PLANT COMMUNITIES OF FIELD MARGINS ъ THE EFFECTS OF MANAGEMENT AND ENVIRONMENTAL FACTORS ON SPECIES COMPOSITION AND DIVERSITY

DOCTORAL THESIS
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CONTRIBUTIONS

The contributions of the authors in the original articles of this thesis are presented in the following table.

	I	II	III	IV
Planning the study	ST, JH	ST, JH	ST, JH	ST
Conducting the experiment	ST, JH	ST	ST	ST
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CONTENTS

ABSTRACT

Agri-environmental schemes have so far resulted in only minor positive implications for the biodiversity of agricultural environments, in contrast to what has been expected. There is still the need for challenging work to improve or even stabilize the current state of biodiversity in agricultural environments. In agriculture, there has always been a continuous tendency towards intensification of production. Farms are often highly specialized, having one main product such as cereals or animals. Land-use intensification has decreased landscape heterogeneity.

Field boundaries are uncultivated areas of permanent vegetation located adjacent to fields. Boundaries are a basic element in agricultural landscapes. Boundary vegetation may become established naturally or can be sown with seed mixtures of few or diverse species. Since the number of boundary habitats is high, investing in their quality may result in more diverse agricultural landscapes. Currently, boundaries can be considered as multifunctional habitats providing agronomic, environmental and wildlife services.

This thesis focused on plant species composition and diversity in field margin habitats, i.e. boundaries, buffer strips and buffer zones. I aimed at describing plant communities and their diversity and the factors affecting plant species diversity and composition. The importance of different factors was studied on regional, landscape and habitat scales. Vegetation surveys were conducted on regional and landscape scales and a field experiment on cutting management was conducted on a habitat scale.

In boundary plant communities, species appeared to be indicators of high or intermediate soil fertility and moist soil conditions. The plant species diversity found in boundaries was rather low, compared with most species-rich agricultural habitats in Finland, such as dry meadows. However, plant species composition and diversity varied between regions and were related to several factors. Land-use history, main production line, natural species and human induced distribution, climate and edaphic factors were elements inducing differences in species composition among regions. The lowest regional species diversity of boundaries was related to intensive and long-term cereal production.

Management by cutting and removal or grazing had a positive effect on plant species diversity. Cutting and removal were the most effective at promoting species diversity. The positive effect on species richness was dependent on the adjacent source of colonizing species. Therefore, in species-poor habitats and

landscapes, establishment of margins with diverse seed mixtures can be recommended for enhancing the development of species richness. Management by cutting for 5 years did not result in a decline in dominance of a harmful weed species, *Elymus repens*, showing that *E*. *repens* probably needs cutting more frequently than once per year. Likewise, soil fertility, especially phosphorus content, did not decrease by boundary management. Therefore, the nutrient load from field to boundaries and waterways should already be reduced in the cultivated area.

It is concluded, that management by cutting and removal is an effective means of enhancing plant species diversity in field margin habitats, although the adjacent species source is also important. Agri-environmental schemes should include long-term contracts with farmers for the establishment and management by cutting and removal of arable field margins that are several metres wide. In such schemes, the timing and frequency of management should be planned so as not to harm other taxa, such as the insects and birds that are dependent on the field margin habitats. No herbicide drifts should be allowed in conventional production to minimize the negative effects of sprayings on field margins. The harmful effects of herbicides can be avoided by organic farming methods.

1 INTRODUCTION

1.1 The features of agriculture in Finland central to farmland biodiversity

In agriculture, there has been a continuous tendency towards intensification of production (Matson et al. 1997). Farms are often highly specialized and may have one main product, such as cereals or animals. Land-use intensification has decreased landscape heterogeneity (Hietala-Koivu 1999, 2002, Luoto 2000). Use of pesticides and artificial fertilizers also belongs to intensified farming.

In Finland, agricultural production experienced remarkable structural changes in the late 19th century. So-called traditional agriculture was coming to an end. At that time, animal production began to increase, followed by the enhanced need for fodder production and the establishment of new fields (Soininen 1974). Moreover, forestry started to become an important source of income and made it possible to invest in agriculture (Soininen 1974). Mechanization of cultivation practices was begun. Use of slash-and-burn method, typical especially of eastern Finland, decreased. These typically stony soils began to be used for livestock grazing.

In the late 1940s after the Second World War the mechanization of agriculture increased at a rapid rate. The use of chemicals also became common (Siiskonen 2000). Regional and farm-level specialization in plant or animal production began to increase. Cereal and animal production were concentrated in separate regions. As a consequence, many ecological features were lost from production and production systems were simplified. Moreover, the local cycling of manure was no longer possible. This led to the increased use of mineral fertilizers in cereal production and, on the other hand, the production of excess amounts of manure as a side product of animal production. Without animals, the less productive grassland areas could no longer be utilized as pastures for grazing animals. These areas have lost their biodiversity and typically have become overgrown with trees.

The considerable loss of heterogeneity in agricultural landscapes is mainly a consequence of mechanization and intensification of cultivation practices (Hietala-Koivu 1999, 2002). The increase in field size and commonly applied subsurface drainage has led to remarkable decreases in small, uncultivated habitats such as boundaries, open ditches, woody patches, stony piles and small wasteland patches of barnyards.

Since joining the European Union (EU) in 1995, Finland has implemented a common agricultural policy (CAP). When the first agri-environmental scheme (AES) was initiated in Finland in 1995, it included hardly any measures aimed at contributing to biodiversity. However, direct pesticide sprayings and fertilization of boundaries have been prohibited since the beginning of the first AES. Since the beginning, further measurements contributing to farmland biodiversity have been included in the scheme. The AES emphasizes that, in the establishment and management of all boundaries, it is important to favour methods that enhance biodiversity. They are aimed at preventing leaching and erosion, promoting biodiversity and having only minor abundances of harmful weeds. Grassy boundaries were chosen for the study object to monitor the effects of AES on biodiversity. Later, since 2000, the monitoring programme has included all types of seminatural habitats.

AESs have so far resulted in only minor positive implications for the biodiversity of agricultural environments (e.g. Kleijn et al. 2001, Kleijn & Sutherland 2003, Blomqvist et al. 2008), in contrast to what has been expected. There is still the need for challenging work to improve or even stabilize the current state of biodiversity in agricultural environments.

1.2 Field boundaries as a part of agricultural landscapes

Field boundaries are uncultivated areas of permanent vegetation located adjacent to the field. Boundaries are a basic element in the field environment and their types vary among the countries. In Finland, they are dominated by herbaceous species and are mainly without trees or bushes. Indeed, the cutting of coppices is obligatory. By comparison, a typical traditional boundary in England consists of hedge with partially planted woody vegetation and herbaceous layer (Marshall & Moonen 2002). The establishment of different types of boundaries is very common in AESs in many European countries and is easily adopted by farmers (Marshall et al. 2006). Boundary vegetation may become established naturally or it can be sown with seed mixtures of few or diverse species. Since the number of boundary habitats is high, investing in their quality may result in more diverse agricultural landscapes.

The functional role of boundary habitats has changed in the course of time. In Finland, during the 16th and 17th centuries grassy margins were used to make hay for animals. After agricultural intensification started during the 1950s, grassy margins were no longer considered useful, but rather as a serious problem, because they acted as a source of weeds, pests and diseases (Hilli 1949, Siiskonen 2000). Farmers were encouraged to reduce the number of boundary areas by subsurface drainage and spray not only the cultivated area but also the grassy margins, as far as to the water's edge (Siiskonen 2000).

In the 1980s, concern over the loss of noncrop habitats of agricultural landscapes became more common. Currently, boundaries can be considered as multifunctional habitats providing agronomic, environmental and wildlife services (see Marshall & Moonen 2002). Boundaries buffer pesticide effects, prevent fertilizer runoff, reduce soil erosion, and promote biodiversity and conservation. Species-diverse boundaries may reduce pesticide use by exploiting pest predators and parasitoids and enhancing crop pollinator populations.

1.3 The role of boundary plant communities for farmland wildlife and cropping

This thesis is focused specifically on plant species composition and diversity in field boundaries. Many studies have shown the importance of margins for different groups of organisms. Not only their area but also their quality plays a significant role. The habitat quality of boundaries for consumers is largely determined by the plant species (producers) diversity and composition. In farmland ecosystems, there are also complex interactions between organisms, and between organisms and human-introduced farming activities.

Plants also obtain ecosystem services from animals, which pollinate flowers and function as seed dispersal vectors. Animals may favour many different types of vegetation, depending on the animal group in question. The richness of nectar- and pollen-producing plants, food plants for larvae, the abundance of tussock-forming grasses or the litter produced may be important for arthropods. Birds may feed and nest in boundaries, which are also movement corridors for other animals. The higher abundance and diversity of food plants providing nectar and pollen have positive effects on bumblebee and butterfly diversity (Dramstad & Fry 1995, Sparks & Parish 1995, Bäckman & Tiainen 2002, Carvell et al. 2007, Ekroos et al. 2008).Predatory arthropods overwinter in boundaries and favour tussock-forming grasses (Dennis & Fry 1992, Lagerlöf & Wallin 1993, Dennis et al. 1994, Pfiffner & Luka 2000). Boundaries are important sources of invertebrate and plant food for birds (Wilson et al. 1999), and birds also use boundaries for nesting.

Margins have only a small influence on the weed flora of arable fields (Marshall & Arnold 1995, Smith et al. 1999, Marshall 2009). Plant species are distributed only short distances from boundaries to field areas (Marshall 1989, Wilson & Aebischer 1995). Species spreading vegetatively, such as *Elymus repens*, may originate from boundaries (Marshall 1989). The establishment of permanent boundary vegetation by sowing variable forbs and grass seed mixtures decreases the abundance of pernicious weeds (West et al. 1997, Bokenstrand et al. 2004, De Cauwer et al. 2008). Simple grass seed mixtures are economical and easily available to the farmer, compared with diverse mixtures of herbs and grasses that may also contain exotic plant species not adapted to local conditions. However, the use of simple grass seed mixtures may decrease species diversity (Kleijn et al. 1998). The use of diverse seed mixtures of meadow plant species may increase the long-term species diversity in field boundary vegetation, although species not adapted to available habitat conditions tend to become extinct (Bokenstrand et al. 2004).

1.4 Key factors affecting plant species diversity and composition in boundaries

In the present study, plant species diversity and composition of field margin habitats were determined at three spatial scales. The regional scale was represented by geographical areas that differed in their climatic conditions, agricultural land-use history and main line of production (see 1.1). The landscape scale was represented as a watershed area, with rather homogenous climatic and edaphic conditions as well as agricultural land use. Boundaries represented a habitat scale. The study, conducted at different spatial scales, aimed at increasing understanding of the factors important at each scale as well as interactions between the scales.

1.4.1 Landscape heterogeneity, land-use history and climate

Landscape heterogeneity is associated with the regional differences in land-use history and landscape structure. Political decisions have also determined the agricultural specialization of regions.

Landscape heterogeneity enhances species richness and geographical variation results in differences in regional species richness (Kivinen et al. 2006). In the study of Billeter et al. (2008), the area of semi-natural habitats and species diversity was positively associated with agricultural landscape. Landscape heterogeneity is crucial for plant species diversity (Le Coeur et al. 1997).

Land-use history can also explain the present species diversity. Lindborg and Eriksson (2004) found that historical land use, mainly habitat connectivity, can explain the present species diversity, especially at the landscape scale. This suggests that the present patterns of species diversity are not necessarily explained by the factors measured currently.

Climatically, differences among the regions can also cause variation in vegetation. Plant species distribution history after the glacial period could also have varied. Many species are also dispersed by human activities.

1.4.2 Boundary management by cutting or grazing

At the habitat and landscape scales, vegetation management plays an important role in species diversity and composition in boundaries. The positive effects of cutting on plant species diversity were shown in several grassland studies (Willems 1983, Hansson & Fogelfors 2000, Maron & Jeffries 2001, Wahlman & Milberg 2002, Pykälä 2004, 2005), but rarely in field boundaries (De Cauwer et al. 2005).

The effects and mechanisms of grazing and cutting differ, but both are effective in maintaining plant species diversity in grasslands (Hansson & Fogelfors 2000). In cutting, all species are treated homogeneously, compared with the heterogeneous effects of grazing, caused mainly by selective grazing of the species and cap formation in the vegetation (Jacquemyn et al. 2003).

For field margin management, cutting is more practical and easier to carry out than grazing. Cutting is rather easily done by machine and cheaper and faster than grazing. Many arrangements, such as fencing, animal transport and control, and arranging of drinking water (Palva 2006) are needed for buffer zone grazing.

To prevent long-term nutrient accumulation in the boundary, not only cutting but also harvesting the cuttings was proposed as important management practices (Kleijn 1996). De Cauwer et al. (2005) reported increased plant species diversity resulting from this type of harvesting of plant biomass from field margins.

Indirectly, management affects plant species richness by the amount of litter and nutrient contents. The accumulation of plant litter negatively affects plant species diversity by reducing seedling establishment and survival (Bobbink & Willems 1991, Tilman 1993, Foster & Gross 1998, Jutila 2003, Ruprecht et al. 2010). However, studies on boundary habitats have not specifically focused on litter.

Cutting management may also depress the populations of harmful weed species, such as *Elymus repens* (L.) Gould. It is an efficient colonizer, especially in fertile soils (Marshall 1990). Once it predominates, however, other species have difficulty colonizing the community (see Werner & Rioux 1977). In a permanent set-aside, cutting diminished the abundance of *E. repens,* especially at the least fertile sites (Hansson & Fogelfors 1998).

1.4.3 Plant species dispersal and colonization

In species-poor agricultural landscapes, species diversity may be limited by the dispersal ability of the species (Leng et al. 2009). In addition to dispersal limitation, unfavourable site conditions may limit the establishment of new species in buffer zones. This colonization limitation may be due to litter accumulation (Bobbink & Willems 1993, Tilman 1993, Ruprecht et al. 2010) or high nutrient levels (Blomqvist et al. 2003, Foster & Gross 1998).

Species source may be a critical factor when increase in species diversity is targeted by management. A clear source for recolonization is the soil seed bank, while less is known about the relative importance of the seed bank and dispersal from neighbouring communities to the maintenance of species diversity in marginal communities. In the margin strips established from a previously cultivated field, the seed bank often reflects the weed community composition of the arable field, which is dominated by early successional species (Kiirikki 1993, Luzuriaga et al. 2005, Boutin 2006). Moreover, the similarity between the old grassland vegetation and its seed bank is typically low, and the seed bank may contain only a few species of value for community restoration (Milberg 1992, Kalamees & Zobel 1998).

1.4.4 Cropping practises and width

Since they are locating adjacent to arable fields, boundaries are exposed, indirectly or directly, to the effects of cultivation practices such as tilling, herbicide sprayings (Marrs et al. 1989) or fertilization (Kleijn 1996, Kleijn & Snoeijing 1997). Wider boundaries have higher species diversity than narrower boundaries (Ma et al. 2002). Vegetation of narrow boundaries is more likely to be affected by herbicide drift from fields (Marrs et al. 1989). Moreover, nutrient loading from fields may negatively affect species richness, especially near field edges (Kleijn & Snoeijing 1997). Species with high nutrient optima survive early establishment in fertile soils and have competitive advantage (Blomqvist et al. 2003). Plant nutrients originating from fertilizers often reach the boundary vegetation through the processes of leaching, runoff and erosion from the field. Boundary vegetation may also be affected by other factors, such as production type and the cultivated plants chosen.

Plant species can be used as indicators to describe the environmental conditions of a certain habitat. The description is often indicative, because species interactions and other factors may also affect species abundance and distribution. In field boundary habitats, species may indicate the use of herbicides, soil fertility, soil moisture or other factors. Ellenberg et al. (1991) described the ecological characteristics of plants, i.e. the environmental conditions that certain plant species is favouring. Classifications for plant species were made according to their optimum for e.g. nitrogen, moisture and light conditions.

2 Aims of the study

This thesis aims at examining the plant communities of different types of field margin habitats and the factors affecting their species diversity and composition. Based on the results, the state of the plant diversity in boundaries is estimated and recommendations for boundary management are given.

At first, my objective was to describe the prevailing plant species diversity and composition in field boundaries of farmland in Finland (**I**). Further, I aimed at classifying the boundaries into vegetation types that were based on their plant community composition (**I**).

Secondly, I aimed at determining more specifically the importance of different factors for species composition at three spatial scales:

At the regional scale, my objective was to study the importance of edaphic, spatial and management factors for species diversity and composition in field boundaries of four geographic regions (**II**).

At the landscape scale, I focused on the role of management and edaphic factors on species diversity and composition of buffer zones within a landscape (**IV**).

At the habitat scale, I aimed at measuring the effects of cutting management on diversity (**III**) and the role of management in decreasing the soil nutrient level (**III**, **IV**). The specific interest was in the effects of cutting and removal on such an existing boundary in which the plant community has already passed through the early stages of succession. In addition, the role of seed bank and adjacent species-rich grassland habitats as species sources was studied (**III**).

3 Material and methods

3.1 Study regions

Two of the studies were carried out in four regions of Finland: Lepsämänjoki 60°20-27' N, 24°37-49' E, Yläneenjoki 60°47-56' N and 22°25-40' E, Lestijoki 63°39-50' N, 24°09-25' E and Taipaleenjoki 62°36-38' N, 29°10-20' E (**I**, **II**). The names of the study regions are the names of rivers, because the study sites were located in the watershed of each river. The average thermal growing season in Yläneenjoki and Lepsämänjoki is 170 days, in Taipaleenjoki 155 days and in Lestijoki 150 days (Finnish Meteorological Institute).

Lepsämänjoki and Yläneenjoki are located in the region of cereal production and Lestijoki belongs to the animal husbandry region. Taipaleenjoki is an animal husbandry area as well, but the farm size is smaller and landscape structure more fine-grained than in the Lestijoki region (Luoto 2000). The typical soil types in Lepsämänjoki and Yläneenjoki are clay and silt. Moraine is the most common soil in Lestijoki, whereas in Taipaleenjoki moraine, gravelly soil and sand are characteristics. In watershed areas, where the study boundaries are located in river, stream or ditch banks, clayey soils were also represented.

The study boundaries at the habitat level (**III)** and landscape level (**IV**) were located in the fields of MTT Agrifood Research Finland in Jokioinen, southern Finland (60°85´ N; 23°46´ E). The region is typically flat agricultural landscape and the average length of the thermal growing season is 165 days in the region. The fields are mainly used for cereal and forage production. The sites were located in a 92 km^2 landscape area (67°45-54' N, 29°79-31°09' E, 9.2 km x 10 km). They were located at the sides of river or streams, all belonging to the watershed area of the Loimijoki River.

3.2 Definition of a boundary

Field boundaries are linear habitats of permanent vegetation surrounding the field. In this thesis, one boundary is measured as starting from one field corner and ending at the next corner. The boundaries of one field are usually connected. However, the environmental conditions may be critically dissimilar, depending on the side of the field. Therefore, the reasonable unit for the boundary habitat in a field environment is a boundary on one side of the field. In the current Finnish AES, three specific types of field margin habitats are defined:

- **Boundaries** of main ditches should be at least 1 m wide, but should not exceed 3 m on average. Mowing is not required, but is necessary if coppices increase in abundance. The requirement applies to all farmland under the scheme.
- **Buffer strips** are established next to larger waterways rather than to main ditches. The width is 3 m and should not exceed 10 m on average. Mowing and removal of cuttings are recommended and necessary if coppices are abundant. If the vegetation is damaged, it should be re-established by sowing as soon as possible. Establishment should be done by sowing, if no previous vegetation exists. It is included to the basic measures of the scheme. The requirement applies to all farmland under the scheme.
- The width of the **buffer zones** is at least 15 m on average. Cutting and the removal of cuttings are compulsory. Grazing is allowed as is the growing of groups of native trees or bushes. The establishment of a buffer zone is a voluntary measure, and extra compensation is paid for it.

In this thesis, these terms are used as defined above. In the original publications, the use of the terms varies. The target field margin habitats of each study are listed in Table 1.

Table 1. Composition of field margin types included in the thesis (I - IV).

Study	Boundary	Buffer strip	Buffer zone
I	x	x	
II	x	x	
III		x	
IV			x

Since management early in the growing season may disturb nesting birds, cutting management should not be done before 1st August. The use of herbicides is restricted; only patches of weeds are allowed to be sprayed if they have very serious weed problems. Fertilizers are not allowed in boundaries. In this thesis, only boundaries next to waterways (ditches, streams or rivers) were examined.

Usually there is a slope between the boundary and waterway. The length and steepness of the slope may vary. Buffer zones are often established on slopes.

3.3 Sampling methods

Boundaries were preselected from aerial photographs to find the sites located next to waterways and open areas, and with no or only minor occurrences of trees or shrubs (**I**, **II**). Plant species abundance and diversity were measured from five 0.25-m² quadrates (0.5 x 0.5 m) 20 m apart from one another (n = 193 **I**). A nine-class scale (1 - Ò0.8%, 2 - Ò1.6%, 3 - Ò3.1%, 4 - Ò6.3%, 5 - Ò12.5%, 6 - Ò25%, 7 - Ò50%, 8 - Ò75%, 9 Ò100%) adopted from Oksanen (1981) was used in estimating plant species coverage (**I**). The width of the boundary in the quadrate locations varied from 4 cm to 860 cm (measured as the even part between the edges of the field and slope). The data of one subset were collected from the boundary areas without quadrates in 1998 (n= 57, **II**). Species abundances were estimated, using five classes of coverage (1 < 1%, 2 = 1-5%, 3 = 5-10%, 4 = 10-50%, 5 > 50%). Since the entire area of each boundary was surveyed, the sampling area varied according to the width and length of each site, but no correlation between the number of species and the area of the boundary was found.

In the study of 15 buffer zones (**IV**), species diversity was estimated from a transect of 50 m² (length 25 m, width 2 m) in each buffer zone. The site width varied from 10 m to 40 m. To estimate species composition, three 1-m^2 quadrates were done along (within) the transect. Two of them were located 2 m from the end of the transect and one in the middle. Plant species coverage percentages were estimated, with absolute coverage values varying from 0.25% to 100% per species. The mean coverage value for each species was counted as an average of the three 1-m^2 quadrates.

Vegetation sampling was performed in July to mid-August (**I),** in July **(II, IV**) and in late July to early August (**III**). Species nomenclature followed that of Hämet-Ahti et al. (1986) (**I**) and (1998) (**II, III, IV**). To describe the ecological characteristics of the species, the indicator values of Ellenberg et al. (1991) were applied (**I**, **II**).

The soil sampling period was as follows: July 1995 and 1997 (**II**), early August 1997 - 2001 (**III**) and July 2003 (**IV**). Several subsamples per site were mixed to obtain a single sample for soil analyses (**II**, **III**, **IV**). Soil phosphorus was also analysed from three depth layers (0 - 2, 2 - 5, 5 - 10 cm) (**IV**). Acid ammonium acetate (pH 4.65) was used to extract exchangeable magnesium, potassium, and calcium and easily soluble phosphorous (Vuorinen and Mäkitie 1955), and water was used for pH measurements (**II, III, IV**). The first three elements were measured using the inductively coupled plasma (ICP) method, and the phosphorus was measured, using a Bran & Luebben autoanalysator (**II, III, IV**).

The environmental factors used as explanatory variables were formed from management practices (no mowing, mowing, combined mowing and grazing), the establishment method (sown grassland, newly established natural vegetation, old natural vegetation) and the use of herbicides in the adjacent field (the number of years the field has been sprayed at least once during the growing season, **II**). The data were based on interviews with farmers conducted by the Finnish Environment Institute. Spatial variables were constructed, by using the longitudinal *y* and latitudinal *x* of the boundaries studied (**II**).

The experiment in cutting management was a randomized complete block design with four replicates (**III**), conducted from 1997 to 2002. Each block of 3 m x 15 m consisted of 3 m x 5 m plots of non-treated control, cutting and cutting with removal. The experiment covered an area of 3 m x 60 m along the margin. In the 5-m-wide margin, 1 m from the field edge and 1 m adjacent to the ditch slope were left outside the experimental area. A scale of five classes was used (see **II**) to estimate the abundances of species in each experimental quadrate plot. The biomass samples were collected by taking three samples from each treatment plot (**III**). The amount of litter was estimated from the areas of biomass samples as an absolute coverage value (0-100%).

The 15 buffer zones were classified into three groups, based on their management intensity (**IV)**. The first group included sites that were managed not more than 4 years, the second group included sites managed during 5 years, and the third group included sites grazed at least in 6 years.

The seed bank samples were collected in May 1998 (**III**) to provide an estimate of the seed bank composition at the beginning of the experiment. A total of 60 soil samples were collected from the experiment area. Five samples were taken from each experimental plot and placed in a greenhouse for germination. Once germinated, the seedlings were identified, counted and removed. The first germination period of 11 weeks occurred during the summer of the sampling and another period of 5 weeks also occurred the next summer after a stratification period in cool, dark storage at a constant temperature of 4 °C.

3.4 Statistical methods

The CANOCO program (Ter Braak 1987) (**I**) and CANOCO for Windows 4.02, Ter Braak & Smilauer 1998, Plant Research International, Wageningen, The Netherlands) (**II**, **III**, **IV**) was used in plant community analyses. Correspondence analysis (CA) was applied to reveal the major variation in the plant communities (**I**). Based on the results of the CA, cluster analysis (Ward's method) was performed with the SAS™ (SAS Institute Inc., Cary, NC, USA) Statistical package (**I**). The mean species richness for each cluster was based only on the boundaries from which all five quadrates were sampled; thus the effect of area on species number was avoided. The relationship between the species richness and distance from the field edge was tested with analysis of variance (ANOVA) performed by SYSTAT™ (SPSS™ Inc. (Chicago, IL, USA) 1997).

The linear redundancy analysis (RDA) of CANOCO was used to study the relationship between species composition and environmental variables (**II**, **IV**). The default options of RDA (i.e. scaling based on interspecies correlations, species scores divided by standard deviation, no transformation, centring by species) were used.

The significance of the explanatory factors was tested, by using the forward selection procedure of CANOCO (Monte Carlo unrestricted permutation test) (**II**, **IV**). Explanatory factors with p-values of conditional variance greater than 0.05 were excluded from further analyses. Furthermore, partial RDA was used to estimate the amount of variation that each variable or group of variables explained (Borcard et al. 1992) (**II**). The variation in statistically significant variables was partitioned (Økland 1999). The coordinates of the study boundaries (longitudinal y and latitudinal x) were used to construct spatial variables that were included in the RDA (**III**). To determine the possible spatial structure in the data, the coordinates were included as covariables (**IV**).

The species composition of the vegetation and the soil seed bank was examined by applying the detrended correspondence analysis (DCA) of CANOCO (**III**). The vegetation analysis is a comparison of the species composition of the early (1998) and the final (2002) stages of the experiment. In the seed bank analysis, the number of seedlings detected was used as a response variable.

Simpson's diversity index (dominance) (**II**, **IV**) and species richness (**I**, **II**, **III**, **IV**) were used as measures of species diversity (see Lande et al. 2000). The reciprocal form of Simpson's index (1/D), in which the index value increases when evenness rises, was used (**IV)** (Magurran 2004). Simpson's index was calculated, using BIODIV® software version 4.1 (Exeter Software, Setauket, NY, USA) (Baev and Penev 1993). ANOVA performed with SYSTAT™ was used to test the effect of distance from the field edge on plant species richness (**I**).

Regression analysis was applied, using SPSS® software to test the dependence of species richness on boundary width, soil pH and easily soluble soil phosphorus concentration, which were statistically significant in the forward selection of CANOCO. To analyse the difference in species diversity and Ellenberg indicator values between the areas, ANOVA and the Games-Howell (GH) multiple comparison test were applied, using SPSS® software (**II**). In addition to regional differences, the interaction of study area and management as well as study area and establishment on species diversity were analysed with the GLM (general linear model) (**II**). The Ellenberg indicator values of species (soil pH, light, moisture and nitrogen) were used to form a value to describe the characteristics of each boundary. The values representing a certain characteristic were summed and then divided by the number of available values per boundary (**II**).

The differences in species richness, coverage and the biomass of herbs and grasses, the biomass of the most abundant grass species (*Elymus repens* and *Phleum pratense* L.), litter coverage and the amount of soil phosphorus were tested among the treatments and study years (**III**). Linear mixed models were applied for analyses of the biomass of the grasses, *E. repens* (log+1-transformed) and *P. pratense* (square root transformed), as well as for the soil phosphorus (log+1 transformed) (**III**). The biomass of herbs was analysed using generalized linear mixed models (log link function and Poisson error distribution). Friedman's nonparametric ANOVA with test parameter W was used to analyse the species richness, coverage of the plants and litter coverage (**III**).

Differences in species richness and evenness, amount of soil phosphorus and calcium, litter coverage and the width and age of the buffer zone were tested among the management intensity levels (**IV**). Mixed GLMs were applied for the analyses. The data on soil phosphorus and species evenness were log+1-transformed prior to the analyses. The statistical tests were conducted, using the statistical package SAS 9.1 for Windows (Littel et al. 2006) (**III**, **IV**).

4 RESULTS AND DISCUSSION

4.1 Landscape heterogeneity, land-use history and climate

Plant species composition alone (**I**) and together with spatial and environmental explanatory factors (**II**) demonstrated the regional differences in boundary vegetation. Of the four study areas, the southern areas (Yläneenjoki and Lepsämänjoki) were more similar than the eastern (Taipaleenjoki) and western (Lestijoki) study areas (**I**). Based on species composition (**I**), seven clusters of boundaries were differentiated. The groupings followed rather strictly the geographical distribution of boundaries. Two groups cached almost half of the sites, with one group (*Ranunculus-Phleum*, n = 37) being the most common in Lestijoki and the other (*Elymus-Anthriscus*, n = 48) the most common in the southern areas (Yläneenjoki and Lepsämänjoki). The mean species richness was highest (24 species on average) in the group of boundaries from the eastern area (Taipaleenjoki) and lowest in the group representing boundaries mainly from Yläneenjoki (14 species on average). Species richness and heterogeneity were also highest in the Taipaleenjoki area, in comparison to the other three study areas (**II**).

Within the regions studied, the landscape heterogeneity was lowest in the Yläneenjoki and Lepsämänjoki areas and highest in the Taipaleenjoki area (Luoto 2000). The higher landscape heterogeneity in Taipaleenjoki probably had a positive effect on species diversity (Kivinen et al. 2006). Landscape heterogeneity plays on important role for species diversity in agricultural environments (Weibull et al. 2000, Benton et al. 2003, Kivinen et al. 2006, Billeter et al. 2008, Lindborg et al. 2008). Of the explanatory factors, spatial variables that include the possible landscape heterogeneity, explained the highest proportion of variation in species composition (**II**). Other significant variables included management practices, width, use of herbicides, soil pH and phosphorus. These variables are affected by field practices that vary regionally, depending on the main production. They indirectly affect boundary plant composition and diversity (Kleijn & Verbeek 2000). This is probably one important explanation for the regional differences in boundary vegetation (**I**, **II**). In RDA, the first two axes explained about half (53%) of the variance in the species-environment relationship. Spatial variables alone explained more than a third (35%) of the variation and jointly with other variables almost a further third of the variation (**II**). Management alone explained the second highest portion (11.6%) and soil characteristics alone the third highest proportion (8.3%) of the variation (**II**).

Species indicating regional differences in land-use history, human-induced or natural distribution of species were also found. Several of these species were not introduced in the original articles, but are only mentioned here. Regional agricultural land use and soil type may have contributed to the abundance of *Phleum pratense* and *Ranunculus repens* L., which were the most frequent and abundant species at the Lestijoki sites (**I**). *Ranunculus repens* is a typical weed in grasslands, while and *P. pratense* probably originated from seed mixtures used for grassland establishment. *Rubus arcticus* L. is naturally distributed throughout Finland, is most vigorous in northern areas and was represented only in Lestijoki.

Species indicating the historical use of slash- and-burn cultivation in the eastern region (Taipaleenjoki), included *Knautia arvensis* (L.) Coult. and *Campanula glomerata* L. The findings of *K. arvensis* were limited only to the eastern region, whereas *C. glomerata* was also found in other regions. A species of eastern origin, *Lactuca sibirica* (L.) Maxim., was found only in the Taipaleenjoki area. Its natural distribution covers eastern and northern Finland.

In the south-western and southern regions, species dispersed by human settlement included *Aegopodium podagraria* L. and *Glechoma hederacea* L. and in the south-west alone, also *Symphytum officinale* L. *Elymus repens* was most frequent and abundant in both regions. Indicators of disturbed and species-poor habitats were characterized especially in the South-western area (**II**).

4.2 Boundary management by cutting or grazing

In the present study, management was a significant factor for species composition and diversity at the regional, landscape and habitat levels. At the regional level (**II**), based on 4 years of information on management practices (Grönroos et al. 1998), management was a significant explanatory factor for species composition but not for species richness. Although the other factors also affected on regional species composition, management alone explained 11.6% and together with other variables 24.5% of the variation in species composition (**II**). Regardless of the short-term data on management, it appeared to play a marked role in explaining the species composition. It seemed to be related to regional field use, in which grasslands for mowing and grazing are commonly found in dairy production areas. The regional-level study did not yet reveal specifically the effects of mowing or grazing on boundary plant communities, but if anything, it described the differences caused by land use of the main production type.

Species richness was positively affected by grazing in the buffer zones (**IV)** and cutting management in the buffer strip (**III**). Species richness was significantly higher in the group in which the sites were managed by grazing for at least 6 years, compared with extensively grazed or cut sites (**IV**). Cutting and removal of biomass resulted in significant increase in species richness, in contrast to cutting or untreated control (**III**). The increase was significant after 3 years of management. All species that appeared after cutting and removal were herbaceous species.

The amount of litter decreased significantly in cutting and removal in contrast to cutting only or control. Litter accumulation was also proposed as preventing new species establishment and thereby decreasing species diversity (Bobbink & Willems 1993, Tilman 1993, Ruprecht et al. 2010). Earlier studies (Foster and Gross 1998, Jutila & Grace 2002) have pointed to the importance of litter in reducing species richness by inhibiting the establishment of seedlings. Their results showed that both an increase in biomass productivity by nitrogen fertilization and an accumulation of litter can independently decrease plant species richness. Both factors contribute to shading, which reduces seedling establishment. In our study, cutting without removal of the cuttings was not effective for the management of species diversity. One clear consequence of biomass removal was reduction in litter formation, pointing to this as a causal factor in the increase of species diversity, as suggested by the study of Foster and Gross (1998).

The mechanisms for enhancing species richness seemed to be different in grazing and cutting. Grazing likely enhanced species richness mainly by disturbance effects. The positive effect of cutting and removal on species richness was most probably a consequence of diminished litter cover from the vegetation ground layer.

Grazing and cutting also affected species composition (**III**, **IV**). Management, litter and aspect were significant explanatory factors for species composition, but did not result in any specific, identifiable type of vegetation (**IV**). Changes in plant communities in response to management are usually slow (Pykälä 2003), especially on formerly arable land, where the period was likely too short for marked changes. After 5 years of management, the cutting and removal plots diverged from the main group of treatment and control plots (**III**). The biomass of *Phleum pratense* increased significantly in the cutting and removal in contrast to the control plots (**III**). No differences in the biomass of *Elymus repens* were detected between the groups. Yearly cutting and removal of biomass did not decrease the abundance of *E. repens* (**III**). Cutting twice per year is effective in formerly arable sites, especially in enhancing the abundance of sown forbs (Lawson et al. 2004). Repeated cutting during a growing season is an effective mechanical control of *E. repens*. However, desirable species sensitive to cutting may not tolerate frequent cutting. Cutting before August may also hinder seed ripening. In Finnish AES the first cutting is recommended after the birds-nesting season in August. Along with warming in autumn as expected by global warming, delaying the cutting to September could be tested. This would allow even late nesting of farmland birds as well as proper ripening of the plant seeds before cutting.

Elymus repens uses nutrients very effectively (Marshall 1990) and probably was even able to utilize light and space more efficiently in plots without nutrient limitations (**III**). In the study of Hansson and Fogelfors (1998), cutting resulted in decrease of *E. repens* in the unfertilized plots. The soil phosphorus level in our study indicated high soil fertility throughout the experiment, irrespective of the management regime. The high fertility probably supported the dominance of *E. repens* and diminished the effects of cutting. Furthermore, our experiment lasted 5 years, which may be a rather short period to draw conclusions on the effects of cutting alone, or of cutting and removal of the cuttings (see Tilman 1993).

Management by cutting or grazing (**III**, **IV**) did not result in decrease in soil phosphorus. In contrast to that expected, the phosphorus level was significantly lower in the most extensively managed group than in the other two groups (**IV)**. The difference was detected in phosphorus measured at variable depths, not in the total (0 ï 20 cm) amount of phosphorus. Cutting with removal may reduce soil phosphorus content even after 4 years of management (Marrs 1993). However, no such reduction was detected (**III, IV**). The sampling method may not have been effective to detect the changes, because there may have been marked differences in soil phosphorus content, depending on the depth of the sample layer (**IV**). This difference according to soil depth was earlier reported by Weaver et al (1988) and Uusi-Kämppä and Jauhiainen (2010) and bears in further study.

4.3 Plant species dispersal and colonization

Species dispersal limitation may be crucial to restricting the increase in species diversity in agricultural landscapes (Leng et al. 2009), where the distance between suitable habitats may be high. Both management methods resulted in the possible colonization of new species. The most important species source was species-rich slopes next to the study area. Seed bank species were mainly species of early successional stages (**III**).

Cutting and removal created opportunities for more plant species to become recruited to the community (**III**). Such recruitment was possible not only through the seed bank in the soil, but also from the adjacent ditch bank habitat. Our results suggest that dispersal from nearby habitats may contribute to the recruitment of new species once the opportunity is created by cutting and removal. The importance of not just cutting, but also the removal of cuttings, was shown in several earlier studies on grasslands (e.g. Willems 1983, Bobbink & Willems 1993, Hansson & Fogelfors 2000), as well as on grassy field margins (Bokenstrand et al. 2004, Lawson et al. 2004, De Cauwer et al. 2005).

As expected, the seed bank was not an important source of species, possibly because the margin studied had been established just 4 years earlier on the arable field. As a result, the seed bank represented species in the initial stages of secondary succession. The role of the annual species therefore remained only minor and they occurred only occasionally during the study. For example, in the restoration of old agricultural grassland habitats, the soil seed bank may play a role, as shown by Maron and Jefferies (2001).

We suggest that cutting and removal also enhanced colonization through its effects on the physical structure of the vegetation. At the beginning of the study, the *E. repens*-dominated vegetation tended to became matted, which flattened and this probably prevented effective light penetration into the topsoil. The matted vegetation kept moisture under the canopy and increased the rate of decay of the lower leaves of the grasses early in the season. The matted canopies remained in the control plots throughout the experiment. Such conditions were also described by Willems (1983) in untreated plots dominated by *Brachypodium pinnatum* (L.) P. Beauv. in chalk grassland. Following cutting and removal, most likely a decrease in the thick litter layer and an increase in *Phleum pratense* resulted in erect canopies. This may explain the unexpected finding of an increase in biomass production and in species coverage along with species richness (Foster & Gross 1998) in the cutting and removal treatment. The decrease in biomass production in the control may also have been due to the loss of biomass by decaying before the samples were taken.

4.4 Cropping practices and width

The regional differences in species composition were also partially associated with field practices. The lowest species richness in Yläneenjoki indicated a long and intensive cereal production history. In cereal production, the yearly use of herbicides is a normal activity. Several studies have demonstrated the negative effect of herbicides on plant species diversity (Marrs et al. 1991, Jobin et al. 1997, Kleijn & Snoeijing 1997). In grasslands used for growing hay, herbicides may not be used yearly. The use of herbicides for control of coppices, which was allowed until 1979 in boundaries in Finland (Siiskonen 2000), has also had harmful effects on boundary vegetation. Moreover, it was normal to spray boundaries in addition to adjacent fields even in the 1980s. The treatments of boundaries with herbicides and other pesticides from the 1940s to 1980s likely modified the species composition, especially in cereal production areas. These mainly field-scale effects of cultivation practices, especially the effects of spraying, should have been diminished after implementation of the AES. The level of exposure is dependent highly on field use, e.g. the need for sprayings or fertilizers.

Even if direct sprayings are not allowed in boundaries, herbicide drift may cause some symptoms in all plant species in the 0-4-m zone downwind (Marrs et al. 1991). However, most plants survive and recover until the end of the growing season. The one important point reported by the study of Marrs et al. (1991) is, that young plants were more susceptible to drift, which may hinder regeneration of new individuals. We point out that this may be crucial for species colonization or regeneration and may explain, at least partially, the poor species diversity in boundaries. Damages caused by sprayings have been frequently reported in field studies (Pakkanen & Helenius 2004, Jauni & Helenius 2008). The frequency of detected damages caused by herbicides was highest in the southern and south-western areas of Finland, which correspond to the previous study areas of Lepsämänjoki and Yläneenjoki.

Distance from the field edge, which was enhanced by increased width of the boundary, was not a statistically significant explanatory variable for species richness (**I**). However, higher width increased the species richness (**II**). The increased distance of the sampling area from the field edge may not have been sufficient to result in higher species richness. The positive effect of width on species diversity has been shown in wider boundaries than those measured here. Marshall et al. (2006) found that 6-m-wide sown marginal strips had a positive effect on species diversity of the adjacent boundary. There are several reasons why increased width may enhance species diversity. Herbicide drift is restricted only to the field side of the boundary in wide boundaries. In the 6-m unsprayed buffer zone, no drift deposition was detected in the ditch (de Snoo & de Wit 1998). This had a positive effect on species diversity and water protection. However, wider buffer zones may be needed to protect neighbouring habitats from the effects of pesticides (de Snoo & de Wit 1998). Marrs et al. (1989) suggested that 6-10-m-wide buffer zones are realistic alternatives for the protection of sensitive habitats. Young plants, especially, are more sensitive to herbicide drift (Marrs et al. 1991). To reduce the negative effects of fertilization, boundaries at least 6 m wide boundaries may be needed (Marshall et al. 2006).

Fertilizer application negatively affects species richness of boundaries by increasing the biomass production (Kleijn & Snoeijing 1997). Ma et al. (2002) also reported that overall species richness in boundaries was positively associated with boundary width and negatively related to soil phosphorus concentration. The negative effect of fertilization may be restricted, at least in 6-m-wide boundaries (Marshall et al. 2006).

The main ecological characteristics of plant species in boundaries are represented by moisture and fertile soil. The main proportion (88%) of the species indicated rather moist conditions typical of boundaries (moderately fresh 52%, moist or nearly wet 25%, wet soils 11%). For mineral nitrogen, 34% of the species indicated high nitrogen levels (nitrogen-rich soil 17%, nitrogen indicators 16%) and almost half of the species (45%) indicated intermediate levels of soil nitrogen (**I**). This fits well with the location of the boundaries studied, which were located beside waterways and fallen away towards the study boundary.

4.5 Management recommendations and conclusions

Management by cutting and removal positively affected plant species diversity. It would be most reasonable to focus the management to the sites, which could benefit most from these activities. However, management should enhance also the diversity of the other groups of organisms. Sites facing south and already rather species rich-sites may increase their diversity when managed. Also other semi-natural grassland areas such as grassland patches can have positive effects e.g. on Lepidopteran species richness (Kuussaari et al. 2007). Mänd et al. (2002) showed that semi-natural grassland areas had significantly higher bumblebee numbers than did adjacent linear habitats of agricultural habitat. Kleijn and van Langevelde (2006) found that habitat quality, i.e. the abundance of flowers, is a significant factor for the richness of bees and hover flies.

Bushes and trees should be allowed in boundaries other than buffer strips. They may aid in preserving avian diversity (Deschênes et al. 2003) and may have positive effects on butterflies when sheltering for wind (Dover 1996, Kuussaari et al. 2007). Management that aims at increasing plant species diversity does not necessarily serve the best interests of all groups of organisms; e.g. some arthropods have more of an advantage in other characteristics of vegetation such as litter abundance or tussock-forming grasses. Only occasional cutting favours araneid species (Baines 1998) and litter dwelling invertebrates favour litter (Smith et al. 2008). Tussock-forming grasses are important for carabid beetles (Asteraki et al. 2004, Woodcock et al. 2008). Sites, such as those facing north or characteristically moist sites, could be left unmanaged.

Landscape-level planning should cover all seminatural grassland areas, not only boundaries. Kleijn and Langevelde (2006) argued that the quality of linear habitats is often low for flower-visiting insects. This confirms the view that conservation and restoration should be directed to the habitats of the highest biodiversity value. Some of the habitats could remain without management and would be valuable as such. Specific management should be supported more efficiently by subsidies of AESs. Tscharntke et al. (2005) highlighted the importance of landscape perspective in AESs. Therefore, the diversity of boundary vegetation should be measured on the landscape scale to estimate the overall heterogeneity of the habitats. One landscape, which may be defined according to the area, should include boundaries from grassy-dominated, species-poor sites to herb-dominated, species-rich sites.

In boundary plant communities, most of the species indicated that soil fertility is high or intermediate and that the soil is most often moist. In contrast to species-rich habitats, such as dry meadows, species diversity in boundaries is rather low. Regional differences in plant species composition and diversity were found. There are several factors contributing to this variation. Land-use history, production line, species natural and human-induced distribution, climate and edaphic factors are elements inducing differences in species composition between regions. The lowest species diversity of boundaries is most likely related to intensive and long-term cereal production.

At the landscape and habitat levels, the overall results indicate that management by cutting and removal or grazing enhances species diversity. The most effective management option for promoting species richness of field margins is management by cutting and removal of the biomass, resulting in the decrease in ground litter. The positive effect seems to be highly dependent on the adjacent source of colonizing species. In species-poor habitats and landscapes, the establishment of margins with diverse seed mixtures may enhance development of further species richness. Five years of cutting management did not diminish the abundance of *Elymus repens.* Reducing the abundance of *E*. *repens* probably needs cutting more frequent than once per year. Moreover, soil fertility measured by phosphorus content, showed no decrease after management. Therefore, the nutrient load should already be diminished in the cultivated area. Careful use of fertilizers, light tilling and field vegetation cover during winter reduce the nutrient load in boundaries.

Together with other measures that target biodiversity, AESs should include long-term contracts with farmers for the establishment and management by cutting and removal of arable field margins that are several metres wide. In such schemes, the timing and frequency of management should be planned so as not to harm other taxa, such as the insects and birds that are dependent on the field margin habitats.

Despite the many ideas suggested for increasing the biodiversity of farmland, political decisions made with in the framework of AESs are probably the most important directional method. There is still an urgent need to develop scheme measures for motivating farmers to improve farmland biodiversity as a part of agricultural production. For example, further studies could investigate the effect of herbicides on species diversity, since practical application of AES rules concerning herbicide sprayings is very much needed.

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REFERENCES

Asteraki, E.J., Hart, B.J., Ings, T.C. and Manley, W.J. 2004. Factors influencing the plant and invertebrate diversity of arable field margins. Agriculture, Ecosystems and Environment 102: 219-231.

Baev, P.V. and Penev, L.D. 1993. BIODIV. Program for calculating biological diversity parameters similarity, niche overlap and cluster analysis. Version 4.1. Pensoft. Sofia, 37 p.

Baines, M., Hambler, C., Johnson, P.J., Macdonald, D.W. and Smith, H. 1998. The effects of arable field margin management on the abundance and species richness of Araneae (spiders). Ecography 21: 74-86.

Benton, T.G., Vickery, J.A. and Wilson, J.D. 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. Evol. 18: 182ï 188.

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., de Cock, R., Diekoetter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J. P., Opdam, P., Roubalova, M., Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M. J. M., Speelmans, M., Simova, P., Verboom, J., van Wingerden, W. K. R. E., Zobel, M. and Edwards, P. J. 2008. Indicators for biodiversity in agricultural landscapes: a pan-European study. Journal of Applied Ecology 45: 141-150.

Blomqvist, M.M., Vos P., Klinkhamer P.G.L. and ter Keurs W.J. 2003. Declining plant species richness of grassland ditch banks ï a problem of colonisation or extinction? Biological Conservation 109: 391-406.

Blomqvist, M.M., Tamis, W.L.M. and de Snoo, G.R. 2008. No improvement of plant biodiversity in ditch banks after a decade of agri-environment schemes. Basic and Applied Ecology 10: 368-378.

Bobbink, R. and Willems, J.H. 1991. Impact of different cutting regimes on the performance of *Brachypodium pinnatum* in Dutch Chalk Grassland. Biological Conservation 56: 1-21.

Bobbink R. and Willems J.H. 1993. Restoration of abandoned chalk grassland in the Netherlands. Biodiversity and Conservation 2: 616-626.

Bokenstrand A., Lagerlöf J. and Redbo Torstensson P. 2004. Establishment of vegetation in broadened field boundaries in agricultural landscape. Agriculture, Ecosystems and Environment 101: 21-29.

Borcard, D., Legendre, P. and Drapeau, P. 1992. Partialling out the spatial component of
ecological variation. Ecology 73: 1045ï 1055.

Boutin, C. 2006. Comparison of the vegetation and seed banks of soybean fields, adjacent boundaries, and hedgerows in Ontario. Canadian Journal of Plant Science 86: 557-567.

Bäckman, J.-P. and Tiainen, J. 2002. Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera: Bombus and Psithyrus). Agriculture, Ecosystems and Environment 89: 53-68.

Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D. and Nowakowski, M. 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee

abundance and diversity on arable field margins. Journal of Applied Ecology 44: 29-40.
De Cauwer, B., Reheul, D., DóHooghe K., Nijs I. and Milbau A. 2005. Evolution of the vegetation of mown field margins over their first 3 years. Agriculture, Ecosystems and Environment 109: 87-96.
De Cauwer, B., Reheul, D., Nijs, I. and Milbau, A. 2008. Management of newly established field margins on nutrient-rich soil to reduce weed spread and seed rain into adjacent crops. Weed Research 48: 102-112.
Dennis, P. and Fry, G.L.A. 1992. Field margins: can they enhance natural enemy population densities and general arthropod diversity on farmland. Agriculture, Ecosystems and Environment 40: 95-115.
Dennis, P., Thomas, M.B. and Sotherton, N.W. 1994. Structural features of field boundaries which influence the overwintering densities of beneficial arthropod predators. Journal of Applied Ecology 31: 361-370.
Deschênes, M., Bélanger, L. and Giroux, J.-F. 2003. Use of farmland riparian strips by declining and crop damaging birds. Agriculture, Ecosystems and Environment 95: 567-577.
De Snoo, G. and De Wit, P. 1998. Buffer zones for reducing pesticide drift to ditches and risks to aquatic organisms. Ecotoxicology and Environmental Safety 41: 112-118.
Dover, J.W. 1996. Factors affecting the distribution of satyrid butterflies on arable farmland. Journal of Applied Ecology 33: 723-734.
Dramstad, W.E. and Fry, G. 1995. Foraging activity of bumblebees (Bombus) in relation to flower resources on arable land. Agriculture, Ecosystems and Environment 53: 123-135.
Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. and Paulißen, D. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18: 1-248.
Ekroos, J., Piha, M. and Tiainen, J. 2008. Role of organic and conventional field boundaries on boreal bumblebees and butterflies. Agriculture, Ecosystems and Environment 124: 155-159.
Foster B.L. and Gross K.L. 1998. Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. Ecology 79: 2593-2602.
Grönroos, J., Rekolainen, S., Palva, R., Granlund, K. Bärlund, I., Nikander, A. and Laine, Y. 1998. Maatalouden ympäristötuki. Toimenpiteiden toteutuminen ja vaikutukset v. 1995-1997. Suomen ympäristö 239. 77 p.
Hansson, M. and Fogelfors, H. 1998. Management of permanent set-aside on arable land in Sweden. Journal of Applied Ecology 35: 758-771.
Hansson, M. and Fogelfors H. 2000. Management of a semi-natural grassland; results from a 15-year-old experiment in southern Sweden. Journal of Vegetation science 11: 31-38.
Hietala-Koivu, R. 1999. Agricultural landscape change: a case study in Yläne, southwest Finland. Landscape and Urban Planning 46: 103-108.
Hietala-Koivu, R. 2002. Landscape and modernizing agriculture: a case study of three areas in Finland in 1954-1998. Agriculture, Ecosystems and Environment 91: 273-281.
Hilli, A., 1949. Piennarkasvustojen maataloudellisesta merkityksestä. Suomen Maataloustieteellisen Seuran julkaisuja 70. 62 p.

Hämet-Ahti, L., Suominen, J., Ulvinen, T., Uotila, P. and Vuokko, S. (Eds.), 1986. Retkeilykasvio. Suomen Luonnonsuojelun Tuki, Helsinki. 598 p.
Hämet-ahti, L., Suominen, J., Ulvinen, T. and Uotila P (eds.) 1998. Retkeilykasvio (Field Flora of Finland), 4th ed, 656 pp, Finnish Museum of Natural History, Botanical Museum, Helsinki, Finland.
Jacquemym H., Brys R. and Hermy, M. 2003. Short-term effects of different management regimes on the response of calcareous grassland vegetation to increased nitrogen. Biological Conservation 111: 137-147.
Jauni, M. and Helenius, J. 2008. Putkilokasvien monimuotoisuus maatalousalueilla 2001-2006. In: Kuussaari, M., Heliölä, J., Tiainen, J., Helenius, J. (Eds.), Maatalouden ympäristötuen merkitys luonnon monimuotoisuudelle ja maisemalle: MYTVAS-loppuraportti 2000ï 2006 (Significance of the Finnish agri-environment support scheme for biodiversity and landscape: Final report 2000ï 2006. Finnish Environment Institute. Helsinki, Finland, pp. 23ï 49. In Finnish with English abstract).
Jobin, B., Boutin, C. and DesGranges, J.-L. 1997. Effects of Agricultural practises on the flora of hedgerows and woodland edges in Southern Quebec. Canadian Journal of Plant Science 77: 293-299.
Jutila, H. M. and Grace, J.B. 2002. Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. Journal of Ecology 90: 291-302.
Jutila, H. M. 2003. Germination in Baltic coastal wetland meadows: similarities and differences between vegetation and seed bank. ï Plant Ecology 166: 275-293.
Kalamees, R. and Zobel, M. 1998. Soil seed bank composition in different successional stages of a species rich wooded meadow in Laelatu, western Estonia. Acta Oecologica 19: 175-180.
Kiirikki, M. 1993. Seed bank and vegetation succession in abandoned fields in Karkali Nature Reserve, southern Finland. Annales Botanici Fennici 30: 139-152.
Kivinen, S., Luoto, M., Kuussaari, M., and Helenius, J., 2006. Multi-species richness of boreal agricultural landscapes: effects of climate, biotope, soil and geographical
location. Journal of Biogeography 33: 862ï 875.
Kleijn, D. 1996. The use of nutrient resources from arable fields by plants in field boundaries. Journal of Applied Ecology 33: 1433-1440.
Kleijn, D. and Snoeijing, I.J. 1997. Field boundary vegetation and the effects of agrochemical drift: botanical change caused by low levels of herbicide and fertilizer. Journal of Applied Ecology 34: 1413-1425.
Kleijn, D., Joenje, W., Le Coeur, D. and Marshall, E.J.P. 1998. Similarities in vegetation development of newly established herbaceous strips along contrasting European field boundaries. Agriculture, Ecosystems and Environment 68: 13-26.
Kleijn, D. and Verbeek, M. 2000. Factors affecting the species composition of arable field boundary vegetation. Journal of Applied Ecology 37: 256-266.
Kleijn, D., Berendse, F., Smit, R. and Gilissen, N. 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. Nature 413: 723-725.

Kleijn, D. and Sutherland, W.J. 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity. Journal of Applied Ecology 40: 947-969.
Kleijn, D. and van Langevelde, F. 2006. Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. Basic and Applied Ecology 7: 201-214.
Kuussaari, M., Heliölä, J., Luoto, M. and Pöyry, J. 2007. Determinants of local species richness of diurnal Lepidoptera in boreal agricultural landscapes. Agriculture, Ecosystems and Environment 122: 366-376.
Lagerlöf, J. and Wallin, H. 1993. The abundance of arthropods along two field margins with different types of vegetation composition: an experimental study. Agriculture, Ecosystems and Environment 43: 141-154.
Lande, R., De Vries P.J. and Walla, T.R. 2000. When species accumulation curves intersect: Implications for ranking diversity using small samples. Oikos 89: 601-604.
Lawson, C.S., Ford, M.A. and Jonathan, M. 2004. The influence of seed addition and cutting regime on the success of grassland restoration on former arable land. Applied Vegetation Science 7: 259-266.
Leng, X., Musters, C.J.M. and De Snoo, G.R. 2009. Restoration of plant diversity on ditch banks: Seed and site limitation in response to agri-environment schemes. Biological Conservation 142: 1340-1349.
Le Coeur, D., Baudry, J. and Burel, F. 1997. Field margins plant assemblages: variation partitioning between local and landscape factors. Landscape and Urban Planning 37: 57-71.
Lindborg, R. and Eriksson, O., 2004. Historical landscape connectivity affects present plant species diversity. Ecology 85: 1840ï 1845.
Lindborg, R., Bengtsson, J., Berg, Å., Cousins, S.A.O., Eriksson, O., Gustafsson, T., Hasund, K.P., Lenoir, L., Pihlgren, A., Sjödin, E. and Stenseke, M. 2008. A landscape perspective on conservation of semi-natural grasslands. Agriculture, Ecosystems and Environment 125: 213-222.
Littel, R.C., Milligen, G.A., Stroup, W.W., Wolfinger, R.D. and Schabenberger, O. 2006. SAS® for mixed models, 2nd ed. SAS Institute Inc., Cary, NC, USA.
Luoto, M., 2000. Spatial analysis of landscape ecological characteristics of five agricultural areas in Finland by GIS. Fennia 178: 15ï 54.
Luoto, M. 2000. Spatial analysis of landscape ecological characteristics of five agricultural areas in Finland by GIS. Fennia 178: 15-54.
Luzuriaga, A.L., Escudero, A., Olano, J.M. and Loidi, J. 2005. Regenerative role of seed banks following an intense soil disturbance. Acta Oecologica 27: 57-66.
Ma, M., Tarmi, S. and Helenius, J., 2002. Revisiting the species-area relationship in a semi-natural habitat: floral richness in agricultural buffer zones in Finland. Agriculture, Ecosystems and Environment 89: 137ï 148.
Magurran, A.E. 2004. Measuring biological diversity. Blackwell Science Ltd., Oxford, UK. 256 p.
Maron, J.L. and Jefferies, R.L. 2001. Restoring enriched grasslands: effects of mowing on species richness, productivity, and nitrogen retention. Ecological Applications 11: 1088-1100.

Marrs, R.H., Williams, C.T., Frost, A.J. and Plant, R.A. 1989. Assessment of the effects of herbicide spray drift on a range of plant species of conservation interest. Environmental Pollution 59: 71-86.

Marrs, R.H., Frost, A.J. and Plant, R.A., 1991. Effects of herbicide spray drift on selected species of nature conservation interest: the effects of plant age and surrounding vegetation structure. Environmental Pollution 69 : 223ï 235.

Marrs, R.H. 1993. Soil fertility and nature conservation in Europe: Theoretical considerations and practical management solutions. Advances in Ecological Research 24: 241-300.

Marshall, E.J.P. 1989. Distribution patterns of plants associated with arable field edges. Journal of Applied Ecology 26: 247-257.

Marshall, E.J.P. 1990. Interference between sown grasses and the growth of rhizome of *Elymus repens* (couch grass). Agriculture, Ecosystems and Environment 33: 11-22.

Marshall, E.J.P. and Arnold, G.M. 1995. Factors affecting field weed and field margin flora on a farm in Essex, UK. Landscape and Urban Planning 31: 205-216.

Marshall, E.J.P. and Moonen, A.C. 2002. Field margins in northern Europe: their functions and interactions with agriculture. Agriculture, Ecosystems and Environment 89: 5-21.

Marshall, E.J.P., West, T.M. and Kleijn, D. 2006. Impacts of an agri-environment field margin prescription on the flora and fauna of arable farmland in different landscapes. Agriculture, Ecosystems and Environment 113: 36-44.

Marshall, E.J.P. 2009. The impact of landscape structure and sown grass margin strips on weed assemblages in arable crops and their boundaries. Weed Research 49: 107-115.

Matson, P.A., Parton, W.J., Power, A.G. and Swift, M.J. 1997. Agricultural intensification and ecosystem properties. Science 277: 504-509.

Milberg, P. 1992. Seed bank in a 35-year-old experiment with different treatments of s semi-natural grassland. Acta Oecologica 13: 743-752.

Mänd, M., Mänd, R. and Williams, I.H. 2002. Bumblebees in the agricultural landscape of Estonia. Agriculture, Ecosystems and Environment 89: 69-76.

Økland, R.H. 1999. On the variation explained by ordination and constrained ordination axes. Journal of Vegetation Science 10: 131-136.

Oksanen, J. 1981. Reindeer lichen (*Cladina*) vegetation of rock outcrops on a coast - inland transect in South Finland. Annales botanici fennici 18: 133-154.

Pakkanen , H. and Helenius, J. 2004. Kasvien monimuotoisuuden seuranta ï toimenpiteiden vaikutukset pientareilla ja suojakaistoilla. In: Kuussaari, M., Tiainen, J., Helenius, J., Hietala-Koivu, R. and Heliölä, J. (eds.), Maatalouden ympäristötuen merkitys luonnon monimuotoisuudelle ja maisemalle. Mytvas ï seurantatutkimus 2000-2003. Suomen ympäristö 709: 30-43.

Palva, R. and Peltonen, M. 2006. Suojavyöhykkeiden hoitomenetelmät ja työn menekki. In: Virkajärvi, P. and Uusi-Kämppä, J. (eds.), Laitumien ja suojavyöhykkeiden ravinnekierto ja ympäristökuormitus. Maa- ja elintarviketalous 76:178-186. Dark Oy. Vantaa. Finland.

Pfiffner, L. and Luka, H. 2000. Overwintering of arthropods in soils of arable fields and adjacent semi-natural habitats. Agriculture, Ecosystems and Environment 78: 215-22

Pykälä, J. 2003. Effects of restoration with cattle grazing on plant species composition and richness of semi-natural grasslands. Biodiversity and Conservation 12: 2211-2226.
Pykälä, J. 2004. Cattle grazing increases plant species richness of most species trait groups in mesic semi-natural grasslands. Plant Ecology 175: 217-226.
Pykälä, J. 2005. Plant species responses to cattle grazing in mesic semi-natural grassland. Agriculture, Ecosystems and Environment 108: 109-117.
Ruprecht, E., Enyedi, M.Z., Eckstein, R.L. and Donath, T.W. 2010. Restorative removal of plant litter and vegetation 40 years after abandonment enhances re-emergence of steppe grassland vegetation. Biological conservation 143: 449-456.
Siiskonen, H. 2000. Myrkyttäkää, ruiskuttakaa, hävittäkää. Ruotsalaisten ja suomalaisten maatalouden ammattilehtien kasvinsuojeluvalistus 1940-1980. Historiallisia tutkimuksia 209. Suomalaisen Kirjallisuuden Seura. Helsinki. 211 p.
Smith, J., Potts, S.G., Woodcock, B.A. and Eggleton, P. 2008. Can arable field margins be managed to enhance their biodiversity, conservation and functional value for soil macrofauna? Journal of Applied Ecology 45: 269-278.
Smith, R.S., Shiel, R.S., Millward, D. and Corkhill, P. 2000. The interactive effects of management on the productivity and plant community structure of an upland meadow: an 8-year field trial. Journal of Applied Ecology 37: 1029-1043.
Soininen, A.M. 1974. Vanha maataloutemme. Maatalous ja maatalousväestö Suomessa perinnäisen maatalouden loppukaudella 1720-luvulta 1870-luvulle. Journal of the Scientific Agricultural Society of Finland 46:1-459.
Sparks, T.H. and Parish, T. 1995. Factors affecting the abundance of butterflies in field boundaries in swavesey fens, Cambridgeshire, UK. Biological conservation 73: 221-227.
SPSS Inc. 1997. SYSTAT for Windows Version 7.
Ter Braak, C.J.F. 1987. CANOCO - a FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Agricultural Mathematics Group, Wageningen. 95 p.
Ter Braak, C.J.F and Smilauer, P. 1998. Canoco for Windows: Software for Canonical Community Ordination (version 4.02) Centre for Biometry Wageningen, CPRO-DLO, Wageningen, The Netherlands.
Tilman, D. 1993. Species richness of experimental productivity gradients: How important is colonization limitation? Ecology 74: 2179-2191.
Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. and Thies, C. 2005. Landscape perspectives on agricultural intensification and biodiversity ï ecosystem service management. Ecology Letters 8: 857-874.
Uusi-Kämppä, J. and Jauhiainen, L. 2010. Long-term monitoring of buffer zone efficiency under different cultivation techniques in boreal conditions. Agriculture, Ecosystems and Environment 137: 75-85.
Vuorinen, J. and Mäkitie, O. 1955. The method of soil testing in use in Finland. Agroecological Publications 63: 1-44.
Wahlman, H. and Milberg, P. 2002. Management of semi-natural grassland vegetation: evaluation of a long term experiment in southern Sweden. Annales Botanici Fennici 39: 159-166.

Weaver, D.M., Ritchie, G.S.P., Anderson, G.C. and Deeley, D.M. 1988. Phosphorus leaching in sandy soils. I. Short-term effects of fertilizer applications and environment conditions. Australian Journal of Soil Research 26: 177-190.

Werner, P.A. and Rioux, R. 1977. The Biology of Canadian Weeds. 24. *Agropyron repens* (L.) Beauv. Canadian Journal of Plant Science 57: 905-919.

Weibull, A.-C., Bengtsson, J. and Nohlgren, E. 2000. Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. Ecography 23: 743-750.

West, T.M., Marshall, E.J.P. and Arnold, G.M. 1997. Can sown field boundary strips reduce the ingress of aggressive field margin weeds? Proceedings of Brighton Crop Protection Conference ï Weeds, 985-990.

Willems, J.H. 1983. Species composition and above ground phytomass in chalk grassland with different management. Vegetatio 52: 171-180.

Wilson, P.J. and Aebischer, N.J. 1995. The distribution of dicotyledonous arable weeds in relation to distance from the field edge. Journal of Applied Ecology 32: 295-310.

Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C. and Bradbury, R.B. 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. Agriculture, Ecosystems and Environment 75: 13-30.

Woodcock, B.A., Westbury, D.B., Tscheulin, T., Harrison-Cripps, J., Harris, S.J., Ramsey, A.J., Brown, V.K. and Potts, S.G. 2008. Effects of seed mixture and management on beetle assemblages of arable field margins. Agriculture, Ecosystems and Environment 125: 246-254.