grazing (G) there was a slight tendency of a lower turnover than for the ungrazed C treatment, which coincides with observations of Milberg & Hansson (1994). On the other hand, Gibson & Brown (1991) found increased rates of appearance and disap- pearance under grazing, but also year-to-year variations in the turnover rates unconnected with grazing which they relate to other environmental forces. Pärtel & Zobel (1995) reported scale-dependent turnover patterns from

grazed Estonian alvar grasslands. Possible explanations for these inconsistent results in the above-mentioned studies may be found in the different degrees of grazing, and the different types of grassland included. Allen et al. (1995) found heavily grazed vegetation in New Zealand to be more susceptible to environmental stress such as drought than ungrazed vegetation; this could also explain our findings.

Drought seems to be the driving force in this type of vegetation; appearance rates around 40% indicate that a large proportion of species involved in the turnover between 1992 and 1993 were newcomers which were not present during the previous recording, but were able to colonize gaps which arose due to die-back of drought-sensitive species.

Similar results have also been mentioned in earlier studies where large fluctuations in the species composition of communities were found (Stephenson & Herendeen 1986; Watkinson 1990; Rusch & van der Maarel 1992). This grassland community seems to be a space-time mosaic of local extinctions and colonizations at a very fine scale (van der Maarel 1996), whereas at a m²-scale it is very stable (Huber 1999). The maintenance of the high richness lies in the fast and large turnover in the species composition on very small patches (Shmida & Ellner 1984; van der Maarel 1993), which bear different species assemblages. This continuous species exchange supports the coexistence of many species.

The absolute number of species that was exchanged in the small 2 cm × 2 cm quadrats was usually greater than in the largest plots; especially the number of disappearing species was, as expected, largest in the small and medium plots, whereas the appearance pattern was not uniform: for a number of treatments the number of newcomers was similar over all scales. Immigration/appearance and extinction/disappearance seem to be two independent, not highly related processes, the first dependent on the frequency of a certain species, the latter independent thereof (Palmer & Rusch 2001).

Another aspect of the large absolute exchange at the fine scale might be the relatively low number of rare species in this grassland combined with a high species richness at the small, but comparatively low one at the large scales (van der Maarel 1988). This may also be an explanation for the different patterns found at the different scales. Palmer & Rusch (2001) found shorter residence times and a more random-like behaviour of species at fine scales. This is supported by this study where the largest turnover (both relative and absolute) and fastest dynamics were found in the small plots.

Still, the mechanisms behind the large turnover and high species richness at these fine levels are not fully understood; a high degree of randomness seems to play an important role, as results from the first year indicate: similarly treated plots showed different patterns. This might also point to the importance of small-scale heterogeneity in chemical soil properties (Ryser et al. 1995) or soil depth (van der Maarel & Sykes 1997). Therefore there is still a need for detailed, long-term, and fine-scale experiments.

Acknowledgements

References

Allen, R.B., Wilson, J.B. & Mason, C.R. 1995. Vegetation change following exclusion of grazing animals in depleted grassland, Central Otago, New Zealand. — J. Veg. Sci. 6: 615-626.

Chesson, P.L. & Huntly, N. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. — Am. Nat. 150: 519-553.

Dai, X. 1998. Small-scale pattern and mobility of plant species in alvar grassland. — Ph.D. Dissertation Uppsala University, Uppsala.

Eek, L. & Zobel, K. 1997. The effect of fertilization and additional illumination on seasonal change of fine-scale community structure in a species-rich grassland. — J. Veg. Sci. 8: 225-234.

Gibson, C.W.D. & Brown, V.K. 1991. The effects of grazing on local colonisation and extinction during early succession. — J. Veg. Sci. 2: 291-300.

Glenn, S.M. & Collins, S.L. 1992. Effects of scale and disturbance on rates of immigration and extinction of species in prairies. — Oikos 63: 273-280.

Glenn, S.M. & Collins, S.L. 1993. Experimental analysis of patch dynamics in tallgrass prairie plant communities. — J. Veg. Sci. 4: 157-162.

Grime, J.P. 1979. Plant strategies and vegetation processes. Wiley, New York, NY.

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

Grubb, P.J. 1988. The uncoupling of disturbance and recruitment, two kinds of seed bank, and persistence of plant populations at the regional and local scales. — Ann. Zool. Fenn. 25: 25-36.

Herben, T., Krahulec, F., Hadincová, V. & Skálová, H. 1993.

Small-scale spatial variability as a mechanism for large-scale stability in mountain grasslands. — J. Veg. Sci. 4: 163-170.

Herben, T., Krahulec, F., Hadincová, V., Pecháčková, S. & Wildová, R. 2003. Year-to-year variation in plant competition in a mountain grassland. — J. Ecol. 91: 103-113.

Holland, P.G. 1978. Species turnover in deciduous forest vegetation. — Vegetatio 38: 113-118.

Huber, R. 1994. Changes in plant species richness in a calcareous grassland following changes in environmental conditions. — Folia Geobot. Phytotax. 29: 469-482.

Huber, R. 1999. Patterns of species richness in a limestone grassland under different treatments in relation to spatial scale. — Appl. Veg. Sci. 2: 257-266.

Huston, M.A. 1994. Biological diversity. The coexistence of species on changing landscapes. — Cambridge University Press, Cambridge.

Kellner, O. 1993. Effects of fertilization on forest flora and vegetation. — Ph.D. Thesis Uppsala University, Uppsala, SE.

Krahulec, F., Rosén, E. & van der Maarel, E. 1986. Preliminary classification and ecology of dry grassland communities on Ölands Stora Alvar (Sweden). — Nord. J. Bot. 6: 797-809.

Lavorel, S., Lepart, J., Debussche, M., Lebreton, J.-D., & Beffy, J.-L. 1994: Small scale disturbances and the maintenance of species diversity in Mediterranean old fields. — Oikos 70: 455-473.

MacArthur, R.M. & Wilson, J. 1967. The theory of island biogeography. — Princeton University Press, Princeton, NJ, US.

Milberg, P. & Hansson, M.L. 1994. Soil seed bank and species turnover in a limestone grassland. — J. Veg. Sci. 5: 35-42.

Mitchley, J. & Willems, J.H. 1995. Vertical canopy structure of Dutch chalk grasslands in relation to their management. — Vegetatio 117: 17-27.

Nilsson, C. & Grelsson, G. 1995. The fragility of ecosystems: a review. — J. Appl. Ecol. 32: 677-692.

Nilsson, J.N. & Nilsson, S.G. 1982. Turnover of vascular plant species on small islands in Lake Möckeln, south Sweden 1976-1980. — Oecologia 53: 128-133.

Nilsson, J.N. & Nilsson, S.G. 1985. Experimental estimates of census efficiency and pseudoturnover on islands: error trend and between-observer variation when recording vascular plants. — J. Ecol. 73: 65-70.

Nilsson, S.G. & Nilsson, J.N. 1983. Are estimated species turnover rates on islands largely sampling errors? — Am. Nat. 121: 595-597.

Novoplansky, A. & Goldberg, D.E. 2001. Effects of water pulsing on individual performance and competitive hierarchies in plants. — J. Veg. Sci. 12: 199-208.

Palmer, M.W. & Rusch, G.M. 2001. How fast is the carousel? Direct indices of species mobility with examples from an Oklahoma grassland. — J. Veg. Sci. 12: 305-318.

Pärtel, M. & Zobel, M. 1995. Small-scale dynamics and species richness in successional alvar plant communities. — Ecography 18: 83-90.

Robinson, G.R. & Quinn, J.F. 1988. Extinction, turnover and species diversity in an experimentally fragmented California annual grassland. — Oecologia 76: 71-82.

Rosén, E. 1982. Vegetation development and sheep grazing in limestone grassland of south Öland, Sweden. — Acta Phytogeogr. Suec. 72: 1-104.

Rusch, G. & van der Maarel, E. 1992. Species turnover and seedling recruitment in limestone grasslands. — Oikos 63: 139-146.

Ryser, P., Langenauer, R. & Gigon, A. 1995. Species richness and vegetation structure in a limestone grassland after 15 years management with six biomass removal regimes. — Folia Geobot. Phytotax. 30: 157-167.

Shmida, A. & Ellner, S. 1984. Coexistence of plant species with similar niches. — Vegetatio 58: 29-55.

Stephenson, S.N. & Herendeen, P.S. 1986. Short-term drought effects on the alvar communities of Drummond Island, Michigan. — Mich. Bot. 25: 16-27.

Tilman, D. 1982. Resource competition and community structure. Monographs in Population Biology 17. — Princeton University Press, Princeton, NJ.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Monographs in Population Biology 26. Princeton University Press, Princeton, NJ.

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

Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. & Webb, D.A. 1964-1980. — Flora Europaea. Cambridge University Press, Cambridge.

van der Maarel, E. 1988. Species diversity in plant communities in relation to structure and dynamics. — In: During; H.J., Werger, M.J.A. & Willems, H.J. (eds.) Diversity and pattern in plant communities, pp. 1-14. The Hague.

van der Maarel, E. 1993. Some remarks on disturbance and its relations to diversity and stability. — J. Veg. Sci. 4: 733-736.

van der Maarel, E. 1996. Pattern and process in the plant community: Fifty years after A.S. Watt. — J. Veg. Sci. 7: 19-28.

van der Maarel, E. & Sykes, M.T. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. — J. Veg. Sci. 4: 179-188.

van der Maarel, E. & Sykes, M.T. 1997. Rates of small-scale species mobility in alvar limestone grassland. — J. Veg. Sci. 8: 199-208.

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. 1999. The relationship between productivity and species richness. — Annu. Rev. Ecol. Syst. 30: 257-300.

Walter, H. 1939. Grasland, Savanne und Busch der ariden Teile Afrikas in ihrer ökologischen Bedingtheit. — Jb. Wiss. Bot. 87: 750-860.

Watkinson, A.R. 1990. The population dynamics of Vulpia fasciculata: a nine-year study. — J. Ecol. 78: 196-209.

Willems, J.H. & Bik, L.P.M. 1998. Restoration of high species density in calcareous grassland: the role of seed rain and soil seed bank. — Appl. Veg. Sci. 1: 91-100.

Willems, J.H. & van Nieuwstadt, M.G.L. 1996. Long-term after effects of fertilization on above-ground phytomass and species diversity in calcareous grassland. — J. Veg. Sci. 7: 177-184.

Zar, J.H. 1984. Biostatistical analysis. — Prentice-Hall, Englewood Cliffs, NJ.

App. 1. Balanced ANOVA for overall heterogeneity at the different scales; df = Degrees of freedom; SS = Sum of squares; MS = Mean square; Trmt = Treatment; Repl = Replicate 1 and 2 in each block.
Trmt*Repl(Block) was the denominator in the *F*-test.

Source	df	SS	MS	F	P	F-test Numerator	df	MS	F	P

Large plots (50 cm × 50 cm)

Appearance

Source	df	SS	MS	F	P	F-test Numerator	df	MS	F	P
Trmt	9	0.23331	0.02592	2.83	0.004	Trmt	9	0.025923	2.03	0.058
Block	4	0.27906	0.06977	7.60	0.000	Block	4	0.069766	5.45	0.001
Trmt*Block	36	0.38065	0.01057	1.15	0.269	Trmt*Block	36	0.010574	0.83	0.721
Repl(Block)	5	0.03193	0.00639	0.70	0.627	Repl(Block)	5	0.006385	0.50	0.775
Trmt*Repl(Block)	45	0.57600	0.01280	1.40	0.066					
Year	4	4.76793	1.19198	129.93	0.000					
Trmt*Year	36	1.47185	0.04088	4.46	0.000					
Block*Year	16	0.24822	0.01551	1.69	0.052					
Trmt*Block*Year	144	1.91351	0.01329	1.45	0.009					
Year*Repl(Block)	20	0.39768	0.01988	2.17	0.004					

Disappearance

Source	df	SS	MS	F	P	F-test Numerator	df	MS	F	P
Trmt	9	0.50837	0.05649	3.78	0.000	Trmt	9	0.056486	4.52	0.000
Block	4	0.07873	0.01968	1.32	0.265	Block	4	0.019684	1.58	0.197
Trmt*Block	36	0.39273	0.01091	0.73	0.868	Trmt*Block	36	0.010909	0.87	0.660
Repl(Block)	5	0.04142	0.00828	0.55	0.735	Repl(Block)	5	0.008284	0.66	0.653
Trmt*Repl(Block)	45	0.56196	0.01249	0.84	0.758					
Year	4	1.75933	0.43983	29.42	0.000					
Trmt*Year	36	1.20514	0.03348	2.24	0.000					
Block*Year	16	0.36697	0.02294	1.53	0.092					
Trmt*Block*Year	144	1.97479	0.01371	0.92	0.705					
Year*Repl(Block)	20	0.33004	0.01650	1.10	0.349					

Turnover

Source	df	SS	MS	F	P	F-test Numerator	df	MS	F	P
Trmt	9	0.887595	0.098622	11.45	0.000	Trmt	9	0.098622	5.06	0.000
Block	4	0.221295	0.055324	6.42	0.000	Block	4	0.055324	2.84	0.035
Trmt*Block	36	0.608910	0.016914	1.96	0.002	Trmt*Block	36	0.016914	0.87	0.668
Repl(Block)	5	0.040501	0.008100	0.94	0.456	Repl(Block)	5	0.008100	0.42	0.836
Trmt*Repl(Block)	45	0.877930	0.019510	2.27	0.000					
Year	4	1.205395	0.301349	34.99	0.000					
Trmt*Year	36	0.715019	0.019862	2.31	0.000					
Block*Year	16	0.326306	0.020394	2.37	0.003					
Trmt*Block*Year	144	1.422889	0.009881	1.15	0.191					
Year*Repl(Block)	20	0.277020	0.013851	1.61	0.055					

Medium plots (10 cm × 10 cm)

Appearance

Source	df	SS	MS	F	P	F-test Numerator	df	MS	F	P
Trmt	9	0.33173	0.03686	2.00	0.043	Trmt	9	0.03686	1.25	0.28
Block	4	0.16596	0.04149	2.26	0.066	Block	4	0.04149	1.41	0.245
Trmt*Block	36	0.70418	0.01956	1.06	0.388	Trmt*Block	36	0.01956	0.67	0.895
Repl(Block)	5	0.12962	0.02592	1.41	0.225	Repl(Block)	5	0.02592	0.88	0.501
Trmt*Repl(Block)	45	1.32218	0.02938	1.60	0.021					
Year	3	2.68524	0.89508	48.67	0.000					
Trmt*Year	27	1.02725	0.03805	2.07	0.004					
Block*Year	12	0.13755	0.01146	0.62	0.820					
Trmt*Block*Year	108	2.55655	0.02367	1.29	0.082					
Year*Repl(Block)	15	0.22325	0.01488	0.81	0.666					

Disappearance

Source	df	SS	MS	F	P	F-test Numerator	df	MS	F	P
Trmt	9	2.71705	0.30189	12.89	0.000	Trmt	9	0.30189	15.66	0.000
Block	4	0.19252	0.04813	2.06	0.090	Block	4	0.04813	2.50	0.056
Trmt*Block	36	0.55734	0.01548	0.66	0.925	Trmt*Block	36	0.01548	0.80	0.750
Repl(Block)	5	0.05738	0.01148	0.49	0.783	Repl(Block)	5	0.01148	0.60	0.704
Trmt*Repl(Block)	45	0.86751	0.01928	0.82	0.771					
Year	3	2.71711	0.90570	38.68	0.000					
Trmt*Year	27	2.19786	0.08140	3.48	0.000					
Block*Year	12	0.21592	0.01799	0.77	0.682					
Trmt*Block*Year	108	2.85207	0.02641	1.13	0.253					
Year*Repl(Block)	15	0.31512	0.02101	0.90	0.569					

App. 1, cont.

Source	df	SS	MS	F	P	F-test Numerator	df	MS	F	p
Turnover										
Trmt	9	1.76370	0.19597	15.37	0.000	Trmt	9	0.19597	7.94	0.000
Block	4	0.09153	0.02288	1.79	0.133	Block	4	0.02288	0.93	0.457
Trmt*Block	36	0.65879	0.01830	1.44	0.073	Trmt*Block	36	0.01830	0.74	0.822
Repl(Block)	5	0.12813	0.02563	2.01	0.081	Repl(Block)	5	0.02563	1.04	0.407
Trmt*Repl(Block)	45	1.11084	0.02469	1.94	0.002					
Year	3	0.06753	0.02251	1.77	0.157					
Trmt*Year	27	0.82291	0.03048	2.39	0.001					
Block*Year	12	0.15788	0.01316	1.03	0.424					
Trmt*Block*Year	108	1.65836	0.01536	1.20	0.152					
Year*Repl(Block)	15	0.21730	0.01449	1.14	0.331					

Small plots (2 cm × 2 cm)

Appearance

Source	df	SS	MS	F	P	F-test Numerator	df	MS	F	p
Trmt	9	0.137488	0.015276	2.46	0.013	Trmt	9	0.015276	2.79	0.011
Block	4	0.043372	0.010843	1.74	0.144	Block	4	0.010843	1.98	0.114
Trmt*Block	36	0.186139	0.005171	0.83	0.736	Trmt*Block	36	0.005171	0.94	0.567
Repl(Block)	5	0.037117	0.007423	1.19	0.316	Repl(Block)	5	0.007423	1.36	0.259
Trmt*Repl(Block)	45	0.246402	0.005476	0.88	0.683					
Year	3	2.286377	0.762126	122.54	0.000					
Trmt*Year	27	0.578287	0.021418	3.44	0.000					
Block*Year	12	0.225206	0.018767	3.02	0.001					
Trmt*Block*Year	108	0.615292	0.005697	0.92	0.681					
Year*Repl(Block)	15	0.041807	0.002787	0.45	0.961					

Disappearance

Source	df	SS	MS	F	P	F-test Numerator	df	MS	F	p
Trmt	9	1.486660	0.165184	28.37	0.000	Trmt	9	0.165184	32.67	0.000
Block	4	0.072664	0.018166	3.12	0.017	Block	4	0.018166	3.59	0.013
Trmt*Block	36	0.182153	0.005060	0.87	0.681	Trmt*Block	36	0.005060	1.00	0.495
Repl(Block)	5	0.027878	0.005576	0.96	0.446	Repl(Block)	5	0.005576	1.10	0.372
Trmt*Repl(Block)	45	0.227556	0.005057	0.87	0.702					
Year	3	2.097277	0.699092	120.05	0.000					
Trmt*Year	27	0.990277	0.036677	6.30	0.000					
Block*Year	12	0.099144	0.008262	1.42	0.165					
Trmt*Block*Year	108	0.581923	0.005388	0.93	0.662					
Year*Repl(Block)	15	0.092166	0.006144	1.06	0.404					

Turnover

Source	df	SS	MS	F	P	F-test Numerator	df	MS	F	p
Trmt	9	1.396791	0.155199	32.84	0.000	Trmt	9	0.155199	13.98	0.000
Block	4	0.034099	0.008525	1.80	0.132	Block	4	0.008525	0.77	0.552
Trmt*Block	36	0.353730	0.009826	2.08	0.001	Trmt*Block	36	0.009826	0.88	0.645
Repl(Block)	5	0.090166	0.018033	3.82	0.003	Repl(Block)	5	0.018033	1.62	0.173
Trmt*Repl(Block)	45	0.499681	0.011104	2.35	0.000					
Year	3	0.141693	0.047231	9.99	0.000					
Trmt*Year	27	0.504213	0.018675	3.95	0.000					
Block*Year	12	0.098672	0.008223	1.74	0.065					
Trmt*Block*Year		100.287540	0.002662	0.56	0.999					
Year*Repl(Block)		10.075095	0.005006	1.06	0.400					

Species mobility and frequency dynamics in a Swiss limestone grassland

Kathrin Studer-Ehrensberger & David M. Newbery[*]

Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland;
[*]Corresponding author; Tel. +41 316318815; Fax +41 316314942; E-mail david.newbery@ips.unibe.ch

Abstract

Community dynamics in a calcareous grassland (*Meso-brometum*) in Egerkingen (Jura mountains, Switzerland) were investigated for 53 non-woody species in 25 1-m^2 plots over 6 years. 50 0.01-m^2 subplots per plot were recorded. The derived variables were spatial frequency, temporal frequency, frequency fluctuation, turnover, and cumulative frequency (each species), and cumulative species richness (all species).

Spectra for 53 species of all variables were different for the two investigated spatial scales (0.01 m^2, 1 m^2). The comparison with other investigations of similar grasslands showed that the behaviour of some species is specific for this type of vegetation in general (e.g. *Achillea millefolium, Arrhenatherum elatius, Bromus erectus*), but most species behaved in a stand-specific way, i.e. they may play another (similar or completely different) role in another grassland stand. Six spatio-temporal patterns were defined across species.

To understand community dynamics, not only the dynamics of mobility but also of frequency fluctuations and spatial distribution of the species are fundamental. In addition, the understanding of temporal behaviour of all species present should be included. Averages always hide important information of vegetation dynamics, as was shown by the present investigation.

Keywords: Contingency; Frequency spectrum; *Meso-brometum*; Mobility behaviour; Mobility spectrum; Niche limitation; Species list; Species richness; Variance deficit; Vegetation dynamics.

Nomenclature: Binz & Heitz (1986).

Abbreviations: CF = Cumulative frequency; FF = Mean frequency fluctuation; SF = Spatial frequency; TF = Temporal frequency.

Introduction

In the last 20 years numerous studies of particular aspects of 'internal community dynamics' (Glenn-Lewin & van der Maarel 1992; van der Maarel 1996a) have been carried out, many of them in grassland vegetation. Species composition and species richness have been shown to be spatially variable and temporally highly dynamic in communities such as the tall-grass prairie of Kansas and Oklahoma, USA (Glenn & Collins 1993), in the meadows of the Krkonoše Mountains (Herben et al. 1993b) and subthermophilous meadows of South Moravia (Klimeš 1995). They are temporally rather stable, however, for instance alvar grassland vegetation on Öland (van der Maarel & Sykes 1993), Australian *Themeda triandra* grassland (Morgan 1998), limestone grassland in Limburg (The Netherlands) and wet grassland in North Carolina and Mississippi (Sykes et al. 1994). Spatial variability of species richness in a tall-grass prairie in southwestern Louisiana was related to environmental effects and not to plant abundance (Grace et al. 2000). A review of influences of ecological factors on species richness is given by Pausas & Austin (2001).

The observation of spatial and temporal variance of species richness other than the one expected from randomness, at scales between 0.01 m^2 and 10 m^2, has been the topic of numerous papers in the last decade (Palmer 1987, Gitay & Agnew 1989, Wilson et al. 1987, Watkins & Wilson 1992, Wilson et al. 1992, Zobel et al. 1993, Bycroft et al. 1993, Wilson & Roxburgh 1994). Variance excess (i.e. the ratio of observed to expected variance in species richness > 1 under a null model) results when the plots are environmentally heterogeneous (e.g. as reported from an abandoned and fertilized meadow by Klimeš et al. 1995), but variance deficit (ratio < 1) may have different causes (Wilson 1995).

A widely discussed cause for variance deficit is niche limitation. Due to niche limitation intense competition occurs and some species become excluded (Wilson et al. 1995a, b). This has, however, been questioned by van der Maarel et al. (1995) and Lepš (1995). Klimeš et al. (1995) did not investigate the variance deficits of all species of their community but those belonging to its internal structure, i.e. those of individual guilds. Since competition between species within one guild is likely to be higher than competition between species of different

guilds (van der Maarel 1988), variance deficit should be more easily detected within guilds. Klimeš et al. (1995) found no variance deficit in any guild for more than 2 out of 5 years, and over this period no significant variance deficits were detected in 0.09-m² subplots of the meadow studied. This is not too surprising perhaps since Gitay & Agnew (1989) had found that a variance deficit was not present in grasslands at scales > 0.005 m². Another reason for a variance deficit may be the limited number of co-existing individual plant modules that can be packed into the area of a plot. This has been tested by Klimeš (1995) who concluded that the limitation of individuals does not completely explain the observed species-richness pattern in his 5 cm × 5 cm subplots.

Quantitative composition of the vegetation also depends spatially on the distribution of environmental factors (Wondzell & Ludwig 1995; Zhang & Skarpe 1995), or temporally on fluctuations in the weather (Stampfli 1995; Stampfli & Zeiter 2004). However, Herben et al. (1993b) found that small-scale variation of species abundance did not correlate with variation at larger scales.

Variation in the spatial patterns of species in a plant community has been studied mainly in herbaceous grassland communities (Herben et al. 1990, 1993a; van der Maarel & Sykes 1993; Zhang & Skarpe 1995; Nordbakken 2000). A classification of distribution patterns of *Mesobromion* species has been proposed by Kammer (1997) and includes criteria of spatial and temporal pattern. Van der Maarel & Sykes (1993) described the small-scale dynamics of vegetation structure and proposed a 'carousel model' (see also van der Maarel 2005). The idea is that over several years, species move around a plant community, a process that enhances species coexistence. High species mobility in different grasslands from four geographically separated areas was found by Sykes et al. (1994). The hypothesis was not corroborated by Herben et al. (1994), however.

This paper presents an analysis of the vegetation dynamics of a central European grassland with the aim of relating small-scale spatial and temporal variability to the composition of the whole community. The central questions were: 1. How mobile are species in this grassland? 2. How important is species mobility in the present community? 3. What implications does a combination of dynamic variables have on the detection of the behaviour of single species and on the whole community?

Methods

Data collection

The study was carried out in a *Mesobrometum* grassland at the southern foot of the Jura mountains near Egerkingen in Switzerland (47°19'46" N, 7°48'29" E). Mean January, July and annual temperatures were 0.5, 18.9 and 9.7 °C,

respectively; annual precipitation averaged 1050 mm (data from MeteoSchweiz for the nearby station Buchs-Suhr, 1985-2005). The 1-ha grassland was surrounded by thermophilous *Fagus sylvatica* forest with *Carpinus betulus* and *Acer campestris*. As in the surrounding grassland, the vegetation was cut in early July and in September.

The area recorded was a square block of 25 1-m² plots separated by pathways of 1 m width. Each plot was divided into 100 0.01-m² subplots. Using a chess-board-type layout 50 subplots were selected for study. Each year at the start of the vegetation period (end March/early April) the vegetation in the plots was examined. Cover of all rooted species was estimated on the scale:
+ = rare; 1 = covering < 0.0025 m²; 2 = 0.0025 - 0.005 m²; 3 = 0.0050 - 0.0075 m²; 4 = 0075 - 0.01 m².

Fifty-three non-woody species were recorded from 1992 to 1997. Generic names will be used, except where a genus had more than one species and then the full names are given. Running species numbers, as presented in square parentheses in Table 1, correspond to the order along the x-axes of the relevant figures, unless otherwise stated.

The study was designed originally as a fertilization experiment. Treatments were found to be almost entirely insignificant ($P \gg 0.05$) as regards species frequency and mobility and the plots were accordingly pooled together as 25 replicates for the analyses in this paper.

Data analysis

Means of species richness were determined at the plot and subplot levels and evenness, calculated as the Shannon index based on plot or subplot frequencies were calculated for each year and for the whole period.

Spatial frequency (SF) of each species, at both plot and subplot levels, was found by counting the numbers of occupied plots, or subplots within plots, firstly across the 6-year period, and secondly for each year individually. Trends in frequency were determined by the significance of linear fits of frequency against time ($P < 0.05$). This led to the definition of three groups: (I) 'increasing', (II) 'fluctuating' (i.e. no significant trend), and (III) 'decreasing'. Temporal frequency (TF) was calculated for each species as the mean number of years that it was present in each plot or each subplot within a plot (maximum 6).

Fluctuation in frequency (FF) for each species was found as the sum of the absolute values of annual frequency differences:

$$FF = f_0 + \sum_{1992}^{1997} \left(f(t) - f(t-1) \right) \tag{1}$$

Gains (g), losses (l) and persistence (p) were respectively the sums of newly occupied, abandoned or continuously occupied subplots (maximum 50) in each plot/species/year. Annual and mean (1992-1997) numbers were expressed in an index of turnover (TO):

$$TO = \frac{(g+l)}{(g+l+p)} \qquad (2)$$

As this measure does not discriminate between g and l, species mobility *per se* was calculated in two ways: firstly, as cumulative species richness (*CSR*):

$$CSR = S_0 + \sum_{1992}^{1997} c(t) \qquad (3)$$

i.e. the number of species in the first year (S_0) plus the number of species newly entering plots and subplots in successive years $c(t)$. This measure takes no account of species identity, and it is not possible to differentiate between species that move around in the community and those that arrive from outside of the area. Secondly, cumulative frequency (*CF*) for each species was calculated as:

$$CF = f_0 + \sum_{1992}^{1997} cf(t) \qquad (3)$$

by adding the number of newly occupied plots or subplots (*cf*) in successive years to the frequency of the first year (f_0). This measure emphasizes spatial expansion into new plots (subplots), but does not take into account the fates of plots occupied earlier.

For each species and for each year the distribution over the 25 plots and subplots was mapped. Species were then qualitatively classified into six broadly-defined species distribution categories (SDP) based on composite visual assessment of spatial patterns, and SF and TF values. The use of statistical methods (i.e. measures of departure from spatial randomness) was prevented because neither plots nor subplots were spatially independent or placed at random: the plots formed a block and the subplots were in a regular grid within each plot. Modelling of spatial autocorrelation was beyond the scope of the present work. The time span of 6-yr was too short for time-series analysis.

Table 1. Classification of 53 species at Egerkingen in the 25 1-m² plots according to the similarity in their distributional patterns (SDP): 1 = regularly distributed species with high frequencies; 2 = irregularly distributed species (also temporarily) with high frequencies; 3 = regularly distributed species with low frequencies; 4 = irregularly distributed species with low frequencies; 5 = spatially and temporally rare species; 6 = spatially rare and temporally stable species. Within each group the species are divided into species with increasing (I), fluctuating (II) and decreasing (III) frequencies. Running species numbers are added in brackets.

| SDP | Species distribution patterns | | |
	I	II	III
1	Arrhenatherum elatius [1]	Avenula pubescens [4]	Bromus erectus [6]
	Carex caryopyllea [2]	Trisetum flavescens [5]	Clinopodium vulgare [7]
	Galium mollugo [3]		Dactylis glomerata [8]
		Leucanthemum vulgare [9]	
		Poa angustifolia [10]	
		Ranunculus bulbosus [11]	
		Salvia pratensis [12]	
2	Coronilla varia [13]		Cerastium holosteoides [15]
	Veronica chamaedrys [14]		Medicago lupulina[1] [16]
		Thlaspi perfoliatum [17]	
		Veronica arvensis [18]	
3	Knautia arvensis [19]	Holcus lanatus [21]	Anthoxanthum odoratum [23]
	Rumex acetosa [20]	Sanguisorba minor [22]	Arabis hirsuta [24]
		Myosotis arvensis [25]	
4	Glechoma hederacea [26]	Plantago lanceolata [28]	Achillea millefolium [31]
	Vicia sativa [27]	Scabiosa columbaria [29]	Anthyllis vulneraria [32]
		Viola hirta [30]	Centaurea jacea [33]
		Daucus carota[2] [34]	
		Festuca pratensis[2] [35]	
		Valerianella locusta[3] [36]	
5	Ajuga reptans [37]	Carex flacca [40]	
	Poa trivialis [38]	Carex ornithopoda [41]	
	Trifolium repens [39]	Hypericum perforatum [42]	
		Leontodon hispidus [43]	
		Linum cartharticum [44]	
		Sedum sexangulare [45]	
		Trifolium pratense [46]	
6	Plantago media [47]	Lotus corniculatus [49]	Prunella vulgaris [53]
	Luzula campestris [48]	Silene vulgaris [50]	
		Thymus serpyllum [51]	
		Primula veris [52]	

1. Spatially ± regular; 2. Transition to 5; 3. Temporarily irregular.
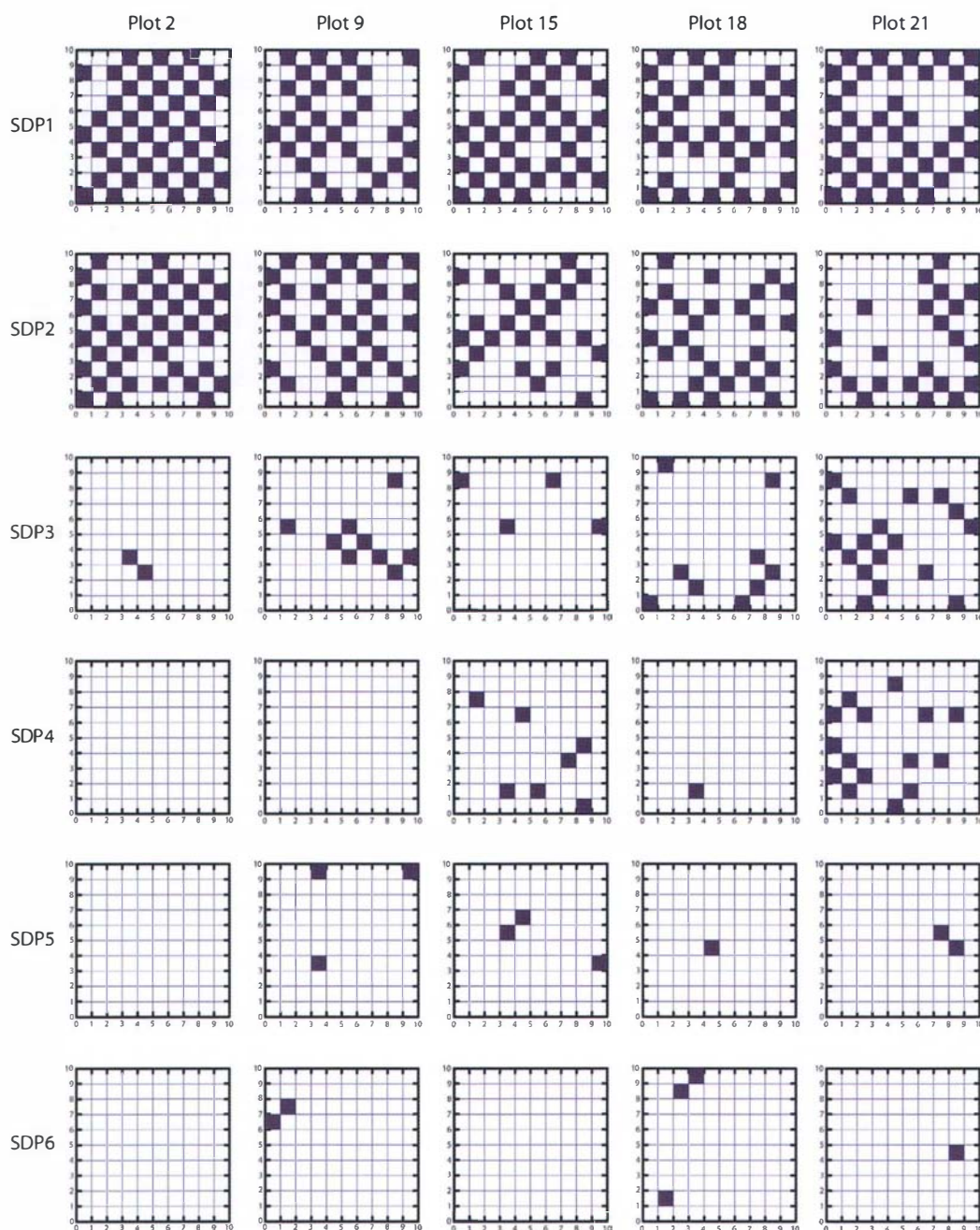
Fig. 1. Spatial variability in species' distribution pattern (SDP) of the six distribution types in five plots of the *Mesobrometum* in 1992. Example species for SDP1: *Arrhenatherum elatius*, SDP2: *Veronica arvensis*, SDP3: *Arabis hirsuta*, SDP4: *Centaurea jacea*, SDP5: *Trifolium pratense*, SDP6: *Lotus corniculatus*.

Results

Distribution of the species

The species distribution patterns of the *Mesobrometum* at Egerkingen as characterized in groups SDP1 to 6, are shown in Table 1. Group 1 contained the species with both high spatial and temporal frequencies (Table 2). Group 2 was heterogeneous: spatial frequency was high in subplots, low to medium in plots, variability of spatial frequency between plots was higher than in group 1 (Fig. 1), and temporal frequency was medium in subplots and plots. In group 3 both spatial and temporal frequency was medium, while the variability of the spatial frequency between the

Table 2. Mean and standard error (SE) of dynamic variables for six species distribution groups (SDP) in the *Mesobrometum* at 0.01m² and 1m². a. SF = Spatial frequency; TF = Temporal frequency; FF = Frequency fluctuation; TO = Turnover; CF = Cumulative frequency; b. P = Persistence; G = Gains, L = losses; CH = changes (G+L) in absolute values.

a.

	SF				TF				FF				TO				CF			
	0.01 m²		1 m²		0.01 m²		1 m²		0.01 m²		1 m²		0.01 m²		1 m²		0.01 m²		1 m²	
SDP	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1	451.9	64.4	24.8	0.1	2.7	0.2	6.0	0.0	437.1	71.9	26.2	0.4	0.6	0.0	0.0	0.0	47.9	4.0	0.0	0.0
2	239.9	52.1	19.7	1.9	1.7	0.2	4.8	0.4	252.8	108.5	40.5	6.2	0.8	0.0	0.3	0.1	43.0	11.0	11.4	8.2
3	122.3	11.6	21.9	0.5	1.6	0.1	5.2	0.1	92.7	22.4	35.0	2.2	0.8	0.0	0.2	0.0	68.8	2.9	8.0	2.1
4	39.2	4.0	12.0	1.2	1.4	0.1	3.5	0.2	31.2	5.0	28.6	3.7	0.8	0.0	0.4	0.1	68.2	3.5	33.8	6.1
5	6.4	2.1	3.4	1.0	1.0	0.0	1.7	0.2	8.9	3.0	12.5	3.1	1.0	0.0	0.8	0.1	86.3	3.5	76.9	6.5
6	14.3	3.4	6.4	1.3	1.7	0.2	3.0	0.3	17.3	4.5	17.0	3.6	0.7	0.0	0.5	0.1	68.2	4.1	47.1	8.2

b.

	P				G				L				CH			
	0.01 m²		1 m²		0.01 m²		1 m²		0.01 m²		1 m²		0.01 m²		1 m²	
SDP	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1	285.0	58.5	24.5	0.2	156.5	12.1	0.2	0.1	169.6	13.8	0.2	0.1	1630.5	109.4	2.0	0.8
2	86.2	24.7	17.0	2.4	110.6	28.1	2.3	0.6	151.2	36.2	2.8	0.9	1308.8	272.6	25.2	6.0
3	45.3	8.9	20.2	0.8	73.8	5.4	1.5	0.2	83.0	8.4	2.2	0.5	784.0	59.0	18.4	3.3
4	11.7	2.3	9.1	1.1	25.4	2.9	2.6	0.4	29.1	3.6	3.2	0.4	272.6	30.8	29.1	3.5
5	0.4	0.2	1.3	0.5	6.2	2.0	2.4	0.5	5.4	1.8	2.1	0.5	58.0	18.6	22.3	4.9
6	5.1	1.3	3.8	0.9	8.7	2.4	2.4	0.5	8.7	2.9	2.4	0.7	86.9	25.6	24.3	6.0
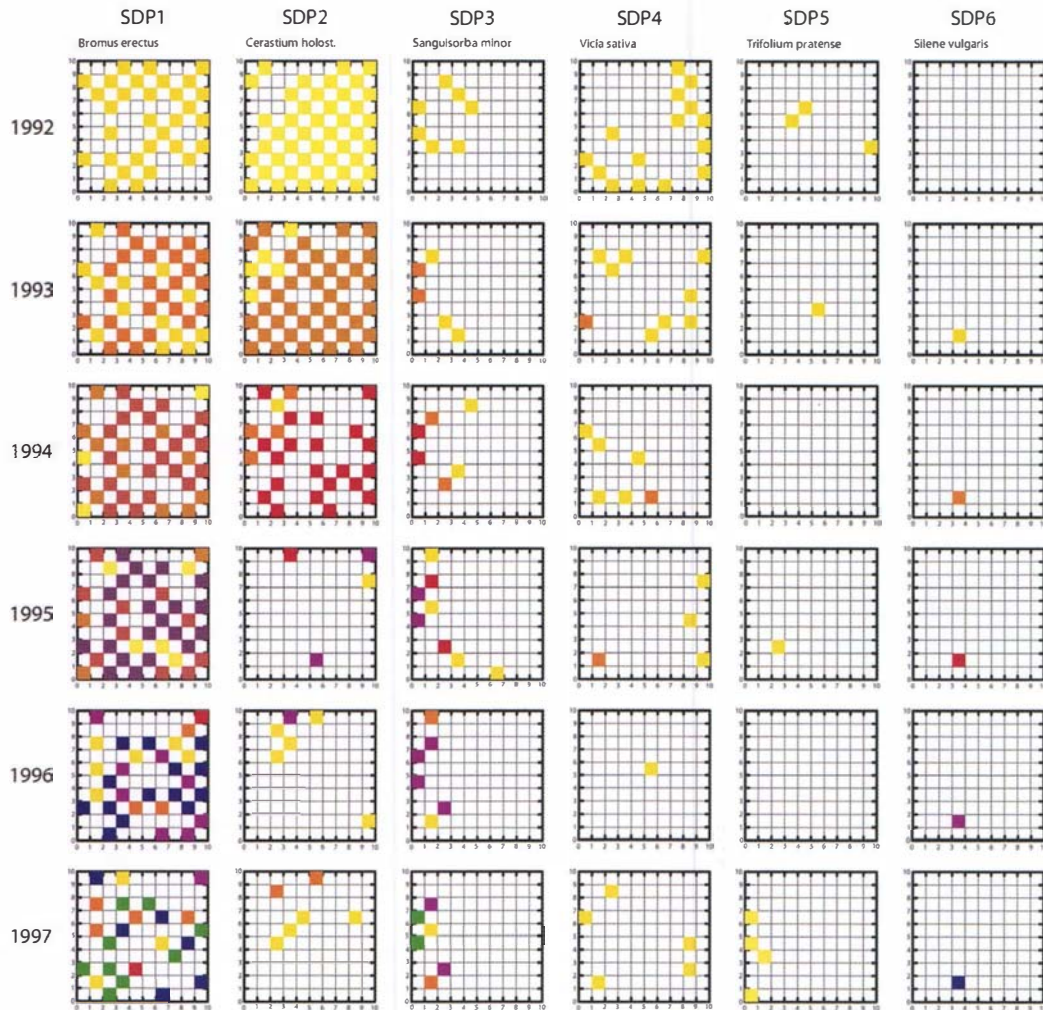
Fig. 2. Temporal variation of species' distribution patterns (SDP) from 1992 to 1997 in plot 15, with *Bromus erectus* (SDP1), *Cerastium holosteoides* (SDP2), *Sanguisorba minor* (SDP3), *Vicia sativa* (SDP4), *Trifolium pratense* (SDP5) and *Silene vulgaris* (SDP6). Yellow: 1 year in the same subplot; orange: 2 years in the same subplot; red: 3 years; violet: 4 years; blue: 5 years; green: 6 years in the same subplot.

a)

b)
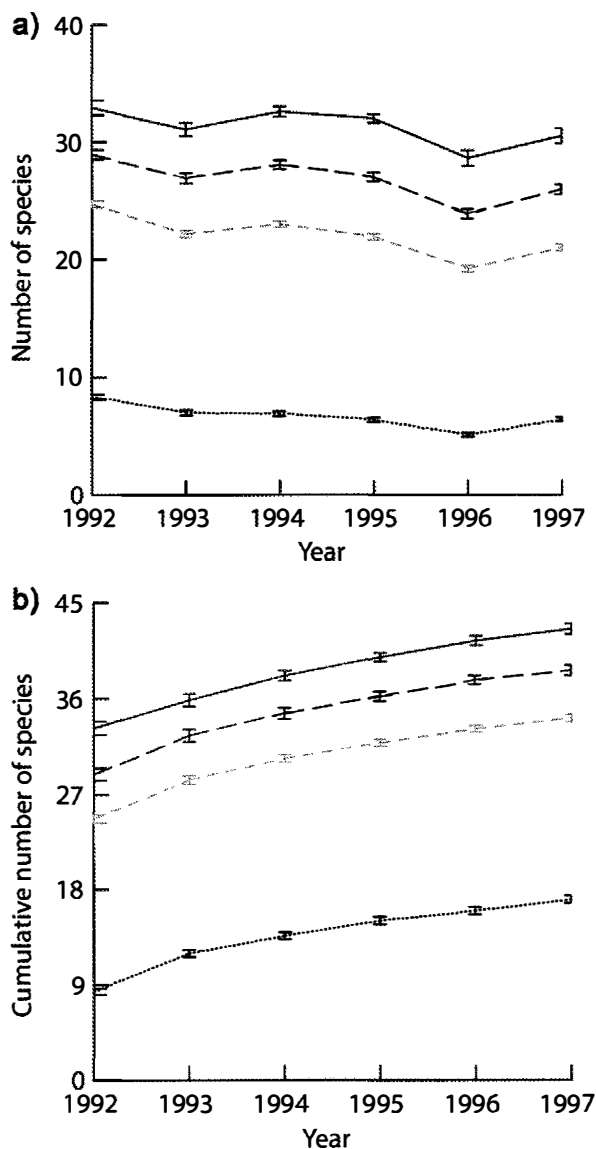
Fig. 3. (a) Mean species richness (± SE); (b) Cumulative species richness in the *Mesobrometum* at Egerkingen 1992-1997 at the scales 0.01 m² (dotted, *n* = 50); 0.25 m² (narrowly broken line, *n* = 100); 0.5 m² (broken line, *n* = 50), and 1 m² (uninterrupted line, *n* = 25).

plots was low. The species of groups 4 to 6 were distributed irregularly in the plots. Spatial and temporal frequencies of group 4 were higher than those in group 5. Many species of group 4 occupied many of the subplots in some of the plots. Species of group 5 were rarely found in the same subplots during two consecutive years, with the exception of *Trifolium pratense*, which may have persisted for 2 years, and *Trifolium repens*, which exceptionally stayed for 5 years in a subplot in plot 15. The species of group 6 occurred in a few subplots in some of the plots and showed a relatively high temporal frequency (3 - 5 years; Fig. 2).

Species numbers and evenness

Mean numbers of species (± 1 SE) in plot sizes of 1, 0.5, 0.25 and 0.01 m² were 31.3 (± 0.6), 26.8 (± 0.5), 22.0 (± 0.5) and 6.7 (± 0.3), respectively. In the smallest plots (0.01 m²), significant differences of species numbers from year to year were most frequent (Fig. 3a). Mean frequency fluctuation FF of the species numbers was 2.6 ± 0.4 species/year for a plot, or 2.0 ± 0.2 species/year for a subplot, between 1992 and 1997.

Cumulative species numbers of the different plot/ subplot series are given in Fig. 3b. They increased from 33.2 to 42.6 in 1-m² plots and from 8.4 to 17.0 in 0.01-m² subplots over 6 years, meaning increases of 28% and 102% respectively. Species accumulation at the 0.01-m² scale did not correlate with the cumulative species number at 1-m² (*r* < 0.001, df = 23, *P* = 0.97).

Evenness was smaller in 0.01-m² subplots (*E* = 0.82) than in 1-m² plots (*E* = 0.95; Fig. 4). Plot sizes of 0.25 m² and 0.5 m² had intermediate frequency distributions and values of evenness (not shown). In the 1-m² plots, ca. 25% of the species were present in 24 - 25 plots (Fig. 4). Nearly 50% of the species were present in less than half of the plots.

Spatial species frequencies over time

Spatial variability of frequency between plots was smallest for *Arrhenatherum*, followed by *Bromus*, *Dactylis*, *Poa angustifolia* and *Medicago* (Table 1). *Achillea*, *Carex flacca*, *Luzula*, *Sedum* and *Silene* showed the most patchy distribution patterns between the investigated plots. The species of group 1 were most regularly dispersed in the plots, whereas those of groups 5 and 6 tended to have patchy distributions. Exceptions existed for all groups (Table 1). Fig. 5 gives the species composition and a spectrum of their relative quantities in the grassland over the 6 years.

The frequency fluctuation varied much amongst the species. In terms of the rank order of species, the most frequent species on the 0.01-m² subplot level from the beginning changed completely in the following 5 years: the first three species of 1992 (1) *Bromus*, (2) *Arrhenatherum*, and (3) *Medicago*, changed rank. *Arrhenatherum* became the most frequent, followed by *Galium* (15 in 1992) and *Veronica arvensis* (4 in 1992). *Bromus* dropped three places (to 4) and *Medicago* was in 21 in 1997. At the plot level the changes were less pronounced (Fig. 5).

The annual changes of the species' abundances showed trends during the investigation period of 6 years. The frequencies of 14 species increased significantly, 21 species decreased in frequency whereas 18 species fluctuated (Table 1).

The degree of frequency fluctuation between 1992 and 1997 of each species was specific. Overall, values of FF at the 0.01-m² scale were least for the group of fluctuating species. The increasing species had smaller FF-values than the decreasing ones (Fig. 6a). At the 1-m² plot scale,
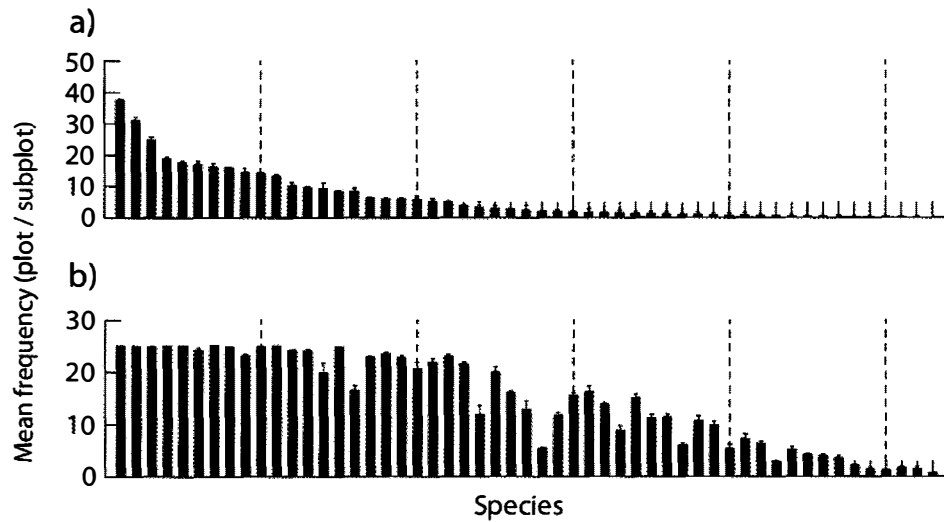
Fig. 4. Mean frequency (± SE, *n* = 6) of 53 species in the *Mesobrometum* during 1992-1997 at (a) 0.01 m², and (b) 1 m². Species sequence: 1, 6, 10, 12, 7, 18, 3, 5, 15, 2 (l) 8, 11, 9, 16, 4, 13, 20, 19, 14, 23, (l), 24, 22, 21, 17, 25, 33, 32, 31, 27, 29, (l) 34, 30, 26, 28, 53, 52, 36, 35, 46, 39 (l) 38, 49, 48, 47, 51, 50, 43, 42, 44, 40, (l) 41, 37, 45. For species names see Table 1.
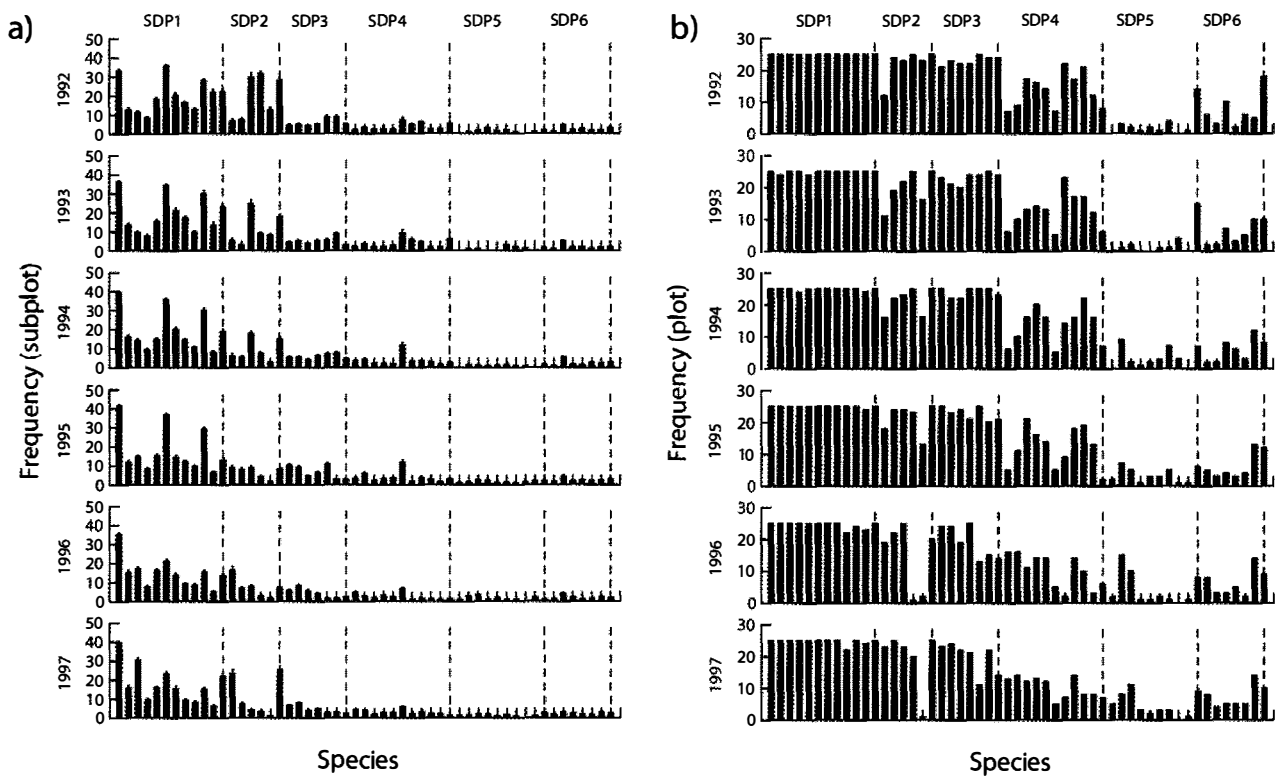
Fig. 5. Development of annual spatial frequency of 53 species in six distribution classes (SDP1 to SDP6) in the Mesobrometum at (a) 0.01 m² (± SE, *n* = 50), and (b) 1 m² (*n* = 25). Species sequence 1 - 53: see Table 1 for names.
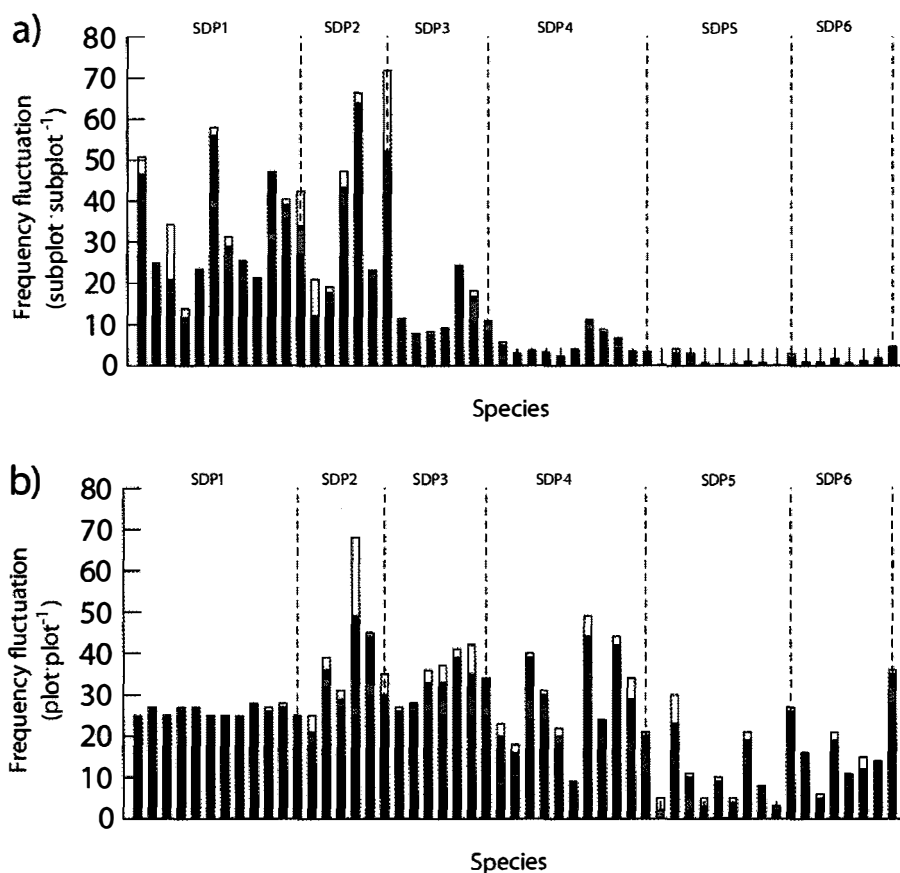
Fig. 6. Frequency fluctuations (absolute amount of annual difference in frequencies) of 53 species in six distribution categories (SDP1 to SDP6) in the *Mesobrometum* during 1992-1997 at (a) 0.01 m^2, and (b) 1 m^2. Black: frequency in 1992, dark grey: fluctuation between 1992/1993, hatched: fluctuation 1993/94, grey: fluctuation 1994/95, hatched: fluctuation 1995/96, and white: net fluctuation 1996/97. Species sequence 1-53; see Table 1 for names.
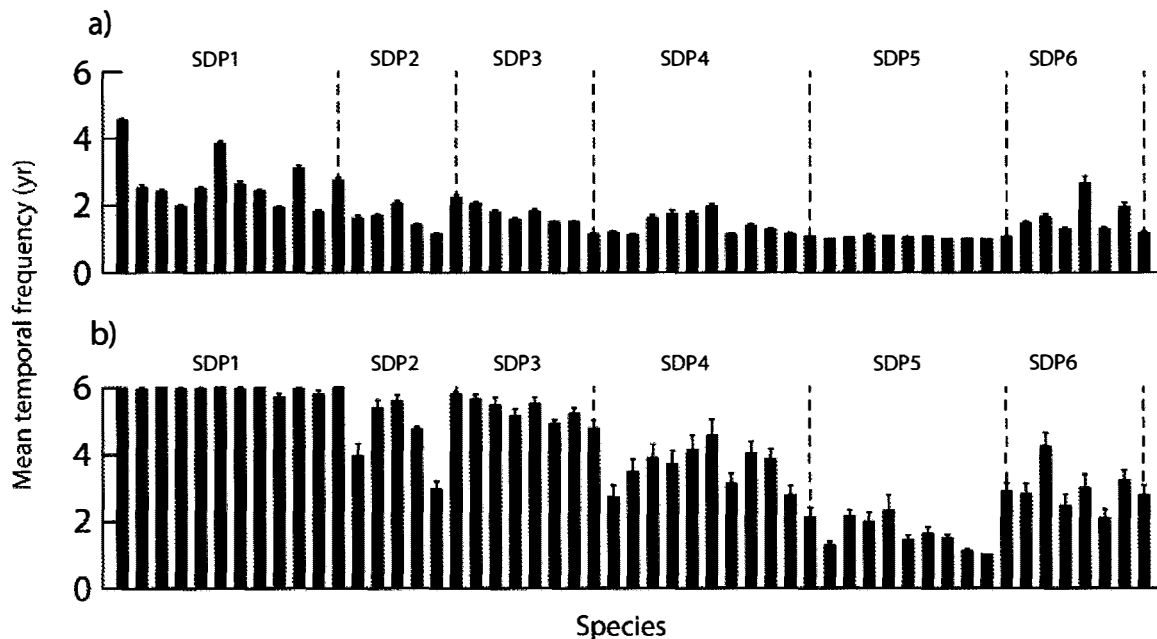
Fig. 7. Mean temporal frequency ($\pm$ SE, $n = 6$) of 53 species of six species' distribution categories (SDP1 to SDP6) in the *Mesobrometum* at (a) 0.01 m^2, and (b) 1 m^2. Species sequence 1-53; see Table 1 for names.

values of FF were almost zero for group 1 but very high for *Medicago* (Fig. 6b).

Temporal frequency of species

For the entire investigated area (25 m^2), all species, except for five rare ones, had TF-values of 100%. The rare species *Ajuga reptans* and *Linum catharticum* were present during 3 of the 6 years, *Sedum* in 4 and *Carex flacca* and *C. ornithopoda* in 5 years. In the *Mesobrometum* at Egerkingen the temporal frequency of the species was higher at the 1-m^2 than at the 0.01-m^2 scale (Fig. 7). Some species had high TF-values in the plots but, on average, they stayed for only 1 year in the subplots (*Anthyllis, Thlaspi, Valerianella*). The others showed means of 2 - 3 years at the subplot level (*Achillea, Silene*).

The six distribution categories showed different spectra of TF-values (Fig. 8). The life-spans of the species of group

1 (long) and those of groups 3 to 5 (short) were contrasting. The species of group 2 were frequent but rather short-lived and SDP6 contained rare species with high numbers of long-lived individuals in their populations.

Persistence, gains and losses

Mean persistence (± SE) for all species was 12.8 ± 1.4 subplots per plot and year, whereas the values for gains and losses were 1.8 ± 0.3 and 2.0 ± 0.4, respectively. Highly frequent species persisted in the subplots and showed gains and losses with high annual variability (e.g. *Galium* and *Medicago*). Rare species added little to the changes in the community. At the 0.01-m^2 scale, two species increased in persistence during the investigated period: *Galium* and *Coronilla*, both perennials (Fig. 9a). Several species were losing persistence at the 0.01-m^2 scale: *Thlaspi* after 1993, *Anthoxanthum* after 1994, *Medicago* after 1995,
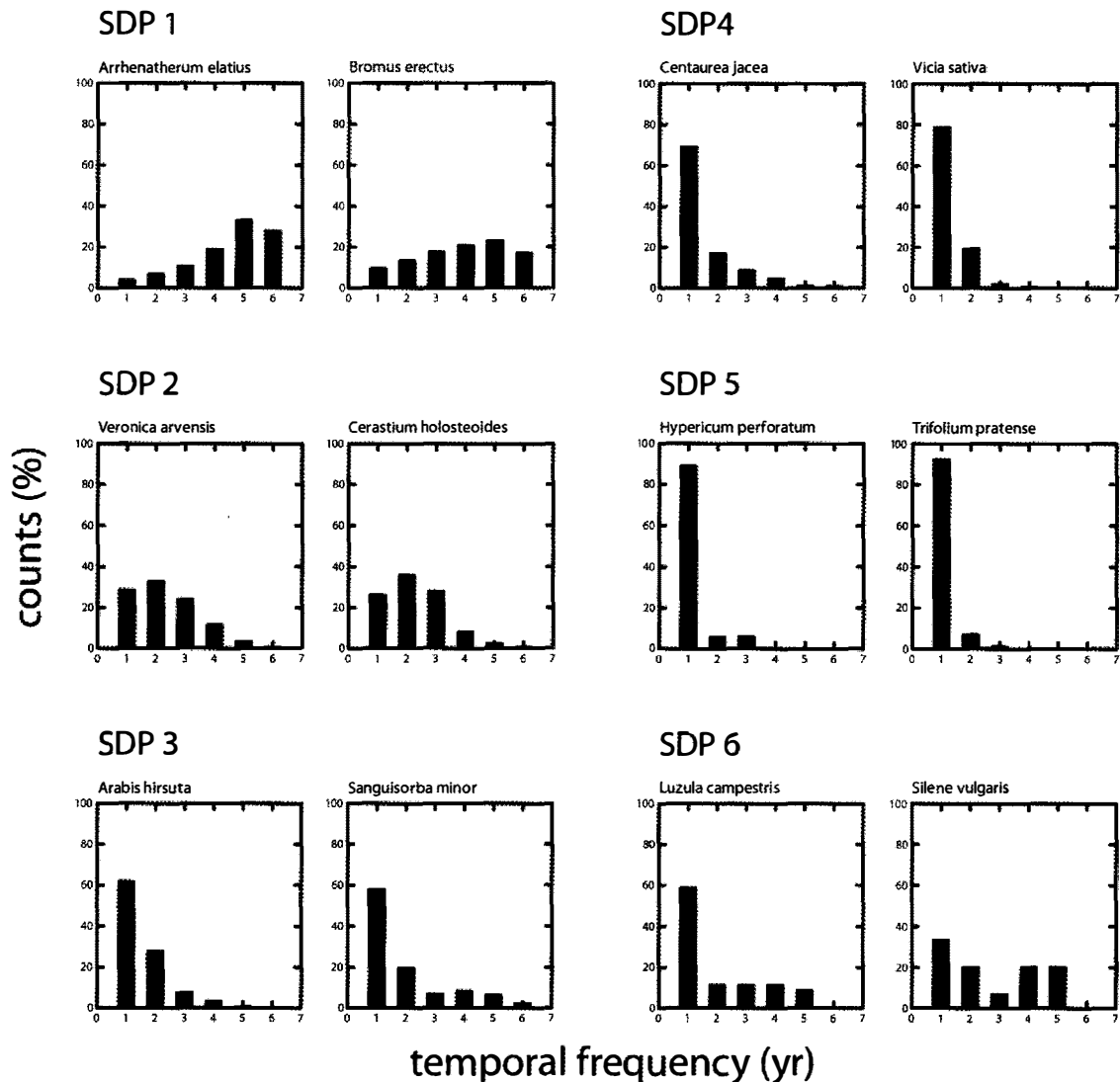
Fig. 8. Spectra of temporal frequencies at the subplot level in the six species distribution categories (SDP1 to SDP6). Two species of each group are given as an example.
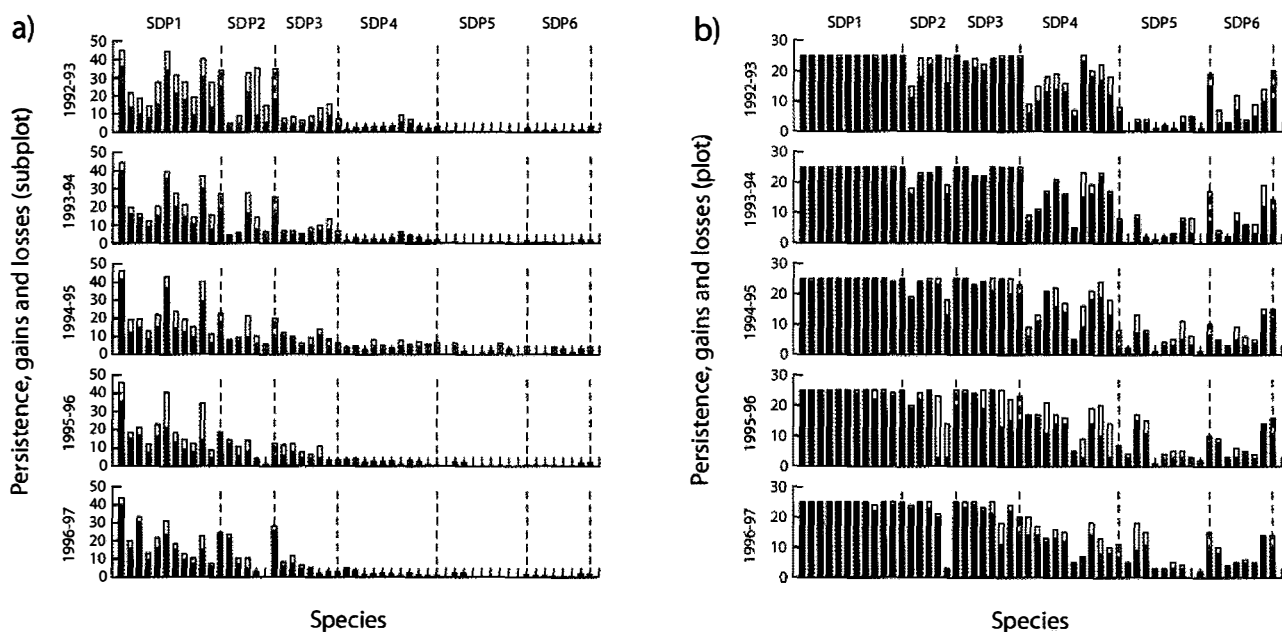
Fig. 9. Mean annual variation of persistence and changes of 53 species of six distribution categories (SDP1 to SDP6) at (a) 0.01 m² and (b) 1 m². Black: persistence, grey: gains, white: losses. Species sequence 1-53; see Table 1 for names.

and also some less frequent ones. The number of subplots in which *Bromus* persisted decreased by 50% during the 6-year study. Persistence of *Bromus* was minimal between 1996 and 1997. *Medicago* had no persistence after 1995 (Fig. 10).

At the plot level, several decreasing species had 100% persistence (Fig. 9b), despite their considerable thinning in the plots: *Bromus*, *Dactylis* and *Salvia* and for all years. *Achillea* (irregularly distributed with low frequencies, group 4) had unchanged persistence for all 6 years, *Prunella* likewise after 1994. Very dynamic species at this scale were *Medicago* and *Thlaspi* (Fig. 9b).

Species turnover

Mean species turnover TO in the subplots during the 6 years of investigation was high (> 66%) for 40 species, medium (< 66%, > 33%) for 12 species, and low (< 33%) for just one species (*Arrhenatherum* [6]; Fig. 11a). Species with low values of TO prevailed in the plots: 9 : 15 : 29 (Fig. 11b). Annual variability of TO was low: TO-values for group 1 were minimal.

Cumulative frequency

Species mobility was spatially restricted. If a species had reached all available positions in the community, CF was maximal and could not increase further (Fig. 12; e.g. *Cerastium* in plot 15 after 1996). All 50 subplots of one single plot had been visited by *Bromus, Cerastium, Poa angustifolia* in

1993, *Arrhenatherum* in 1994, *Veronica arvensis* in 1995, and *Clinopodium* and *Salvia* in 1997. No species reached all possible subplots: the three most frequent and mobile species *Arrhenatherum*, *Bromus* and *Poa angustifolia* reached 1242, 1214 and 1176 out of the 1250 subplots, respectively. The highest increases in CF occurred for (1) *Galium* (plus 707 subplots), (2) *Coronilla* (562 subplots; 13 plots), and (3) *Trisetum* (487 subplots).

With a mean increase of 4.7 subplots, *Galium* showed the highest annual rate of increase of CF. *Coronilla* followed with 3.7 subplots and 2.2 plots at the 1-m² scale. *Poa angustifolia* (3.2 subplots/year) was faster than *Arrhenatherum* (2.7) and *Bromus* (2.1). Some less frequent species such as *Primula* (plus 74 subplots and 16 plots) and *Poa trivialis* (77; 17) had high increases also at the plot level, and were, together with *Trifolium repens* (71; 15), most efficient in gaining new space at medium distances (Fig. 13a). The CF of *Achillea* increased only at the subplot level (67; 0).

It took 6 years at the most for all the plots to be visited by species from groups 1, 2 and 3. The species of the other groups would probably need several years to some decades (e.g. *Achillea* and *Luzula*, to reach all plots (Fig. 13b). At the subplot level the estimated time could be 15 years for the species of group 1, increasing for groups 2 - 6 to perhaps 20, 30, 60, 60-80 to 120 years respectively (Fig. 13a).
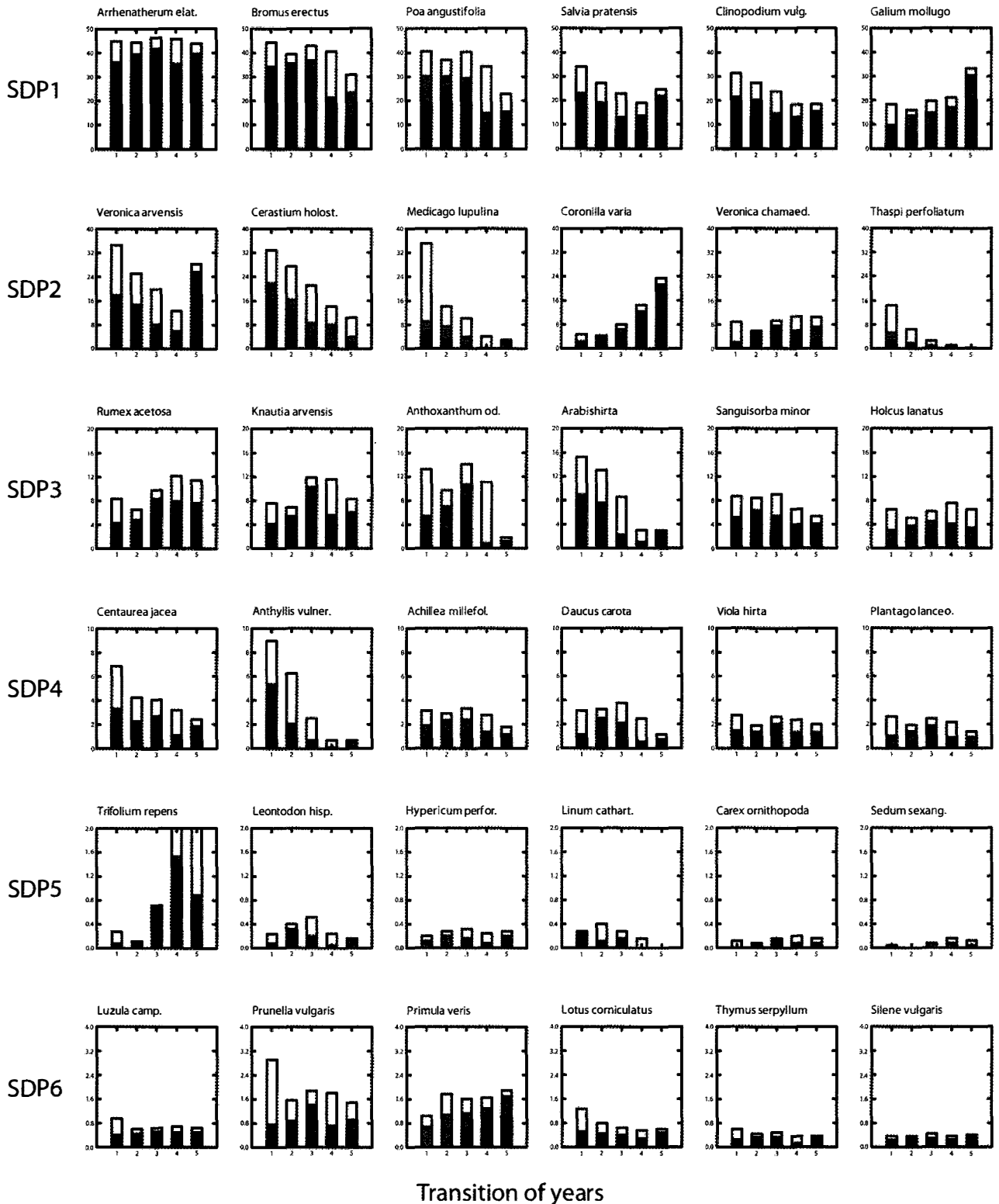
Fig. 10. Annual variation of persistences (black), gains (grey) and losses (white) in the six species' distribution categories (SDP1 to SDP6) at 0.01 m² between 1992 and 1997.
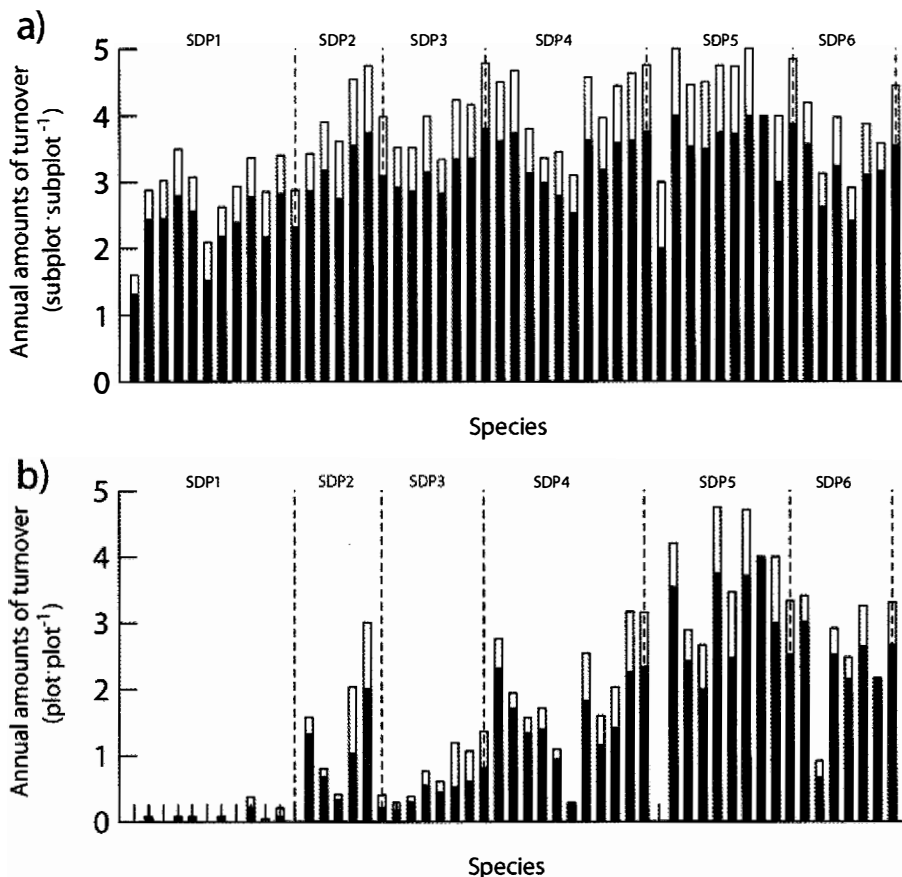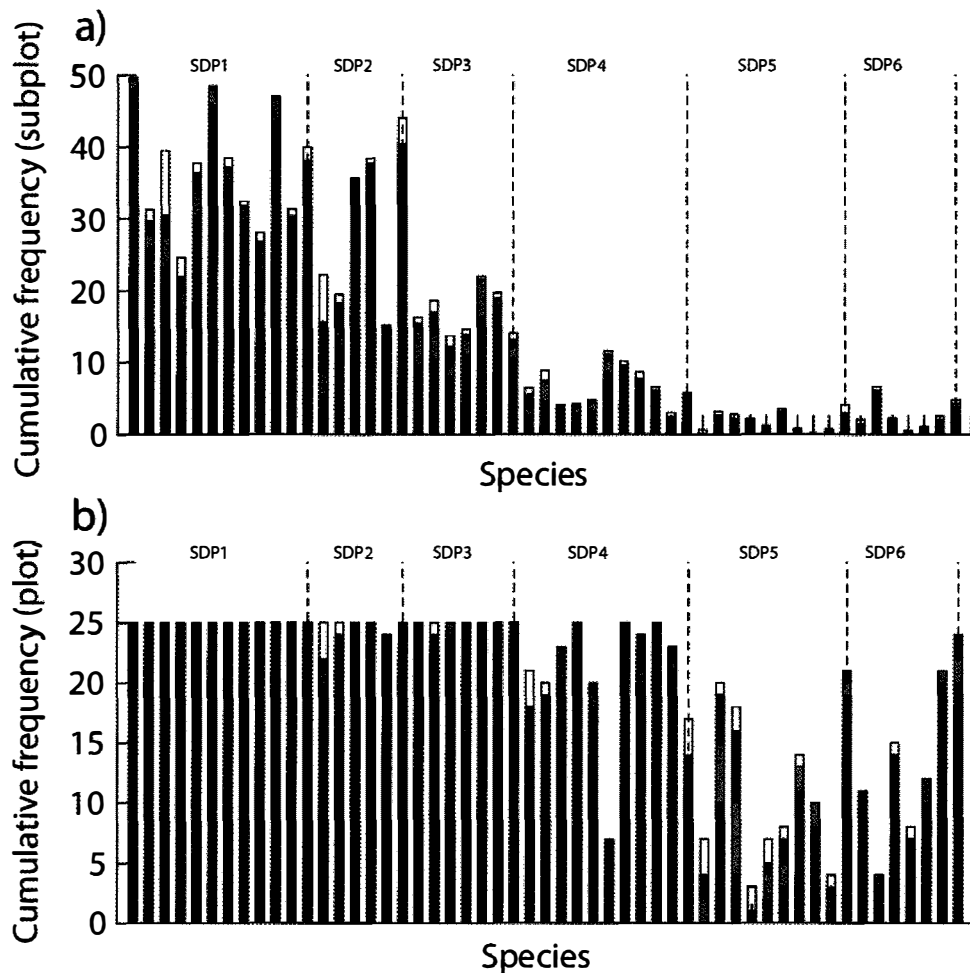
Fig. 11. Mean annual amounts of turnover of 53 species of six distribution patterns (SDP1 to SDP6) in the *Mesobrometum* at (a) 0.01 m² and (b) 1 m². Maximal annual turnover is 1. black: turnover between 1992 and 1993, hatched: TO (1993/1994), grey: TO (1994/1995), hatched: TO (1995/ 1996), and white: TO (1996/1997). Species sequence 1-53; see Table 1 for names.

Discussion

Spatio-temporal species distribution maps

All of the species present behaved individually in the *Mesobrometum* plots. Nevertheless, spatial and temporal arrangements occurred which were similar for several species. The annual distribution maps of all 53 species in the 25 investigated plots were classified in six species distribution categories (Tables 1 and 2). Round 90% of the species were easily added to one of the 6 SDPs because of their SF (Fig. 1) or temporal appearances (Figs. 2 and 12). For the rest of the species a compromise had to be found. *Leucantheumum* (group 1), for instance, had low SF (0.01-m² scale) and TF values. However, FF was too small to add it to group 2. *Thlaspi*, an irregularly occurring species, had low SF for group 2, but was too frequent for group 4. In group 4, *Achillea* behaved completely individually, because this species had high TF, no accumulation (CF) in the plots, low TO and low FF. *Valerianella* could also have been classified in group 5, but would be equally conspicuous there. Due to its exceptionally high abundance

at specific plots and times, it was classified in group 4.

The spectrum of spatio-temporal distribution categories depends on the individual combination of the ecological factors of the community under study (see '*species classifications based on distribution patterns*'), and gives a method to compare the community dynamics in different communities. It is an abstraction of the real vegetation dynamics. These dynamics can not be described by a single variable such as SF, TF, persistence, gains and losses, TO, CSR or CF and not even by a combination of several of them, but have to be read from the distribution maps. The success of a considerable number of species coexisting in the *Mesobrometum* at Egerkingen is not due to its precise fit to any of the SPDs, but rather to the many-fold possibilities of the species to react differently.

Each of the above variables, that are frequently used to describe vegetation dynamics in a community, has limited possibilities of providing a full reflection of each species' dynamics, as will be shown in the following paragraphs.
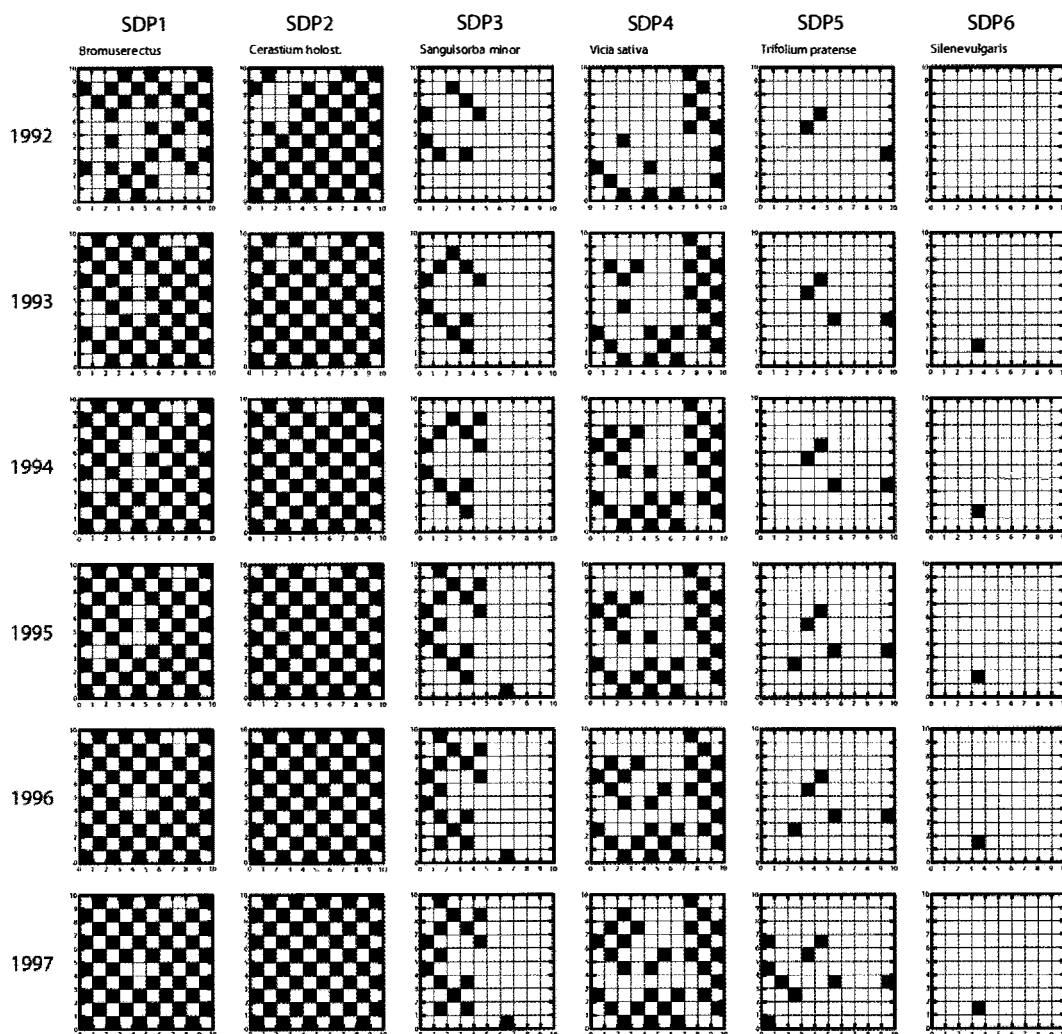
Fig. 12. Cumulative frequency of species' distribution patterns (SDP) between 1992 and 1997 in plot 15. SDP1: *Bromus erectus*, SDP2: *Cerastium holosteoides*, SDP3: *Sanguisorba minor*, SDP4: *Vicia sativa*, SDP5: *Trifolium pratense*, and SDP6: *Silene vulgaris*.

Species' dynamics variables

Spatial frequency and frequency fluctuation

Spatial frequency SF is a coarse measurement of a species' relative occupancy of space. SF is a relative measure, and no information about the location of the individuals in the community is involved. Spatial variability of SF is species-specific. Furthermore, SF at one scale is not derivable from that at another scale.

Frequency fluctuation FF is a net value, which is not related to space. It remains unclear whether decreases in the fluctuation occur because (a) individuals just disappear and the population does not rejuvenate, or (b) individuals disappear and rejuvenation continues. The biological consequences of these two situations are completely different. Even when FF is zero, all individuals can change position, i.e. vegetation dynamics remain undetected.

Between 1992 and 1997, net FF (i.e. the absolute difference between the number of subplots from which a species emigrates and the ones into which it immigrates) of *Salvia* (with a decreasing frequency), *Viola* (fluctuating frequency) and *Veronica chamaedrys* (increasing frequency) was ca. 1 % of the absolute FF (sum of changes, i.e. (gains + absolute values of losses; Table 2). Therefore, in this period, the quantities of the three species fluctuated 100 times more than indicated by FF (Fig. 6). They had high ephemeral presence. For *Veronica arvensis* the given FF was 5.5% of the absolute FF. In contrast, FF of the small *Cerastium*, *Medicago* and *Thlaspi* (all with decreasing frequency, and the last two being monocarpic) as well as the clonally spreading *Coronilla*, *Galium* and *Ajuga* (all increasing frequency; Table 2) corresponded to the absolute FF during the 6 years of investigation. The other species showed intermediate patterns of behaviour.

Fig. 13. Mean annual increase of cumulative frequency of 53 species of six distribution patterns (SDP1 to SDP6) in the *Mesobrometum* at (a) 0.01 m², and (b) 1 m². Black: frequency in 1992, dark grey: increase of cumulative frequency 1992/1993, hatched: 1993/94, grey: 1994/95, hatched: 1995/96, white: 1996/97. Species sequence 1-53; see Table 1 for names.

Temporal frequency of species

The duration of the continuous survival of a species in the vegetation is indicated by the temporal frequency TF of a species. This value does not give the exact life-span of an individual. It depends on the size of the investigated plot. In a larger plot TF may be substantially higher (e.g. *Avenula*: 6 years at the plot, 2 years at the subplot scale). A species population in a vegetation patch has a spectrum of TF-values (Fig. 8). *Arrhenatherum* and *Bromus* had the highest TF-values of all the species. The conclusion that TF corresponded to the effective life expectancy of a species can only be demonstrated by experiments of a population's biological nature.

Species turnover and persistence

Species turnover TO is a relative measure of change in a vegetation patch. It is complete if all individuals of a species have changed positions in a plot. TO does not

increase with the number of changed positions. It does not make any difference whether there are gains or losses. If all the occupied places are abandoned in a subsequent year or all (empty) subplots become colonised, TO is maximal.

Thus, the vegetation is completely restructured. Persistence reduces TO. Only *Bromus* and *Arrhenatherum* remained in more plots than they colonised. In relation to persistence, the proportions of gains and losses were lowest for these species: 25% gains, 20% losses for *Arrhenatherum*, 30% gains and 40% losses for *Bromus* (Table 2). Interestingly, the polycarpic species *Ajuga*, *Leontodon*, *Sedum*, and also partly *Glechoma* with its long runners, *Festuca pratensis*, *Trifolium pratense*, *Poa trivialis* and *Carex ornithopoda* behaved in the same way as real therophytes, notably *Thlaspi*, *Vicia*, *Valerianella*, *Linum*, *Myosotis*, and partly *Medicago* and *Anthyllis*. The former were not as vital and competitively successful in the present community as the two perennial grass species.

Turnover was minimal for *Arrhenatherum* (< 30%),

for *Bromus* up to 40%. The species of the SDP1 group (*Avenula* with 70%), but also *Achillea* (SDP group 4) and *Silene* in group 6, showed similar values (≤ 60%). Species of group 5 newly colonized 90 - 100% of the subplots annually (Table 2).

For the species at Egerkingen, TO was calculated with the same method used by Morgan (1998) and his spectra with categories low (< 33%), medium (> 33% and < 66%) and high (> 66%) may therefore be directly compared with the values of the present study. Morgan (1998) found spectra which varied annually. At both spatial scales, the species with low TO prevailed for 1 year and those with high TO for a further 1 year. At Egerkingen, most species had constantly high TO in the subplots, whereas in the plots the ones with low values prevailed. A slightly similar tendency may be seen in Morgan's data. However, his values varied widely, possibly because his 0.01-m² plots were not situated within 1-m² plots and TO varied most as a consequence of presence or absence of the species.

In 2 cm × 2 cm plots, Otsus & Zobel (2002) found the highest TO (mean of 3 years) for *Prunella vulgaris*, followed by *Carex ornithopoda*, *C. flacca*, *Thymus serpyllum* and *Achillea millefolium*. In the plots/subplots at Egerkingen, these species had different sequences each year and only *Achillea* showed the lowest TO at both scales. At Egerkingen, as well as in the small subplots of the Estonian calcareous grassland, the last-mentioned species was practically immobile. In contrast to Otsus & Zobel (2002), who exclusively found high TO-values for sedges, in the *Mesobrometum* not only the sedges *Carex flacca* and *C. ornithopoda* had high TO-values, but also the grass *Poa trivialis*. Nevertheless, another sedge, *C. caryopyllea,* had a low TO as did the other common species in the *Poaceae*: *Arrhenatherum*, *Avenula*, *Bromus* and *Trisetum*.

Cumulative frequency

Cumulative frequency CF increased when new areas were occupied. Even if a species loses all its previous positions and appears in a single new one, or if it adds to all the former ones a new one, this is not expressed in CF *per se*. The FFs remain hidden. In a certain way, species of SDP groups 2, 4 and 5 increased their presence in the community by moving annually from subplot to subplot and so they were able to compensate their short stays (Fig. 2; cf. Fig. 12). A species with very low CF was *Silene*, which remained for 4 years in the same subplot, whereas at the same time *Trifolium pratense* occurred in nine different subplots of plot 15. *Veronica arvensis*, a therophyte, showed a relatively high CF, as did the therophytes of Klimeš (1999), but in general the non-clonal *Mesobrometum* plants were not the most mobile ones. The therophyte *Thlaspi* had a conspicuously low mobility, yet *Galium*, a clonal plant, had very high mobility.

In the *Avenetum* of Öland (van der Maarel & Sykes 1993), the species, which occurred in > 80% of the sub-

plots (*n* = 40) more than trebled (from 5 to 18), i.e. after 6 years, 40% of the species became highly frequent. In the *Mesobrometum* at Egerkingen, in the same period, only four species accumulated high frequency (*n* = 1250), another six species arrived in 60 - 80% of all subplots, i.e. nearly 25% of the species substantially increased their cumulative presence. Furthermore, 50% of the species of the *Mesobrometum* (10% in the *Avenetum* referred to) occurred in a maximum of 20% of subplots. Therefore, the species of the Öland *Avenetum* showed much higher mobility than those of the Swiss *Mesobrometum*, a fact that is possibly due to the extreme ecological factors affecting the former.

Community organisation

Constancy of species list but varying frequency of the species

During the period of investigation, no trend in the development of species richness and high persistence was observed. Furthermore, no major change in the species composition was detected and hence the grassland community was considered to be a stable ecosystem.

However, in the whole of the investigated area, SF decreased for 40% of the species, and for 26% of them it increased. Therefore, nearly half of the species had continuously less individuals and were in danger of disappearing, whereas a quarter of the species increased their presence significantly at the cost of the former ones. The species with decreasing frequency are mainly found in Central-European semi-natural grasslands, half of which are indicators of calcareous and nutrient-poor soils (Studer 2000). Four decreasing species are indicators of moderately nutrient-rich and moist soils; another seven species indicate nutrient-rich and humid soils. Half of the increasing species are indicators of nutrient-rich and humid soils, half are indicators of soils with low nutrient content and moderate dryness (Studer 2000). The trend in the abundance of the species was probably the result of nitrogen input from the air. At Egerkingen the annual amount of nitrogen deposited corresponded to the fertilisation in a typical Swiss hay meadow, one which is harvested twice a year (Rihm 1996).

A continuous decrease of SF in 40% of the species (down to their final disappearance), and the increase of 26% of other species, would decrease species richness, and alter species composition, at the site considerably.

Cumulative species numbers

The increase in cumulative species numbers within the investigated *Mesobrometum* was of the same order as that in plots with corresponding dimensions in Öland, Limburg, North Carolina and the Mississippi region (Sykes et al. 1994). In a *Bromus* grassland in the Bilé Karpaty Mountains, a similar number of species were found at the

0.01-m^2 scale (Klimeš 1999). However, on a scale 0.25 m^2, cumulative species richness was considerably higher: 32 - 45 species in the *Bromus* grassland, compared with 25 - 32 in the *Mesobrometum* at Egerkingen.

Species classifications based on distribution patterns

Kammer (1997) described species distribution patterns for another *Mesobrometum* in Switzerland. The aim of his investigation was to detect the amount of species spatial variability on an increasing scale. He distinguished four different distribution patterns. These patterns did not seem to have satisfactory details for the present investigations. In addition to Kammer's spatially and temporally regularly distributed species with high frequency, irregularly distributed species occurred at Egerkingen (SDP2). Furthermore, not only sporadically allocated and coincidentally occurring species (SDP5, Kammer 1997), but also sporadically and continuously occurring ones (SDP6) were classified at Egerkingen.

Two different classifications of species mobility types have been published (Herben et al. 1993a; van der Maarel 1996a). The classification by Herben et al. ordinates the species along the two axes 'persistence' (as a combination of spatial and temporal occurrences of species) and 'long-distance spread'. The four resulting types were: (1) 'sitters' (high persistence), (2) 'phalanx' (medium persistence), (3) 'short-range guerrilla' (low persistence) and (4) 'long-range guerrilla species and annuals' (low persistence and high degrees of long-distance spread). These axes are appropriate for the grassland vegetation in which Herben et al. (1993a) worked, i.e. a *Nardetum* with relatively few long-lived species, but were not straightforward to understand as they involved sophisticated calculations which in the *Mesobrometum* were not of the same biological importance.

In the simpler and more universal classification by van der Maarel (1996b) TF and SF are the main ordination axes. Five types are distinguished: the highly frequent 'constants', medium-frequent 'pulsating' (fluctuating) species and 'circulating' (accumulating) species and the rare 'occasionals' and 'locals'. Van der Maarel's classification was applied to an Australian grassland by Morgan (1998). In the Australian *Themeda* grassland, as well as in the *Mesobrometum* at Egerkingen, species occurred that fitted in the classes of the extreme values: constants (SDP1), occasionals (SDP5) and locals (SDP6). By contrast, the differentiation of the spatially and temporally medium-frequent species 'pulsating' and 'circulating' species posed problems also for Morgan (1998). He redefined these two groups more widely as 'low to medium SF and large yearly FF' and 'medium SF and low yearly FF, appearing in new plots regularly and accumulating in space over time', respectively. His two types included SDP2 to SDP4. Morgan's method of classification seems

inappropriate for the reason that one and the same species may belong to different mobility types, depending on spatial scale at which it has been investigated. However, more interesting biologically is the fact that in two different stands of *Themeda*-grassland species existed which showed the same mobility type, e.g. *Themeda triandra* (constant), *Pentagopon* (circulating) and *Juncus bufonius* (occasional). Nevertheless, in Morgan's *Themeda*-grassland, species which behaved differently in the two stands were more numerous. The same stand-specific classification of mobility types may be stated for the species of the *Mesobrometum* at Egerkingen in comparison to the one by Kammer (1997).

It seems reasonable to suppose a species spectrum of mobility behaviour which depends on its specific surroundings, i.e. one that is contingent. This spectrum of species may be abstracted in species classifications as e.g. Grime's universal competitor class (Grime 2001). For the study of a specific vegetation stand such abstract types are not intended to be used directly, but may have possibilities of application in a similar way to the ecological indicator values of Ellenberg (1974) and Landolt (1977).

The spectrum of mobility types of a whole community (and not the spectrum of mobility possibilities of a single species, as above), may be an expression of various ecological factors forming the community. This is the reason why van der Maarel (1996b) defined mobility types for the ecologically extreme *Avenetum* of Öland which were different from the ones of the temperate Australian *Themeda*-grassland of Morgan (1998) and the present *Mesobrometum* at Egerkingen.

Carousel time

For the carousel model of van der Maarel & Sykes (1993), Palmer & Rusch (2001) defined a 'carousel time'. This is the time that a species needs to visit all places in the community. Palmer & Rusch (2001) concluded from their analysis of data from an Oklahoma grassland that carousel time for the species would have the dimension of centuries. Single species also have shorter values: *Ambrosia psilostachya* with minimal carousel time would need 13.4 years for the 1 m^2-scale or 33.6 years for one of 0.0125 m^2. In the plots of the present study, all species of SDP1 to SDP3 had estimated carousel times of up to 6 years (except for *Thlaspi*, 12 years). As also observed by Palmer & Rusch (2001), the estimated carousel time in the subplots of the *Mesobrometum* was (much) longer (Fig. 13a and b). For the visit of 25 subplots, carousel time of SDP1 would be 6 years (except *Avenula*, 7 years), of SDP2 6 - 8 years (except *Thlaspi*, 26 years) and SDP3 12 years. For all 50 subplots more time would be necessary.

If carousel time is defined as the time it takes to visit all sites of a given grain within a community, Palmer & Rusch (2001, pp. 316/317) note that CT will be extremely long at a fine grain. In addition, they state that with another

definition, i. e. number of quadrats where this number is equal across grain sizes, CT is usually longer at larger than smaller grain. Contrary to this statement of the two authors, carousel time in the subplots of the *Mesobrometum* was longer than in the plots, even though, instead of 50 subplots only 25 (same number as plots) had to be reached (e.g. for *Coronilla* 6 years for 25 plots and 7 and 15 years for 25 and 50 subplots, respectively). The only exceptions were *Achillea* and *Luzula* with more accumulation of places at small scales, i.e. shorter CT (Fig. 13a and b).

Palmer & Rusch (2001) calculated their carousel times for 14 widespread non-matrix species only and therefore it remains unclear whether the spectrum of carousel times of the species in Oklahoma grassland is comparable to the one of the *Mesobrometum*. Such comparisons could help to reveal to what extent ecological factors influence carousel time.

Conclusions

In a community all the species present are equally important. Vegetation dynamics can only be understood if all occurring species are considered. The size of the investigated subplots in this study was suitable for the detection of individual plants and partly showed their behaviour. An annual observation of single individuals or ramets of all species would have been even more desirable, as recommended by Mason et al. (2002). The plot (100-fold larger) revealed spatial patterns of single species in the grassland community with satisfactory results. The entire study used a small area (25 1-m^2 plots, each separated by a gap of 1 m), since no larger homogeneous *Mesobrometum* was available. Had the possibility of a larger area been there, further understanding of spatial variability of the grassland could have been investigated.

The investigation period of 6 years was an absolute minimum. For most species, the characteristics of individual behaviour could be detected during this time. Of course it would have been desirable to continue the observations in order to investigate further whether the behaviour of the species continued to correspond to the designated SDPs or whether the species would change their SDP and even new SDPs would arise.

Important insights into the processes of vegetation dynamics may be gained if the present methods are applied to other geographically and ecologically different plant communities. Additionally important to these insights is the necessity of studying the specific behaviour of all species present, and to describe their dynamics with a combination of several simple variables, that can be directly evaluated.

Acknowledgements

References

Binz, A. & Heitz, C. 1986. Schul- und Exkursionsflora für die Schweiz. 18. Aufl.. Schwabe, Basel.

Bycroft, C.M., Nicolaou, N., Smith, B. & Wilson, J.B. 1993. Community structure (niche limitation and guild proportionality) in relation to the effect of spatial scale, in a Nothofagus forest sampled with a circular transect. —N. Z. J. Ecol. 17: 59-65.

Ellenberg, H. 1974. Zeigerwerte der Gefässpflanzen Mitteleuropas. —Scripta Geobot. 9: 1-122.

Gitay, H. & Agnew, A.D. 1989. Plant community structure, connectance, niche limitation and species guilds within a dune slack grassland. —Vegetatio 83: 241-248.

Glenn, S.M. & Collins, S.L. 1993. Experimental analysis of patch dynamics in tallgrass prairie plant communities. — J. Veg. Sci. 4: 157-162.

Glenn-Lewin, D.C. & van der Maarel, E. 1992. Patterns and processes of vegetation dynamics. In: Glenn-Lewin, D.C., Peet, R.K. & Veblen T.T. (eds.) Plant succession: Theory and prediction, pp. 11-59. Chapman and Hall, New York.

Grace, J., Allain, L. & Allen, C. 2000. Factors associated with plant species richness in a coastal tall-grass prairie. — J. Veg. Sci. 11: 443-452.

Grime, J.P. 2001. Plant strategies, vegetation processes, and ecosystem properties. 2nd ed. — John Wiley & Sons, Chichester.

Herben, T., Krahulec, F., Kovářová, M. & Hadincová, V. 1990. Fine-scale dynamics in a mountain grassland. In: Krahulec F., Agnew A.D.Q., Agnew S. & Willems J.H. (eds.) Spatial processes in plant communities, pp. 173-184. SPB Academic Publishing, The Hague.

Herben, T., Krahulec, F., Hadincová, V. & Kovářová, M. 1993a. Small-scale spatial dynamics of plant species in a grassland community over six years. — J. Veg. Sci. 4: 171-178.

Herben, T., Krahulec, F., Hadincová, V. & Skalová, H. 1993b. Small-scale variability as a mechanism for large-scale stability in mountain grasslands. — J. Veg. Sci. 4: 163-170.

Herben, T., Krahulec, F., Hadincová, V. & Pecháčková, S. 1994.

Is a grassland community composed of coexisting species with low and high spatial mobility? — Folia Geobot. Phytotax. 29: 459-468.

Kammer, P.M. 1997. Räumliche, zeitliche und witterungsbedingte Variabilität eines Trespen-Halbtrockenrasens (Mesobromion) im Schweizer Mittelland. Ein Beitrag zur Methodik der Dauerflächenbeobachtung. Dissertationes Botanicae 272, Cramer, Berlin.

Klimeš, L. 1995. Small-scale distribution of species richness in a grassland (Bile Karpaty Mts, Czech Republic). — Folia Geobot. Phytotax. 30: 499-510.

Klimeš, L. 1999. Small-scale plant mobility in a species-rich grassland. — J. Veg. Sci. 10: 209-218.

Klimeš et al. 1995. Variability in species richness and guild structure in 2 species-rich grasslands. —Folia Geobot. Phytotax. 30: 243-253.

Landolt, E. 1977. Ökologische Zeigerwerte zur Schweizer Flora. —Veröff. Geobot. Inst. Rübel, ETH Zürich 64.

Lepš, J. 1995. Variance deficit is not reliable evidence for niche limitation. —Folia Geobot. Phytotax. 30: 455-459.

Mason, N.W.H, MacGillivray, K., Steel, J.B. & Wilson, J.B. 2002. Do plant modules describe community structure better than biomass? A comparison of three abundance measures. — J. Veg. Sci. 13: 185-190.

Morgan, J.W. 1998. Small-scale plant dynamics in temperate *Themeda triandra* grasslands of southeastern Australia. — J. Veg. Sci. 9: 347-360.

Nordbakken, J.F. 2000. Fine-scale persistence of boreal bog plants. — J. Veg. Sci. 11: 269-276.

Otsus, M. & Zobel, M. 2002. Small-scale turnover in a calcareous grassland, its pattern and components. — J. Veg. Sci. 13: 199-206.

Palmer, M.W. 1987. Variability in species richness within Minnesota oldfields: a use of the variance test. —Vegetatio 70: 61-64.

Palmer, M.W. & Rusch, G.M. 2001. How fast is the carousel? Direct indices of species mobility with examples from an Oklahoma grassland. — J. Veg. Sci. 12: 305-318.

Pausas, J.G. & Austin, M.P. 2001. Patterns of plant species richness in relation to different environments: an appraisal. — J. Veg. Sci. 12: 153-166.

Rihm, B. 1996. Critical loads of nitrogen and their exceedances; eutrophying atmospheric deposition. —Environmental Series No. 275, Air, 74. Federal Office of Environment, Forests and Landscape (FOEFL), Bern.

Stampfli, A. 1995. Species composition and standing crop variation in an unfertilized meadow and its relationship to climatic variability during 6 years. — Folia Geobot. Phytotax. 30: 117-130.

Stampfli, A. & Zeiter, M. 2004. Plant regeneration directs changes in grassland composition after extreme drought: a 13-year study in southern Switzerland. — J. Ecol. 92: 568-576.

Studer, K. 2000. Synthesis of semi-natural grassland vegetation of a biogeographically heterogeneous area: mesophilous species-rich meadows in Switzerland. — Folia Geobot. Phytotax. 35: 289-313.

Sykes, M.T., van der Maarel, E., Peet, R.K. & Willems, J.H. 1994. High species mobility in species-rich plant communities: an intercontinental comparison. — Folia Geobot. Phytotax. 29: 439-448.

van der Maarel, E. 1988. Floristic diversity and guild structure in the grassland of Öland's Stora Alvar. — Acta Phytogeogr. Suec. 76: 53-65.

van der Maarel, E. 1996a. Vegetation dynamics and dynamic vegetation science. —Acta Bot. Neerl. 45: 421-442.

van der Maarel, E. 1996b. Pattern and processes in the plant community: fifty years after A.S. Watt. — J. Veg. Sci. 7: 19-28.

van der Maarel, E. 2005. Vegetation ecology. Blackwell Publishing, Oxford.

van der Maarel, E. & Sykes, M.T. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. — J. Veg. Sci. 4: 179-188.

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

Watkins, A.J. & Wilson, J.B. 1992. Fine-scale community structure of lawns. — J. Ecol. 80: 15-24.

Wilson, J.B. 1995. Variance in species richness, niche limitation, and vindication of patch models. —Oikos 73: 277- 279.

Wilson, J.B. & Roxburgh, S.H. 1994. A demonstration of guild-based assembly rules for a plant community, and determination of intrinsic guilds. —Oikos 69: 267-276.

Wilson, J.B., Gitay, H. & Agnew, A.D.Q. 1987. Does niche limitation exist? — Funct. Ecol. 1: 391-397.

Wilson, J.B., Roxburgh, S.H. & Watkins, A.J. 1992. Limitation to plant species coexistence at a point: a study in a New Zealand lawn. — J. Veg. Sci. 3: 711-714.

Wilson, J.B., Peet, R.K. & Sykes, M.T. 1995a. What constitutes evidence of community structure? A reply to van der Maarel, Noest & Palmer. — J. Veg. Sci. 6: 753-758.

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

Wondzell, S. & Ludwig, J.A. 1995. Community dynamics of desert grasslands: influences of climate, landforms, and soils. — J. Veg. Sci. 6: 377-390.

Zhang W. & Skarpe, C. 1995. Small-scale species dynamics in semi-arid steppe vegetation in Inner Mongolia. — J. Veg. Sci. 6: 583-592.

Zobel, K., Zobel, M. & Peet, R.K. 1993. Change in pattern diversity during secondary succession in Estonian forests. — J. Veg. Sci. 4: 489-498.

Re-establishment of alvar plant species in abandoned arable fields on Öland

Jan P. Bakker[1]*, Ejvind Rosén[2] & Karin Steg[1]

[1]*Community and Conservation Ecology, University of Groningen, P.O.Box 14, NL-9750 AA Haren, The Netherlands;*
[2]*Department of Plant Ecology, Evolutionary Biology Centre, Uppsala University, Villavägen 14,
SE-75236 Uppsala, Sweden;*
* *Corresponding author; E-mail j.p.bakker@rug.nl*

Abstract

In the past, arable fields were established locally on the alvar on Öland. Several persisted until the present time, but some of them were abandoned shorter or longer ago. We found a series of arable fields forming a chronosequence: still cultivated, ca. 20 years abandoned, ca. 50 years abandoned, and never cultivated. Species of man-influenced habitats gradually disappeared from the former arable fields, but a few persisted after 50 years. A group of alvar species had re-established after 20 years, but others did not re-establish even after 50 years of abandonment, although they are present in the local species pool. We found no evidence of dispersal as a constraint for re-establishment.

Keywords: Dispersal; Seed bank; Seed mass; Seed shape; Soil fertility; Species pool.

Nomenclature: Lid (1987); *Hieracium praealtum* was identified according to Mossberg (1992).

Introduction

Many reclaimed arable fields established on former semi-natural vegetation in many parts of the world have now been abandoned. Authorities in charge of nature conservation often try to restore the plant communities present before cultivation, e.g. species-rich grassland or heathland on nutrient-poor soil. Such attempts often fail, which can be attributed to the eutrophicated soil conditions or dispersal limitations of the characteristic species of the former communities (Bakker & Berendse 1999). Intensive management aiming to reduce the nutrient surplus by top soil removal is often not sufficient for the re-establishment of the target species (Verhagen et al. 2001). In many agricultural landscapes, the re-establishment site is surrounded by agricultural fields, hence the target species are lacking in the local species pool (Zobel et al. 1998).

The present study focuses on the spontaneous re-establishment of the original dry alvar grasslands of Öland. Alvar refers to the system of dry grassland plant communities growing on thin soil over limestone bedrock (Rosén 1982). This vegetation harbours the species-rich *Veronica spicata-Avenula pratensis* community (Krahulec et al. 1986; Bengtsson et al. 1988; Löbel & Dengler 2007). This community can disappear either by overgrowing with *Juniperus communis* shrubs, or by transformation into arable fields. In both cases re-establishment of dry alvar grassland species from the community species pool (Zobel et al. 1998) will be restricted, as the long-term persistent seed bank of these species is poor (Bakker et al. 1996, 1997). Locally cultivated fields have been abandoned in the alvar area of Öland (Fig. 1). The longer ago cultivated fields have been abandoned, the lower the cumulative nutrient input, the better the starting position for re-establishment of species of nutrient-poor soil conditions (Bakker & Olff 1995). With likely favourable abiotic conditions, dispersal of propagules may be a constraint for the re-establishment of dry alvar grassland species.

The aim of the present study is to establish how fast the

dry alvar grassland community can re-establish in previously cultivated arable fields. As these cultivated fields are surrounded by extensive, never-reclaimed species-rich dry alvar grasslands, dispersal of propagules is unlikely to be a constraint. Hence, we hypothesize that all dry alvar grassland species have re-established after some decades.

Methods

Study site

The study site is situated at 'Stora Alvaret' in the southern part of Öland. It is part of the abandoned hamlet of Dröstorp (56°35' N, 16°34' E), ca. 3 km west of Skarpa Alby. The site has 10-50 cm deep brown soils developed in reworked glaciofluvial deposits on Ordovician limestone (Rosén 1982; Krahulec et al. 1986).

Cultivation at Dröstorp started in 1757 by two boatswains from Skarpa Alby. At this time Dröstorp was mentioned as an uninhabitated homestead. The land belonged to the community of Skarpa Alby. After some time the two man moved up there and each of them established a farm. Somewhat later one or more farmers from Skarpa Alby also cultivated some land. The two farms remained until the end of the 19th century, when people returned to Skarpa Alby. However, the cultivation of the now uninhabited homestead continued. In the 1990s only four agricultural fields, including the 'still cultivated' field in the present study, were still exploited as a sown hayfield with artificial fertiliser (Fig. 2). Since the 1960s, the four fields still cultivated have been alternately used as arable field (oat, rye and barley), and as hayfield including grazing the aftermath. The fields have not been ploughed since 1988 when barley was sown together with a grass mixture including *Dactylis glomerata*. After harvest-

ing barley, the field was cut annually for hay and grazed afterwards by cattle. During the past decades artificial fertilisers have been applied. It implies that the fields in the study sites have been cultivated without interruption during about 200 years.

Five areas have been included in the present study, (1) a field still cultivated, (2, 3) two fields abandoned for ca. 26 years, (4) a field abandoned for 48 years, and (5) an area which has never been cultivated. The afore-mentioned application of fertilisers has probably been the same in all cultivated fields. The two fields abandoned 26 years ago differ in conditions before abandonment. One has been used as a hayfield for some years (3), and is left as such. The other (2) has been ploughed (but not further treated) after six years of abandonment, 20 years ago (the vegetation, including already established small junipers was only partly damaged). This field is referred to as 20-26 year abandoned. From Fig. 2 it is clear that the group of fields is surrounded by an extensive uncultivated area. Land use has been livestock grazing and collection of *Juniperus communis* for fuel for many centuries (Rosén 1982).

In all former cultivated fields, at the start of this study, 12 junipers were cut to examine their age by counting tree rings. It is likely that they started to establish immediately after cessation of agriculture in the bare soil, and thus could give extra information about the periods the fields were abandoned.

In 1994 the study in the uncultivated area and in the still cultivated field took place (Bakker et al. 1996, 1997), whereas the abandoned fields were studied in 1996. To ascertain similar abiotic conditions at the various fields, sample plots were chosen so as to avoid *Juniperus communis* shrubs and thinner soil. Juniper shrubs which were very abundant in the 48-year abandoned field, could have caused shading effects (Rejmánek & Rosén 1988) and a locally lower pH

Fig. 1. Abandoned arable field near Dröstorp, Öland, with encroachment of *Juniperus communis*.

(Rosén 1982; Bengtsson et al. 1988). Thinner soils were avoided since the major trends in plant community composition were associated with soil moisture levels, which are correlated to the thickness of the soil (Bengtsson et al. 1988). The thickness of the soil overlying the limestone was measured at ten points in each of the ten plots for vegetation monitoring with a little auger.

Vegetation and seed bank sampling

The established vegetation was monitored from early June until late July by recording the presence of all species in ten subplots of 1 m × 0.4 m in each of ten plots of 2 m × 2 m in each individual field. Moreover, an inventory was carried out to record species present in the fields but not found in the plots. Specimens of *Polygala vulgaris* may have included some *P. amarella. Cerastium* species without flowering parts were considered *Cerastium* cf. *fontanum*, but may in part have been *Cerastium semidecandrum*.

The species were divided into four ecological groups according to van der Maarel (1988) and Rejmánek & Rosén (1988):
A: Dry alvar grasslands on either shallower or deeper soils;
W: Scrub, woodland and understorey in woodland;
D: Wetlands in depressions, ranging from temporary pools to alvar lakes;
M: Man-made and/or strongly human-influenced habitats

To calculate a weighted nitrogen figure for each site according to Ellenberg (1979), the original N-values of

the species were multiplied by the number of 1 m × 0.4 m subplots in which the species was found, and the product was divided by the total number of 2 m × 2 m plots per site in which the species occurred.

The seed bank was studied using the concentration method (ter Heerdt et al. 1996). Soil samples were taken in April prior to the fresh seed rain of the season. Natural stratification of the seeds has taken place in the field during the previous winter period. Ten cores (4 cm diameter) were taken adjacent to each of the ten plots per site, in which the established vegetation was monitored. After removal of the litter, the samples were subdivided into 0-5 cm and 5-10 cm layers. The samples per depth interval per plot (volume 0.7 l) were pooled. The pooled samples were washed on a fine sieve (mesh width 0.2 mm). The reminder was spread in a thin layer over a 6 cm layer of sterilised potting soil covered with 1 cm sterile sand in individual trays of 30 cm × 30 cm. The trays were put into the greenhouse and watered daily. Temperature was 15 °C during the night (20:00 - 08:00) and ranged between 25 - 45 °C during the day. The seedlings emerged were identified and removed as soon as possible, counted and removed.

The relationship between the presence of species in the established vegetation and the seed bank, including depth of the soil layer allows the classification into transient, short-term and long-term persistent according to Thompson et al. (1997).

Species were classified according to seed size and shape. *Carex* spp. were measured without their utricules, grass species without lemmas and awns, and *Asteraceae* were measured without their pappus. Data on 101 species were thus analysed. The size of a diaspore was quantified as the air-dry weight. The shape was quantified by the extent to which it differed from a sphere, using the variance of diaspore length, width and depth, after transforming all values so that the length was unity (see Bakker et al. 1996).

Data analysis

Comparisons of the thickness of the soil layer in the five sites were made by a non-parametric Kruskal-Wallis one-way ANOVA.

The means of the number of species per 2 m × 2 m plots and 1 m × 0.4 m subplots in all sites were also compared by a non-parametric Kruskal-Wallis one-way ANOVA. Differences among sites were assessed by a non-parametric Student Newman Keuls test (Zar 1984).
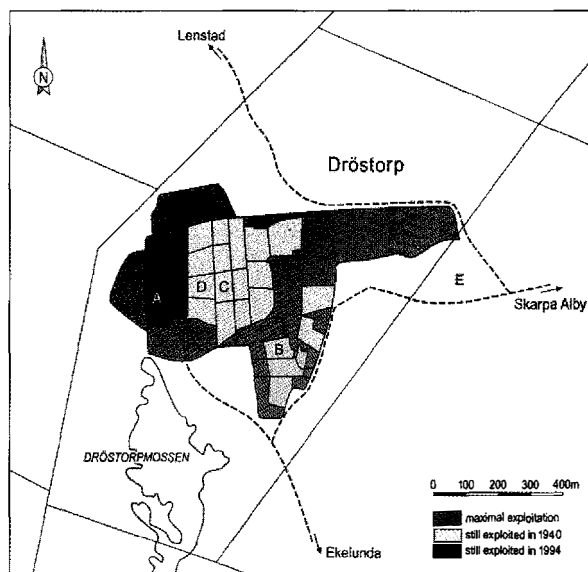
To check on differences in the occurrence of individual species in the 1 m × 0.4 m subplots, the frequencies of occurrence in the 2 m × 2 m plots were compared. This was done by a non-parametric Kruskal-Wallis one-way ANOVA. Differences among sites were assessed by a non-parametric Student Newman Keuls test (Zar 1984).

Fig. 2. Map of the abandoned hamlet of Dröstrop. Indicated are the still cultivated fields (A), the field abandoned 20-26 years ago (B), the field abandoned 26 years ago (C), the field abandoned 48 years ago (D), and the never cultivated site (E).

Results

The sites

The depth of the soil layers on top of the limestone bedrock ranged from 15-25 cm in all five sites, and did not significantly differ among sites (Table 1). The weighted Ellenberg nitrogen figures indicate that the still cultivated field harbours plant species bound to a relatively high nutrient availability, while the never cultivated site on the alvar harbours species with a low nitrogen figure, but differences were not significant (Table 1). In the fields abandoned ca. 48 and 26 years ago, junipers with an estimated age of 48 and 26 years, respectively, were found.

The species

The total number of plant species in the established vegetation was significantly lower in the still cultivated field as compared to the field that has been abandoned for 26 years and ploughed 20 years ago, and in the field abandoned for 48 years, both in the 2 m × 2 m plots and in the 1 m × 0.4 m subplots (Table 2). The total number of germinated species found in the seed bank did not differ for the sites. The number of species and seedlings germinated from the top soil (0 - 5 cm) was higher than that germinated from the deeper soil layer (5 - 10 cm) (Table 2).

A group of 19 species with *Festuca ovina* and *Filipendula vulgaris* was present in the uncultivated site, absent in the still cultivated site, but had returned in the abandoned sites (App. 1). With the exception of *Viola hirta*, all are A-species characteristic of dry alvar grasslands. Most of these species are classified as having a transient seed bank. A group of 17 species with *Helianthemum nummularium*

and *Asperula tinctoria* had not yet returned 48 years after abandonment. Except for *Sesleria caerulea* and *Anthoxanthum odoratum*, these are A-species as well, and again most have a transient seed bank (App. 1).

The following three groups of species in App. 1 are largely M-species, characteristic of man-made and/or human-influenced habitats. A group with *Medicago sativa* and *Lolium perenne* had disappeared after 26 years of abandonment. A second group with *Daucus carota* had disappeared after 48 years of abandonment. A third group with *Dactylis glomerata* includes species which were still present after 48 years of abandonment; these are common grassland species.

Most of the species of the group with *Carex flacca* and *Chrysanthemum leucanthemum* (often common grassland species) are frequent in the fields abandoned for 26 years and ploughed 20 years ago, whereas the group with *Arabis hirsuta* and *Fragaria viridis* (many species characteristic of dry alvar grasslands) have a significant high frequency in all previously cultivated fields (App. 1).

Five species (*Raphanus raphanistrum*, *Rumex crispus*, *Alyssum alyssoides*, *Galium aparine* and *Silene vulgaris*) only occur in the still cultivated field, have a transient seed bank, and most of them are characteristic of man-made habitats.

Finally, 34 species in the group of *Juncus articulatus* and *Juncus bufonius* were only found in the seed bank. Often only one or two seedlings were found. The species with more seedlings were often classified as having a persistent seed bank (App. 1).

Mean seed weight and variance of shape did not differ among the groups (Table 3). The nitrogen figures of species not yet returned after 48 years are low, whereas those of species that had initially established in the abandoned sites,

Table 1. Mean thickness of the soil (± SE, $n = 100$) and weighted nitrogen figure according to Ellenberg, in the five study sites: still cultivated, abandoned since 20-26 years, 26 years, 48 years ago, and not cultivated

	Cult.	20-26 years ab.	26 years ab.	48 years ab.	Not cult.
Mean thickness (cm)	17.6 ± 0.3	22.4 ± 0.5	21.2 ± 0.6	20.6 ± 0.6	16.8 ± 0.4
Weighted Nitrogen figure	3.7	2.2	2.6	2.3	1.9

Table 2. Total and mean (± SE) number of species in the established vegetation in the five investigated fields. Total number of species and seedlings in the seed bank. Different superscripts indicate significant differences ($P < 0.05$), assessed by a non-parametric multiple range Student Newman Keuls test.

		Cult.	20-26 years ab.	26 years ab.	48 years ab.	Not cult.
Number of species	per 40 m^2 ($n =1$)	40	91	69	82	64
	per 4 m^2 ($n = 10$)	20.2^c ± 0.6	58.1^a ± 1.3	38.9^{bc} ± 2.0	46.5^{ab} ± 1.7	38.5^{bc} ± 1.4
	per 0.4 m^2 ($n = 100$)	9.4^c ± 0.2	36.9^a ± 0.4	22.7^{bc} ± 0.5	29.1^{ab} ± 0.5	22.8^{bc} ± 0.8
Number of species in seed bank	0-5 cm depth	39	54	43	42	49
	5-10 cm depth	32	43	30	33	32
	0-10 cm depth	48	56	45	47	51
Number of seedlings in seed bank	0-5 cm depth	431	1111	789	443	1025
	5-10 cm depth	261	706	324	318	653
	0-10 cm depth	692	1817	1113	761	1678

but disappeared later, are high. However, the differences were not significant (Table 3).

Discussion

Numbers of plant species

The sites do differ somewhat in thickness of the soil layer, but they can all be considered deep silicious alvar soils (15 - 50 cm) according to Bengtsson et al. (1988). Hence, abiotic differences between the five sites are unlikely. The estimation of the age of the junipers confirms the information from other sources such as aerial photographs and farmers of the nearby villages of Skarpa Alby and Ekelunda, that the sites represent a chronosequence from a still cultivated field to long-term abandoned fields with a never cultivated site as a reference system. The differences in the established vegetation and the soil seed bank can, therefore, be attributed to the various periods of abandonment from cultivation.

The number of plant species in the study area differed considerable among the fields, and ranged between 20 and 58 species per 4 m^2. The decrease in the number of species characteristic of man-made habitats upon abandonment is in agreement with the decrease of commonly cultivated species after abandonment (Kiirikki 1993). The field abandoned for 26 years was exploited as a hayfield before abandonment. The stand with tall grasses such as *Dactylis glomerata*, *Arrhenatherum elatior* and *Poa angustifolia* caused competition for light, especially for seedlings (Lodge 1993). Old fields previously planted with *Dactylis glomerata* showed a lower species turnover than fields with other final crops. It dominated early succession stages by inhibiting other species to establish (Myster & Pickett

1990). In contrast, the field ploughed 20 years ago is very rich in species compared to other calcareous grasslands (Bengtsson et al. 1988, Willems & Bobbink 1990, Gibson & Brown 1991). This can be explained by the combined occurrence of many alvar species as well as a number of species characteristic of man-made habitats. It is likely that ploughing made the site accessible for species that could establish with a little competition for light during some time. This field might also be trampled by livestock, because it is situated closer to the well of Dröstorp than the other fields. Livestock included cattle and, during the last five years, also sheep. Trampling may cause more bare soil, which makes the field more accessible for species to establish (Rusch 1992).

The group of species established after abandonment in the present study are partly the same as those described in the study by Gibson & Brown (1991) on calcareous grassland after abandonment of cultivated sites. Six out of the 15 species found to return early (20-26 years) after abandoning in the present study were classified by them as 'already present in early (1-10 years) or mid (11-100 years) succession': *Avenula pratensis*, *Anthyllis vulneraria*, *Briza media*, *Cirsium acaule*, *Linum catharticum* and *Viola hirta*.

After the initial establishment of species characteristic of dry alvar grasslands. no new species established between 26 and 48 years of abandonment. It seems that the window of opportunity for establishment becomes closed after stabilisation of the sward. This is in agreement with results from old fields in North America (Myster & Pickett 1994). Newman (1993) suggested, according to studies on calcareous grasslands in southern England, that re-creation of a 'complete' community by unassisted succession can take at least 100 years after abandonment.

Table 3. Total numbers of species, and total numbers of species of group A (characteristic of dry alvar grasslands on either shallower or deeper soils), M (characteristic of man-made and/or strongly human-influenced habitats), D (characteristic of wetlands in depressions, ranging from temporary pools to alvar lakes) and W (characteristic of scrub, woodland and understorey in woodland), differentiated according to their relation to field abandonment: ret26 = returned after 26 years; notret48 = not returned after 48 years; dis26 = disappeared after 26 years; dis48 = disappeared after 48 years; pres48 = still present after 48 years; pres26 = only present in 20-26 years abandoned field; prescult = only present in former cultivated fields. Mean (± SE) nitrogen figure according to Ellenberg and mean (± SE) seed weight and variance of seed shape for each of the groups. Also indicated is the number of species found to have LP (long-term persistent) seeds in the soil seed bank.

Position	ret26	notret48	dis26	dis48	pres48	pres26	prescult
Total numbers of species in group	19	17	7	3	6	13	12
Number of A species	18	15	3	0	2	3	8
Number of M species	0	1	4	3	4	4	1
Number of D species	0	1	0	0	0	4	1
Number of W species	1	0	0	0	0	2	2
Nitrogen figure	2.3 ± 0.2	2.0 ± 0.2	4.8 ± 1.0	6.0 ± 2.0	5.8 ± 1.0	3.8 ± 0.6	3.8 ± 0.6
Seed weight	0.8 ± 0.2	0.6 ± 0.1	1.3 ± 0.6	2.0 (n = 1)	4.4 ± 3.1	0.5 ± 0.2	0.5 ± 0.2
Variance of seed shape	0.07 ± 0.01	0.07 ± 0.01	0.10 ± 0.01	0.10 (n = 1)	0.07 ± 0.02	0.06 ± 0.02	0.06 ± 0.02
Number of species with LP seeds	3	1	1	0	0	2	4

Characteristics of species

The group of 19 species with *Festuca ovina* and *Filipendula vulgaris* that had returned in the abandoned sites, and the group of 17 species with *Helianthemum nummularium* and *Asperula tinctoria* that had not yet returned 48 years after abandonment apparently differ in dispersal capacity. Both groups feature seeds that can be classified as having a short-lived seed bank. Seeds of both groups do not differ in mean seed weight and variance. Nevertheless they might differ in some other characteristics. Viable seeds of *Festuca ovina*, *Avenula pratensis*, *Potentilla tabernaemontani*, *Galium verum*, *Thymus pulegioides* and *Linum catharticum* found in dung at the alvar suggest that at least part of the species of the group of *Festuca ovina* occurring after about 20 years of abandonment (Table 2) can be dispersed by cattle (Dai 2000). However, also *Helianthemum nummularium*, *Prunella grandiflora*, *Phleum phleoides*, *Veronica spicata*, *Agrostis vinealis* and *Helianthemum oelandicum* of the group of *Helianthemum nummularium* that did not occur after 20 years of abandonment, can be spread through cattle dung (Dai 2000).

When taking into account all vectors of dispersal (wind, water, birds, other vertebrates and man), as is adopted for the Northwest European flora (see the LEDA database, Knevel et al. 2003), six out of the 19 species of the *Festuca ovina* group may be dispersed by two or more vectors, whereas this holds for two out of the 17 species of the *Helianthemum nummularium* group (Tamis et al. 2004). Both groups harbour about seven species that may be dispersed by a single vector. Unfortunately the dipsersal vector of six species of the *Helianthemum nummularium* group is not known.

We conclude that there is not enough evidence to suggest that the group of species that did not establish after ca. 20 years of abandonment has poorer dispersal capacity than the group that did establish. Introduction experiments may reveal whether abiotic conditions might be the constraints for establishment of plant species that apparently did not spread over a distance of a few hundred metres.

References

Bakker, J.P. & Berendse, F. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. — Trends Ecol. Evol. 14: 63-68.

Bakker, J.P. & Olff, H. 1995. Nutrient dynamics during restoration of fen meadows by hay-making without fertiliser application. In: Wheeler, B.D., Shaw, S.C., Foyt, W.J. & Robertson, R.A. (eds.). Restoration of temperate wetlands. pp 143-166. — Wiley, Chichester.

Bakker, J.P., Bakker, E.S., Rosén, E., Bekker, R.M. & Verweij, G.L. 1996. The soil seed bank composition along a gradient from dry alvar grassland to *Juniperus* scrubland. — J. Veg. Sci. 7: 196-176.

Bakker, J.P., Bakker, E.S., Rosén, E. & Verweij, G.L. 1997. The soil seed bank of undisturbed and disturbed limestone grassland. — Z. Ökol. Nat.schutz 6: 9-18.

Bengtsson, K., Prentice, H., Rosén, E., Moberg, R. & Sjögren, E. 1988. The dry alvar grasslands of Öland: ecological amplitudes of plant species in relation to vegetation composition. — Acta Phytogeogr. Suec. 76: 21-46.

Dai, X. 2000. Impact of cattle dung deposition on the distribution pattern of plant species in an alvar limestone grassland. — J. Veg. Sci. 11: 715-724.

Ellenberg, H. 1979. Zeigerwerte Gefässpflanzen Mitteleuropas. — Scripta Geobotanica 9: 1-122.

Gibson, C.W.D. & Brown, V.K. 1991. The nature and rate of development of calcareous grassland in southern Britain. — Biol. Conserv. 58: 297-316.

Kiirikki, M. 1993. Seed bank and vegetation succession in abandoned fields in Karkali Nature Reserve, southern Finland. — Ann. Bot. Fen. 30: 139-152.

Knevel, I.C., Bekker, R.M., Bakker, J.P. & Kleyer, M. 2003. Life-history traits of the Northwest European flora: The LEDA traitbase. — J. Veg. Sci. 14: 611-614.

Krahulec, F., Rosén, E., & van der Maarel, E. 1986. Preliminary classification and ecology of dry grassland communities on Ölands Stora Alvaret (Sweden). — Nord. J. Bot. 6: 797-809.

Lid, J. 1987. Norsk, Svensk, Finsk Flora. Det Norske Samlaget, Oslo.

Löbel, S. & Dengler, J. 2007. Dry grassland communities on southern Öland: phytosociology, ecology, and diversity. — Acta Phytogeogr. Suec. 88: 13-32 (this volume).

Lodge, D.M. 1993. Species invasions and deletions: community effects and responses to climate and habitat change. In: Kreiva, P.M., Kingsolver, J.G. & Huey, R.B. (eds.) Biotic interactions and global change, pp. 367-387. — Sinauer, Sunderland, MS.

Mossberg, B., Stenberg, L. & Ericsson, S. 1992. Den nordiska floran. — Wahlström & Widstrand, Stockholm.

Myster, R.W. & Pickett, S.T.A. 1990. Initial conditions, history and successional pathways in ten contrasting old fields. — Am. Nat. 124: 231-238.

Myster, R.W. & Pickett, S.T.A. 1994. A comparison of rate of succession over 18 yr in 10 contrasting old fields. — Ecology 75: 387-392.

Newman, E.I. 1993. Conservation and management of wild species. — Blackwell Scientific Publications, Oxford.

Rejmánek, M. & Rosén. E. 1988. The effects of colonizing

shrubs (*Juniperis communis* and *Potentilla fruticosa*) on species richness in the grasslands of Stora Alvaret, Öland (Sweden). — Acta Phytogeogr. Suec. 76: 67-72.

Rosén, E. 1982. Vegetation development and sheep grazing in limestone grasslands of south Öland. — Acta Phytogeogr. Suec. 72: 1-172.

Rusch, G. 1992. Spatial pattern of seedling recruitment at two different scales in a limestone grassland. — Oikos 65: 433-442.

Tamis, W.L.M., van der Meijden R., Runhaar, J., Bekker, R.M., Ozinga, W.A., Odé, B. & Hoste, I. 2004. Standaardlijst van de Nederlandse flora 2003. — Gorteria 30: 101-195.

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

Van der Maarel, E. 1988. Floristic diversity and guild structure in the grasslands of Öland's Stora Alvaret. — Acta Phytogeogr. Suec. 76: 53-76.

Verhagen, R., Klooker, J., Bakker, J.P. & van Diggelen, R. 2001. Restoration success of low-production plant communities on former agricultural soils after top soil removal. — Appl. Veg. Sci. 4: 75-82.

Willems, J.H. & Bobbink, R. 1990. Spatial processes in the succession of chalk grassland on old fields in the Netherlands. In: Krahulec, F., Agnew, A.D.Q. & Willems, J.H. (eds.) Spatial processes in plant communities, pp. 237-249. — SPB, The Hague.

Zar, J.H. 1984. Biostatistical analysis. — Prentice Hall, Englewood Cliffs, NJ.

Zobel, M., van der Maarel, E. & Dupré, C. 1998. Species pool: the concept, its determination and significance for community restoration — Appl. Veg. Sci. 1: 55-66.

App. 1. Total number of 0.4 m^2 plots in which species occur in the established vegetation of the five investigated field sites (abbreviations as in Table 1). Species represented by 'x' were found in the field but outside the recorded plots. In parentheses total number of viable seeds/125 cm^2 in the respectively 0-5 cm depth layer (devided from 10 replicates). Species characteristics of dry alvar grassland are indicated by A, of wetlands in depressions by D, of scrub and woodland by W, and of heavily man-influenced habitats by M. The Nitrogen figure according to Ellenberg is indicated (1 = lowest, 9 = highest). Then weight (mg) and variance of shape (length, width and height) of seeds is indicated. In the last column the type of seed bank derived from this study is indicated. T = transient, SP = short-term persistent and LP = long-term persistent. Data for species with very few seeds in a layer, i.e. < 3 seeds per site, were left out of consideration while classifying species into T, SP or LP. Species marked with * are not classified because their seeds did not germinate in the greenhouse. Different letters a, b, c indicate significant ($P < 0.05$) differences of frequencies in the established vegetation.

Species	Still cult.	20-26 years ab.	26 years ab	48 years ab.	Not cult.	N-figure Ellenberg	Seed weight (mg)	Seed shape variance	Seed bank class.
Species returned after 26 years									
A *Anthyllis vulneraria*	_b	100a(4/1)	13b	75a	48ab(3/2)	3	1.72	0.05	T
A *Avenula pratensis*	_b	41ab	47ab	90a	94	2	1.78	0.15	T
A *Avenula pubescens*	_c	70ab	99a	82ab	69bc	4	-	-	T
A *Briza media*	_b	92a(13/1)	53ab(35/2)	93a(3/-)	48ab(1/-)	2	0.27	0.06	T
A *Campanula persicifolia*	_b	70a(13/5)	47ab	88a(21/8)	55ab(1/3)	3	0.05	0.06	SP/T/LP
A *Carex caryophyllea*	_b	21ab	2b	26ab	74a(18/3)	2	0.72	0.04	T/SP
A *Carlina vulgaris*	4ab	35a	_b	9ab	2b	3	0.92	0.13	T
A *Centaurea jacea*	2ab	35a	1b	10a	35ab(1/-)	-	0.89	0.09	T
A *Cirsium acaule*	_b	41a	2ab	12ab	26ab	2	3.55	0.10	T
A *Festuca ovina*	2c	56ab(1/-)	14bc(1/-)	99a(1/4)	99a(7/1)	-	0.50	0.13	T/LP
A *Filipendula vulgaris*	_b	100a(7/1)	76a(2/-)	90a(2/-)	99a	2	0.62	0.12	T
A *Galium verum*	_b	100a(36/3)	100a(28/-)	100a(11/1)	89a(2/-)	3	0.24	0.01	T/SP
A *Linum catharticum*	_c	93ab(44/11)	36bc(11/-)	93a(66/28)	21bc(159/37)	1	0.13	0.11	SP
A *Luzula campestris*	_c	46ab	28abc	32bc(2/-)	79a(6/2)	2	0.95	0.02	T
A *Galium boreale*	_b	4b	27ab	20ab(1/-)	67a	2	0.59	0.04	T
A *Orchis ustulata*	_b	14ab	xb	11ab	13a	3	-	-	T
A *Potentilla tabernaemontani*	1b(-3)	92a(11/-)	20b(19/4)	94a(29/3)	a91a(76/17)	2	0.71	0.05	SP/T/LP
A *Thymus serpyllum*	_b	43ab(3/-)	_b	32ab	65a(1/-)	1	0.10	0.03	T
A *Trifolium campestre*	_b(10/4)	27a(7/3)	3ab	16ab(3/2)	1ab(7/2)	3	0.30	0.03	T/SP
W *Viola hirta*	_b	25ab	32ab	47a	11ab	2	-	-	T
Species not returned after 48 years									
A *Agrostis vinealis*	_b	_b	_b	_b	22a(9/3)	1	-	-	SP
A *Antenneria dioica*	_b	3b	_b	_b	53a	3	0.06	0.11	T
M *Anthoxanthum odoratum*	_b	8ab	_b	_b	13a(3/-)	-	0.80	0.09	T
A *Artemisia oelandica*	_b	_b	_b	_b	17a	-	0.22	0.09	T
A *Asperula tinctoria*	_b	3b	4b	6b	99a(3/-)	3	0.65	0.01	T
A *Calluna vulgaris*	_b	_b	_b	_b	43a(451/459)	1	0.05	0.04	LP
A *Carex ericetorum*	_b	4b	_b	_b	59a(45/15)	2	0.80	0.02	SP/T
A *Danthonia decumbens*	_b	5b	_b	_b	55a(6/-)	2	0.80	0.12	T
A *Helianthemum nummularium*	_b	xb	_b(2/-)	xb	100a(27/1)	1	0.72	0.04	T
A *Helianthemum oelandicum*	_b	_b	_b	_b	17a	-	0.64	0.03	T
A *Oxytropis campestris*	_b	_b	1b	3b	62a(17/2)	-	1.85	0.05	T
A *Phleum phleoides*	_b	xb	1b	8b	59a	1	0.14	0.09	T
A *Prunella grandiflora*	_b	xb	4b	_b	73a	3	0.68	0.07	T
A *Pulsatilla pratensis*	_b	xb	_b	_b	19a	2	1.04	0.11	T
D *Sesleria caerulea*	_b	10ab	_b	8b	59a	2	1.03	0.06	T
A *Veronica spicata*	_b	11ab(3/-)	_b	xb	53a(15/6)	2	0.09	0.09	SP/T
A *Viola canina*	_b	_b	_b	_b	35a(1/-)	2	-	-	T
Species disappeared after 26 years									
M *Carum carvi*	17a(36/21)	_b	_b	_b	_b	6	-	-	SP
A *Erophila verna*	34a(11/8)	6b(6/-)	_b(4/4)	1b(4/9)	_b	2	0.03	0.09	LP/SP/T
M *Lolium perenne*	91a(3/-)	_b	_b	_b	_b	7	2.40	0.13	T
M *Medicago sativa*	48a	_b	xb	_b	_b	3	2.31	0.07	T
M *Poa pratensis*	56a(1/-)	_b	_b	_b	_b	6	0.26	0.09	T
M *Polygonum aviculare*	6a(10/7)	_b(1/2)	_b(-/2)	_b(-/2)	_b(1/-)	-	-	-	SP/T
A *Veronica arvensis*	74a(5/-)	_b	1b	_b	_b	-	-	-	T
Species disappeared after 48 years									
M *Convolvulus arvensis*	36a	16ab	40a	_b	_b	-	-	-	T
M *Daucus carota*	_b(2/1)	88a(17/1)	24ab(9/5)	14b	_b	4	-	-	SP/T
M *Elymus repens*	20a	7ab	24ab	xb	_b	8	1.97	0.13	T
Species still present after 48 years									
A *Allium vineale*	32a	44a	15ab	11ab	_b	7	16.66	0.05	T
M *Arrhenatherum elatius*	_b	xb	100a	100a	_b	7	-	-	T
M *Dactylis glomerata*	100a(-/1)	97a	100a(4/-)	76a	_b	6	1.06	0.12	T
M *Plantago lanceolata*	5b	99a(39/2)	88a(25/-)	90a(3/2)	76ab(3/-)	-	0.85	0.09	T
A *Ranunculus bulbosus*	83a	98a(2/-)	79a(7/3)	89a(7/4)	1b	3	2.65	0.09	T/SP
M *Vicia cracca*	23ab	33ab	22ab	64a	_b	-	0.74	0.02	T

App. 1, cont.

Species	Still cult.	20-26 years ab.	26 years ab	48 years ab.	Not cult.	N-figure Ellenberg	Seed weight (mg)	Seed shape variance	Seed bank class.
Species only significantly present in field abandoned for 20-26 years									
D *Agrostis gigantea*	_b	53a(120/65)	_b	_b	_b	-	0.08	0.08	SP
D *Carex flacca*	_b	92a(109/17)	6b(5/-)	10b(5/9)	10b(5/2)	-	0.97	0.02	LP/SP/T
M *Chrysanthemum leucanthemum*	_b	81a(9/-)	xb	8b	_b	-	-	-	T
M *Cynosurus cristatus*	_b	28a	xb	5b	_b	4	0.47	0.08	T
W *Fraxinus excelsior*	_b	11a	_b	_b	_b	7	-	-	T
A *Hieracium praealtum*	_b	64a(6/1)	_b	8	_b	-	-	-	T
W *Hieracium umbellatum*	_b	30a	1b	xb	_b	2	-	-	T
D *Inula salicina*	_b	77a(37/-)	5b	11b	_b	2	-	-	T
A *Myosotis stricta*	_b	24a	_b	2b	_b	-	-	-	T
M *Phleum pratense pratense*	4ab	18a	_b	_b	_b	6	0.56	0.05	T
A *Polygala vulgaris*	_c	72a	10bc	35ab	15 bc(1/1)	2	1.70	0.05	T
M *Rumex acetosa*	_b	67a(1/-)	2b	_b	_b	5	-	-	T
D *Sagina nodosa*	_b	6a(82/73)	_b	_b	_b(2/1)	5	0.04	0.03	LP/T
A *Satureja acinos*	_b	30a(7/2)	_b	_b	_b	..	0.22	0.06	T
Species only significantly present in the former cultivated fields									
W *Agrimonia eupatoria*	_b	61a	56a	76a	_b	4	-	-	T
A *Arenaria serpyllifolia*	5ab(167/88)	17b(5/21)	2ab(29/26)	36a(8/3)	1b(9/3)	-	0.05	0.03	SP/LP
M *Anagallis arvensis*	_b	33a(3/40)	12ab	3ab	_b	6	-	-	LP/T
A *Arabis hirsuta*	_b	66a(11/1)	12ab(-/1)	12ab(-/1)	5b(3/-)	-	0.10	0.13	T
A *Cerastium* cf. *fontanum*	_b	45a	29ab	44a	_b	5	-	..	
A *Fragaria viridis*	_c(7/-)	79ab	5ab (2/3)	19ab(4/9)	xb(-/1)	1	0.03	0.09	LP/T
A *Hypericum perforatum*	_b	90a(118/101)	28ab(21/17)	54a(61/28)	xb	-	-	-	SP
A *Lotus corniculatus*	_c	73a(3/-)	12bc	36ab(2/-)	9bc(1/-)	3	0.93	0.03	T
M *Medicago falcata*	_b	3b	60a(4/1)	68a(1/-)	_b	-	-	-	T
M *Medicago hybrida*	_b	_b	68a	17ab	_b	-	-	-	T
A *Medicago lupulina*	21bc	100a(20/6)	53ab(58/6)	77ab(21/5)	xc(-/1)	-	1.37	0.02	SP/T
A *Phleum pratense bertolonii*	_b	14ab	15a	7ab	_b	4	0.20	0.04	T
W *Poa angustifolia*	_b(3/3)	88a(5/2)	100a(28/1)	71ab(2/3)	_b	3	0.18	0.10	LP/T
A *Polygala amarella*	_b	37a	11ab(1/-)	25ab	_b	-	..	..	T
D *Potentilla reptans*	6b(4/19)	63a(51/40)	68a(255/142)	55a(114/153)	_b	5	0.24	0.03	LP/SP
A *Primula veris*	_b	8ab	7ab	38a	xb	3	0.96	0.03	T
A *Prunella vulgaris*	_b	77a(27/15)	_b	12ab(3/1)	_b	-	0.46	0.05	T/SP
A *Sedum acre*	_b(-/3)	16a(5/4)	100a(22/1)	100a(5/-)	17bc	3	0.35	0.04	T
A *Trifolium pratense*	_b	81a(1/-)	32ab	26ab(1/-)	_b	..	1.43	0.03	T
Species without a significant preference									
M *Achillea millefolium*	75ab(13/13)	99a(1/2)	74ab	62ab	46b(1/-)	5	0.12	0.14	T/LP
A *Agrostis capillaris*	-	-	1	9	2(9/3)	3	-	-	T/SP
A *Agrostis stolonifera*	..	x(5/1)	-	-	-	5	-	-	T
W *Alchemilla glaucescens*	..	1	-	4	-	-	0.51	0.03	T
A *Allium oleraceum*	-	x	2	2	-	4	-	-	T
M *Alyssum alyssoides*	1	..	-	-	-	1	-	-	T
A *Artemisia campestris*	-	-	-	-	x	2	-	-	T
M *Barbarea vulgaris*	2(3/3)	x(3/1)	-	-	-	6	-	-	LP/T
M *Bellis perennis*	-	1	-	-	-	5	-	-	T
A *Bromus hordeaceus*	3	-	2	-	x	3	3.73	0.14	T
A *Campanula rotundifolia*	_b	9ab(1/-)	3ab	5b	37bc(20/15)	2	0.06	0.09	T/SP
D *Carex tomentosa*	-	x	-	x(1/-)	-	-	-	-	T
A *Centaurea scabiosa*	20(1/-)	x	-	-	-	3	-	-	T
A *Cerastium fontanum*	59a(29/9)	38ab(52/14)	15b(32/8)	43ab(13/6)	19ab(42/9)	5	0.10	0.02	SP
A *Cerastium glutinosum*	3	2(1/1)	-	-	1	-	-	-	T
A *Cerastium pumilum*	-	3	-	-	-	-	-	-	T
A *Cerastium semidecandrum*	-	3	3	x	1	-	-	-	T
W *Crataegus laevigata*	-	1	1	2	..	-	-	-	T
A *Dactylorhiza sambucina*	-	-	-	-	x	-	-	-	T
M *Festuca pratensis*	2	-	-	4	-	6	-	-	T
M *Festuca rubra*	-	-	1	-	-	-	-	-	T
W *Galium aparine*	1	-	-	-	-	8	-	-	T
A *Geranium columbinum*	-	x	6	-	-	-	-	-	T
M *Geranium molle*	2	-	x	-	..	4	-	-	T
A *Globularia vulgaris*	-	x	-	-	1(1/-)	-	..	-	T
D *Gymnadenia conopsea*	-	1	-	-	-	-	-	-	T
M *Heracleum sphondylium*	-	-	x	-	-	8	-	-	T
A *Hieracium pilosella*	_b	45ab	35b	94a	23 b	2	0.15	0.13	T
A *Juniperus communis*	_c	55ab	9c	30ab	13 bc	-	6.84	0.06	T
A *Knautia arvensis*	-(1/-)	4	21	9	3	3	2.25	0.09	T
M *Linaria vulgaris*	-(1/1)	x(-30?)	3(1/-)	-	-	3	-	-	LP/T
A *Luzula multiflora*	-	x	x	-	-	3	-	-	T
A *Myosotis ramosissima*	3	-	x	..	x	-	-	-	T
A *Orchis mascula*	-	-	x	2	5	3	-	-	*
D *Orchis militaris*	-	x	8			2	..	-	*

App. 1, cont.

Species	Still cult.	20-26 years ab.	26 years ab.	48 years ab.	Not cult.	N-figure Ellenberg	Seed weight (mg)	Seed shape variance	Seed bank class.
A *Pimpinella saxifraga*	-	15	-	30	-	2	-	-	T
A *Poa compressa*	-[b](1/1)	74[a](25/16)	88[a](20/11)	3[b](4/6)	-[b](2/1)	2	0.12	0.10	SP/LP/T
D *Platanthera chlorantha*	-	34	13	14	1	-	-	-	*
A *Potentilla argentea*	4(1/2)	6(7/6)	23(82/23)	7(14/15)	-	1	-	-	SP/T
D *Potentilla erecta*	-	1	-	-	-	2	0.36	0.02	T
W *Prunus spinosa*	-[c]	15[c]	83[a]	63[ab]	30 [bc]	-	106.79	0.05	T
W *Pyrus communis*	-	-	-	1	-	-	-	-	T
M *Raphanus raphanistrum*	2	-	-	-	-	5	-	-	T
W *Rosa* cf. *canina*	-	11	8	13	x	-	-	-	T
M *Rumex crispus*	2	-	-	-	-	5	-	-	T
A *Saxifraga tridactylites*	-	2(54/144)	-(16/40)	-(1/1)	-	1	-	-	LP/T
A *Scabiosa columbaria*	20[a]	-[b]	-[b]	-[b]	16[ab]	3	0.56	0.09	T
A *Scleranthus perennis*	-	-	19	-	-	1	-	-	T
A *Sedum album*	-	-	-	-(3/5)	1	1	-	-	SP/T
A *Sedum reflexum*	-(-/1)	-	5	-	9(7/2)	-	0.02	0.09	T
A *Silene nutans*	-	-	-	-	1	3	-	-	T
A *Silene vulgaris*	1	-	-	-	-	2	-	-	T
A *Stellaria graminea*	-(1/-)	-	p	-(2/-)	-(1/-)	-	-	-	T
M *Trifolium dubium*	7	-	-	-	-	4	-	-	T
W *Trifolium medium*	-	-	p	10	-	3	-	-	T
W *Trifolium montanum*	-	1	2	x	-	2	0.57	0.03	T
A *Trifolium repens*	-(2/1)	x	3(1/1)	x	1(12/22)	7	-	-	LP/T
A *Trifolium striatum*	-(1/-)	-	-	2	-(2/-)	-	-	-	T
W *Veronica officinalis*	-(1/-)	1	-	12(-/1)	-	4	-	-	T
D *Veronica serpyllifolia*	-	-(23/28)	-(1/1)	-(1/1)	-	-	-	-	LP/T
A *Vicia hirsuta*	3(3/1)	-	-	-	-	3	-	-	T
? *Taraxacum* spec.	78[a](1/1)	2[b](1/-)	22[ab]	30[ab]	12 [b](2/1)	-	-	-	T
Species only occurring in the seedbank									
A *Arabis glabra*	-(1/-)	-	-	-	-	5	-	-	T
M *Atriplex littoralis*	-(-/1)	-	-	-	-	7	-	-	T
W *Betula pubescens*	-	-	-	-	-(1/-)	3	-	-	T
M *Capsella bursa-pastoris*	-(2/1)	-	-	-	-	5	-	-	T
D *Carex oederi*	-	-	-	-	-(1/-)	2	-	-	T
A *Chaenorrhinum minus*	-	-(20/19)	-(4/5)	-(2/3)	-	-	-	-	LP/SP
M *Chenopodium album*	-(63/55)	-	-(1/1)	-(1/2)	-	7	-	-	SP/T
A *Draba incana*	-(11/8)	-	-	-	-	-	-	-	SP
D *Eleocharis uniglumis*	-	-(1/-)	-(1/-)	(1/-)	-(1/-)	5	-	-	T
M *Erigeron canadensis*	-(1/-)	-	-	-	-	-	-	-	T
A *Erodium cicutarium*	-(3/-)	-	-	-	-	-	-	-	SP
A *Herniaria glabra*	-(3/1)	-(20/5)	-	-	-(-/1)	4	-	-	SP/T
A *Hornungia petraea*	-(1/-)	-	-	-	-	1	-	-	T
D *Juncus articulatus*	-(5/3)	-(5/3)	-(13/5)	(4/1)	-(18/19)	2	-	-	SP/LP/T
D *Juncus bufonius*	-	-(13/10)	-(2/4)	-(2/2)	-(13/16)	-	-	-	LP/SP/T
A *Leontondon autumnalis*	-	-	-	-	-(1/-)	5	-	-	T
M *Medicago minima*	-(4/1)	-	-	-	-	1	-	-	SP
M *Papaver dubium*	-(-/1)	-	-	-	-	5	-	-	T
M *Papaver rhoeas*	-(-/1)	-	-	-	-	6	-	-	T
D *Salix caprea*	-	-	-	-	-(-/1)	7	-	-	T
A *Senecio sylvaticus*	-	-	-	-	-(-/1)	8	-	-	T
M *Sinapis arvensis*	-(1/-)	-	-	-	-	6	-	-	T
M *Sonchus arvensis*	-	-(2/-)	-	-	-	-	-	-	T
M *Papaver agremone*	-	-	-(-/1)	-	-	5	-	-	T
M *Plantago major*	-	-(2/12)	-	-	-	6	-	-	LP/T
M *Thlaspi arvensis*	-(-/1)	-	-	-	-	6	-	-	T
D *Typha angustifolia*	-	-(-/1)	-(1/-)	-(4/1)	-(1/-)	7	-	-	SP/T
W *Veronica chamaedrys*	-(24/2)	-	-	-	-	-	-	-	SP
M *Viola arvensis*	-(5/-)	-	-(-/3)	-(-/1)	-	-	-	-	SP/LP/T
A *Viola rupestris*	-	-	-	-	-(6/-)	2	-	-	SP
A *Viola tricolor*	-(2/3)	-	-	-	-	6	-	-	T
? *Crepis* spec.	-(1/-)	-	-	-	-	-	-	-	T
? *Juncus* spec.	-	-	-(1/-)	-	-	-	-	-	T
Unidentified species	-	(2/-)	(1/-)	(2/-)	-	-	-	-	T1

Fragmented grasslands on the Baltic island of Öland: Plant community composition and land-use history

Honor C. Prentice[1],*, B. Olle Jonsson[1,2], Martin T. Sykes[3],
Margareta Ihse[4] & Merit Kindström[4]

[1]*Plant Ecology & Systematics, Department of Ecology, Lund University, SE-223 62 Lund, Sweden;* [2]*Länsstyrelsen i Östergötland, Miljövårdsenheten, SE-581 86 Linköping, Sweden;* [3]*Geobiosphere Science Centre, Department of Physical Geography & Ecosystems Analysis, Lund University, SE-223 62 Lund, Sweden;* [4]*Department of Physical Geography, Stockholm University, SE-106 91 Stockholm, Sweden;*
**Corresponding author; E-mail honor_c.prentice @ekol.lu.se*

Abstract

The relationships between properties of present landscapes and species diversity within fragmented grasslands have been the subject of many studies. However the potential roles of grassland history and past landscape structure as determinants of diversity have not been widely studied. We therefore focus on these roles with an overview of patterns of variation in plant community composition in grassland fragments, of known ages, within a 22 km^2 site around the village of Jordtorp on the Baltic island of Öland. While the frequencies of individual vascular plant species in 328 50 cm × 50 cm quadrats showed trends related to grassland continuity and previous land use, the dominant gradients of plant community composition were interpreted in terms of gradients of soil moisture and eutrophication. Because relationships between grassland age and plant community composition are confounded by local grassland eutrophication, it is difficult to use the present grassland data set to draw conclusions about the extent to which the distributions of individual species reflect a long history of continuous grassland management or an absence of eutrophication. Our results suggest that studies that attempt to explore associations between grassland age and fine-scale species richness, or the occurrence of individual species, should be based on sampling rules that standardize the type of plant community that is to be compared between grassland fragments.

Keywords: Eutrophication; Gradient; Grassland history; Habitat continuity; Plant species occurrence.

Nomenclature: Karlsson (1998).

Abbreviations: CIR = Colour infra-red; PA = Previously arable; PF = Previously forest; RA = Recently arable.

Introduction

The structure of European agricultural landscapes is changing rapidly. Landscapes with a long land-use history and a close connection between local animal husbandry and crop production are increasingly being replaced by regionally specialized landscapes (e.g. Jongman 1996; Stoate et al. 2001).

Traditionally-managed cultural landscapes are often characterized by a high structural diversity (e.g. Skånes & Bunce 1997) and support high levels of species diversity (e.g. Bernes 1994). These types of economically-unproductive grassland habitats are becoming increasingly rare in Europe (e.g. Bruun et al. 2001; Poschlod & WallisDeVries 2002). For example, within Sweden, the area occupied by unimproved pastures and hay meadows has decreased by more than 90% since the 1870s (Bernes 1994) and the remaining traditionally-managed grasslands are fragmented and disjunct. There is currently considerable interest in the conservation and management of pastures and meadows, and their rich floras and faunas (e.g. Blackstock et al. 1999; Norderhaug et al. 2000; WallisDeVries et al. 2002; Pärtel et al. 2005).

Pastures and hay meadows are among the most species-rich habitats in Europe (e.g. Kull & Zobel 1991; van der Maarel & Sykes 1993; Dupré & Diekmann 2001). Abandonment of grazing and mowing and the rapid fragmentation of such grassland habitats is accompanied by the local extinction of grassland plants, the isolation of the remaining populations and the loss of both species and gene diversity (e.g. Rejmánek & Rosén 1988; Fischer & Stöcklin 1997; Rosquist & Prentice 2000; Cousins & Eriksson 2001, 2002; Kiviniemi & Eriksson 2002; Pluess & Stöcklin 2004).

The current interest in biodiversity in agricultural landscapes has not only focussed attention on the relationships between present landscape structure and species diversity but also on the possibility that levels of species

diversity may reflect historical processes within earlier landscapes.

Different classic ecological models predict how species co-existence and diversity may be influenced by factors such as disturbance or nutrient-availability (e.g. Connell 1978; Grime 1979). Other diversity models include stochastic processes (e.g. van der Maarel & Sykes 1993, 1997) or the dynamics of species pools (e.g. Eriksson 1996; Pärtel et al. 1996; Zobel 1997). However, it is becoming increasingly clear that field-based attempts to test hypotheses about the control of species diversity may be severely limited by the fact that present levels of diversity may depend on historical processes – as well as on the present demographic and structural properties of populations and landscapes (e.g. Norderhaug et al. 2000; Eriksson et al. 2002; Lindborg & Eriksson 2004; Helm et al. 2006).

We have established a study area, including the village of Jordtorp, on the Baltic island of Öland that will allow the inclusion of data on historical landscape structure and habitat continuity in investigations of the mechanisms controlling species diversity and genetic diversity within grasslands. The mosaic structure of the landscape means that there is spatial replication of different present-day land-use categories/vegetation types. The grassland fragments that represent different historical continuity classes are also spatially scattered within the landscape (Johansson et al. in press).

As a first step in the design of future sampling protocols for species diversity, we require an overview of the major gradients of vegetation composition in the species-rich grasslands within the Jordtorp area. Here we characterize gradients of grassland community composition and explore the extent to which the distributions of individual species, as well as variation in vegetation composition, are related to grassland continuity and previous land use.

Material and Methods

The Jordtorp study area: The present landscape

The study site (centred on 56°40'49" N, 16°33'58" E) is located in the parish of Algutsrum in the central part of the Baltic island of Öland, covers an area of ca. 22 km² and includes the land associated with Jordtorp and four adjacent villages: Övetorp, Holmetorp/Hässleby, Hult and Törnbotten. The limestone bedrock of the area is mostly overlain by varying depths of neutral to weakly-acidic moraine. The topography is generally flat, but the area is crossed by a few low ridges of coarse sedimentary material (Forslund 2001) (Fig. 1). The annual mean temperature on Öland is 7 °C, with a July mean of 17 °C and a January mean of –1 °C (Alexandersson et al. 1991). The island is in the rain shadow of the Swedish mainland and the mean annual precipitation is low (400 mm).

The present landscape consists of a mosaic of arable cultivation (mostly concentrated within the areas adjacent to the villages), semi-natural grasslands and deciduous forest (cf. Göransson 1969). There are small disjunct fragments of alvar vegetation (cf. Ekstam & Forshed 2002) in sites with flat, outcropping limestone bedrock and thin base-rich soils. The area also contains a number of small fens and shallow (often ephemeral) wetlands.

Much of the forest vegetation in the area has an open character and the underlying herb layer contains many grassland species. These open forests appear to represent a succession from more-or-less sparsely tree-covered outfield pastures, whereas forest areas with a typical forest herb layer flora are often found in enclosed areas nearer to the villages (cf. Göransson 1969).

Most fragments of semi-natural grassland within the study area contain dry grassland vegetation although there are a few patches of moist grassland with a flora that indicates previous management as hay meadows (Lindahl & Vik 1997).

Fig, 1. View to the east along the glacio-fluvial ridge of Jordtorpsåsen. The dry grasslands belong to the continuity category OLD (see Table 1) and have had at least 270 years of grassland continuity. The trees are *Sorbus intermedia* (photo: Triin Reitalu).

Land-use history and the historical map database

Animal husbandry was historically important on Öland. Until the middle of the 18th or the early 19th century, the common pastures ('utmarker' or out-fields, comprising both grasslands and unfenced, open wooded pastures) lay outside the villages and were shared by the farms belonging to the village (Göransson 1969). Most of the land used for arable cultivation and hay production was restricted to small fields ('inägor' or in-fields), adjacent to the villages (Göransson 1969). An attempt to rationalize the agricultural landscape was made in a series of Enclosure Acts during the late 18th century and the first half of the 19th century (Tollin 1991). The villages in the Jordtorp area are covered by survey maps dating from 1723-33 as well as by cadastral maps (1801-1810; 1821-1851) that were produced in connection with the Enclosure Acts (cf. Tollin 1991). In addition, data on historical land use are available from black and white aerial photographs (1938; 1959) and the modern landscape is covered by colour infra-red (CIR) aerial photos from 1994.

A map database has been constructed to cover the land-use history of the Jordtorp area from 1723/33 to the end of the 20th century (Johansson et al. in press). The base map for the database is a land-use/vegetation map for 1994/1997 derived from the interpretation of CIR aerial photos (taken in 1994) supported by ground validation in 1997. This base map is at the scale of 1:10 000 and all the maps for the earlier time periods are rectified and justified relative to the base map. GIS overlay analysis was used to determine continuity classes for all the map polygons (ranging in size from ca. 0.1 ha to 14.0 ha) that were classed as 'semi-natural grassland' in the 1994/1997 base map of the Jordtorp area (Johansson et al. in press).

Grassland continuity classes

In the present study, we defined the time categories for the different classes of grassland continuity in relation to 1998, the year when the vegetation sampling was carried out (Table 1).

The map polygons from which we recorded vegetation data are assigned to four main land-use history categories:
OLD (old grassland), PF (grassland that was previously forest), PA (grassland that was previously under arable cultivation) and RA (young grasslands on recently abandoned arable land). The polygons that belong to the historical land-use categories (OLD, PF and PA) were classified as 'semi-natural grassland' in the 1994/1997 base map. The land-use category RA polygons were classified as 'cultivated grassland' in the 1994/1997 base map (Johansson et al. in press).

The old grasslands (category OLD) have had a continuous history of at least 270 years as grassland. The pre-1700 history of the old grasslands is not known, but it is likely that many of these grasslands are considerably older than 300 years.

The categories PF and PA represent intermediate-aged grasslands that were forested or used for arable cultivation at some stage during the last 177 years and which have had a grassland history of less than 177 years. Both the PF and PA grasslands are divided into three subcategories based on the age of their transition from forest or arable to grassland. The PF_{100} polygons have been grassland since at least 1938 but were classed as forest in 1821/1851 (ca. 100 years of grassland continuity; Table 1), and the PF_{50} polygons have been grassland since at least 1959 but were classed as forest in 1938 (ca. 50 years of grassland continuity; Table 1). The PA_{100} polygons have been grassland at least since 1938 but were arable in 1821/1851 (ca. 100 years of grassland continuity; Table 1). The PA_{50} polygons have been grassland at least since 1959 but were arable in 1938 (ca. 50 years grassland continuity; Table 1).

The PF_{25} and PA_{25} polygons (ca. 25 years of grassland continuity; Table 1) were classified as forest and arable, respectively, in 1959 (Johansson et al. in press).

It takes at least 15 years for abandoned arable fields to develop a 'signature' that allows them to be scored as semi-natural grassland in CIR photographs (M. Ihse pers. obs.). Therefore the fact that the PA_{25} polygons were recognizable as 'semi-natural grassland' in the 1994 IR aerial photos indicates that arable cultivation ceased at least 15 years earlier and, in 1998, these polygons had had a grassland continuity that was longer than 19 years. In contrast, because much of the forest in the Jordtorp area is open and characterized by a grassland flora (cf. Ekstam & Forshed 1992), the transition to semi-natural grassland after forest clearance may be more rapid than the arable-to-grassland transition. PF_{25} polygons that were interpreted

Table 1. Numbers of sampled map polygons and vegetation quadrats within different grassland continuity classes in the Jordtorp area. Details of the land-use history categories are given in the text: all time intervals are given in relation to 1998 (the year of the vegetation survey).

Land-use history category /grassland continuity class	No. sampled polygons	No. sampled quadrats
Polygons classified as 'semi-natural grassland' in the 1994/1997 base map		
Grassland ca. 270 years ago (OLD)	45	174
Forest 60–177 years ago (PF_{100})	5	25
Forest 39–60 years ago (PF_{50})	1	4
Forest ca. 5–39 years ago (PF_{25})	6	20
Arable 60–177 years ago (PA_{100})	10	24
Arable 39–60 years ago (PA_{50})	7	17
Arable ca. 19–39 years ago (PA_{25})	15	44
Grasslands with no historical documentation (G)	5	13
Polygons classified as 'cultivated grassland' in the 1994/1997 base map		
Recently arable (RA)	2	7
Total	96	328

as 'semi-natural grassland' in the 1994 IR aerial photos might thus have been cleared only a few years earlier.

Polygons in the category 'recently arable' (RA) were interpreted as 'cultivated grassland' (including both grass leys and recently-abandoned arable fields) in the 1994 aerial photos. In 1998, these grasslands were still in the process of reverting to semi-natural grassland.

Collection of vegetation data

Vegetation data were collected between 3 June and 13 July 1998, from semi-natural grassland polygons that were spread throughout the study area and represented the range of polygon sizes as well as the seven different historical land-use classes (Table 1). We also collected data from a limited number of polygons that were classified as 'cultivated grassland' in the 1994/1997 base map. Data were not collected from wetland vegetation, from moist grasslands (dominated by *Sesleria uliginosa* or *Molinia caerulea*) or from 'alvar' vegetation on thin base-rich soils.

Within each sampled polygon, we divided up the grassland plant communities into 'vegetation types' and randomly laid out 50 cm × 50 cm quadrats within each of the vegetation types. Frequency data (based on presence/absence in 25 5 cm × 5 cm sub-quadrats within each quadrat) were collected for vascular plant species.

The nutrient status of each quadrat was subjectively assessed (in terms of overall appearance, vegetation colour and lushness, and presence/absence of animal dung). Nutrient status was scored as: 0 = no indication of eutrophication; 1 = indications of some eutrophication; 2 = indications of heavy eutrophication.

Data analyses

Data were analysed using Detrended Correspondence Analysis (DCA) (program MVSP; Kovach 1998) to produce quadrat- and species-ordinations based on frequency data for the individual species in the 328 sampled quadrats. Ellenberg nitrogen (N) values (Ellenberg et al. 1991), were assigned, where available, to individual species and plotted on the species-ordination. These N-values provided additional qualitative information on nutrient status that was used in the interpretation of the ordination axes. A number of recent studies support the validity of using Ellenberg values as habitat indicators, even in areas outside their original central European context (e.g. Ekstam & Forshed 1992; Diekmann 1995; Diekmann & Falkengren-Grerup 1998; Hill et al. 1999).

Results

Species occurrences in relation to grassland continuity

The occurrences of the individual species (percentage quadrat presence and average frequency within quadrats) in the different grassland continuity categories are summarized in App. 1. Of the grassland species that were present in five or more of the 328 quadrats, few (e.g. *Antennaria dioica, Sagina nodosa, Sedum rupestre, Silene nutans,* and *Vicia tetrasperma*) were restricted to OLD grasslands. No grassland species was found exclusively in the quadrats from previously forested (PF) grassland polygons. The species that were restricted to polygons classed as either OLD or PF, and were absent from previously arable (PA) polygons, included, for example, *Artemisia campestris, Orchis mascula, Sedum album* and *Trifolium medium.*

A larger set of species had their highest presence and frequencies in quadrats from OLD and PF polygons, had lower presence and frequencies in the PA_{100}, PA_{50} and PA_{25} polygons, and were absent from the recently arable (RA) polygons (see App. 1). This set of species included *Agrostis vinealis, Anemone pratensis, Asperula tinctoria, Danthonia decumbens, Festuca ovina, Helianthemum nummularium, Melampyrum cristatum, Poa compressa, Prunella grandiflora, Satureja acinos, Sedum acre* and *Thymus serpyllum.* Ekstam & Forshed (1992) classed many of these species as being characteristic of traditionally-managed pastures.

A suite of species that had their highest frequencies and/or percentage presence (see App. 1) in grasslands from previously arable (PA) polygons included, for example, *Briza media, Campanula persicifolia, Cerastium arvense, Convolvulus arvensis, Fragaria viridis, Helictotrichon pubescens, Knautia arvensis, Medicago lupulina, Polygala comosa, Rumex acetosa, Veronica chamaedrys.*
Species with their highest frequencies and/or percentage presence in grasslands on recently abandoned arable fields included *Daucus carota, Festuca rubra, Prunella vulgaris* and *Saxifraga granulata.*

A set of annual species, including for example, *Aphanes arvensis, Rumex tenuifolius, Vicia lathyroides* and *Viola arvensis* was largely absent from the PA quadrats, but present in both OLD/PF and RA quadrats.

Gradients of plant community composition

The grassland history/continuity category (Table 1) for each quadrat is superimposed on the DCA (axes 1 and 2) quadrat-ordination (Fig. 2). The first two axes of the quadrat ordination had eigenvalues of 0.472 and 0.319, and the cumulative variance accounted for by these axes was 9.33%. While there is no obvious relationship between species composition and grassland history/continu-

Fig. 2. Grassland continuity categories plotted on the first two axes of the quadrat-ordination from a DCA based on the frequencies of 217 species of vascular plants in 328 quadrats from fragmented grasslands in the Jordtorp area on the Baltic island of Öland. The grassland continuity classes (see Table 1) are indicated by the following symbols:

● = OLD, ▲ = PF100, ■ = PF50,
◆ = PF25, □ = PA100, ◇ = PA50,
▽ = PA25, △ = RA, ○ = G.

The %-presence and frequencies of the individual species in the continuity/land-use categories OLD, PF, PA_{100}, PA_{50}, PA_{25} and RA are summarized in App. 1.
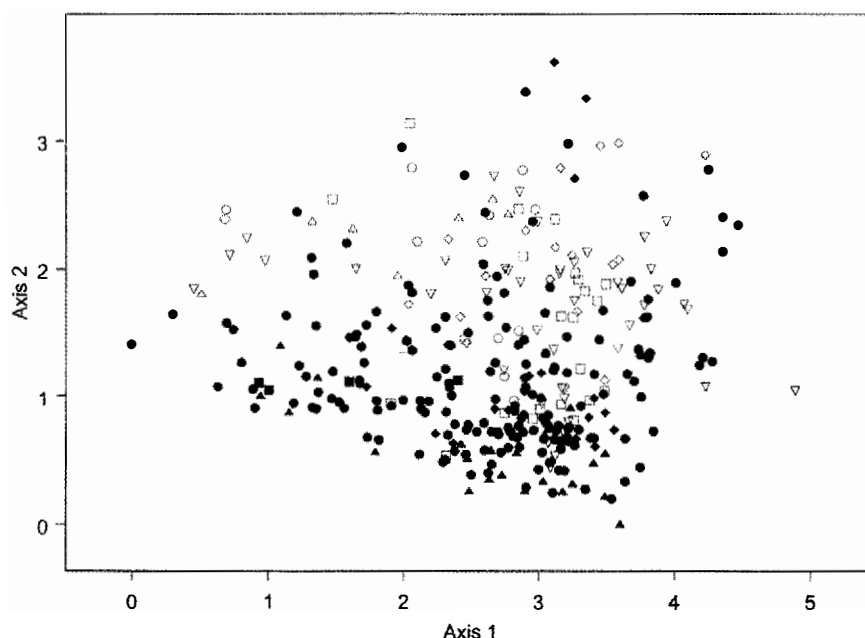
Fig. 3. Plots of within-quadrat frequencies for eight vascular plant species. The plots are based on the same quadrat-ordination (DCA) as Figs. 2 and 4. The species illustrate different types of distribution in relation to gradients of moisture (axis 1), eutrophication (axis 2; cf. Figs. 4 & 5) and categories of grassland continuity (cf. Fig. 2 & App. 1) *Anemone pratensis* (highest presence/frequency in OLD and PF; no eutrophication), *Artemisia campestris* (only in OLD and PF; no eutrophication), *Sedum acre* (highest presence/frequency in OLD and PF; dry; no eutrophication), *Asperula tinctoria* (highest presence/frequency in OLD and PF; moist; no eutrophication), *Bromus hordeaceus* (highest presence/frequency in OLD and PF; dry; indifferent to eutrophication), *Centaurea jacea* (highest presence/frequency in PA; moist; indifferent to eutrophication), *Lolium perenne* (highest presence/frequency in RA and PA; dry to moist; eutrophicated) and *Potentilla reptans* (moist; eutrophicated). The quadrats in which a species occurred are indicated by filled circles, and the within-quadrat frequency of the species is indicated by the size of the circle. Quadrats in which the species was absent are indicated by dots.
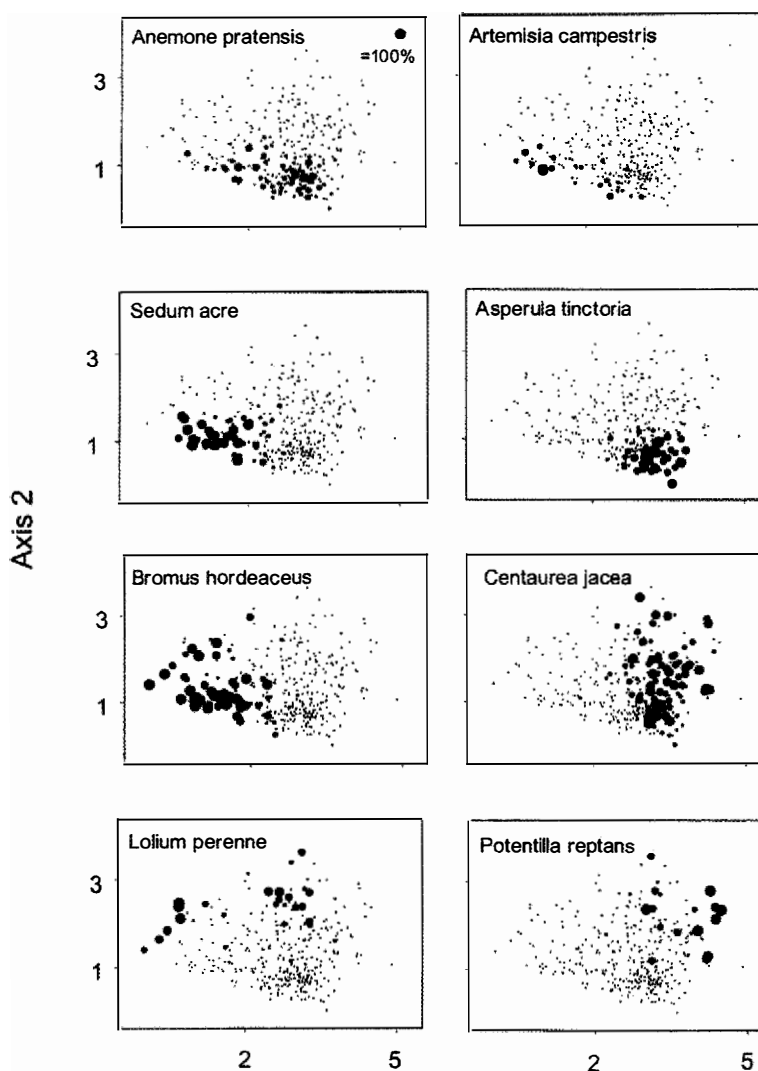
ity on the first axis, there is a tendency for quadrats from younger grasslands on previously arable sites (PA$_{25,50,100}$) to have higher scores on axis 2. Quadrats from the OLD grasslands are mostly concentrated on the lower half of the second axis, but some OLD grasslands also have high scores on axis 2.

The first ordination axis represents a moisture gradient (cf. Bengtsson et al. 1988). Species such as *Bromus hordeaceus* (Fig. 3), *Scleranthus annuus* and *Sedum acre* (Fig. 3) that are typically associated with dry grassland habitats on Öland have low scores on axis 1. Species that are characteristic of somewhat moister grasslands (e.g. *Asperula tinctoria* (Fig. 3), *Centaurea jacea* (Fig. 3), *Danthonia decumbens, Potentilla reptans* (Fig. 3) *Sesleria uliginosa* and *Succisa pratensis*) have high scores on axis 1.

The field assessment of the nutrient status of the individual quadrats is superimposed on the quadrat-ordination

in Fig. 4. This figure suggests that the second ordination axis represents a nutrient/eutrophication gradient. All the quadrats scored as showing indications of heavy eutrophication (2) have high scores on axis 2, while quadrats scored as having no indication of eutrophication (0) are mostly concentrated towards the bottom of the axis.

The plot of Ellenberg N-values on the species-ordination in Fig. 5 supports the interpretation that axis 2 represents a eutrophication gradient. No species with N-values of 1 (i.e. species that are intolerant of N; e.g. *Festuca ovina, Helianthemum nummularium, Sedum acre* (Fig. 3)) are found in the upper half of axis 2. Species with high (4-8) N-values (e.g. *Bellis perennis, Lolium perenne* (cf. Fig. 3), *Potentilla reptans* (cf. Fig. 3)) are predominantly found in the upper half of axis 2, while most occurrences of species with N-values of 3 or less (cf. *Anemone pratensis* and *Asperula tinctoria* in Fig. 3) are found in the lower
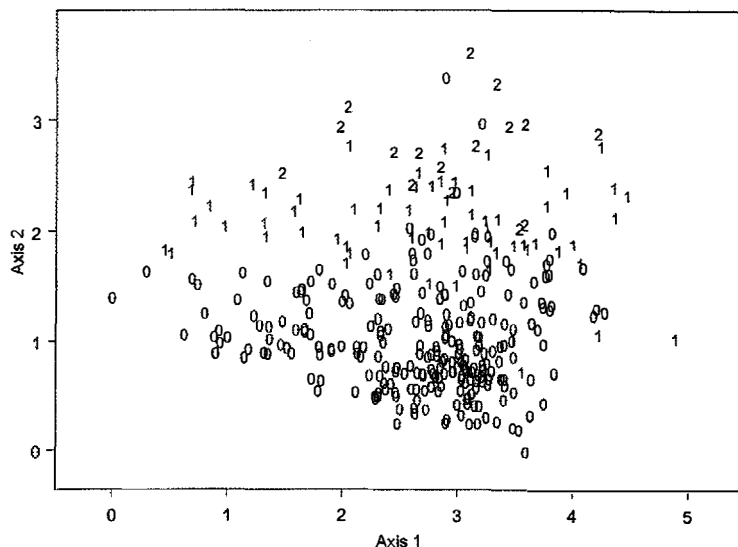

Fig. 4. Eutrophication categories plotted on the first two axes of the same DCA (quadrat) ordination as in Fig. 2. The quadrats were assigned in the field to three, subjectively assessed, categories: 0 (no indication of eutrophication), 1 (some indication of eutrophication) and 2 (indications of heavy eutrophication).
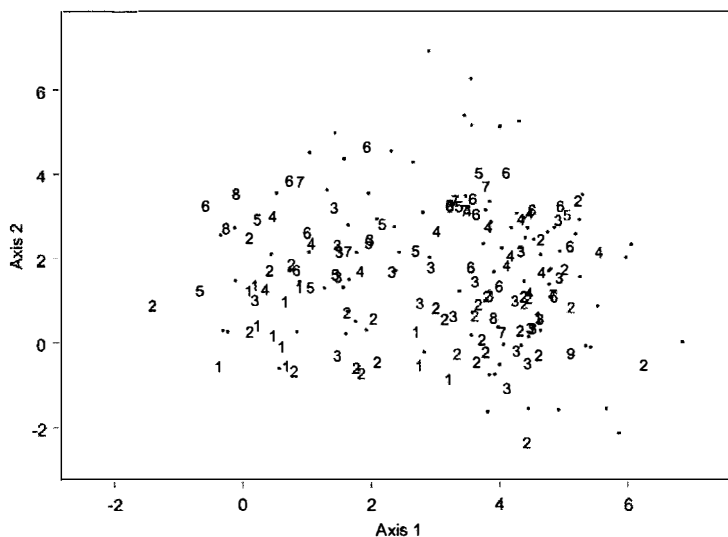

Fig. 5. Ellenberg nitrogen (N) values (Ellenberg et al. 1991) plotted on the species-ordination from the same DCA analysis as in Figs. 2 & 4. The Ellenberg N values 1 to 8 indicate species that are associated with low to high levels of nitrogen. Other species are indicated by dots.

half of axis 2. A few species, such as *Geranium dissectum*, *Draba muralis* and *Vicia tetrasperma*, have high Ellenberg N-values (4-6), yet have low scores on axis 2. These annual species also have low scores on axis 1 and are restricted to dry habitats. They characteristically occur in small gaps in the grass sward that are associated with fine-scale disturbance, trampling and dung-deposition by cattle. A few other species with high (6-8) N-values and low scores on axis 2 have high scores on axis 1 (i.e. occur in moister vegetation). This group of species also includes annuals that rely on disturbance and gap-formation for their establishment (e.g. *Myosotis arvensis*), as well as tree (*Fraxinus excelsior*) seedlings.

Discussion

A survey of dry alvar grasslands on Öland (Bengtsson et al. 1988) showed that the main gradients of variation in unimproved grassland vegetation types on the island are related to pH/soil depth, and to soil moisture. The Bengtsson et al. (1988) survey included both true alvar (shrub-heath) vegetation on thin soils overlying limestone bedrock (cf. Ekstam & Forshed 2002) as well as species-rich grasslands on deeper, neutral to weakly acidic morainic soils. The few patches of true alvar vegetation that occur on thin calcareous soils on outcropping limestone bedrock in the Jordtorp area were not included in the present study and the plant communities described here represent a limited subset of those described by Bengtsson et al. (1988). The first and second ordination axes are short, and the main trends of variation in the studied vegetation are not related to soil pH. The majority of the grassland fragments in the Jordtorp area occur on neutral (pH 6.5 - 7.0) morainic soils (T. Reitalu & M. Vandewalle, unpubl. data). The main gradient of variation in plant community composition, represented by the first ordination axis, in the Jordtorp study is explained by soil moisture. In contrast to the unimproved grasslands that were the focus of the Bengtsson et al. (1988) survey, a proportion of the grasslands in the Jordtorp area are close to villages or farms. These grasslands are subject to eutrophication by concentrations of cattle (or, less commonly, sheep). Variation in plant community composition along the second ordination axis is interpreted in terms of a nutrient/eutrophication gradient.

The presence and frequencies of many plant species in the Jordtorp area are related to grassland age and the previous land use of the younger grasslands (see App. 1). Some species have their highest percentage presence and/or frequencies in young grasslands on previously arable sites (PA) and decline in presence/frequency with increasing grassland age. This suite of species includes species that are characteristic of recently abandoned arable fields (e.g. *Veronica chamaedrys* and *Convolvulus arvensis*). A number of species (e.g. *Briza media*, *Phleum phleoides*

and *Saxifraga granulata*) that are generally regarded as indicators of traditionally-managed grasslands (cf. Ekstam & Forshed 1992) also have their highest presence and/or frequency values in young and intermediate-aged grasslands (see App. 1). While these species are typical constituents of old grassland communities in the Jordtorp area, the present study shows that they are also relatively early colonizers of grasslands developing on previously arable sites (cf. Prentice et al. 2006).

A large suite of species shows an opposite trend, with percentage-presence and frequencies that increase to their maxima in the OLD grasslands. Many of these species are regarded as indicators of old, long-continuity grasslands (see e.g. Eriksson 1998; Ekstam & Forshed 1992). Only a small number of species are exclusively found in OLD grasslands and absent from grasslands belonging to the other grassland land-use/continuity categories. However, a larger suite of species is restricted to OLD grasslands together with grasslands that were previously classed as forest (PF), and absent from grasslands that were previously arable (PA). The distinction between forest and grassland within the out-field areas in the study area is often unclear, and areas classed as forest on the basis of tree canopy cover at the present-day may have a field-layer that is rich in grassland species. It is likely that the tree cover on the grazed out-field areas also varied historically (cf. Danielson 1918) – but that much of this area nevertheless supported an unbroken continuity of grassland vegetation. The fact that many species that typically indicate traditionally-managed grassland in Sweden (Ekstam & Forshed 1992) show their highest presence and/or frequencies in the PF, rather than in the OLD grasslands, may be explained by the observation that few quadrats in the PF grasslands show indications of eutrophication.

Although the occurrences of individual plant species show trends that are related to grassland continuity and previous land-use history (App. 1), relationships between the age and previous land use of the grasslands and plant community composition (Fig. 2) are confounded by local eutrophication. The majority of the OLD grasslands (with more than ca. 270 years' continuity as grassland) have low scores on the second ordination axis. The fact that quadrats from the grasslands on previously arable sites ($PA_{25, 50, 100}$), tend to have higher scores on the axis is consistent with the expectation that nutrients will persist in the soil during the succession from arable to grassland. However, a proportion of the quadrats from the OLD grasslands also have high scores on the second ordination axis. Even in old sites, with a long documented history of grassland continuity, local eutrophication may result in the presence of species that are typical of younger grasslands, and the absence of grassland species that are intolerant of eutrophication. It is thus difficult to use the present grassland data set to draw conclusions about the extent to which the distributions of species such as *Artemisia campestris* or *Asperula tinctoria*

(Fig. 3) reflect a long history of continuous management as grassland or an absence of eutrophication. The present results suggest that studies that aim to investigate associations between grassland age or structure (the present and past sizes and distributions of grassland fragments) and fine-scale species richness, or the occurrence of individual species, should be based on sampling rules that standardize the type of plant community that is to be compared in the different grassland fragments.

Acknowledgements

References

Alexandersson, H., Karlström, C. & Larsson-McCann, S. 1991. Temperaturen och nederbörden i Sverige 1961-1990. Referensnormaler — SMHI Meteorologi, rapport 81, 87 pp.

Bengtsson, K., Prentice, H.C., Rosén, E., Moberg, R. & Sjögren, E. 1988. The dry alvar grasslands of Öland, Sweden: ecological amplitudes of plant species in relation to vegetation composition. — Acta Phytogeogr. Suec. 76: 21-46.

Bernes, C. 1994. Biological diversity in Sweden: a country study. — Naturvårdsverket, Solna, 280 pp.

Blackstock, T.H., Rimes, C.A., Stevens, D.P., Jefferson, R.G., Robertson, H.J., Mackintosh, J. & Hopkins, J.J. 1999. The extent of semi-natural grassland communities in lowland England and Wales: a review of conservation surveys 1978-96. — Grass & Forage Sci. 54: 1-18.

Bruun, H.H., Fritzbøger, B., Rindel, P.O. & Hansson, U.L. 2001. Plant species richness in grasslands: the relative importance of contemporary environment and land-use history since the Iron Age. — Ecography 24: 569-578.

Connell J.H. 1978. Diversity in tropical rain forests and coral reefs. — Science, 199: 1302-1310.

Cousins, S.A.O. & Eriksson, O. 2001. Plant species occurrences in a rural hemiboreal landscape: effects of remnant habitats, site history, topography and soil. — Ecography 24: 461-469.

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 Ecol. 17: 517-529.

Danielson, U. 1918. Anteckningar om de Öländska skogarnas historia och utveckling. — Skogsvårdsföreningens Tidskrift 16: 201-262.

Diekmann, M. 1995. Use and improvement of Ellenberg's indicator values in deciduous forests of the Boreo-nemoral zone in Sweden. — Ecography 18: 178-189.

Diekmann, M. & Falkengren-Grerup, U. 1998. A new species index for forest vascular plants: development of functional indices based on mineralization rates of various forms of soil nitrogen. — J. Ecol. 86: 269-283.

Dupré, C. & Diekmann, M. 2001. Differences in species richness and life-history traits between grazed and abandoned grasslands in southern Sweden. — Ecography 24: 275-286.

Ekstam, U. & Forshed, N. 1992. Om hävden upphör: kärlväxter som indikatörarter i ängs- och hagmarker [If grassland management ceases: vascular plants as indicators in meadows and pastures]. — Naturvårdsverket, Solna, 135 pp.

Ekstam, U. & Forshed 2002. Svenska alvarmarker. — Naturvårdsverket Förlag, Stockholm, 222 pp.

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. 1991. Zeigerwerte von Pflanzen in Mitteleuropa (Scripta Geobotanica 18) — Verlag E. Goltze KG., Göttingen, 248 pp.

Eriksson, Å., 1998. Regional distribution of *Thymus serpyllum*: management history and dispersal limitation. — Ecography 21: 35-43.

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

Eriksson, O., Cousins, S.A.O & Bruun, H.H. 2002. Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. — J. Veg. Sci. 13: 743-748.

Fischer, M. & Stöcklin, J. 1997. Local extinctions of plants in remnants of extensively used calcareous grasslands 1950-1985. — Conserv. Biol. 11: 727-737.

Forslund, M. 2001. Natur och kultur på Öland. — Länsstyrelsen i Kalmar län, Kalmar, 463 pp.

Göransson, S. 1969. Morphogenetic aspects of the agrarian landscape of Öland. — Oikos Suppl. 12: 68-78.

Grime, J.P. 1979. Plant strategies and vegetation processes. — John Wiley & Sons, Chichester, 222 pp.

Helm, A., Hanski, I. & Pärtel, M. 2006. Slow response of plant species richness to habitat loss and fragmentation.. — Ecol. Lett. 9: 72-77.

Hill, M.O., Mountford, J.O., Roy, D.B. & Bunce, R.G.H. 1999. Ellenberg's indicator values for British plants. — *ECOFACT*, 2a -Technical Annex. Institute of Terrestrial Ecology, Monks Wood, 46 pp.

Johansson, L.J., Hall, K., Prentice, H.C., Ihse, M., Reitalu, T., Sykes, M.T. & Kindström, M. In press. Semi-natural grassland continuity, long-term land-use change and plant species richness in an agricultural landscape on Öland, Sweden. — Landscape Urb. Plan. (doi:10.1016/j.landurbplan.2007.08.001).

Jongman, R.H.G. (ed.) 1996. Ecological and landscape consequences of land use change in Europe. — Man and Nature 1. European Centre for Nature Conservation, Tilburg, 410 pp.

Karlsson, T. 1998. Förteckning över svenska kärlväxter. — Sven. Bot. Tidskr. 91: 241-560.

Kiviniemi, K. & Eriksson, O. 2002. Size-related deterioration of semi-natural grassland fragments in Sweden. — Divers. Distrib. 8: 21-29.

Kovach, W.L. 1998. MVSP – A MultiVariate Statistical Package for Windows, ver. 3.0. — Kovach Computing Services, Pentraeth.

Kull, K. & Zobel, M. 1991. High species richness in an Estonian wooded meadow. — J. Veg. Sci. 2: 711-714.

Lindahl, C.H. & Vik, P. (eds.) 1997. Ängs- och hagmarker i Sverige. — Naturvårdsverket Förlag, Stockholm.

Lindborg, R. & Eriksson, O. 2004. Historical landscape connectivity affects present plant species diversity. — Ecology 85: 1840-1845.

Norderhaug, A., Ihse, M. & Pedersen, O. 2000. Biotope pattern and abundance of meadow plant species in a Norwegian rural landscape. — Landscape Ecol. 15:201-218.

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

Pärtel, M., Kalamees, R., Reier, Ü., Tuvi, E.-L., Roosaluste, E., Vellak, A. & Zobel, M. 2005. Grouping and prioritization of vascular plant species for conservation: combining natural rarity and management need. — Biol. Conserv. 123: 271-278.

Pluess, A.R. & Stöcklin, J. 2004. Genetic diversity and fitness in *Scabiosa columbaria* in the Swiss Jura in relation to population size. — Conserv. Genetics 5: 145-156.

Poschlod, P. & WallisDeVries, M.F. 2002. The historical and socioeconomic perspective of calcareous grasslands — lessons from the distant and recent past. — Biol. Conserv. 104: 361-376

Prentice, H.C., Lönn, M., Rosquist, G., Ihse, M. & Kindström, M. 2006. Gene diversity in a fragmented population of *Briza media*: grassland continuity in a landscape context. — J. Ecol. 94:87-97.

Rejmánek, M. & Rosén, E. 1988. The effects of colonizing shrubs (*Juniperus communis* and *Potentilla fruticosa*) on species richness in the grasslands of Stora Alvaret, Öland (Sweden). — Acta Phytogeogr. Suec. 76: 67-72.

Rosquist, G. & Prentice, H.C. 2000. Habitat fragmentation and the structure of genetic diversity within disjunct isolates of *Anthericum ramosum* L. (Anthericaceae) in Scandinavia. — Biol. J. Linn. Soc. 69: 193-212.

Skånes, H.M. & Bunce, R.G.H. 1997. Directions of landscape change (1741-1993) in Virestad, Sweden – characterised by multivariate analysis. — Landscape Urb. Plan. 38: 61-75.

Stoate, C., Boatman, N.D., Borralho, R.J., Rio Carvalho, C., de Snoo, G.R. & Eden, P. 2001. Ecological impacts of arable intensification in Europe. — J. Environ. Manage. 63: 337-365.

Tollin, C. 1991. Ättebackar och ödegärden. De äldre lantmäterikartorna i kulturmiljövården. — Riksantikvarieämbetet, Uppsala.

van der Maarel, E. & Sykes, M.T. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. — J. Veg. Sci. 4: 179-188.

van der Maarel, E. & Sykes, M.T. 1997. Rates of small-scale species mobility in alvar limestone grassland. — J. Veg. Sci. 8: 199-208.

WallisDeVries, M.F., Poschlod, P. & Willems, J.H. 2002. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. — Biol. Conserv. 104: 265-273.

Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? — Trends Ecol. Evol. 12: 266-269.

App. 1. Species-occurrences (in vegetation quadrats) in relation to grassland history within the Jordtorp study area. Species present in less than five quadrats are listed at the end of the Appendix. Grassland history categories (cf. Table 1): OLD (174 quadrats) = more than 270 years of grassland continuity; Previously forest: PF (pooled data from categories PF_{100}, PF_{50} and PF_{25}, 49 quadrats) = transition from forest 177-4 years ago; Previously arable: PA_{100} (24 quadrats) = transition from arable land 60-177 years ago; PA_{50} (17 quadrats) = transition from arable 39-60 years ago; PA_{25} (44 quadrats) = transition from arable ca. 19-39 years ago; Recently arable: RA (7 quadrats) = recently arable land. '%' = the percentage of quadrats within which a species was present; 'frq' = the mean frequency of a species within the quadrats. Data from 13 quadrats from polygons with unknown grassland history (Table 1) are not included.

	OLD		PF		PA_{100}		PA_{50}		PA_{25}		RA	
	%	frq	%	frq	%	frq	%	frq	%	frq	%	frq
Achillea millefolium	65	5.4	47	4.2	58	6.3	65	9.4	73	8.8	89	12
Agrimonia eupatoria	1.7	0.0	6.1	0.1	13	0.4	12	0.3	9.1	0.2	-	-
Agrostis capillaris	49	4.9	55	5.7	25	2.5	53	7.2	25	3.2	89	12
Agrostis gigantea	8.6	0.7	-	-	4.2	0.0	29	5.1	-	-	-	-
Agrostis vinealis	35	2.8	51	4.5	21	2.6	-	-	2.3	0.0	-	-
Alchemilla glaucescens	5.2	0.4	4.1	0.2	4.2	0.1	-	-	-	-	-	-
Allium oleraceum/vineale	15	0.6	2.0	-	4.2	0.0	12	0.3	9.1	0.2	33	1.3
Anemone pratensis	32	1.4	47	1.4	25	0.9	5.9	0.1	9.1	0.5	-	-
Antennaria dioica	2.9	0.3	-	-	-	-	-	-	-	-	-	-
Anthoxanthum odoratum	30	2.9	18	1.0	25	1.1	35	1.4	9.1	0.3	22	1.1
Anthyllis vulneraria	32	1.9	29	1.1	33	0.9	5.9	0.1	39	3.5	11	0.1
Aphanes arvensis	5.2	0.2	-	-	-	-	-	-	4.5	0.0	22	0.4
Arabis hirsuta	9.8	0.2	4.1	0.1	17	0.5	5.9	0.1	16	0.3	22	0.4
Arabidopsis thaliana	3.4	0.1	-	-	-	-	-	-	-	-	-	-
Arenaria serpyllifolia	40	3.0	31	1.3	42	1.7	24	1.2	25	1.1	44	0.8
Arrhenatherum elatius	7.5	0.3	-	-	13	0.7	18	1.6	16	1.2	11	1.9
Artemisia absinthium	1.1	0.1	-	-	-	-	-	-	6.8	0.2	-	-
Artemisia campestris	7.5	0.2	25	1.1	-	-	-	-	-	-	-	-
Asperula tinctoria	18	1.3	47	4.0	4.2	0.5	5.9	0.2	4.5	0.6	-	-
Bellis perennis	18	1.5	22	1.1	29	2.1	29	0.7	34	3.4	22	5.6
Brachypodium sylvaticum	2.3	0.1	4.1	0.4	-	-	-	-	-	-	-	-
Briza media	41	3.0	47	2.9	54	6.2	41	2.2	55	6.5	-	-
Bromus hordeaceus	29	3.1	33	5.3	8.3	0.5	-	-	11	1.6	11	2.6
Campanula persicifolia	5.2	0.3	4.1	0.4	13	0.4	18	0.5	16	3.0	11	0.3
Campanula rotundifolia	24	1.3	33	3.2	17	1.5	29	1.3	25	2.1	22	5.2
Capsella bursa-pastoris	1.7	0.0	2.0	0.1	-	-	-	-	9.1	0.2	11	0.2
Carex caryophyllea/ericetorum	51	4.9	69	7.2	25	1.9	18	2.1	27	3.0	-	-
Carex flacca/panicea	20	2.3	10	0.8	17	2.3	47	4.5	21	1.9	-	-
Centaurea jacea	31	2.5	25	1.7	50	4.3	41	3.2	48	3.7	-	-
Centaurea scabiosa	5.7	0.2	-	-	13	0.5	12	0.9	9.1	0.6	22	0.3
Cerastium arvense	1.1	0.1	-	-	4.2	0.3	5.9	0.1	4.5	1.0	-	-
Cerastium semidecandrum	23	1.7	18	1.3	13	0.5	-	-	14	0.9	56	4.1
Cerastium fontanum	56	2.5	43	1.8	71	3.5	82	6.3	64	2.2	67	5.3
Cirsium acaule	6.3	0.3	2.0	0.0	4.2	0.4	5.9	0.1	2.3	0.1	-	-
Cirsium arvense	1.7	0.1	4.1	0.1	-	-	-	-	-	-	-	-
Convolvulus arvensis	4.0	0.2	-	-	17	0.3	5.9	0.3	16	0.7	-	-
Cynosurus cristatus	7.5	0.8	2.0	0.2	17	1.6	47	5.6	21	1.5	22	2.9
Dactylis glomerata	17	1.3	12	0.8	42	3.7	59	4.4	50	3.8	22	2.2
Danthonia decumbens	11	0.9	12	0.3	4.2	0.0	5.9	0.1	4.5	0.0	-	-
Daucus carota	1.1	0.1	4.1	0.4	-	-	-	-	9.1	0.2	22	3.0
Dianthus deltoides	12	0.4	8.2	0.3	4.2	0.2	12	0.4	-	-	11	0.2
Draba muralis	8.0	0.5	2.0	0.0	8.3	0.2	5.9	0.1	4.5	0.1	11	0.1
Erodium cicutarium	11	0.5	16	0.9	-	-	-	-	6.8	0.1	11	0.2
Erophila verna	27	1.1	22	0.5	17	0.2	24	0.8	16	0.4	67	3.4
Festuca ovina	89	17	94	18	71	11	53	6.5	71	9.4	-	-
Festuca pratensis	3.4	0.1	2.0	0.2	13	0.8	53	4.6	14	1.2	-	-
Festuca rubra	14	0.7	10	1.1	13	1.4	59	4.5	41	3.8	67	8.0
Filipendula vulgaris	43	5.4	22	3.3	54	7.0	53	6.9	23	2.2	-	-
Fragaria vesca	39	3.5	37	2.3	54	5.9	24	0.9	52	5.5	11	0.3
Fragaria viridis	35	2.8	27	0.9	46	3.1	41	4.4	46	2.6	22	3.1
Fraxinus excelsior	1.7	0.0	-	-	4.2	0.0	-	-	-	-	11	0.1
Galium boreale	19	1.7	12	1.4	17	2.0	24	1.8	6.8	0.6	-	-
Galium verum	86	13	86	14	92	16	77	9.5	86	15	44	5.3
Geranium columbinum	12	0.8	8.2	0.3	8.3	0.8	12	0.7	2.3	0.0	22	0.4
Geranium dissectum	2.3	0.0	2.0	0.1	-	-	-	-	2.3	0.0	-	-
Geranium molle	22	0.9	-	-	21	0.6	5.9	0.1	11	0.7	78	3.9
Geum rivale	3.4	0.2	-	-	-	-	-	-	2.3	0.1	-	-
Geum urbanum	-	-	-	-	-	-	18	0.2	4.5	0.1	-	-
Geum urbanum/rivale	1.7	0.0	2.0	0.0	8.3	0.1	-	-	6.8	0.2	-	-
Helianthemum nummularium	58	8.6	63	11	38	4.6	12	0.3	21	2.3	-	-
Helianthemum oelandicum	5.7	0.5	10	1.2	4.2	0.1	-	-	9.1	0.5	-	-

App. 1, cont.	OLD		PF		PA$_{100}$		PA$_{50}$		PA$_{25}$		RA	
	%	frq	%	frq	%	frq	%	frq	%	frq	%	frq
Helictotrichon pratensis	45	6.1	53	9.4	42	7.1	5.9	0.9	43	5.5	-	-
Helictotrichon pubescens	24	1.1	27	1.7	42	3.3	41	3.6	52	3.2	-	-
Herniaria glabra	2.9	0.0	-	-	4.2	0.1	-	-	-	-	-	-
Hypericum perforatum	13	0.4	6.1	0.2	17	0.5	29	0.6	11	0.3	-	-
Juncus articulatus	2.3	0.1	-	-	-	-	12	0.9	-	-	-	-
Knautia arvensis	2.9	0.1	-	-	21	0.4	-	-	21	0.5	-	-
Lathyrus pratensis	2.9	0.1	-	-	-	-	-	-	11	0.8	-	-
Leontodon autumnalis	2.3	0.1	-	-	8.3	1.0	-	-	14	0.5	22	0.4
Leucanthemum vulgare	1.7	0.0	-	-	4.2	0.1	-	-	2.3	0.6	-	-
Linum catharticum	36	1.7	27	0.8	21	0.4	24	0.3	39	2.2	-	-
Lolium perenne	6.3	0.4	6.1	0.7	17	1.0	5.9	0.3	21	2.0	22	0.6
Lotus corniculatus	40	1.4	37	1.0	38	1.8	24	1.8	27	0.7	-	-
Luzula campestris	56	3.6	65	5.7	50	3.3	41	4.4	66	4.5	33	0.8
Medicago falcata s.l.	24	2.9	6.1	0.8	58	4.3	29	2.5	50	5.6	11	0.3
Medicago lupulina	39	1.5	14	0.5	67	4.3	35	3.2	68	5.3	11	0.1
Melampyrum cristatum	8.0	0.4	10	0.3	-	-	-	-	-	-	-	-
Myosotis arvensis	2.3	0.0	-	-	-	-	5.9	0.1	-	-	-	-
Myosotis ramosissima	20	0.8	18	0.7	8.3	0.1	18	0.3	9.1	0.2	22	0.7
Myosotis stricta	1.7	0.0	6.1	0.1	-	-	-	-	-	-	22	0.2
Orchis mascula	1.7	0.1	6.1	0.1	-	-	-	-	-	-	-	-
Oxytropis campestris	5.2	0.2	4.1	0.1	13	0.2	-	-	-	-	-	-
Phleum phleoides	40	3.0	6.1	0.6	50	5.8	12	0.9	21	1.1	-	-
Phleum pratense pratense	0.6	0.0	-	-	13	0.3	12	0.2	2.3	0.0	11	0.8
Phleum pratense serotinum	9.2	0.3	-	-	17	0.8	18	0.5	9.1	0.3	-	-
Pilosella lactucella	5.7	0.4	-	-	4.2	0.0	-	-	2.3	0.0	-	-
Pilosella officinarum s.l.	38	3.7	49	2.6	38	4.0	35	1.7	36	3.0	22	3.1
Plantago lanceolata	91	12	82	9.9	71	7.0	65	5.7	77	7.3	67	11
Poa annua	2.9	0.3	2.0	0.0	-	-	18	0.6	2.3	0.0	11	0.1
Poa bulbosa	4.0	0.4	-	-	-	-	-	-	-	-	22	2.9
Poa compressa	14	0.9	18	1.7	8.3	0.6	5.9	0.3	6.8	0.1	-	-
Poa pratensis pratensis	13	0.9	6.1	0.8	17	2.5	29	0.6	21	2.0	78	14
Poa pratensis angustifolia	76	6.7	61	6.7	79	12	94	8.4	75	10	89	2.7
Polygala amarella	2.3	0.1	-	-	-	-	-	-	4.5	0.1	-	-
Polygala comosa	6.9	0.2	4.1	0.0	25	0.8	5.9	0.3	18	0.9	-	-
Polygala vulgaris	1.7	0.0	8.2	0.2	-	-	-	-	4.5	-	-	-
Potentilla argentea	24	1.1	22	0.7	-	-	-	-	16	1.3	22	1.2
Potentilla erecta	1.1	0.0	-	-	-	-	-	-	6.8	0.7	-	-
Potentilla reptans	6.3	1.0	4.1	0.3	8.3	0.6	5.9	0.8	16	1.3	-	-
Potentilla tabernaemontani	69	5.1	76	5.7	75	4.2	35	1.5	59	4.0	33	1.2
Primula veris	14	0.7	8.2	0.9	21	0.6	5.9	0.1	11	0.6	-	-
Prunella grandiflora	13	0.9	18	1.4	-	-	18	0.3	9.1	0.2	-	-
Prunella vulgaris	4.6	0.5	4.1	0.5	4.2	0.0	12	0.4	9.1	0.1	22	3.6
Prunus spinosa	20	0.5	12	0.2	33	0.9	29	0.9	14	0.3	-	-
Ranunculus acris	4.6	0.4	4.1	0.5	-	-	12	0.4	11	0.7	-	-
Ranunculus bulbosus	82	5.1	67	3.4	83	4.0	77	6.4	77	4.4	67	4.2
Rosa spec.	2.3	0.0	-	-	8.3	0.1	-	-	2.3	0.0	-	-
Rumex acetosa	7.5	0.2	6.1	0.4	17	0.4	41	1.2	25	0.5	11	0.1
Rumex acetosella tenuifolius	7.5	0.4	2.0	0.0	-	-	-	-	-	-	11	0.3
Sagina nodosa	5.2	0.2	-	-	-	-	-	-	-	-	-	-
Sanguisorba minor	-	-	-	-	8.3	0.9	-	-	18	1.3	-	-
Satureja acinos	16	0.6	12	0.5	8.3	0.3	-	-	2.3	0.1	-	-
Saxifraga granulata	17	0.4	12	0.4	4.2	0.1	24	1.5	2.3	-	44	1.4
Scabiosa columbaria	1.7	0.1	-	-	8.3	0.4	-	-	-	-	-	-
Scleranthus annuus	9.8	0.7	12	1.1	-	-	-	-	6.8	1.0	33	1.3
Sedum acre	24	2.3	29	2.7	21	1.5	-	-	6.8	0.2	-	-
Sedum album	2.3	0.2	2.0	0.0	-	-	-	-	-	-	-	-
Sedum rupestre	4.0	0.2	-	-	-	-	-	-	-	-	-	-
Senecio jacobaea	1.7	0.1	-	-	-	-	29	1.5	14	0.2	11	0.6
Sesleria uliginosa	13	1.8	2.0	0.0	4.2	0.3	41	1.4	16	0.7	-	-
Silene nutans	5.2	0.2	-	-	-	-	-	-	-	-	-	-
Stellaria graminea	2.9	0.2	-	-	8.3	0.3	35	1.8	-	-	56	6.3
Taraxacum sect. *Erythrosperma*	37	1.1	51	1.4	25	0.8	12	0.2	30	0.9	44	1.7
Taraxacum sect. *Ruderalia*	14	0.8	8.2	1.0	33	1.8	53	1.3	36	1.5	44	1.1
Thlapsi caerulescens	1.7	0.0	-	-	8.3	0.5	-	-	2.3	0.4	-	-
Thymus serpyllum	26	2.4	45	4.1	4.2	0.4	-	-	18	2.3	-	-
Trifolium arvense	14	0.5	20	1.8	4.2	0.1	12	0.1	-	-	11	0.4
Trifolium dubium/campestre	43	2.4	43	2.4	17	0.8	29	1.0	27	1.5	44	5.3
Trifolium medium	3.4	0.2	4.1	0.6	-	-	-	-	-	-	-	-
Trifolium montanum	0.6	0.0	-	-	-	-	12	0.2	4.5	0.3	-	-
T. pratense	19	1.2	25	1.2	17	0.3	29	1.2	34	4.2	11	0.1

App. 1, cont.	OLD		PF		PA$_{100}$		PA$_{50}$		PA$_{25}$		RA	
	%	frq	%	frq	%	frq	%	frq	%	frq	%	frq

	OLD %	OLD frq	PF %	PF frq	PA$_{100}$ %	PA$_{100}$ frq	PA$_{50}$ %	PA$_{50}$ frq	PA$_{25}$ %	PA$_{25}$ frq	RA %	RA frq
Trifolium repens	22	1.5	22	1.1	33	3.8	77	8.3	25	2.3	44	1.9
Trifolium striatum	21	2.1	-	-	4.2	0.0	5.9	1.1	6.8	0.8	-	-
Ulmus minor	5.2	0.1	-	-	-	-	–	-	-	-	-	-
Valerianella locusta	2.9	0.3	2.0	0.0	-	-	5.9	0.2	2.3	0.2	11	0.4
Veronica arvensis	41	3.1	29	1.5	21	0.9	12	0.2	27	1.7	89	8.9
Veronica chamaedrys	11	0.4	-	-	25	1.5	24	0.5	16	1.3	11	1.8
Veronica officinalis	2.3	0.1	14	0.8	-	-	–	-	2.3	0.1	-	-
Veronica serpyllifolia	4.0	0.1	4.1	0.2	-	-	12	0.2	6.8	0.1	22	0.3
Veronica spicata	25	2.3	39	3.6	8.3	0.8	–	-	2.3	0.2	11	1.4
Vicia hirsuta	4.6	0.1	2.0	0.0	-	-	5.9	0.1	4.5	0.2	11	0.6
Vicia lathyroides	4.6	0.1	-	-	-	-	-	–	-	-	22	0.7
Vicia tetrasperma	4.6	0.1	-	-	-	-	-	-	-	-	-	-
Viola arvensis	7.5	0.1	–	-	-	-	-	-	6.8	0.4	11	0.1
Viola hirta	18	0.6	25	0.8	46	1.3	41	1.2	32	0.8	-	-
Viola riviniana/reichenbachiana / canina	4.0	0.1	-	-	-	-	-	-	-	-	-	-

Species recorded in less than five quadrats: *Acer platanoides, Aira praecox, Alopecurus geniculatus, Alyssum alyssoides, Anchusa officinalis, Anemone hepatica, Anthemis arvensis, Arabis glabra, Artemisia rupestris, Barbarea vulgaris, Betula pendula/pubescens, Bromus* sp., *Calluna vulgaris, Cardamine pratensis, Carex hirta, C. muricata, C. tomentosa, C.* sp., *Centaurium pulchellum, Cerastium pumilum, Cirsium vulgare, Corylus avellana, Cynoglossum officinale, Dechampsia caespitosa, Elytrigia repens, Erigeron acer, Euphrasia stricta, Galium aparine, Geranium pusillum, G. sanguineum, Glechoma hederacea, Hypochoeris radicata, Inula salicina, Juncus bufonius, Juniperus communis, Luzula multiflora, L. pilosa, Lychnis viscaria, Melampyrum pratense, Moehringia trinervia, Ononis spinosa* ssp. *arvensis, Ononis spinosa* ssp. *maritima, Orchis ustulata, Origanum vulgare, Pilosella dichotoma, Plantago major, Platanthera* sp., *Quercus robur, Ranunculus auricomus, R. ficaria, R. illyricus, Rhamnus cathartica, Rhinanthus minor, Salix repens* ssp. *argentea, Satureja vulgaris, Scleranthus perennis, Scorzonera humilis, Scutellaria hastifolia, Sherardia arvensis, Silene vulgaris, Stellaria media, Succisa pratensis, Thalictrum flavum, Thlaspi perfoliatum, Trisetum flavescens, Valeriana officinalis, Veronica hederifolia, Vicia cracca, Viola rupestris.*

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