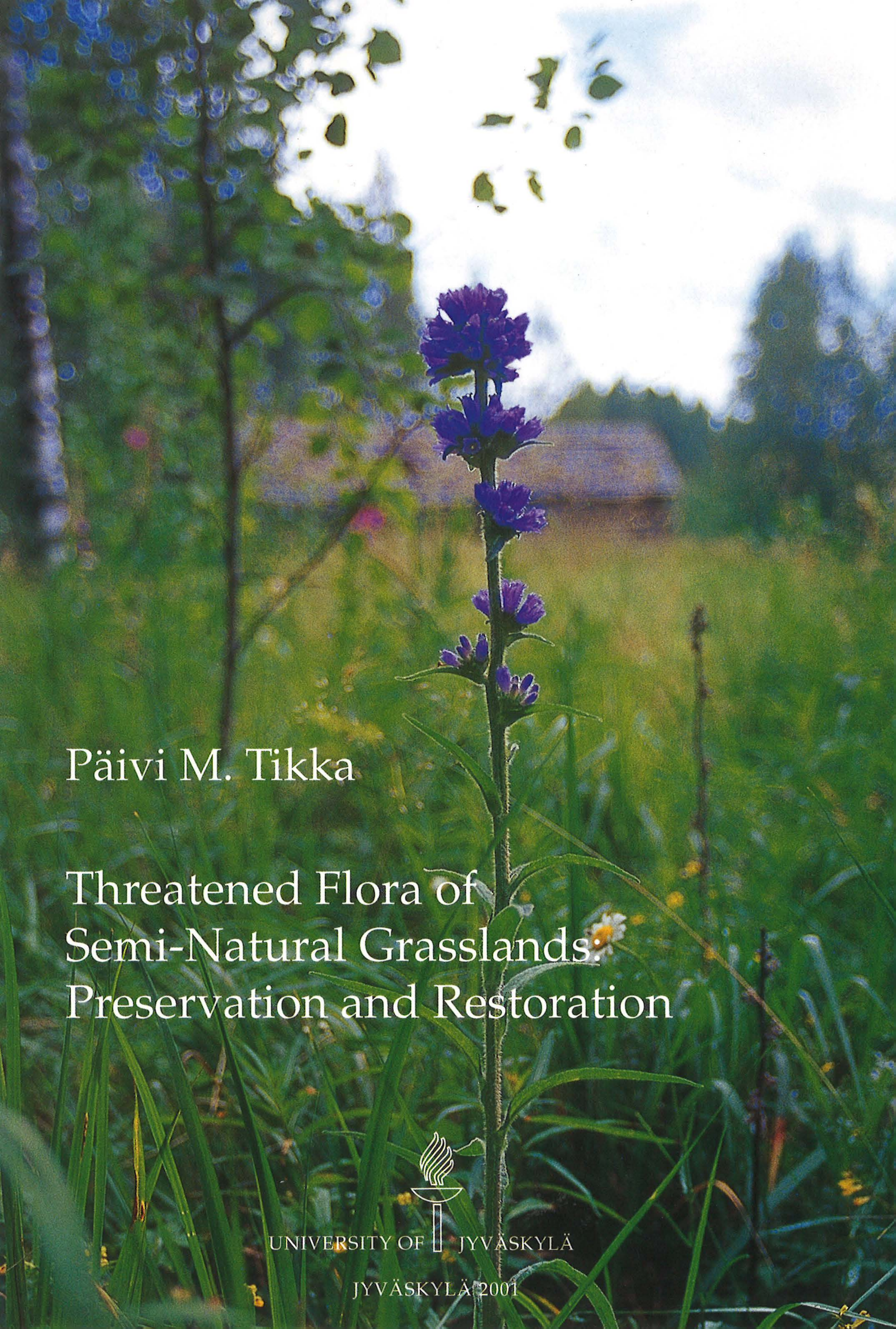

Päivi M. Tikka

Threatened Flora of Semi-Natural Grasslands: Preservation and Restoration

UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2001

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE 93

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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi yliopiston Ambiotica-rakennuksen salissa YAA 303
helmikuun 24. päivänä 2001 kello 12.

Academic dissertation to be publicly discussed, by permission of
the Faculty of Mathematics and Natural Sciences of the University of Jyväskylä,
in the Building Ambiotica, Auditorium YAA 303, on February 24, 2001 at 12 o'clock noon.

UNIVERSITY OF JYVÄSKYLÄ

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Publishing Unit, University Library of Jyväskylä

Cover picture: Päivi M. Tikka

URN:ISBN:978-951-39-8627-8
ISBN 978-951-39-8627-8 (PDF)
ISSN 1456-9701

ISBN 951-39-0885-2
ISSN 1456-9701

Jyväskylä University Printing House,
Jyväskylä and ER-Paino, Lievestuore 2001

ABSTRACT

Tikka, Päivi M.
Threatened flora of semi-natural grasslands: preservation and restoration
Jyväskylä: University of Jyväskylä, 2001, 35 p.
(Jyväskylä Studies in Biological and Environmental Science,
ISSN 1456-9701; 93)
ISBN 951-39-0885-2
Yhteenveto: Niittykasvillisuuden säilyttäminen ja ennallistaminen
Diss.

Semi-natural grasslands play an important role in the modern environments, serving as refuges for a number of threatened plant and animal species. In this thesis I concentrate on the problems of identifying, maintaining and recreating plant communities typical of these grasslands. First I used field data to study whether the most species-rich grasslands were characterised by common variables describing land use and environment. However, these variables proved to be of little use. No shortcut was found to discovering the individual grasslands with the richest flora or a set of sites with the highest total species-richness. Instead, comprehensive species inventories are necessary when searching and monitoring the floristically valuable areas. Besides semi-natural grasslands, the occurrence and success of grassland species were also studied on a restored meadow and in alternative habitats that they invade spontaneously. Grassland plants were regularly found bordering roads and railways, and they even appeared capable of using such routes as dispersal corridors. They thrived especially on the verges of small, unpaved roads in open environments. However, entire plant communities similar to those on semi-natural grasslands were not identified, probably due to excessive disturbance and an unfavourable management regime. An appropriate mowing frequency and avoidance of the use of de-icing salt may, nevertheless, increase the number of grassland species along roads and railways. As an example, a rare grassland species *Campanula cervicaria* succeeded equally well on roadsides as on meadows, provided that the vegetation remained open. Its population sizes decreased with shading, and small populations had an elevated risk of losing all fertile plants. For preservation of *C. cervicaria* and other rare, short-living grassland species, recreating a grassland failed to be a viable alternative. Therefore, in the protection of grassland communities the importance of preservation and management of existing semi-natural grasslands cannot be over-emphasised.

Key words: Corridors; dispersal; grassland plants; management; population size; rarity; restoration; sides of roads and railways; semi-natural grasslands.

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following articles, which will be referred to in the text by their Roman numerals. I planned and produced a significant portion of papers I-V. I wrote papers II and V and am the main writer of papers I and III. I also wrote a significant portion of paper IV.

I Tikka, P. M., Virolainen, K. M. & Kivelä, R. A. 2000. Identification of species-rich semi-natural grasslands. Manuscript.

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

III Tikka, P. M., Högmander, H. & Koski, P. S. 2000. Road and railway verges serve as dispersal corridors for grassland plants. Manuscript (submitted).

IV Eisto, A.-K., Kuitunen, M., Lammi, A., Saari, V., Suhonen, J., Syrjäsuo, S. & Tikka, P. M. 2000. Population persistence and offspring fitness in the rare bellflower *Campanula cervicaria* in relation to population size and habitat quality. Conservation Biology 14: 1413-1421.

V Tikka, P. M., Heikkilä, T. Heiskanen, M. & Kuitunen, M. 2000. The role of competition and rarity in restoration of a dry grassland in Finland. Applied Vegetation Science (in press).

1 INTRODUCTION

1.1 General introduction

Semi-natural grasslands are extraordinary biotope types that have originated as a result of traditional, long-term hay making and grazing. Continuous disturbance arrests the successional change, resulting in low-growing, light-demanding plant communities that require active management to prevent overgrowing and loss of species (Ellenberg 1988, Kull & Zobel 1991, Eriksson et al. 1995, Norderhaug 1996). The agricultural use of semi-natural grasslands has, however, become economically unprofitable during recent decades. Consequently, the majority of them have been abandoned, afforested, or transformed into fertilised fields or pastures. This development has lead to a drastic decline in the area of semi-natural grasslands throughout Europe, awakening concern and inducing scientific studies on their role in the protection of biodiversity (e.g., Garcia 1992, Bastian & Bernhardt 1993, Pärtel et al. 1999, Stampfli & Zeiter 1999).

The area of semi-natural grasslands has similarly decreased in the Nordic countries, where they belong to the most species-rich vegetation types (Ihse & Norderhaug 1995, Kotiranta et al. 1998, Norderhaug et al. 2000, Rassi et al. 2000). In Finland, the proportion of remaining semi-natural grasslands may regionally be as low as 0.4% compared to their area at the beginning of the 20th century (Marttila et al. 1999). Insight on the species composition of semi-natural grasslands at the time they were routinely utilised is given in classical botanical studies. For instance, species-richness was as high as 30 – 36 species per square metre on the meadows described by Linkola & Tiirikka (1936). Examples of species typically occurring on these meadows are given in Table 1. In addition to the current loss of grassland area, the quality of semi-natural grasslands has also deteriorated. A Swedish study showed a 50% reduction in the amount of grassland plants where the sites were subjected to fertilisation (Bengtsson-Lindsjö et al. 1991). Even those grasslands that are still traditionally managed have often become small and fragmented, which increases the risks of extinction of native species, the invasion of exotic species, and a reduction in population size (MacArthur & Wilson 1967, Drayton and Primack 1996).The disappearance and fragmentation of open, semi-natural biotope types is considered to be the main reason for the current status of 31% of the threatened vascular plants, 38% of the threatened heteroptera, 57% of the threatened lepidoptera, and 59% of the threatened hymenoptera in Finland (Rassi et al. 2000).

TABLE 1 Examples of species co-occurring on old, traditionally managed meadows according to Linkola & Tiirikka (1936).

Alchemilla pastoralis	*Knautia arvensis*
Antennaria dioica	*Leucanthemum vulgare*
Anthoxanthum odoratum	*Luzula multiflora*
Campanula rotundifolia	*Lychnis viscaria*
Dianthus deltoides	*Nardus stricta*
Festuca rubra	*Pimpinella saxifraga*
Galium verum	*Potentilla argentea*
Hypochoeris maculata	*Veronica verna*

Even though the importance of semi-natural grasslands for the survival of several organisms is recognised, attempts to protect them have also raised philosophical debate. As these grasslands are maintained by human actions, they are in a sense artificial environments, and the meaningfulness of their preservation has sometimes been questioned. However, many plant species typical of semi-natural grasslands are native to Finland and thought to have invaded the country independently of humans (Hämet-Ahti et al. 1998). Originally these species probably grew in open areas created by natural disturbances such as fires or grazing by contemporary herbivores. In consequence they indisputably belong to our natural flora. In the present situation, with rapidly changing environmental conditions, biotope types with diverse flora and fauna – such as semi-natural grasslands – are important reserves of genetic diversity needed to ensure adequate evolutionary potential (Primack 1993). Furthermore, flowering grasslands can be of direct significance for human society, serving as a source of recreational and aesthetic experiences.

Several alternatives have been proposed for maintaining species diversity in semi-natural grasslands. The simplest and most reliable option seems to be the continuation of traditional management on existing grasslands. The restoration of recently abandoned grasslands by re-starting grazing or mowing may also be successful (Bakker & Berendse 1999). The creation of new grasslands by sowing or planting native plants is the last option and the subject of various recent studies (e.g., Chapman et al. 1996, Hutchins & Booth 1996a, b, Snow et al. 1997, Muller et al. 1998, Mentis 1999).

1.2 Objectives

In this thesis I study plant species and communities typical of semi-natural grasslands – both in their natural habitats and in alternative or recreated habitats. I aim in particular to identify the environment types, conditions, and management systems favourable for grassland species. Simultaneously, an attempt is made to outline scientifically-based principles for the maintenance of these species and communities.

In order to localise the biologically and aesthetically valuable semi-natural grasslands in Finland, a nation-wide inventory was carried out during the 1990s. In the data collection greatest effort was concentrated on describing the floristic diversity of these grasslands. Since the species composition of grasslands is prone to change with alterations in management regime, even a species-rich site may lose its value if the management changes or ceases (Herben et al. 1993, Smith and Rushton 1994). Therefore, the state of valuable semi-natural grasslands should be re-assessed at regular intervals. In this thesis grasslands are considered valuable if they have high species-richness, and more specifically, a high number of grassland species. To facilitate the identification and monitoring of species-rich grasslands, it would be useful to find background variables serving as reliable tools for predicting the quality of the flora. When searching such tools I tested whether the quality of variables collected during the national inventory of semi-natural grasslands was adequate for predicting the species-richness of grasslands and for selecting the best grasslands under management. Thus, the first central question addressed here was as follows: what is the role of environmental and land use data when the objective is to identify semi-natural grasslands with a high floristic value (I)?

It is known that individual plant species typical of semi-natural grasslands also occur in alternative environments, such as road and railway verges (Anon. 1996a, b, Schaffers 2000). Here, however, the objective was to study whether these habitat types are also able to compensate for disappearing semi-natural grasslands. Therefore, the second central question was: do entire plant communities similar to those of semi-natural grasslands occur on the sides of roads and railways, and what management systems or environmental factors are most likely to maintain grassland flora (II)? As local conditions may change, ability to invade new habitats is essential for grassland plants. That is why I thirdly studied whether road and railway verges are capable of serving as dispersal corridors for plants typical of semi-natural grasslands. Instead of single species, the focus was on the dispersal of grassland plants as an entire group (III).

As a representative of rare grassland plants thriving on road verges the bellflower *Campanula cervicaria* was studied more closely. I tried to identify reasons for its decreasing population density, and the fourth central question was: what are the effects of population size and habitat quality on the persistence of populations and the performance of offspring in *Campanula cervicaria* (IV)?

Finally, I examined whether habitat recreation is a viable option for the preservation of rare grassland plants in boreal latitudes, and the fifth central question was as follows: how does outside competition affect species performance in a restored meadow, and does the performance of rare species differ from that of more common species(V)?

2 METHODS

2.1 The study area

All the studies were performed in the Central Finland region (61.5 - 63.5°N, 24.0 - 27.0°E) which mainly belongs to the southern boreal vegetation zone and is dominated by taiga forests (Ahti et al. 1968). Seasonal differences in temperature are remarkable: the mean temperature in January is between –8 and –10 °C while it varies from +16 to +17 °C in July. Annual precipitation is 500-600 mm (Alalammi 1987). The bedrock in the region is mainly composed of acidic rocks such as granite, granodiorite and quartz diorite. There are only patchy deposits of alkaline rock types and limestone is virtually absent (Alalammi 1990), which is reflected in the relative scarcity of plant species, especially in the northern part of the region (Lahti et al. 1988). The first people arrived in the area about 9000 years ago, soon after the Ice Age (Winqvist & Ursin 1992), and have influenced the vegetation ever since. The early development of field husbandry was rather slow but then the region remained dominated by agriculture until the 1950s (Laitinen 1983). However, by 1995 the proportion of inhabitants having agriculture as their main source of income had dropped to 9% (Anon. 1998a). Also the landscape has changed as a consequence of this transition of agriculture and the loss of open, semi-natural grasslands has been a quick process.

2.2 The study species and their habitats

In this thesis I concentrate on vascular plants occurring on different grasslands, either as individual species or as plant communities. Depending on local conditions, grasslands may include weeds and forest species in addition to grasses and flowering herbs. Therefore, those plant species that are specially adapted to conditions on traditionally-managed grasslands were separately identified (I, II, III, V). In paper I identification was based on combining the information presented by Pykälä et al. (1994), Ekstam & Forshed (1997), and Hämet-Ahti et al. (1998). In papers II and III the lists are based on Ekstam & Forshed (1997) and in paper V on Hämet-Ahti et al. (1998). *Botrychium lunaria, Centaurea phrygia, Lychnis viscaria,* and *Nardus stricta* are examples of grassland species found on the sites studied.

Some of the floristic data was collected in connection with the national inventory of semi-natural grasslands (I, II). The inventory of the grasslands used in this study was performed during the summers of 1992-1994. In 1997 we collected floristic data from 90 road and railway verges (II, III), studying an equal number of sites along paved main roads, gravel roads and railways. Along each route type, half the sites were located in a forested environment and the remainder in a non-forested environment surrounded by fields or settlements. As a representative of rare grassland plants, a monocarpic, short-living perennial bellflower *Campanula cervicaria* was comprehensively monitored in its natural habitats in the region (IV). As its primary habitats in glades created by slash-and-burn agriculture have already returned to forest, *C. cervicaria* now occurs in old fields and grassland strips next to road verges and under power lines (Ryttäri & Kettunen 1997, Nurmi 1998). It is classified as vulnerable in Finland (Rassi et al. 2000). Isolated populations may suffer from a lack of pollinators, and in *C. cervicaria* self-pollination results in lower seed production than cross-pollination by insects (Eisto 1990).

2.3 The flora of grassland plant communities

2.3.1 Semi-natural grassland

In order to obtain a set of semi-natural grasslands with a comparable vegetation structure, only relatively open grassland types were used in the studies. Paper I included open meadows and pastures, wooded pastures with occasional scattered tree groups, and also old fields where diverse grassland flora had recovered as a consequence of management by grazing or mowing, making 69 grasslands in total. In addition to the grasslands referred to above, paper II also covered those forest pastures that had a maximum of 35% canopy shading, amounting to 92 sites altogether. To determine species composition on semi-natural grasslands, all vascular plant species growing on the sites studied were listed. The total species number, number of grassland species (I, II), and restricted range diversity (II) were then calculated for each site. Restricted range diversity describes the floristic uniqueness of a site within a known data set. To calculate this index, each component species is first given a score that is the inverse number of sites in which it occurs. The scores of individual species are then summed within a site, and the sum is expressed as a percentage of the total scores for all the species in all the studied sites (Kershaw et al. 1994, 1995).

In order to assess the effects of land use and the characteristics of the environment on species composition, the background variables collected on semi-natural grasslands were used (I). During the national inventory, the percentage coverage of tree and shrub canopies and the moisture level of the soil were assessed. The area of the site, its geographical location, and the date of inventory were determined. The ages of sites were indicated by interviewing the landowners and the sites were classified according to the prevailing land use as abandoned, mown, or grazed. For this study, the grazed sites were further ranked as follows: no grazing in the year of inventory; strongly under-grazed; slightly under-grazed; appropriately and evenly grazed; slightly over-grazed; and strongly over-grazed. A variable symbolising the tilling history of the sites was formulated as follows: never tilled; partly tilled; and entirely tilled but tilling ceased over 30 years ago. At the end of the field inventories the sites were given relative rank values according to the directions for inventory, combining the floristic data and the variables describing the environment and land use (Pykälä et al. 1994). The value categories indicating the relative importance of grasslands on a national scale were as follows: 1) no particular value, 2) local -, 3) local, 4) local +, 5) regional -, 6) regional, 7) regional +, and 8) national.

The management or protection of all desired sites is normally impossible due to limitations of funding and other resources. Consequently, actions must be concentrated on the sub-set of sites that represents the desired attributes in the best possible way. However, if the sites under management are selected on the basis of simple scores, e.g. species number per site, any set of highest–ranking sites may include some species several times and simultaneously miss others. Therefore, we identified the sets of semi-natural grasslands with the highest total number of all species or grassland species using an heuristic site selection algorithm (Pressey and Nicholls 1989, Pressey et al. 1993, Williams 1999) (I). The algorithm proceeds iteratively, first selecting a grassland with the highest number of species and removing all species encountered at this site from the data set. The number of remaining species is then recalculated for each remaining grassland, and the grassland with the highest recalculated species number is selected next. If several sites have an equal number of species, the grassland with the highest initial species number is selected. If there are still several candidates, the site is selected randomly. The algorithm continues until all species or a desired number of sites are selected, giving an order of priority for grasslands. We compared the efficiency of the heuristic algorithm and the relative value of grassland in identifying a set of grasslands including the highest total number of all species or grassland species.

2.3.2 Road and railway verges

Each study site was a 200 m strip at the side of a road or railway, the breadth of which was determine as the distance from the edge of the tarmac or gravel to the outer edge of the verge (II, III). Also on these sites the species number, number of grassland species and restricted range diversity were calculated (II).

To study the potential factors affecting flora on road and railway verges, the values of the following environmental variables were measured or assessed: the area of the site, the coverage of tree and shrub canopies, the variation in soil moisture, and the angle of inclination of the embankment. As regards management, the sites were classified as unmown, mown once, and mown twice in a summer. With regard to the use of de-icing salt and herbicides, the sites were simply divided into two groups, indicating whether these agents had been employed or not (II).

2.4 Use of corridors by grassland plants

Whether plants are able to use corridors for dispersal or not is difficult to measure directly due to their sessile nature. Therefore, the dispersal ability of grassland species was assessed by studying the spatial pattern of their occurrence on road and railway verges. The key question was: is the species composition of neighbouring sites more similar than would be expected if the sites were inhabited independently? The nearest neighbour for each of the 90 study sites was defined as the site at the shortest distance measured along intersecting traffic routes. If two sites formed a symmetric pair being the nearest neighbours to each other, this pair was included only once. As a consequence, the data included 61 pairs of nearest neighbours, the distance between which varied from 400 m to 11 km (median = 1.9 km). To study the spatial randomness of inhabited sites for the grassland species, the binomial test was applied as described in detail in paper III. The 67 grassland species that inhabited more than one site were included in the test. For individual species, the number of inhabited sites varied between 2 and 82 (mean = 33). Respectively, the number of pairs of neighbouring sites inhabited by the same species ranged from 0 to 54 (mean = 14).

2.5 Persistence of a rare grassland species

2.5.1 Monitoring and vegetation analyses

During the summers of 1987-1989, 52 populations of the bellflower *C. cervicaria* were located (IV). Most of the populations occurred on road and railway verges (roadside populations, n = 40), while the rest were found in power line corridors, abandoned fields, and dry meadows (meadow populations, n = 12). The number of flowering, fertile individuals was used to indicate population size. As populations usually also include sterile rosettes, the abundance of fertile plants does not determine the exact population size. However, it serves as an indicator of the population's viability. The number of fertile plants encountered during the first population check in 1987-1989 is referred to as the initial population size. All 52 populations were re-examined in 1995 and long term change in population size was measured as the difference between the initial population size and the population size in 1995. The degree of isolation of each population was measured as the distance to the nearest known population, the size of which was also determined.

Between 1995 and 1998 the number of fertile plants was counted annually in 26 easily accessible populations, 18 of which had already been included in 1987-1989, the rest having been found later. The current population size for these 26 populations was calculated as the mean of the population sizes between 1995 and 1998. The long-term variation in population size for each population was defined using a few variables: the average population size in the 1980s (i.e., the mean size in 1987–1989), average population size during the entire period (1987-1998), and the relative range, indicated as a percentage of the maximum population size during the entire period [(maximum - minimum) x 100 / maximum].

To evaluate the influence of co-occurring vegetation on the performance of *C. cervicaria*, 23 stable populations consisting of plants observed every year were chosen for vegetation analyses in 1998. In each population, five quadrates (1 x 1 m) were selected for a visual estimation of the percentage coverage of tree and shrub canopy and all vascular plant species in the field layer. The coverage of each species in each quadrate were summed to determine the total coverage of field layer vegetation. The mean of the total coverage obtained from the five quadrates in each population was used as a measure of field layer coverage and tree and shrub canopy coverage.

2.5.2 Germination

Ripe seeds were encountered in 24 of the 26 populations in the autumn of 1996 and in 19 populations in 1997. After collection, the seeds were cold-stratified at +5°C for four months. To determine the germination ability of the seeds, 50 seeds from one naturally pollinated plant per population were then placed on moistened paper inside petri dishes. Since the smallest populations had only a single fertile individual, seeds from one randomly selected plant per population were used in all germination and raising of seedlings. In both 1996 and 1997 the seeds were germinated under greenhouse conditions employing a light regime 12 hours light and 12 hours dark for four weeks. Subsequent to this the germination percentages were calculated. To achieve a slightly wider figure of germination ability, the germination percentage by population was also calculated as the mean of the values obtained in 1996 and 1997.

To compare the growth of seedlings between populations, ten seedlings from each population were grown for eight weeks in both 1996 and 1997. Seeds were sown in pots in boxes that were covered with plastic, and the seedlings were watered daily. After eight weeks in greenhouse conditions the seedlings were harvested, dried and weighed. In addition to determining the biomass per population separately in both years, the average seedling biomass for each population was also calculated as the mean of the values obtained in 1996 and 1997.

2.6 Restoring grassland vegetation

2.6.1 The species and the site

In this experiment (V) I used 13 species, domestic seeds of which were available and which are adapted to conditions in semi-natural grasslands and open cultural habitats. These test species were divided into two sets according to their expected height (Table 2). Due to the limited supply of grass seeds, *Festuca ovina* was used in both sets. The rarity of the test species in their natural habitats, termed regional frequency, was calculated from the inventory data of semi-natural grasslands (I, II). The number of grasslands where each species occurred was given as a percentage of the total number of grasslands studied. The seed weight was also indicated for each species (Table 2).

The experiment was set up in Jyväskylä, Central Finland in the early summer of 1997. The study site was an old, clayey field that had been abandoned seven years earlier. In order to impoverish the soil and reduce the amount of weeds, a 10 cm layer of topsoil was removed by a caterpillar tractor. In order to improve the permeability of the soil to water, a 3 cm thick layer of sand was then spread on the ground and mixed to a depth of about 10 cm.

TABLE 2 The species sets used in this study, the regional frequencies (%) of the species and seed weights of the species (mg).

Low-growing species (50-60 cm)	Tall-growing species (up to 150 cm)
Campanula rotundifolia, 11.8 %, 0.05 mg	*Anthemis tinctoria*, 0 %, 0.24 mg
Dianthus deltoides, 18.2 %, 0.21 mg	*Campanula cervicaria*, 0.9 %, 0.05 mg
Festuca ovina, 28.2 %, 0.35 mg	*Centaurea cyanus*, 0.9 %, 5.07 mg
Lychnis viscaria, 1.8 %, 0.08 mg	*Centaurea jacea*, 0.9 %, 2.66 mg
Pilosella officinarum, 38.2 %, 0.15 mg	*Festuca ovina*, 28.2 %, 0.35 mg
Trifolium spadiceum, 2.7 %, 0.67 mg	*Leucanthemum vulgare*, 76.4 %, 0.42mg
Viola tricolor, 1.8 %, 0.61 mg	*Verbascum thapsus*, 1.8 %, 0.09 mg

2.6.2 The experimental design

For both sets of test species 45 experimental plots of 1 x 1 m were marked out. The plots were randomised into three treatments: weeded (all except the test species were rooted out a couple of times per summer), non-weeded (other species were allowed to grow among the test species), and control (no planting, all emerging species were allowed to grow). By virtue of the weeding treatment the potential success of the test species in the absence of outside competition was compared to their success in a situation where competing species were present. To describe the initial conditions in the field, a soil sample was taken from each plot, and total amounts of calcium (Ca), phosphorus (P), potassium (K), magnesium (Mg), and nitrogen (NO_3-N), as well as pH and soil texture fractions were analysed.

C. cervicaria and *C. rotundifolia* were grown into seedlings beforehand because bellflowers (Campanulaceae) are known to germinate poorly in artificial environments (e.g. Kivi 1991). The seeds were sown in pots and grown in a greenhouse for six weeks before planting. In early June 1997 the seeds and seedlings were planted on the experimental plots, in which 100 points at equal intervals had been marked. Each species had been randomised beforehand to an equal number of these planting points. The purpose of this design was to assess the relative ability of each species to become established and invade the surrounding ground. To imitate traditional management, the vegetation in each plot was clipped and removed every year in the late summer. In early August 1999, before clipping, the percentage coverage was visually assessed for each vascular plant species in each plot. The coverage figures for individual species were summed into two variables: test species coverage and other species coverage. All the results represented here are from the third growing season.

2.7 Statistical analyses

One-way analysis of variance (ANOVA) and factorial ANOVA were used to study the effects of environmental and management variables of nominal scale on species numbers or coverage (I, II, V). Where the number of independent factors was two, a t-test was performed. When the assumptions of parametric tests were not met, Kruskal-Wallis one-way ANOVA or the Mann-Whitney test was applied. The relations of species number or coverage to those background variables having ordinal, interval, or ratio scale were tested with Spearman rank correlation, Pearson's correlation, and multiple regression analysis. For *C. cervicaria* (IV) a logistic regression analysis was used to test whether the initial population size, the distance and the size of the nearest population, and the habitat type affected the persistence of populations. The change in population size from the 1980s to 1995 was tested with a paired t-test. Spearman rank correlation was used to test the associations between germination percentage, coverage of surrounding vegetation, and the variables related to population size and variation in size. All these tests were performed using SPSS for Windows. CANOCO (ter Braak & Šmilauer 1998) was used to group the semi-natural grasslands and road and railway verges on the basis of their species composition (II). The statistical tests are described in detail in papers I-V.

3 RESULTS AND DISCUSSION

3.1 Flora of semi-natural grasslands (I)

3.1.1 The role of background variables

In general, the environmental and land use variables collected during the national inventory of semi-natural grasslands were fairly inefficient in predicting species numbers and the numbers of grassland species in the grasslands studied. However, certain trends emerged. The area of grassland indisputably affected species number and the number of grassland species, both of which tended to increase with growing area. This result is in line with two well-know hypotheses. Firstly, a large site may simply include more individuals and, consequently, more species than a corresponding smaller site (MacArthur and Wilson 1963, 1967, Ås et al. 1992). Secondly, the heterogeneity of the environment often increases with area, allowing the co-existence of several species with slightly differing habitat requirements (Williams 1964, Ås et al. 1992). Although species richness is presumably highest on the largest sites, the superiority of large grasslands in species preservation is not guaranteed. Depending on local conditions, small grasslands in a systematically and traditionally managed landscape may be more favourable than a large grassland in a degraded environment (Norderhaug 1996). Therefore, the value of individual grasslands should always be evaluated in the context of the surrounding landscape.

With regard to grazing pressure, the number of grassland species was significantly higher in the slightly under-grazed than in the strongly under-grazed grasslands. Although the other differences between grazing categories were statistically non-significant, both species number and the number of grassland species tended to peak at the intermediate grazing intensities. This result gives some support for the intermediate disturbance hypothesis (Grime 1973, 1979,Connell 1978). According to this hypothesis the highest diversity is found on moderately disturbed sites. At low disturbance levels strongly competing species are likely to monopolise the community, while intensive disturbance prevents the regeneration of most species. This hypothesis, just like any attempt to generalise ecological phenomena, has failed to be universally applicable. Studies testing its validity in areas with differing grazing pressure have produced contrasting results (e.g., Prober & Thiele 1995, Olff & Ritchie 1998, Proulx & Mazumder 1998, Rambo & Faeth 1999, Stohlgren et al. 1999), and the scale of measurements, as well as the local characteristics of the environment, held to be at least as important as disturbance in determining species diversity.

No other connections were found between the environmental or land use variables and the variables describing species-richness although such relations have been identified earlier. Among others, Ejrnæs & Bruun (1995) have recorded a positive relation between species diversity and age in Scandinavian grasslands. Such a relation is to be expected, as the highest ecological value is supposed to be associated with the oldest landscape elements (Ihse & Norderhaug 1995). Continuous, long-term management prevents the progress of succession and controls for the content and availability of nutrients in the soil, thereby maintaining favourable conditions for high species diversity (e.g., Ellenberg 1988, Morris 1991, Eriksson et al. 1995, Smit et al. 2000). In the inventory data, however, the information on age was available for only one third of the grasslands studied. Based on the recollections of the landowners, the age estimates probably undervalued the real age of the grasslands, which reduces the reliability of the result.

The generally weak connections between species-richness and management in this study are probably due to inadequate quality of the data collected during the national inventory of semi-natural grasslands. Due to the limited time and funding, the values of most variables were based on visual assessments or interviews with the landowners instead of exact analyses. Provided that the data is appropriately collected, some connections should emerge. Schaffers (2000) has namely shown that species diversity in semi-natural vegetation primarily depends on environmental factors and management.

3.1.2 Floristic priority sites

The identification of a set of grasslands with the highest total species-richness is important when selecting sites under management; it is rarely possible to include all sites in management programs. The relative value of grassland, combining the environmental and floristic data collected during the national inventory, was in a positive and highly significant correlation with both species number and the number of grassland species. However, when a set of grasslands with the highest total species number was searched on the basis of the relative value of grassland, the result did not exceed the maximum species number obtainable by random selection. An heuristic selection was more efficient than selection based on the relative value or random selection, and the result was independent of the number of grasslands in a set. The results were similar when selection was based on the number of grassland species instead of all species. As a scoring procedure the relative value concentrates on one grassland at a time, ignoring the species composition on the other grasslands. Therefore, a set of sites with high relative values may include some species several times and simultaneously miss others (Smith & Theberge 1987, Pressey & Nichols 1989). When searching a network of sites under management, a more sophisticated area selection method should be used instead of scoring procedures that combine several estimated variables. An heuristic area selection method based purely on species composition appears to be a suitable alternative. Correspondingly, the various environmental and land use variables collected during the national inventory can be used to describe the habitats and to identify culturally or aesthetically remarkable grasslands, but they appear not be suitable for assessing the species-richness of sites.

3.2 Road and railway verges as grassland plant habitats and movement corridors (II, III)

3.2.1 Grassland plants on the sides of roads and railways (II)

Strips of vegetation along roads and railways resemble dry semi-natural grasslands in several aspects. Their soil is normally permeable to water and they are kept open by mowing. When compared to the semi-natural grasslands in our study, the mean species number and the restricted range diversity per site were higher on road and railway verges. In contrast, grassland species were more abundant on grasslands. In a comparison of entire floras, the plant communities on road and railway verges were shown to be strikingly different from those of grasslands. Verges were characterised by occasionally occurring cultivated species and species typical of disturbed areas, and only one site next to a gravel road had a species composition comparable to that of grasslands. On one hand, this difference may be caused by the invasion of alien species with the soils used in road construction (Greenberg et al. 1997) and by the spread of species from the surrounding habitats (Stottele 1994). On the other hand, the growth and survival of sensitive species may be reduced due to the dust that spreads from roads, reduces photosynthesis, interferes with respiration and facilitates the penetration of pollutants (Farmer 1993). Gaseous pollutants, such as oxides of nitrogen, may further damage plant tissues, disturb metabolism and cause premature senescence of plants (Flückiger et al. 1979, Viskari 1999). Even though the affecting mechanisms cannot be identified in this study, it is clear that the current vegetation on road and railway verges is cannot substitute for the plant communities of semi-natural grasslands. A similar result was recently obtained in a Norwegian study (Norderhaug et al. 2000).

On the sides of roads and railways, however, we found a number of factors that tended to enhance the occurrence of grassland species. Firstly, grassland plants were more abundant along gravel roads than along paved main roads and railways. The construction and maintenance of gravel roads cause lower levels of disturbance than those of paved roads or railways. They often pass through a more varied landscape than main roads (Norderhaug et al.

2000) and are thus surrounded by a more diverse species pool. As the verges of gravel roads often lack sown grass, the species growing on them have mainly spread from these diverse, natural seed sources. More grassland species also occurred along roads in cultural, non-forested environments than in forested areas. This result can be explained by the fact that grassland plants generally thrive in areas that enjoy abundant sunlight and have low-growing vegetation (e.g. Kull & Zobel 1991). Therefore, more grassland species can spread to verges from open areas than from shady, forested environments. Furthermore, the number of grassland species was higher on the verges of unsalted than salted roads. It also differed in regard to mowing with the highest numbers of grassland species on sites that were mown once a summer. In some earlier studies, mowing twice during the growing season has maintained the most species-rich vegetation (Parr & Way 1988, Melman & Verkaar 1991). Here, however, all the twice-mown sites were also salted, which reduced the abundance of grassland species. The use of de-icing salt raises the concentrations of inorganic pollutants, such as Na^+ and Cl^- (Viskari et al. 1997). Salt may also damage the surface tissues of plants and cause deterioration of the soil structure, leading to compaction and disturbed water transportation (Bäckman & Folkeson 1995). Taken together, these stress factors may reduce the survival of plant species.

Under the current management regime road and railway verges are not able to compensate for the loss of plant communities in semi-natural grasslands. However, the chances of grassland plants surviving on verges can apparently be improved by avoiding the use of salt and by specially planning the treatment of verges in open environments near seed sources. Mowing twice during the summer and gathering the cuttings immediately have been shown to efficiently remove nutrients, thus promoting species richness (Persson 1995, Schaffers et al. 1998). In addition to frequency, the timing of mowing should also be considered. To guarantee the chances of survival and dispersal of grassland plants the sward should be mown only after the seed shed in the late summer.

3.2.2 Movement corridors (III)

The combinations of grassland species occurring at the nearest neighbouring sites along roads and railways were more similar than would be expected if the species inhabited the sites with no mutual spatial dependence. This distribution pattern reflecting spatial dependence among sites supports the hypothesis that grassland species disperse along road and railway verges.

Alternatively, floristic similarity may also be caused by factors different from active dispersal along corridors. One such factor is the sowing practised in connection with road construction. However, in only five cases in our data had both sites within the pair been sown, and these sowings had mostly been performed over 20 years ago. Only three of the 67 grassland species in this study have always been included in the seed mixture used on roadside verges, and the coverage figures for most sown species decrease drastically within just a few years after sowing (Suominen 1974, Anon. 1991, 1998b). Therefore, the role of sowing is negligible when explaining the high similarity of species composition at the nearest sites which was observed.

Spatial autocorrelation is another possible reason for the similarity of flora at neighbouring sites (Legendre 1993, Brown et al. 1995). A similar species composition could simply reflect similar abiotic and biotic conditions at these sites. However, this is not likely in our data. First, in the majority of neighbouring pairs the sites were in different environment types, one in a forested and the other in a cultural, non-forested environment. Second, the distances between nearest neighbours were relatively long and varied considerably, from a few hundred metres to several kilometres. The relatively large scale emphasises the mutual independence of the sites with respect to their surroundings.

Moreover, road and railway verges constitute the most hospitable and probable route for dispersal to the majority of grassland plants. Different forestry lands cover approximately 75 % of the total area in Finland (Sevola 1997), and the majority of sites in this study were separated by coniferous forests. For grassland plants dispersal through such forests is difficult when compared to dispersal along open verges. Furthermore, along road and railways the seeds may be transported by means cars and trains (Schmidt 1989; Ernst 1998) or by the machinery used for mowing (Strykstra et al. 1997). Therefore I conclude that the distribution pattern of grassland plants which was identified reflects the use of road and railway verges as dispersal corridors. Even though such verges could not replace semi-natural grasslands, the ability to disperse to new habitats along verges is encouraging for the persistence of grassland species.

3.3 *Campanula cervicaria* – an example of rare grassland species (IV)

The initial size of bellflower populations ranged from 1 to 240 fertile individuals. The average size was only 24, and almost half the populations had five or fewer fertile plants. After eight years, in 1995, the population sizes had generally decreased, and 24 out of 52 populations had lost all fertile individuals. According to the logistic regression model, the risk of losing all fertile plants was over 50% if the initial population size was less than six. Habitat type (meadow or roadside) or size and distance of the nearest population had no significant effect on the probability of losing the fertile individuals. Therefore, the modern, regularly disturbed grasslands along roads and railways seem as suitable for this bellflower as the habitat types closer resembling traditional meadows. In fact, Lesica & Allendorf (1992) have argued that moderate stress may even help to maintain genetic diversity and the viability of populations, as well as being thought to promote the species diversity of plant communities (Grime 1973, 1979,Connell 1978). Since geographic isolation did not raise the risk of losing the flowering plants, it would be tempting to infer that isolation has not caused crucial genetic differences. However, geographic distances do not necessary predict genetic distances between populations (Godt et al. 1996, Lammi et al. 1999), and in small populations demographic uncertainty may be a more probable cause of decreasing population sizes and extinction than genetic problems (Shaffer 1987). For those populations that were monitored until 1998, the mean population size from the study period as a whole and the relative range of population size were negatively correlated. In addition to a raised risk of losing all fertile plants, the smallest populations exhibited the greatest fluctuation in population size, which again reflect demographic stochasticity.

Neither the ability of the seeds to germinate nor the growth rate of the seedlings were clearly connected to the current population size or to the variables describing variation in population size. Also in a recent experiment, in which several bellflowers were grown per population, the population size did not affect the size of seedling after the first growing season (T. Siippainen, unpublished data). As the viability of the early life-stages is independent of population size, small populations do not appear to suffer from inbreeding depression. However, in-depth studies covering the entire life cycles of plants coming from different-sized populations are needed before the possibility of genetic deterioration can be excluded. In contrast, the role of the surrounding environment in affecting population performance was obvious in our data. The current size of populations was negatively correlated with the percentage coverage by trees and shrubs. As canopy coverage in the original habitat had no effect on seed germination or growth in the laboratory, shading appears to be an external factor that deterministically reduces the survival of *C. cervicaria*, regardless of the potential viability of the plants. The same phenomenon has also been reported for other species that thrive in open environments (e.g., Oostermeijer et al. 1994). The decreasing amount of suitable, well-lit vegetation types appears thus to be an important reason for the diminishing size and number of bellflower populations. However, the open verges along roads and railways appear to present a continuous network of potential habitats, provided that they are appropriately managed. Being a monocarpic species that can wait for suitable flowering conditions as a rosette for several years, *C. cervicaria* appears to be adapted even to verges where management is irregular.

3.4 Protection of grassland plants by restoration (V)

Efforts to recreate a grassland produced somewhat discouraging results. As expected, mechanical removal of extra species affected the abundance of test species in the experimental field. In both species sets the mean coverage of test species as a group grew systematically from control plots to non-weeded and weeded plots but failed to exceed 60% even when outside competition was minimised. When the coverage figures for test species were broken up into their component species, half of the species had a higher coverage in weeded than in non-weeded plots. However, the mean coverage of no more than four species exceeded ten percent – even in the weeded plots – and no species achieved a remarkable coverage in the control plots. These results indicated rather low establishment and dispersal in most species.

On average, the rarer the test species were in the nature, the lower their coverage remained. Most of the rare and poorly surviving species were annuals or short-living monocarpic plants, the regeneration of which relies on successful seed production and germination. However, the weight of the seeds, indicating the amount of endosperm, was not related to the success of the species in the experiment. When setting up the experiment and collecting the results, the summer months happened to be exceptionally dry (e.g., Anon. 1997, 1999). Since regeneration from seeds is strongly dependent on weather conditions (Stampfli & Zeiter 1999), germination and growth were undoubtedly restricted by the water shortage and hardening of the soil surface. As an exception among the rare species, the perennial *C. jacea* reached the highest mean coverage of all test species. Once established it survived excellently in spite of the prevailing weather conditions or competition. Since *C. jacea* lacks adaptations to wind dispersal (Polunin 1969), its regional rarity is probably due to difficulties in spreading to fragmented grassland plots rather than reproductive problems.

With regard to other, non-test species, their summed coverage was the lowest in weeded and the highest in non-weeded or control plots. Similarly to the test species, only four individual non-test species (*Agrostis gigantea, Trifolium hybridum, T. repens,* and *Vicia cracca*) reached a mean coverage of over 10 percent in any of the treatments. When compared to a sample of Finnish semi-natural meadows (Kivi 1991), the quantities of certain nutrients at the beginning of the experiment were remarkably high. The tendency of a few species to dominate the sward gives support to the generally accepted paradigm of decreasing floristic diversity in productive environments (e.g. Anderson 1995). However, even productive sites may maintain relatively high species richness if the standing biomass is kept low by frequent management (Schaffers 2000). In this study the clipping of vegetation once a year was seemingly not enough to counteract the competitive effect.

On the basis of this experiment the success of rare grassland plants on a recreated grassland was uncertain. Especially the rare, short-living species that regenerate by the means of seeds achieved only low coverage figures, whether they were assisted by weeding or not. Even though the removal of other species relieved the test species from outside competition, the exposed soil surface became hardened and unsuitable for germination during the dry summers. The problematic soil conditions probably controlled the dispersal of well-established species as well, since the summed coverage of grassland species still remained as low as 60 % still in the third growing season. The difficulties in recreating meadow vegetation emphasise the need to maintain currently existing grasslands and to re-start management of recently abandoned ones. This need is further highlighted by an estimate according to which recreating a diverse grassland may require decades, even a century (Ihse & Norderhaug 1995). If, however, new grasslands are created, the initial sowing rate must clearly be high enough to thoroughly cover the whole area. Furthermore, introduction of fast-germinating nursing species may create safe sites and facilitate the establishment of grassland plants.

4 CONCLUSIONS

When using the data from the national inventory of semi-natural grasslands, no reliable tool was found for the identification of grasslands with the highest plant species richness. Only the area of the grassland was indisputably connected to the number of all species and grassland species. As the restricted time and funding available for the inventory project prevented chemical soil analyses and other exact surveys, such as measurement of illuminance, the accuracy of the background variables assessed appeared to be inadequate to establish the differences in species richness. Unless the environmental variables can be objectively measured, their collection is of little use in detecting the most species-rich areas. Instead, floristic diversity can be determined most reliably and cost-effectively by means of comprehensive species inventories in the field. Similarly, to cover the highest total species richness, the selection of priority sites for monitoring and management should be based on the use of objective area selection methods instead of scores which combine various floristic and non-floristic variables but failing to relate sites to each other.

Finding and maintaining representative semi-natural grasslands is critical for the preservation of plant communities typical of them, since the strips of grassland vegetation along roads and railways cannot fill the place of traditionally-managed grasslands. However, appropriate timing and frequency of mowing, removal of the cuttings and avoidance of the use of salt help to create more favourable conditions for grassland species along traffic routes, especially along small roads in open environments with human influence. Once they have landed on a favourably managed verge, the seeds of grassland plants dispersing along roads and railways may establish new populations, again serving as propagule sources for further dispersal. The rare bellflower *Campanula cervicaria* is an example of species that have successfully invaded the sides of roads and railways. Although the bellflower populations appear to be in a state of general decline, the roadside populations do not face an elevated risk of losing individuals when compared to populations in habitats closer resembling traditional meadows. In fact, the decreasing population sizes may not even be disastrous for the persistence of the species. Those species with a monocarpic life history typically occur on temporary habitats, and the life span of individual populations may be short (Often 1999). Therefore, the survival of the species *C. cervicaria* can probably be safeguarded by frequently providing open, slightly disturbed habitats along dispersal routes. If managed appropriately, road and railway verges serve as a continuous network of potential habitats.

For other grassland species too the maintenance of existing populations on semi-natural grasslands or roadsides appears to be far more favourable than the creation of new grasslands in altered environments. The common grassland species also survived moderately well in the recreated meadow, but the establishment of rare, short-living species was highly insecure. Even though roadsides are artificial habitats as well, their existing vegetation probably provides suitable microhabitats for the germination and establishment of the occasional rare grassland species thriving on them. Therefore, if attempts are made to recreate grassland vegetation, reliable methods are also needed to provide safe sites for germination, in addition to effective soil impoverishment techniques. In any case, my results support the argument that systematic management of existing semi-natural grasslands is the most effective and advisable instrument for the maintenance of viable communities of grassland plants (Anderson 1995, Bekker et al. 1997, Bakker & Berendse 1999).

Acknowledgements

This research was carried out at the Department of Biological and Environmental Science, University of Jyväskylä. Firstly, I would like to thank my supervisor Markku Kuitunen, who encouraged me to begin and continue with this work. I thank Markku and also prof. Aimo Oikari for providing working facilities at the University of Jyväskylä.

I wish to express my gratitude to all the colleagues and students who have helped me during this project. I am thankful to Reija Kivelä for allowing me to use her data on semi-natural grasslands and for commenting on the manuscripts. I would also like to thank Kaija Virolainen, who has been an excellent co-author and critic. I am grateful to Tuula Heikkilä, Mira Heiskanen, Tuula Häkkinen, Ari Jäntti, Pirjo Kuitunen, Outi Lehtinen, Tanja Siippainen and Hanna-Leena Keskinen, who have helped in different phases of the endless, laborious restoration experiment. I also wish to thank Piia Koski for her work with the roadside flora. Anna-Kaija Eisto, Antti Lammi, Veli Saari, Jukka Suhonen and Susanna Syrjäsuo have provided valuable information and practical help in work with the interesting bellflower *Campanula cervicaria*. Harri Högmander has helped me with statistical problems and shown me that writing an article can be fun. I am indebted to Veikko Salonen and Elisa Vallius for their comments on my texts and to Tony Melville for checking the language of this thesis. I also wish to thank all the other people working at the department, in the offices and in the library for their encouragement and assistance. Furthermore, I would like to express my thanks to the staff of Laukaa Research and Elite Plant Station, especially Marjatta Uosukainen, Asko Kukkonen and Satu-Marja Kinnunen, for their help and advice in raising the seedlings for the restoration experiment. I am similarly grateful to the horticultural authorities of the city of Jyväskylä, especially Mauri Lehtinen who provided us with the peaceful experimental area.

Next, I wish to address my special thanks to Elisa Vallius, Hanna Pasonen, Antti Haapala, Kaija Virolainen, Veikko Salonen, and Harri Högmander for their pleasant company at the department and/or during scientific meetings in different parts of the world.

My parents Hilkka and Tarmo, as well as my brother Juha and his wife Marita deserve my warmest thanks for their support, and I thank my nieces Tiia and Niina for sometimes playing with me. I am grateful to Tomi's parents Hilkka and the ate Erkki for always taking care of me at their city-farm when needed. Moreover, I wish to express my gratitude to all my friends for sharing normal life with me during these years. I would also like to thank all the people with whom I practised judo in Jigotai – after a couple of kata-gurumas it was impossible to think about science. Above all, I address my warmest thanks to Tomi, my Winnie-The-Pooh, for his endless encouragement, patience and helpfulness with practical problems. He has given me the strength to get through the hard times and he has shared the joy of the good moments.

My work has been financed by the Academy of Finland, the Maj and Tor Nessling Foundation and the University of Jyväskylä.

YHTEENVETO

Niittykasvillisuuden säilyttäminen ja ennallistaminen

Väitöskirjassani tutkin niittykasviyhteisöjen esiintymistä erilaisissa ympäristöissä sekä tarkastelen niittylajiston säilyttämis- ja ennallistamismahdollisuuksia. Niittykasvit, kuten kissankello (*Campanula rotundifolia*), ketoneilikka (*Dianthus deltoides*) ja nurmitatar (*Bistorta vivipara*), ovat perinnemaisemille eli luonnonniityille, -laitumille ja hakamaille tyypillisiä lajeja. Maa- ja metsätaloutta tehostettaessa perinnemaisemien määrä on romahtanut, ja monet niittykasveista ovat muuttuneet uhanalaisiksi. Niistä riippuvaiset hyönteiset ovat samalla harvinaistuneet, joten jäljellä olevien perinnemaisemien säilyttäminen tai korvaavien elinympäristöjen luominen on välttämätöntä useiden taksonomisten ryhmien suojelemiseksi.

Kansallisen perinnemaisemainventoinnin yhteydessä kerättyjä lajisto- ja ympäristötietoja käyttämällä arvioin, voiko kasviston monipuolisuutta ennustaa taustamuuttujien avulla. Hoitoon otettavien kohteiden valinta ja seuranta helpottuisivat, mikäli olemassa olevia taustamuuttujia voisi käyttää työkaluina lajimäärän ja erityisesti niittylajien lukumäärän arvioinnissa. Pinta-alaa lukuunottamatta mikään yksittäinen muuttuja ei kuitenkaan selvästi ennustanut lajimääriä. Vaikka kasvisto- ja ympäristömuuttujista yhdistetty, kohteen kansallista merkittävyyttä kuvaava arvoluokka korreloi kokonaislajimäärän ja niittylajien määrän kanssa, sen käyttö ei ollut tehokasta etsittäessä suurimman mahdollisen yhteislajimäärän sisältävää perinnemaisemajoukkoa. Taustamuuttujat sopivat kohteiden kuvailuun mutteivät lajiston ennustamiseen. Kasvistoltaan rikkaimpien kohteiden etsinnässä tulee käyttää huolellisia lajistoinventointeja sekä objektiivisia valintamenetelmiä, esim. heuristista menetelmää.

Niittykasveja esiintyy säännöllisesti myös vaihtoehtoisissa elinympäristöissä, kuten teiden ja ratojen pientareilla. Vertaillessani kokonaisia kasviyhteisöjä huomasin kuitenkin, etteivät pientareet kelpaa perinnemaisemien korvikkeiksi. Rikka-, viljelys- ja satunnaislajiston osuus teiden ja ratojen varsilla oli yleisesti liian suuri, mutta pientareiden välillä oli kuitenkin eroja. Asfaltoitujen ja suolattujen pääteiden metsäosuuksien pientareet olivat lajistoltaan köyhimpiä, kun taas avoimissa kulttuuriympäristöissä kulkevien sorateiden varsilla niittykasvit viihtyivät parhaiten. Välttämällä suolausta ja niittämällä kasvusto vasta siementämisen jälkeen niittylajien selviämisedellytyksiä ainakin avoimissa ympäristöissä voitaneen parantaa nykyisestä. Tulosteni mukaan niittykasvit kykenevät myös käyttämään tien ja radan varsia leviämiskäytävinä. Jos sopivalla hoidolla luodaan potentiaalisten kasvupaikkojen verkosto, leviämiskyky edistää niittylajiston entistä parempaa vakiintumista pientareille. Esimerkkinä uhanalaisista, tien varsille kotiutuneista niittylajeista olen tutkinut hirvenkelloa (*Campanula cervicaria*). Sen populaatiokoot pienenivät kahdeksan vuoden seurantajakson aikana, ja pienimmillä populaatioilla oli suurin riski menettää kaikki kukkivat yksilöt. Riski ei kuitenkaan ollut sen suurempi tienpientareilla kuin niittymäisemmillä kasvupaikoillakaan, vaan liittyi lähinnä ympäröivän kasvillisuuden varjostuksen voimakkuuteen. Koska hirvenkello on jo sopeutunut pientareille, kannan vahvistaminen onnistunee suunnittelemalla niittoaikataulut ja avoimena pidettävien pientareiden leveys lajia suosiviksi.

Olemassa olevien populaatioiden ja kasvupaikkojen säilyttäminen näyttää varmimmalta suojelukeinolta niin hirvenkellon kuin muidenkin harvinaisten tai uhanalaisten niittykasvien kohdalla. Entiselle pellolle perustetulla uudisniityllä menestyivät hyvin vain muutamat yleiset tai vahvasti kilpailevat lajit, mutta nekin levittäytyivät suhteellisen hitaasti. Vielä kolmantenakin kasvukautena niittylajien yhteispeittävyys koeruuduilla jäi noin 60 %:iin, vaikka ympäristöstä levinneet rikkakasvit oli kitketty pois. Kitkemättömillä ruuduilla niittylajien osuus jäi vielä huomattavasti alhaisemmaksi. Kitkemiskäsittelyn tarkoituksena oli minimoida ulkopuolinen kilpailu ja tarkastella niittylajien potentiaalista menestystä uudisympäristössä. Koekaudelle osui kuitenkin kaksi poikkeuksellisen kuivaa ja lämmintä kesää, joiden aikana kitkemisen paljastama maa kovettui vaikeuttaen itämistä ja kasvullista lisääntymistä. Tämän vuoksi kasvit eivät luultavasti pystyneet täysin hyödyntämään kitkemisen tuomaa kilpailuetua. Mikäli keinotekoisia niittyjä yritetään perustaa suojelutarkoituksessa, kylvötiheyden tulee olla niin korkea, ettei nousevaan kasvustoon jää suuria, kuivumiselle tai rikkojen leviämiselle alttiita aukkoja. Myös maaperän köyhdytyksen on oltava tehokasta. Tässä kokeessa maan ravinnetasot olivat luonnonniityiltä mitattuja korkeammat, mikä luultavasti suosi rikkalajeja niittykasvien kustannuksella. Niittykasvillisuuden vakiintuminen on lisäksi hidasta, joten kolme kasvukautta on varmastikin liian lyhyt aika lajikohtaisen menestyksen lopulliseen arviointiin.

Koska uusien kasvupaikkojen luomiseen liittyy riski- ja epävarmuustekijöitä, suojeluresurssit on syytä keskittää runsaslajisten perinnemaisemien tai piennarpopulaatioiden hoitoon ja kunnostukseen. Kun niiden riittävä hoitotaso on turvattu, alueiden verkostoa voidaan harkinnan mukaan koettaa täydentää uudisniityillä. Ennen kuin niittyjen perustamista voi suositella luonnonsuojelullisena keinona, vaaditaan kuitenkin perusteellisia tutkimuksia mm. kasvien paikallisista geneettisistä eroista ja eri kantojen sekoittumisen vaikutuksista jälkeläisten kasvuun ja lisääntymiseen.

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ORIGINAL PAPERS

I

Identification of species-rich semi-natural grasslands.

Tikka, P. M., Virolainen, K. M. & Kivelä, R. A.

Manuscript

II

Can grassland plant communities be preserved on road and railway verges?

Tikka, P. M., Koski, P. S., Kivelä, R. A. & Kuitunen, M. T., 2000.

Applied Vegetation Science 3: 25-32

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https://doi.org/10.2307/1478915

III

Road and railway verges serve as dispersal corridors for grassland plants

Tikka, P. M., Högmander, H. & Koski, P. S.

Manuscript (submitted)

https://doi.org/10.1023/A:1013120529382

IV

Population persistence and offspring fitness in the rare bellflower *Campanula cervicaria* in relation to population size and habitat quality

Eisto, A.-K., Kuitunen, M., Lammi, A., Saari, V., Suhonen, J.,
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Conservation Biology 14: 1413-1421

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https://doi.org/10.1046/j.1523-1739.2000.99283.x

V

The role of competition and rarity in restoration of a dry grassland in Finland

Tikka, P. M., Heikkilä, T. Heiskanen, M. & Kuitunen, M., 2001

Applied Vegetation Science (in press)

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https://doi.org/10.1111/j.1654-109X.2001.tb00244.x