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Road verges: potential refuges for declining grassland species despite remnant vegetation dynamics

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Whether road verge vegetation can be manipulated to resemble traditionally managed grassland has been much debated. This short-term study compared management effects on road verge and pasture vegetation in western Norway. We quantified vegetation change and explored whether it occurred along underlying environmental gradients. We found management-related variation in species richness and vegetation physiognomy, but high resistance in species composition prevented directional changes in vegetation dynamics. Initial differences between the habitats indicated historical management effects on traditionally managed pastures and road verges. Given proper management, road verges may have a nature conservation potential. Moreover, their linear structure may enable fine-scale mosaic management that allows the coexistence of a wide range of grassland species.

Introduction

Disturbance is widely acknowledged to be a key process in all ecosystems (White 1979, Fraterrigo & Rusak 2008). In semi-natural grasslands, man-made disturbance is considered to be crucial in maintaining open vegetation, since mowing and grazing act as reset mechanisms for succession (Glenn-Lewin & van der Maarel 1992). The response pattern of a particular system determines its ability to maintain its properties (e.g. vegetation composition, species richness or physiognomy) when the management regime changes (often termed 'resistance'), and also its ability to return to its former state after a period under a different management regime (often termed 'resilience'; Mitchell *et al*. 2000).

Understanding these response patterns is crucial for sustainable conservation management (Chapin *et al*. 1996). Traditional management regimes for north-western European semi-natural grasslands included summer mowing and spring and/or autumn grazing (Losvik & Austad 2002, Jefferson 2005, Hellström *et al*. 2006). This prevented tall species from ousting smaller ones and provided gaps where regeneration could take place. Combined with low input of fertilisers, these management regimes gave rise to grassland habitats of great value, such as pastures and meadows (Hellström *et al*. 2006, Pärtel *et al*. 2007). Grassland management for conservation purposes is therefore generally designed to resemble traditional regimes as closely as possible (Jefferson 2005).

Land-use changes throughout Europe are proving to be a serious threat to semi-natural grasslands (Lennartsson & Oostermeijer 2001, Bennie *et al*. 2006, Hamre *et al*. 2007). They are being abandoned and become overgrown, and many species adapted to such habitats decline (Hellström *et al*. 2006). In Norwegian semi-natural grasslands that are still managed, the traditional regime of summer cutting and spring and autumn grazing is often replaced by grazing only (Norderhaug *et al*. 2000). Meanwhile, the area of another type of grassland habitat, road verges, increases with the expansion of the road network. Road verges are kept mown for traffic safety purposes, creating treeless, open vegetation resembling traditional semi-natural grasslands (Parr & Way 1988, Jantunen *et al*. 2007). Appropriately managed road verges have therefore been proposed as suitable habitats for declining grassland species (Parr & Way 1988, Norderhaug *et al*. 2000, Huhta & Rautio 2007). However, it cannot be assumed that managing road verges like traditional meadows will result in the preferred vegetation type, or that results from studies of e.g. meadows are transferrable to road verges. There is no traditional management regime for road verges that could serve as a template, and for safety reasons, spring and autumn grazing (important elements of the traditional management regimes) cannot be applied in road verges. Experimental studies of the effects of specific treatments on vegetation dynamics are therefore needed to identify suitable disturbance regimes and make recommendations for restoration and management. The resulting vegetation should ideally be compared with reference vegetation (Bakker *et al*. 2002, Moog *et al*. 2002), such as well-managed, mown grasslands. This is often lacking in the modern landscape. One solution is to compare the effects of road verge management with the responses of semi-natural grassland to the reintroduction of traditional management.

In our study, we compared the effect of various management regimes on the vegetation of road verges and nearby pastures. We looked at changes in vegetation height, litter depth, floristic similarity and vegetation dynamics along underlying environmental gradients in response to different treatments. We specifically addressed the following questions: (1) Is pasture vegetation a suitable reference for evaluating the effects of management on road verge vegetation dynamics? (2) How do various management methods affect road verge vegetation dynamics (physiognomy, species richness, successional rates and variation along environmental gradients)? (3) Which characteristics of the grassland vegetation could explain the observed response patterns to management? (4) Do road verges have specific properties that affect their potential as refuges for traditional grassland species?

Material and methods

Study site

We studied six semi-natural grassland sites, three pastures and three road verges, in Lærdal, the Sogn og Fjordane county, western Norway (61°04´N, 7°32´–49´E). This is a glaciated region with mountains reaching 1600 m and with areas of small-scale traditional agricultural landscape including species-rich grasslands. The sites are less than 11 km apart at altitudes varying from 35 to 420 m a.s.l., and all face south (from SE to SW). The pastures vary in area from 2.8 to 7.5 ha, while the road verges are narrow (3–5 m) strips 50–100 m in length. The sites are situated in the southern boreal, slightly continental region (Moen *et al*. 1999), with low annual precipitation (ca. 500 mm) and an annual mean temperature of ca. 5.9 °C for the normal period 1961–1990 (eKlima 2008). Precipitation in the growing season (March–August) varied during the study period (2003–2006), the last year being particularly dry (cumulative precipitation was only 65% of the normal precipitation for the growing season, *see* Appendix 1). We have no data on the 'historical' species content of the pastures, but our observations indicate that they are examples of traditional species-rich grasslands (Losvik 2007). They are currently grazed by sheep in spring and autumn. Two of the three sites were also mown annually until 10–20 years ago, while the third site has never been mown, only grazed. A three-metre wide strip of the road verges is cut in in August, and the 1–2 m zone closest to the road bed is also cut in June (*see* Auestad *et al*. 2008 for further information), resulting in fine-scale variation of the management regime along the verges. Grass is not removed after cutting.

Study design

We used stratified random sampling (Aubry & Debouzie 2001) and assigned six blocks to each site, measuring 3 m × 5 m in road verges (2 m × 7.5 m in the narrowest verge) and 4 m × 4 m in pastures. The blocks were placed in clearly homogenous areas and spanned the apparent local environmental variation. We randomly laid out permanent plots (0.5 × 0.5 m with buffer zones of 0.25 m on all sides) within each block, four in each road verge block and three in each pasture block. We used small plots to enable replication of all treatments in each block at every site. Plots (including buffer zones) were not allowed to share sides, ensuring a minimum between-plot distance of 0.7 m (for further details, *see* Auestad *et al*. 2008). If stone/rock covered more than 25% of a potential plot, it was rejected, and a substitute was chosen from a fixed priority list of adjacent positions.

For annual records of species composition (recorded in mid-June to mid-July; all years prior to the management treatments), we divided each 0.25-m^2 plot into 16 subplots of 0.0156 m^2, and used subplot shoot frequency (0–16) as a measure of abundance of vascular plant species in the plot. We recorded vegetation physiognomy by measuring maximum vegetation height and thickness of litter at eight fixed points in each plot in the first (2003) and the last (2006) season. We calculated species richness as the plot-wise species number per year.

We investigated how different treatments affected various aspects of vegetation dynamics during the study period (2003–2006). Treatments were applied to buffer zones as well as plots, while vegetation records were made in the plots only, always before cutting. The treatments were replicated in a hierarchical design with 124 plots in 36 blocks nested in six sites (Auestad *et al*. 2008). We applied four different treatments to the road verges, replicated within each block (Table 1). V1 mimicked the current management of the outer part of the verge, and comprised early (June) and late (August) cutting, with no removal of hay. V2 was a more labour-intensive regime, as it also included hay removal. V3 involved cutting and removing hay in August only. Finally, V4 involved no active management. We investigated three management regimes for the pastures, replicated within each block. P1 was a continuation of the current regime (spring and autumn sheep grazing), while P2 replicated the more labour-intensive traditional regime (spring and autumn sheep grazing, late cutting and removal of hay). P3 resembled P2, but with more intensive raking to remove both cut hay and litter, increasing gap formation. Some road verge plots had to be excluded because they were accidentally cut by the road authorities in 2005. One V2 and one V4 plot were therefore discarded from the total dataset (2003–2006), and four V4 plots from the 2006 dataset, giving a total of 492 plots over the four years. We mowed the grass 5–10 cm above the ground in late June (early cut) and

Table 1. The seven treatments applied to road verges and pastures in the management experiment.

	Treatment	Cutting time	Hay removal	Spring + autumn grazing	No. plots per year
Road verges	V1	June + August	–	–	18
	V2	June + August	+	–	17*
	V3	August	+	–	18
	V4	–	–	–	17(13*)
Pastures	P1	–	–	+	18
	P2	August	+	+	18
	P3	August	+	+	18

* One V2 and one V4 plot were discarded from the total dataset (2003–2006), and four V4 plots were excluded from the 2006 dataset because they were accidentally cut by the road authorities in 2005.

in late August (late cut, after census) in all four years of the study. Stocking rates at the pasture sites varied: one had high stocking rates in both spring and autumn, the second experienced varying grazing pressure in spring and high stocking rates in autumn, and the third had generally low stocking rates.

Data analyses

We calculated the Bray-Curtis floristic dissimilarity (BC) for each plot between the initial year (2003) and each of the following years to measure overall vegetation change. We also calculated BC between subsequent years to examine turnover rates (Helle & Mönkkönen 1985). For analyses of changes in vegetation height, litter depth and species richness trends, we included only the plots that were analysed in all four years. Thus, $n = 18$ for all treatments except V2 ($n = 17$) and V4 ($n = 13$). We zero-skewness transformed and standardised data before testing for differences between years and treatments in vegetation height, litter depth, species richness and floristic dissimilarity using a linear mixed-effect model (LME; Pinheiro & Bates 2000). This procedure accounted for the nested structure of the plots and the repeated measurement of the individual plots. We used year and treatment as factors in a two-way approach, with random effects of site, block and plot, plots nested within blocks and blocks nested within sites. The initial differences in vegetation height, litter depth and plot-wise species number between pastures and road verges were tested by the Mann-Whitney *U*-test.

To clarify whether vegetation change was directional rather than reflecting fluctuations, we examined displacements of plot positions in DCA ordination space (Myster & Pickett 1994, Rydgren *et al*. 2004). We summarised vegetation variation along main environmental gradients and compared treatment-related vegetation dynamics by means of DCA ordination of the total data set ($n = 492$). We had previously (Auestad *et al*. 2008) evaluated the vegetation–environment relationships of the plots in the 2003 data subset by using the DCA score of each plot as response variable and one explanatory variable in turn as predictor in a split-plot GLM (Venables & Ripley 2004) analysis, specifying error components at three hierarchical levels. Based on this study, we interpreted the main vegetation variation (DCA axis 1) as a gradient in the historical (1931–2003) management regime, reflecting a gradual change from pastures with a long management history to grasslands with a shorter or different management history, i.e. the road verges. We interpreted DCA axis 2 as a gradient in soil moisture and soil element concentrations. We confirmed the correspondence between the axes of the DCA ordination of all 492 plots and the previous ordination of the 124 plots from 2003 (Auestad *et al*. 2008) by correlating the plot scores of the 2003 ordination with the corresponding scores of the 2006 ordination (non-parametric correlation coefficient Kendall's τ, DCA axis 1: $\tau = 0.86$, $p < 0.001$ and DCA axis 2: $\tau = -0.59$, $p < 0.001$, $n = 124$). All statistical analyses were performed using R version 2.6.2 (R Development Core Team 2008).

Results

Litter thickness and vegetation height increased with no active management

Average vegetation height was initially significantly higher ($W = 2615$, df = 1, $p < 0.001$) and the litter layer thicker ($W = 2845$, df = 1, $p < 0.001$) in road verges than in pastures (Fig 1). Vegetation height changed significantly from 2003 to 2006 ($F_{1,113} = 27.13$, $p < 0.001$) in response to treatment ($F_{6,78} = 12.57$, $p < 0.001$). It declined significantly under all pasture regimes (P1–3) and all road verge regimes except V4 (no active management) (*see* Fig. 1a). The rate of change varied between treatments (time by treatment: $F_{6,113} = 4.15$, $p < 0.001$). Different treatments affected the thickness of the litter layer over time ($F_{6,78} = 6.02$, $p < 0.001$) to varying degrees (time by treatment: $F_{6,113} = 27.96$, $p < 0.0001$). Litter depth increased under the current pasture regime (P1) and under V4, but decreased under all other pasture and road verge treatments (Fig. 1b). The rate of change varied significantly between treatments ($F_{6,113} = 9.62$, $p < 0.001$).

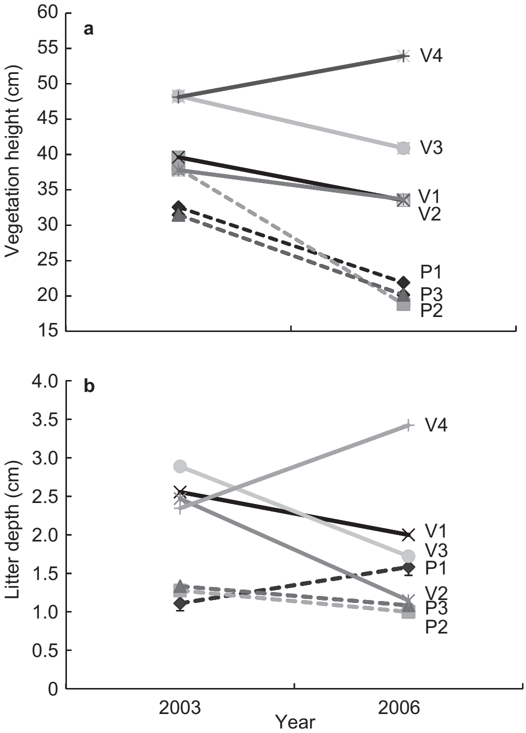

Fig. 1. (**a**) Mean vegetation height, and (**b**) mean litter thickness under the seven treatments in 2003 and 2006. *See* Table 1 for key to treatments. Note the different scaling of the *y*-axes.

Largest increase in species richness under intensive management

We recorded 93 vascular plant species during the study (Appendix 2). Initially, there was no difference between road verges and pastures in plot-wise species number (W = 1521, df = 1, p = 0.178). Plot-wise species richness increased significantly under all treatments ($F_{3,339}$ = 34.57, p < 0.001) until the last year, when it levelled off or decreased (Fig. 2). Species richness differed between the treatments ($F_{6,78}$ = 2.57, p = 0.025) with the rate of change varying significantly between treatments (time by treatment: $F_{18,339}$ = 1.87, p = 0.017). For the pastures, the treatment that gave the largest average increase in species richness (3.5) was P3 (grazing, cutting and hard raking). Treatment P2 (cutting and normal raking) and P1 (grazing only) gave intermediate average increases (2.3 and 1.6 respectively). For

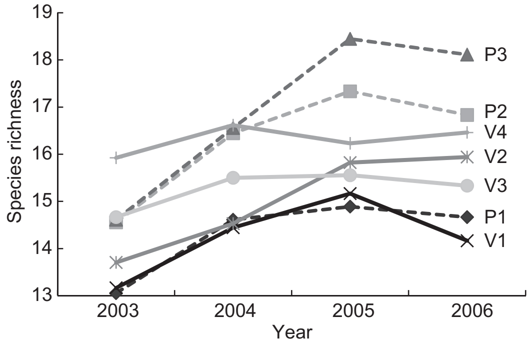

Fig. 2. Plot-wise mean species richness per year for the seven treatments. *See* Table 1 for key to treatments.

the road verges, treatment V2 (cut twice, hay removed) gave the largest average increase in species number between 2003 and 2006 (2.2), while V1 (cut twice, no removal of hay) gave a net average increase of 1.0. Treatments V3 (cut once, hay removed) and V4 (no active management) gave the smallest increases in species richness (0.7 and 0.5, respectively).

Species abundance is related to habitat and management over time

The most abundant species in the road verges included perennial grassland herbs such as *Pimpinella saxifraga* (Fig. 3a) and *Campanula rotundifolia* (Fig. 3b) and tall grasses such as *Dactylis glomerata* (Fig. 3c) and *Poa pratensis*. Nine of the ten most frequent pasture species were also among the top ten species in road verges, the only exception being *Agrostis capillaris* (found in 92% of the pasture plots but only 30% of road verge plots, Fig. 3d). A number of relatively common species were clearly associated with pastures, e.g. *Veronica chamaedrys*, *Euphrasia stricta*, *Viola tricolor*, *Sedum acre* and *Cerastium fontanum*. Others were found only in the road verges, e.g. *Thlaspi caerulescens*, *Equisetum pratense*, *Alopecurus pratensis*, *Poa nemoralis*, *Rubus idaeus*, juvenile *Ulmus glabra* (Fig. 3e) and *Betula pubescens* agg. (*see* Appendix 2). Many species showed only a slight response to management, however, the abundance of some species (*Lychnis viscaria*, Fig. 3f and *Cam-*

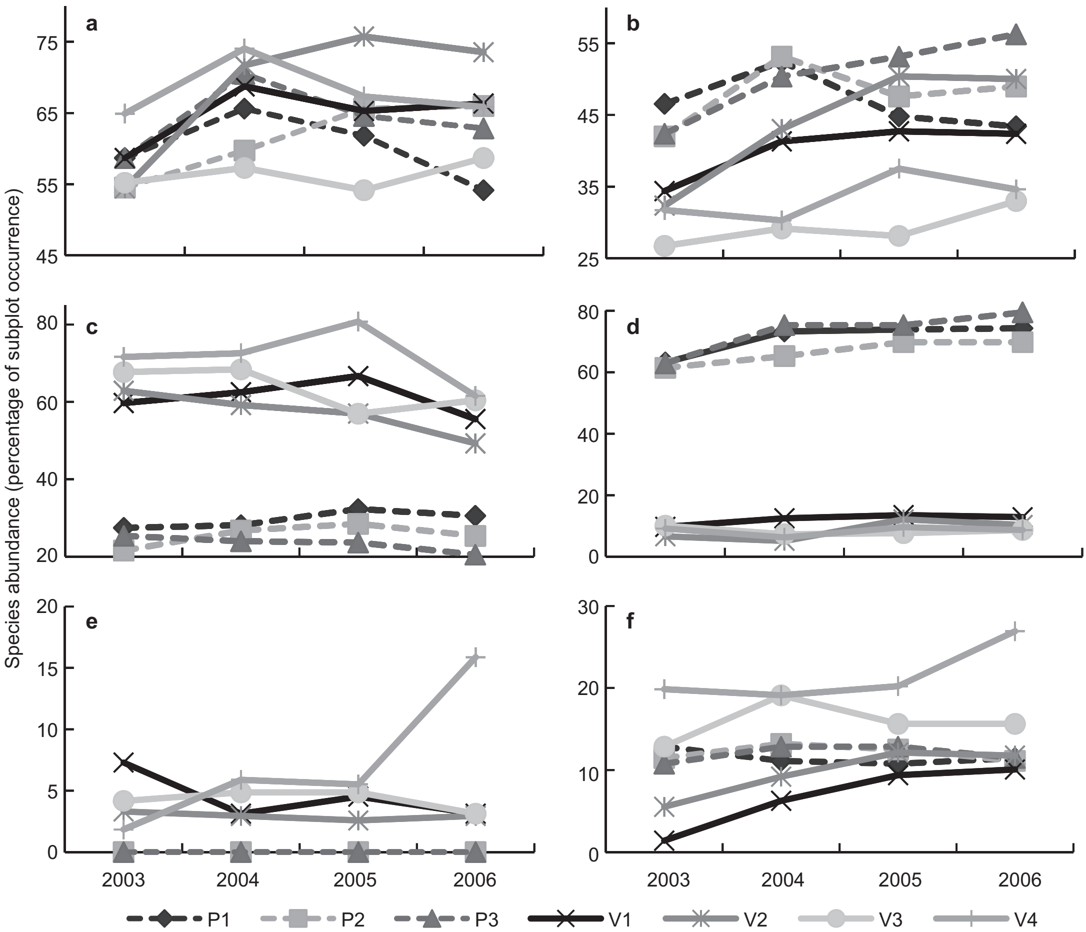

Fig. 3. Abundances (measured as percentage subplot occurrence) for six species showing different occurrence patterns over four successive years: (**a**) *Pimpinella saxifraga*, (**b**) *Campanula rotundifolia*, (**c**) *Dactylis glomerata*, (**d**) *Agrostis capillaris*, (**e**) *Ulmus glabra*, and (**f**) *Lychnis viscaria*. *See* Table 1 for key to treatments. Note the different scaling of the *y*-axes.

panula rotundifolia, Fig. 3b) increased under road verge treatments V1 and V2. Abundance of *Ulmus glabra* increased under V4 (no active management), but decreased under V1 and V2. Treatment V4 had a moderate impact on the abundance of certain low-growing species such as *C. rotundifolia*.

Floristic dissimilarity increased, but was not related to treatment

Species composition became more dissimilar to the initial situation (Fig. 4a) over the years ($F_{2,242} = 135.99$, $p < 0.0001$), as measured by the Bray-Curtis floristic dissimilarity (BC). Treatment V3 gave the largest overall vegetation change (2003–2006; 26%, Fig. 4a). However, there were no significant differences between the seven treatments ($F_{6,82} = 0.96$, $p = 0.46$) and they followed the same pattern over time (time by treatment: $F_{12,320} = 0.34$, $p = 0.98$).

The initial (2003–2004) vegetation change was largest for the road verge treatments (16–17%), and lower for the pasture treatments (11%–13%) (*see* Fig 4b). The turnover rates, computed as BC between successive years, varied significantly between time periods ($F_{2,242} = 7.84$, $p < 0.0001$). Turnover rates were generally higher in road verges than in pastures, but by 2005–2006, the rate for treatment V2 had declined below that of P2 and P3. For most treat-

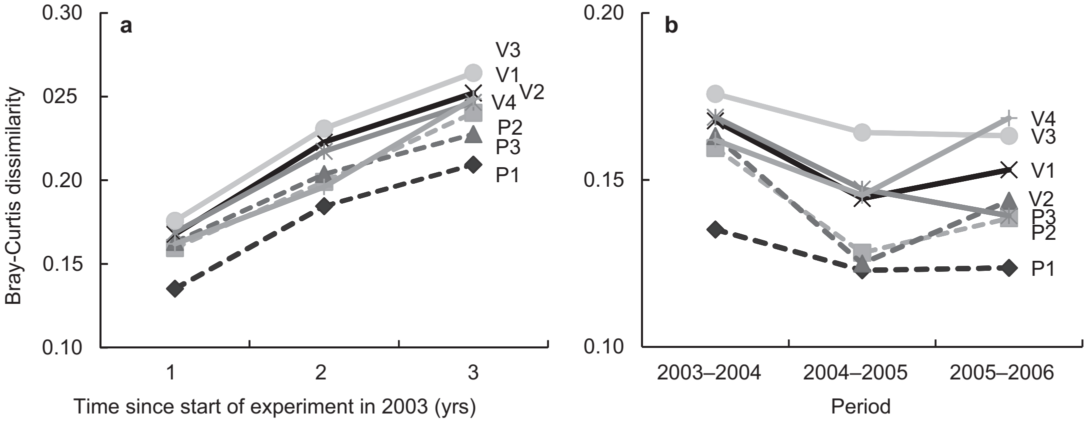

Fig. 4. Mean Bray-Curtis floristic dissimilarity index for each plot separated between treatments (**a**) between the initial year (2003) and each of the three following years (2004–2006), and (**b**) between subsequent years; turnover rate. *See* Table 1 for key to treatments. Note the different scaling of the two graphs.

ments, the rate levelled off between the two first periods but increased slightly between the two last periods. Overall, the treatments followed the same pattern over time (time by treatment: $F_{12,320} = 0.41$, $p = 0.96$) and the seven treatments did not differ ($F_{6,82} = 1.16$, $p = 0.34$; Fig. 4b).

DCA ordination: no directional change along underlying ecological gradients

The DCA ordination of the 492 plots revealed that the mean axis scores of the pasture treatments were located at lower values of DCA axis 1 (the historical management gradient) than the road verge scores (Fig. 5), but more or less at the same location along DCA axis 2 (gradient in soil moisture and soil element concentrations). Over the years, we observed no directional movement in response to the various treatments along either of the main gradients (Fig. 5).

Discussion

This short-term experiment explores how management affects the vegetation of road verges and pastures. To ensure a relevant basis for comparison of road verge treatments, we used traditional management techniques in the pastures, but found no clear distinctions in vegetation dynamics between grazing-only (P1) and grazing and cutting (P2–3) treatments. Long-term studies comparing effects of grazing and mowing indicate that different species thrive under these treatments (Tamm 1956, Wahlman & Milberg 2002), but regeneration processes after reintroduction of management are usually slow (Aavik *et al.* 2008). Moreover, traditionally managed grasslands (mowing followed by grazing) may differ less from grazed-only grasslands than from (non-grazed) hay meadows (Wahlman & Milberg 2002). In our study, there were similarities in species composition between pastures and road verges, but pastures had shorter vegetation, a thinner litter layer, and a higher content of traditional grassland species, showed a smaller change in floristic dissimilarity and occupied a different position along the historical management gradient. This indicates that although road verge habitats resemble pastures, they are not identical (Norderhaug *et al.* 2000, Tikka *et al.* 2000). However, pastures do provide a relevant basis for evaluating road verge management.

Road verges that were not actively managed (V4) showed a pronounced increase in vegetation height and litter depth; in contrast, the other three treatments (V1–3) all resulted in vegetation physiognomy resembling that of pastures. This supports the accepted view that biomass removal decreases competition for light, favouring low-growing grassland species (Klimeš & Klimešová 2002). Our analyses show that treatments V1–3 all enhanced biodiversity in road verges,

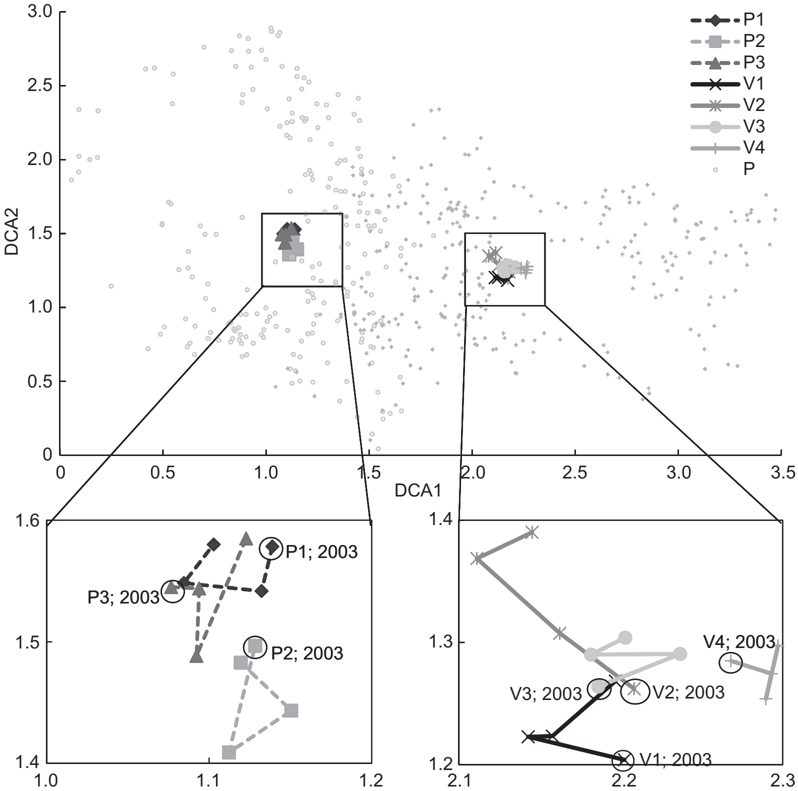

Fig. 5. DCA ordination for the total data set (n = 492) for the sample years 2003–2006 (DCA axis 1: λ = 0.39, gradient length = 3.48 SD units and DCA axis 2; λ = 0.25, gradient length = 2.90 SD units). Pasture (P) and road verge (V) plots and the mean plot score for each of seven treatments are indicated by symbols, see legend. The enlarged sections of the ordination space show the details of the treatment-related vegetation dynamics, with the starting points indicated by circles. *See* Table 1 for key to treatments.

increasing their similarity to valuable grasslands (Poschlod & WallisDeVries 2002, Losvik 2007). Increasing vegetation height and litter thickness (the result of treatment V4) is expected to hinder the growth of small-stature grassland species and reduce the number of microsites for seed germination (Ruprecht *et al*. 2010), thus preventing the increase in species richness observed under more intensive treatments (V1–2).

The analyses of species composition revealed changes not attributable to different treatments (floristic dissimilarity) and no directional change at all along underlying environmental gradients (ordination analysis). This indicates that although the treatments used did affect the vegetation, species composition resisted short-term changes in management. Most species occurred at high frequencies, but showed no coordinated response to the treatments, thus confirming the results of Parr and Way (1988) who found that 1/3 of species in a road verge management experiment were unaffected by the treatment after 18 years. Moreover, our study sites were dominated by long-lived perennials (83 of 93 species). Such communities tend to exhibit slow or remnant population dynamics (Eriksson 1996), which may have prevented a quick response to the minor changes in management in this study (Morris *et al*. 2008). The generally arid conditions at the study sites probably cause further deceleration of the vegetation dynamics, as turnover rates are usually slow under such conditions (Prach *et al*. 1993). However, the dry period in 2006 probably increased turnover rates in the last year of the study period (2005–2006) by eradicating many species that had emerged from the seed bank during the experiment. Species richness for most treatments declined in 2006, further supporting this conclusion. Very dry periods occur regularly in the study area, and may delay overgrowing and allow low-growing, light-demanding species to colonise gaps (Bartha *et al*. 2003) and persist for a relatively long time, even after abandonment (Bennie *et al*. 2006). This may explain why the “no active management” option in road verges (V4) failed to induce overgrowth (i.e. movement away from the pasture plots along the first DCA axis in the ordination analysis), so that the vegetation appeared resistant to lack of active management.

Although the ordination analysis gave no indication of directional vegetation change, the floristic dissimilarity measures revealed changes in species composition under all treatments. The vegetation includes many clonal species which stabilise vegetation dynamics on a larger spatial and temporal scale. However, the same species may speed up the fine-scale spatial vegetation dynamics, as species move in and out of the plots by means of organs such as rhizomes or creeping stems (Kalamees & Zobel 2002). The inherent fine-scale heterogeneity of grasslands (Jackson & Caldwell 1993) may form a template on which the observed fine-scale vegetation dynamics is superimposed. Plants respond to mosaics of variability in moisture, nutrients, and so on by exhibiting phenotypic plasticity in time and space (Wildova *et al.* 2007). The small plot size we used (0.25 m^2) probably allowed fine-scale variations to amplify temporal changes, which in turn increased the floristic dissimilarity. Interannual fluctuations in species' abundance have also been observed in long-term studies of presumably stable road verge vegetation in the UK (Dunnett *et al.* 1998). Small plots are more strongly influenced by the surroundings (Pakeman *et al.* 2002), whereas in large plots the statistical assumptions may not be met (Kiehl & Wagner 2006). In their ten-year study of management effects in a dry–mesic hay meadow in northern Finland, Hellström *et al.* (2006) used a plot size similar to ours and also observed little response in overall measures of vegetation change (e.g. species richness) but considerable temporal changes at plot level.

The initial differences between the two habitats probably indicate longer-term management effects on the vegetation (Bakker *et al.* 2002, Auestad *et al.* 2008), as pastures were dominated by light-demanding grassland species such as *Veronica chamaedrys* and *Botrychium lunaria*, while woody species such as *Betula pubescens* and *Ulmus glabra* occurred only in the road verges. This indicates that different treatments affect vegetation composition even in these resistant systems, but a longer time scale is needed to draw detailed conclusions (Baasch *et al.* 2010). It should also be noted that while most management studies (including ours) focus on cutting in summer or autumn (Bakker *et al.* 2002, Hellström *et al.* 2006, Jantunen *et al.* 2007, Noordijk *et al.* 2009), Parr and Way (1988) found in their classical road verge management study that cutting in May both increased species richness and improved traffic safety. Plants tolerate biomass removal better early in the growing season (Maschinski & Whitham 1989). We therefore recommend that further studies should include a spring cutting regime (in May in southern Scandinavia, parallel to the period of spring grazing in the pastures) in addition to a late summer cut (August), to investigate whether this controls woody species and encourages vulnerable grassland species (Jantunen *et al.* 2007).

The search for an optimal grassland management regime is inevitably complicated by wide life-history variations among grassland species. Road verges, however, may allow the coexistence of a wide range of species, as management intensity often decreases with increasing distance to the road bed, providing long, parallel sections of vegetation managed in different ways. Different treatments affect closely situated plant populations in various ways, and such 'mosaic' management may allow metapopulation dynamics. This was observed in the road verges for the late-flowering *Pimpinella saxifraga* (Auestad *et al.* 2010); cutting in June (V1 and V2) prevented seed production but increased survival, whereas no cutting (V4) allowed seed production but lowered survival. Such negative life-history correlations may reflect adaptability to environmental changes, which reduces extinction risk (Menges 2000). Noordijk *et al.* (2009) proposed a mosaic regime for promotion of insect diversity and abundance in road verges, arguing that cutting various sections of the road verges at different times ensures continuous flowering throughout summer. This is a good example of the situation described by Seastedt *et al.* (2008): novel ecosystems have novel properties, and a sound knowledge base is needed to recommend a suitable management regime.

Concluding remarks

Road verges share many species with pastures, and their potential as refuges for semi-natural grassland species should therefore be enhanced. The apparent short-term resistance of the vegetation to management is in contrast to the clear differences in vegetation between the two habitats that have been differently managed over a long period of time. The positive response to all active road verge treatments indicates that biomass removal (in some form) is needed to encourage low-growing vegetation. More longer-term studies, perhaps including other aspects of management, will be needed to provide more detailed recommendations. We advise the inclusion of several various measures of vegetational change to reveal different aspects of vegetation dynamics. The linear structure of road verges means that different management regimes can be applied in a fine-scale pattern, thus providing suitable conditions for a range of grassland species.

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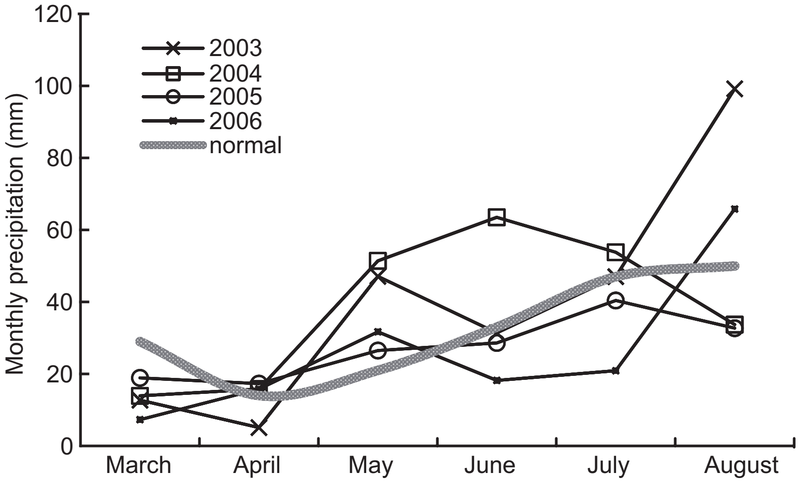

Appendix 1. Monthly precipitation in the study area during the growing season (March–August) for the four years of the study, and monthly averages for the normal period 1961–1990.

Appendix 2. Species occurring in the total data set, frequency given as C^{MFS}; C = constancy percentage, MFS = mean frequency in subplots in the seven treatments over the four years of the study. For treatment abbreviations, *see* Material and methods.

Treatment	P1				P2				P3			
Year	2003	2004	2005	2006	2003	2004	2005	2006	2003	2004	2005	2006
Number of plots	18	18	18	18	18	18	18	18	18	18	18	18
Species frequency	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}
Achillea millefolium	61^{11}	67^{11}	67^{11}	61^{11}	67^{7}	67^{7}	72^{7}	67^{7}	56^{10}	61^{10}	67^{9}	67^{9}
Agrostis capillaris	94^{11}	94^{12}	83^{14}	83^{14}	83^{12}	94^{11}	89^{13}	94^{12}	83^{12}	100^{12}	100^{12}	100^{13}
Alopecurus pratensis	.	.	.	.	.	.	.	.	.	.	.	.
Anthoxanthum odoratum	11^{3}	11^{8}	17^{5}	11^{5}	22^{6}	28^{7}	28^{8}	28^{6}	22^{7}	17^{10}	22^{7}	17^{7}
Anthriscus sylvestris	.	.	.	6^{1}	.	6^{2}	6^{1}	6^{1}	.	.	.	.
Anthyllis vulneraria ssp. *carpatica*	.	6^{3}	6^{1}	.	.	.	.	.	6^{1}	6^{1}	11^{1}	6^{1}
Avenula pubescens	67^{9}	78^{9}	78^{10}	78^{8}	72^{10}	83^{10}	83^{10}	83^{10}	67^{12}	72^{11}	83^{10}	83^{8}
Betula pubescens agg.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula rotundifolia	72^{10}	78^{11}	78^{9}	78^{9}	78^{9}	83^{10}	89^{9}	89^{9}	78^{9}	83^{10}	83^{10}	83^{11}
Carex spicata	6^{5}	6^{2}	6^{3}	6^{3}	11^{7}	11^{6}	11^{8}	6^{11}	6^{2}	6^{1}	11^{1}	11^{1}
Carum carvi	6^{1}	11^{4}	11^{5}	11^{4}	6^{13}	11^{10}	11^{10}	11^{12}	.	6^{1}	11^{1}	6^{1}
Cerastium fontanum	6^{8}	17^{9}	17^{9}	28^{5}	11^{4}	33^{6}	50^{8}	39^{7}	6^{2}	28^{3}	33^{6}	22^{6}
Cuscuta europaea	11^{3}	6^{1}	6^{2}	.	28^{5}	11^{5}	17^{11}	11^{4}	17^{6}	6^{2}	6^{13}	11^{4}
Dactylis glomerata	61^{7}	56^{8}	61^{8}	67^{7}	56^{6}	50^{9}	50^{9}	50^{8}	67^{6}	56^{7}	61^{6}	56^{6}
Deschampsia flexuosa	.	.	6^{1}	6^{1}	6^{5}	11^{7}	17^{3}	17^{2}	11^{4}	11^{6}	11^{6}	6^{7}
Dianthus deltoides	22^{4}	22^{5}	28^{6}	28^{4}	22^{4}	28^{4}	33^{5}	28^{5}	22^{4}	22^{5}	28^{4}	22^{2}
Elymus repens	6^{1}	11^{2}	11^{1}	11^{3}	11^{3}	11^{9}	11^{11}	11^{12}	6^{12}	6^{12}	11^{9}	11^{11}
Equisetum arvense	.	.	.	.	.	.	.	.	.	.	.	.
Euphrasia stricta	39^{9}	44^{11}	50^{13}	56^{7}	39^{10}	44^{9}	44^{10}	39^{7}	39^{12}	44^{10}	50^{9}	50^{7}
Festuca ovina	44^{11}	39^{13}	39^{13}	39^{13}	33^{11}	39^{10}	50^{9}	50^{9}	39^{11}	39^{13}	50^{11}	44^{12}
Festuca pratensis	28^{7}	28^{8}	28^{9}	22^{11}	22^{9}	33^{8}	33^{9}	33^{9}	17^{10}	28^{6}	22^{7}	28^{6}
Festuca rubra	78^{10}	78^{10}	72^{10}	67^{10}	72^{11}	72^{13}	78^{12}	78^{11}	56^{9}	67^{9}	78^{8}	72^{8}
Fragaria vesca	17^{9}	17^{8}	17^{6}	22^{5}	17^{9}	17^{7}	17^{8}	17^{8}	17^{7}	17^{6}	17^{7}	17^{7}
Galium boreale	22^{13}	22^{12}	22^{12}	22^{12}	33^{11}	33^{11}	33^{11}	33^{12}	39^{10}	39^{10}	39^{10}	39^{8}
Galium verum	83^{11}	83^{10}	83^{10}	83^{9}	89^{12}	89^{10}	89^{10}	89^{8}	94^{12}	94^{11}	94^{10}	94^{9}
Geranium sylvaticum	.	.	.	6^{3}	6^{3}	6^{7}	6^{8}	6^{6}	11^{2}	11^{2}	11^{5}	17^{3}
Geum urbanum	.	6^{1}	6^{3}	6^{4}	.	.	6^{1}	6^{2}	.	6^{2}	17^{2}	.
Hieracium spp.	.	6^{3}	11^{3}	11^{3}	.	.	.	.	.	11^{4}	22^{2}	28^{3}

continued

Appendix 2. Continued.

Treatment	P1				P2				P3			
Year	2003	2004	2005	2006	2003	2004	2005	2006	2003	2004	2005	2006
Number of plots	18	18	18	18	18	18	18	18	18	18	18	18
Species frequency	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}
Hieracium umbellatum	11^{5}	11^{12}	11^{8}	11^{7}	17^{2}	22^{3}	22^{4}	22^{4}	.	.	.	.
Knautia arvensis	28^{3}	22^{4}	28^{4}	22^{4}	11^{6}	17^{3}	22^{4}	17^{5}	28^{2}	22^{4}	22^{5}	22^{4}
Leontodon autumnalis	.	.	.	.	.	.	.	.	.	.	.	.
Linaria vulgaris	28^{6}	28^{8}	28^{6}	28^{4}	28^{6}	28^{6}	28^{4}	28^{3}	39^{6}	28^{4}	28^{3}	11^{3}
Lotus corniculatus	33^{3}	28^{5}	28^{5}	22^{4}	17^{2}	28^{2}	22^{2}	28^{1}	33^{4}	44^{5}	33^{4}	33^{3}
Luzula multiflora	.	.	6^{2}	.	.	.	.	.	.	.	.	.
Lychnis viscaria	28^{7}	22^{8}	22^{8}	28^{7}	33^{6}	33^{6}	33^{6}	33^{5}	22^{8}	22^{9}	28^{7}	28^{7}
Myosotis arvensis	.	22^{3}	17^{1}	6^{2}	6^{2}	28^{7}	33^{6}	22^{3}	6^{2}	33^{8}	56^{5}	22^{3}
Phleum pratense	22^{9}	22^{9}	28^{8}	28^{8}	33^{5}	28^{7}	33^{8}	33^{8}	28^{5}	22^{9}	28^{10}	28^{10}
Pimpinella saxifraga	94^{10}	100^{11}	100^{10}	100^{9}	94^{9}	94^{10}	89^{12}	89^{12}	100^{9}	100^{11}	100^{10}	100^{10}
Plantago media	6^{8}	6^{9}	6^{9}	6^{10}	.	.	.	6^{1}	6^{3}	6^{3}	6^{3}	6^{1}
Poa nemoralis	.	.	.	.	.	.	.	.	.	.	.	.
Poa pratensis	61^{8}	72^{7}	78^{7}	78^{8}	89^{8}	94^{9}	94^{9}	83^{9}	67^{10}	72^{10}	83^{9}	94^{9}
Potentilla argentea	11^{2}	6^{1}	.	.	6^{4}	6^{3}	11^{2}	11^{3}	6^{5}	11^{3}	11^{3}	11^{3}
Ranunculus acris	33^{3}	39^{5}	33^{6}	44^{4}	33^{7}	39^{7}	44^{7}	44^{6}	28^{5}	39^{6}	44^{6}	39^{6}
Rhinanthus minor	6^{1}	6^{4}	6^{8}	6^{3}	11^{3}	6^{6}	11^{8}	6^{7}	22^{4}	22^{5}	28^{5}	28^{5}
Rosa spp.	6^{3}	6^{2}	11^{3}	6^{6}	6^{1}	6^{2}	6^{2}	6^{2}	6^{16}	6^{9}	6^{8}	6^{8}
Rubus idaeus	.	.	.	.	.	.	.	.	.	.	.	.
Rumex acetosella	11^{12}	11^{15}	22^{9}	22^{11}	28^{9}	28^{11}	28^{12}	28^{9}	22^{8}	22^{8}	22^{9}	22^{9}
Rumex acetosa	17^{2}	28^{3}	33^{2}	22^{3}	22^{4}	39^{4}	44^{6}	44^{4}	17^{6}	39^{5}	44^{4}	33^{6}
Sedum acre	11^{10}	11^{10}	11^{10}	11^{9}	17^{13}	17^{11}	17^{9}	17^{11}	17^{5}	28^{3}	28^{5}	22^{10}
Silene vulgaris	6^{1}	6^{4}	6^{3}	6^{2}	6^{1}	6^{6}	6^{3}	6^{4}	17^{2}	22^{4}	17^{3}	22^{4}
Stellaria graminea	17^{10}	22^{8}	22^{10}	22^{9}	11^{6}	17^{7}	22^{6}	17^{5}	22^{4}	28^{7}	33^{8}	33^{5}
Tanacetum vulgare	.	.	.	.	.	6^{1}	6^{1}	6^{1}	.	.	.	.
Taraxacum sect. *Ruderalia*	.	11^{2}	.	.	17^{4}	11^{8}	11^{5}	6^{4}	6^{2}	6^{6}	11^{2}	6^{5}
Thlaspi caerulescens	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium medium	33^{14}	39^{13}	39^{13}	39^{13}	33^{14}	39^{13}	44^{12}	44^{11}	44^{12}	50^{11}	44^{13}	39^{13}
Trifolium pratense	39^{10}	56^{9}	50^{10}	50^{7}	39^{5}	50^{5}	50^{6}	50^{5}	44^{6}	61^{9}	61^{10}	78^{6}
Trifolium repens	28^{9}	28^{10}	22^{13}	22^{11}	39^{11}	39^{11}	50^{9}	50^{9}	44^{6}	44^{9}	61^{9}	61^{7}
Ulmus glabra	.	.	.	.	.	.	.	.	.	.	.	.
Verbascum nigrum	.	.	.	.	.	.	.	.	.	.	.	6^{1}
Veronica chamaedrys	11^{9}	11^{9}	11^{9}	11^{8}	11^{2}	17^{4}	17^{4}	22^{4}	11^{3}	11^{4}	17^{4}	17^{5}
Vicia cracca	.	6^{1}	.	.	.	.	.	.	6^{1}	.	.	.
Vicia sepium	.	.	.	.	.	.	.	.	.	.	.	.
Viola canina	11^{4}	17^{5}	17^{5}	17^{6}	17^{4}	22^{3}	17^{4}	28^{4}	28^{4}	28^{5}	33^{6}	39^{5}
Viola tricolor	.	22^{4}	22^{4}	22^{4}	6^{3}	11^{8}	17^{7}	11^{4}	.	11^{3}	22^{5}	28^{5}

Treatment	V1				V2				V3				V4			
Year	2003	2004	2005	2006	2003	2004	2005	2006	2003	2004	2005	2006	2003	2004	2005	2006
Number of plots	18	18	18	18	17	17	17	17	18	18	18	18	17	17	17	13
Species frequency	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}
Achillea millefolium	44^{6}	50^{7}	50^{6}	39^{6}	47^{4}	41^{5}	41^{6}	41^{6}	39^{7}	39^{6}	39^{6}	33^{7}	47^{4}	41^{9}	41^{7}	38^{11}
Agrostis capillaris	22^{7}	28^{7}	44^{5}	44^{5}	12^{9}	18^{5}	35^{6}	41^{4}	33^{5}	28^{4}	28^{4}	28^{5}	29^{4}	29^{3}	29^{4}	31^{5}
Alopecurus pratensis	17^{6}	17^{5}	17^{4}	28^{3}	29^{6}	35^{5}	35^{5}	29^{4}	22^{6}	28^{6}	33^{4}	28^{4}	35^{6}	35^{6}	35^{7}	38^{6}
Anthoxanthum odoratum	6^{4}	6^{4}	6^{4}	6^{3}	6^{10}	6^{11}	6^{13}	6^{14}	6^{3}	6^{5}	6^{4}	6^{7}	6^{8}	6^{8}	6^{3}	8^{5}
Anthriscus sylvestris	17^{5}	28^{3}	28^{6}	33^{5}	12^{3}	18^{5}	29^{4}	29^{4}	17^{5}	22^{4}	22^{6}	17^{7}	18^{4}	24^{3}	24^{3}	38^{5}
Anthyllis vulneraria	6^{2}	6^{1}	6^{3}	6^{2}	6^{1}	18^{2}	12^{3}	.	.	6^{1}	.	11^{1}	12^{3}	18^{2}	6^{1}	8^{1}
Avenula pubescens	67^{8}	67^{11}	56^{14}	61^{10}	71^{7}	71^{9}	71^{10}	65^{9}	56^{10}	61^{10}	61^{10}	61^{9}	65^{9}	65^{8}	71^{8}	62^{11}
Betula pubescens agg.	22^{11}	22^{6}	22^{5}	22^{7}	29^{11}	24^{8}	24^{7}	24^{8}	22^{13}	22^{10}	17^{12}	17^{13}	18^{10}	24^{11}	24^{12}	31^{10}

continued

Appendix 2. Continued.

Treatment	V1				V2				V3				V4			
Year	2003	2004	2005	2006	2003	2004	2005	2006	2003	2004	2005	2006	2003	2004	2005	2006
Number of plots	18	18	18	18	17	17	17	17	18	18	18	18	17	17	17	13
Species frequency	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}
Campanula rotundifolia	78^{7}	67^{10}	72^{9}	67^{10}	88^{6}	88^{8}	88^{9}	82^{10}	78^{6}	72^{6}	61^{7}	72^{7}	76^{6}	71^{6}	76^{7}	92^{6}
Carex spicata	17^{4}	22^{3}	22^{3}	17^{6}	12^{8}	18^{6}	18^{4}	18^{3}	28^{4}	28^{4}	33^{3}	28^{3}	18^{6}	18^{6}	18^{8}	23^{4}
Carum carvi	6^{2}	6^{4}	17^{1}	.	6^{1}	6^{5}	6^{4}	6^{1}	11^{6}	11^{2}	11^{3}	11^{3}	.	.	.	.
Cerastium fontanum	.	.	.	.	.	.	.	.	.	.	6^{5}	6^{14}	.	.	.	.
Cuscuta europaea	.	.	.	.	.	.	6^{2}	.	6^{6}	6^{3}	11^{5}	6^{6}	6^{1}	.	6^{4}	.
Dactylis glomerata	94^{10}	94^{11}	100^{11}	100^{9}	100^{10}	100^{9}	100^{9}	100^{8}	94^{11}	94^{12}	94^{10}	94^{10}	94^{9}	100^{9}	100^{10}	100^{10}
Deschampsia flexuosa	17^{16}	22^{13}	22^{13}	17^{16}	29^{13}	24^{16}	24^{15}	24^{14}	28^{11}	33^{11}	28^{13}	28^{12}	29^{6}	24^{10}	24^{6}	23^{7}
Dianthus deltoides	11^{9}	17^{7}	22^{8}	22^{8}	12^{9}	18^{8}	18^{11}	18^{9}	17^{9}	17^{12}	17^{13}	22^{11}	18^{4}	18^{4}	18^{4}	23^{4}
Elymus repens	28^{11}	28^{12}	22^{12}	28^{9}	29^{12}	29^{11}	35^{10}	29^{10}	28^{9}	28^{9}	22^{11}	22^{11}	29^{9}	29^{8}	24^{11}	15^{16}
Equisetum arvense	11^{4}	22^{2}	33^{3}	33^{1}	29^{3}	29^{3}	35^{5}	47^{3}	17^{4}	22^{3}	28^{3}	17^{4}	12^{2}	6^{2}	12^{2}	15^{3}
Euphrasia stricta	.	.	.	.	.	.	.	.	.	.	.	6^{3}	.	.	.	.
Festuca ovina	11^{8}	11^{8}	17^{9}	17^{6}	18^{7}	18^{9}	35^{7}	24^{9}	22^{7}	28^{7}	22^{10}	22^{9}	12^{5}	12^{6}	12^{5}	15^{8}
Festuca pratensis	17^{6}	11^{8}	17^{8}	11^{4}	24^{6}	24^{4}	24^{7}	24^{6}	28^{3}	28^{3}	33^{3}	22^{2}	6^{3}	12^{3}	12^{3}	15^{4}
Festuca rubra	78^{10}	94^{8}	78^{9}	72^{9}	65^{11}	76^{9}	71^{9}	65^{9}	67^{12}	67^{11}	72^{10}	72^{9}	71^{12}	71^{12}	71^{12}	69^{8}
Fragaria vesca	50^{9}	44^{12}	44^{12}	44^{12}	24^{15}	24^{15}	24^{15}	24^{15}	39^{6}	33^{5}	28^{7}	33^{7}	24^{6}	24^{8}	24^{8}	23^{10}
Galium boreale	6^{1}	6^{2}	.	.	12^{14}	12^{10}	12^{10}	12^{10}	11^{8}	11^{6}	11^{6}	11^{8}	6^{7}	6^{3}	6^{1}	8^{2}
Galium verum	39^{7}	39^{7}	33^{7}	33^{6}	35^{8}	29^{7}	41^{4}	29^{5}	56^{7}	56^{5}	50^{6}	44^{6}	47^{9}	53^{7}	47^{7}	38^{10}
Geranium sylvaticum	.	.	.	.	6^{2}	12^{3}	18^{3}	18^{2}	17^{4}	17^{2}	17^{3}	22^{3}	18^{2}	18^{1}	18^{2}	31^{4}
Geum urbanum	6^{3}	11^{3}	11^{7}	11^{3}	12^{4}	18^{5}	18^{5}	24^{4}	22^{2}	22^{3}	17^{6}	17^{8}	.	6^{2}	.	.
Hieracium spp.	6^{3}	6^{4}	11^{3}	11^{2}	.	.	6^{3}	12^{6}	6^{1}	6^{3}	6^{5}	11^{3}	.	.	.	.
Hieracium umbellatum	39^{4}	33^{4}	33^{6}	33^{7}	41^{5}	41^{5}	41^{9}	47^{8}	17^{8}	22^{9}	22^{10}	22^{9}	24^{4}	24^{7}	24^{7}	31^{8}
Knautia arvensis	39^{5}	39^{5}	39^{4}	28^{6}	12^{5}	12^{5}	29^{3}	29^{4}	22^{4}	28^{4}	33^{3}	22^{4}	53^{4}	47^{4}	47^{4}	54^{4}
Leontodon autumnalis	17^{4}	17^{4}	22^{3}	22^{2}	12^{3}	12^{5}	12^{5}	18^{3}	17^{4}	17^{5}	17^{6}	22^{7}	6^{2}	6^{6}	6^{4}	15^{5}
Linaria vulgaris	17^{6}	11^{7}	11^{3}	6^{2}	.	6^{1}	6^{3}	6^{1}	17^{9}	22^{4}	22^{4}	17^{2}	29^{3}	24^{4}	12^{7}	23^{4}
Lotus corniculatus	.	6^{1}	6^{1}	.	.	6^{1}	6^{3}	6^{2}	.	.	.	6^{2}	.	.	.	.
Luzula multiflora	6^{1}	6^{3}	6^{1}	6^{1}	12^{2}	6^{3}	18^{3}	12^{3}	6^{5}	17^{2}	17^{4}	11^{3}	12^{3}	6^{1}	6^{2}	.
Lychnis viscaria	11^{2}	33^{3}	44^{3}	44^{4}	18^{5}	35^{4}	41^{5}	53^{4}	33^{6}	44^{7}	44^{6}	50^{7}	41^{8}	35^{9}	35^{9}	54^{8}
Myosotis arvensis	6^{2}	17^{3}	6^{2}	.	12^{2}	24^{2}	18^{6}	6^{1}	.	17^{3}	17^{6}	.	.	.	.	.
Phleum pratense	11^{7}	17^{6}	28^{6}	33^{6}	24^{4}	24^{5}	24^{6}	35^{5}	28^{3}	28^{3}	28^{5}	33^{5}	29^{6}	35^{6}	35^{9}	46^{7}
Pimpinella saxifraga	94^{10}	94^{12}	94^{11}	94^{11}	100^{9}	100^{11}	100^{12}	100^{12}	89^{10}	89^{10}	89^{10}	94^{10}	94^{11}	94^{11}	94^{11}	92^{11}
Plantago media	6^{13}	6^{14}	6^{12}	6^{11}	24^{6}	24^{6}	24^{5}	24^{5}	6^{3}	6^{2}	6^{2}	6^{2}	6^{1}	6^{1}	.	.
Poa nemoralis	39^{6}	33^{7}	33^{8}	33^{7}	35^{9}	47^{5}	41^{6}	35^{7}	44^{6}	50^{7}	50^{7}	50^{8}	47^{7}	59^{8}	59^{9}	85^{9}
Poa pratensis	61^{5}	72^{7}	78^{7}	83^{8}	59^{8}	65^{8}	82^{7}	88^{8}	83^{6}	83^{6}	94^{6}	94^{7}	71^{7}	76^{5}	76^{6}	92^{7}
Potentilla argentea	.	.	.	.	.	.	.	6^{1}	11^{3}	6^{5}	11^{3}	11^{3}	6^{1}	12^{1}	12^{1}	.
Ranunculus acris	11^{3}	11^{3}	17^{3}	11^{3}	18^{6}	18^{6}	29^{5}	24^{5}	6^{15}	11^{7}	11^{9}	17^{7}	12^{3}	12^{4}	6^{2}	8^{2}
Rhinanthus minor	.	6^{2}	6^{4}	6^{1}	.	.	.	6^{1}	.	6^{2}	6^{1}	6^{1}	.	.	.	.
Rosa spp.	22^{9}	22^{7}	22^{5}	17^{4}	6^{1}	.	6^{1}	6^{1}	11^{2}	6^{2}	11^{3}	6^{3}	6^{1}	.	.	.
Rubus idaeus	11^{5}	11^{3}	6^{1}	11^{3}	6^{2}	6^{2}	6^{1}	6^{1}	6^{5}	6^{2}	17^{2}	17^{2}	29^{4}	24^{5}	29^{4}	23^{3}
Rumex acetosella	.	.	.	.	.	.	.	.	6^{1}	.	6^{3}	11^{2}	.	.	.	.
Rumex acetosa	.	11^{1}	6^{1}	6^{1}	6^{1}	6^{1}	6^{1}	6^{1}	.	11^{1}	6^{1}	.	.	6^{2}	6^{1}	8^{1}
Sedum acre	.	.	.	.	.	.	.	.	11^{4}	11^{4}	11^{5}	6^{10}	.	.	.	8^{1}
Silene vulgaris	17^{3}	22^{3}	22^{3}	17^{3}	12^{4}	6^{3}	12^{3}	18^{2}	22^{1}	6^{4}	6^{2}	6^{3}	12^{5}	24^{2}	18^{3}	15^{3}
Stellaria graminea	.	.	6^{7}	6^{1}	6^{2}	6^{2}	6^{10}	6^{3}	.	.	.	6^{1}	.	.	.	.
Tanacetum vulgare	22^{2}	33^{2}	22^{2}	17^{2}	12^{6}	18^{3}	6^{3}	6^{3}	22^{5}	28^{3}	22^{2}	22^{2}	29^{7}	29^{5}	24^{6}	23^{5}
Taraxacum sect. *Rud.*	28^{9}	28^{11}	33^{11}	28^{11}	47^{6}	41^{6}	47^{4}	47^{4}	33^{10}	33^{10}	39^{10}	28^{12}	24^{8}	24^{11}	24^{9}	23^{10}
Thlaspi caerulescens	6^{4}	6^{13}	11^{9}	17^{6}	12^{3}	18^{7}	18^{6}	24^{5}	11^{5}	17^{5}	17^{7}	17^{8}	24^{7}	24^{6}	24^{6}	23^{3}
Trifolium medium	17^{12}	17^{13}	17^{13}	28^{9}	18^{16}	18^{15}	18^{16}	24^{14}	28^{13}	28^{14}	28^{15}	33^{13}	18^{15}	18^{16}	18^{16}	23^{15}
Trifolium pratense	50^{9}	50^{9}	61^{8}	56^{5}	59^{7}	59^{9}	59^{10}	53^{9}	56^{7}	50^{10}	50^{10}	56^{5}	53^{7}	53^{7}	53^{8}	69^{5}
Trifolium repens	22^{5}	28^{4}	33^{5}	6^{6}	12^{9}	18^{8}	18^{8}	12^{10}	6^{8}	17^{4}	17^{2}	6^{2}	6^{5}	12^{3}	18^{5}	8^{1}
Ulmus glabra	22^{5}	22^{2}	22^{3}	22^{2}	12^{5}	6^{8}	12^{4}	18^{3}	17^{4}	17^{5}	11^{7}	11^{5}	18^{2}	24^{4}	24^{4}	46^{6}
Verbascum nigrum	17^{2}	17^{2}	11^{2}	.	18^{1}	12^{1}	12^{1}	12^{2}	11^{1}	6^{1}	6^{1}	6^{2}	18^{7}	18^{5}	18^{4}	15^{4}

continued

Appendix 2. Continued.

Treatment	V1				V2				V3				V4			
Year	2003	2004	2005	2006	2003	2004	2005	2006	2003	2004	2005	2006	2003	2004	2005	2006
Number of plots	18	18	18	18	17	17	17	17	18	18	18	18	17	17	17	13
Species frequency	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}	C^{MFS}
Veronica chamaedrys	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vicia cracca	11^{2}	6^{1}	6^{1}	.	18^{5}	18^{1}	6^{1}	6^{1}	22^{6}	17^{6}	17^{1}	17^{3}	6^{2}	.	6^{1}	8^{4}
Vicia sepium	6^{4}	6^{5}	17^{2}	11^{1}	6^{2}	.	.	.	17^{5}	17^{5}	17^{3}	17^{3}	47^{5}	47^{5}	47^{6}	46^{3}
Viola canina	.	.	.	.	.	.	6^{1}	6^{1}	.	.	.	.	6^{1}	12^{1}	6^{2}	15^{2}
Viola tricolor	.	.	.	.	.	.	.	6^{1}	.	.	.	.	.	.	.	.

Additional species [C < 5% in the total data set (all treatments over all years)]: *Alchemilla vulgaris* P1(....), P2(....), P3(....), V1(....), V2($6^{3}6^{2}6^{4}6^{8}$), V3(..$6^{1}6^{3}$), V4(....); *Allium oleraceum* P1(....), P2(6^{2}.6^{3}.), P3(....), V1(....), V2(....), V3(....), V4(....); *Alnus glutinosa* P1(....), P2(....), P3(....), V1(....), V2(6^{2}...), V3(....), V4(....); *Alnus incana* P1(....), P2(....), P3(....), V1(....), V2($6^{2}6^{1}6^{1}$.), V3(.6^{2}.6^{1}), V4($12^{10}12^{12}12^{15}12^{12}$); *Angelica sylvestris* P1(....), P2(....), P3(....), V1(....), V2($6^{2}6^{1}6^{1}6^{1}$), V3(....), V4(....); *Antennaria dioica* P1(....), P2(....), P3(....), V1(.$6^{2}6^{4}6^{4}$), V2(....), V3(....), V4(....); *Arenaria serpyllifolia* P1(....), P2(.6^{3}..), P3(....), V1(....), V2(....), V3(....), V4(....); *Botrychium lunaria* P1(....), P2($6^{3}6^{1}6^{2}6^{2}$), P3($6^{1}6^{1}6^{1}6^{1}$), V1(....), V2(....), V3(....), V4(....); *Bromus tectorum* P1(....), P2(....), P3(...6^{1}), V1(....), V2(....), V3(....), V4(....); *Calamagrostis epigejos* P1(..$6^{1}6^{1}$), P2(....), P3(....), V1(....), V2(....), V3(....), V4(....); *Campanula latifolia* P1(....), P2(....), P3(....), V1(....), V2(....), V3(....), V4(...8^{4}); *Carex pallescens* P1(....), P2(....), P3(....), V1($6^{1}6^{2}6^{4}6^{3}$), V2($6^{4}6^{3}6^{2}6^{3}$), V3(....), V4(....); *Chenopodium album* P1(....), P2(.6^{1}..), P3(....), V1(....), V2(....), V3(.6^{1}..), V4(....); *Deschampsia cespitosa* P1(....), P2(....), P3(....), V1($11^{4}11^{8}11^{8}11^{17}$), V2($6^{3}6^{5}6^{3}6^{4}$), V3($6^{6}6^{9}6^{2}6^{5}$), V4($18^{4}12^{4}12^{4}$.); *Draba incana* P1($11^{1}6^{1}11^{1}6^{1}$), P2($11^{2}11^{4}$..), P3(....), V1(....), V2(....), V3(....), V4(....); *Epilobium montanum* P1(....), P2(....), P3(....), V1(....), V2(....), V3(....), V4($12^{2}6^{2}6^{2}$.); *Erigeron acer* P1(....), P2(....), P3(....), V1(....), V2(...6^{2}), V3(....), V4(....); *Galeopsis sp.* P1($6^{4}6^{13}6^{10}6^{2}$), P2($6^{3}11^{5}6^{2}6^{1}$), P3($11^{1}11^{1}11^{1}11^{1}$), V1(....), V2(.6^{1}..), V3($11^{5}6^{2}6^{1}$.), V4(6^{2}...); *Galium aparine* P1($6^{5}6^{2}$.6^{1}), P2($6^{1}6^{2}$..), P3($17^{1}6^{1}$.6^{1}), V1(.$6^{3}6^{1}6^{1}$), V2(....), V3($6^{7}6^{5}6^{1}6^{1}$), V4(....); *Galium uliginosum* P1(....), P2(...6^{1}), P3(...17^{1}), V1(....), V2(....), V3(....), V4(....); *Heracleum sibiricum* P1(....), P2(....), P3(....), V1($6^{2}6^{4}6^{5}6^{7}$), V2($6^{3}6^{2}6^{3}6^{3}$), V3(.$6^{3}6^{5}6^{7}$), V4(....); *Pinus sylvestris* P1(....), P2(....), P3(....), V1(....), V2(6^{4}...), V3(....), V4(....); *Poa glauca* P1(....), P2(....), P3(....), V1(...6^{1}), V2(....), V3($6^{8}6^{11}6^{4}6^{3}$), V4(..$6^{2}8^{2}$); *Potentilla crantzii* P1(....), P2(....), P3($6^{2}6^{4}6^{3}6^{3}$), V1(....), V2(....), V3(....), V4(....); *Prunella vulgaris* P1(....), P2(....), P3(...6^{2}), V1(....), V2(6^{2}...), V3(....), V4(....); *Salix caprea* P1(....), P2(....), P3(....), V1($11^{6}6^{3}6^{2}$.), V2(.6^{2}..), V3($11^{5}6^{2}6^{2}6^{2}$), V4(....); *Senecio viscosus* P1(..6^{4}.), P2(6^{2}...), P3(...6^{1}), V1(....), V2(...12^{1}), V3(...6^{1}), V4(...8^{3}); *Veronica officinalis* P1(....), P2($6^{4}6^{11}6^{7}11^{4}$), P3(.6^{2}.11^{1}), V1(....), V2($6^{2}12^{2}12^{3}12^{2}$), V3($6^{3}6^{2}6^{3}6^{2}$), V4(...8^{3}); *Veronica serpyllifolia* P1(.$6^{1}6^{5}11^{6}$), P2(.$6^{2}11^{4}11^{7}$), P3(.$6^{11}11^{8}11^{9}$), V1(....), V2(....), V3(....), V4(....).