

**RESTORATIVE MOWING ON
SEMI-NATURAL GRASSLANDS:
COMMUNITY-LEVEL CHANGES
AND SPECIES-LEVEL
RESPONSES**

**ARI-PEKKA
HUHTA**

Department of Biology,
University of Oulu

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Department of Biology, University of Oulu, P.O.Box 3000, FIN-90014 University of Oulu, Finland
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Abstract

This thesis operates at two levels of ecological research, describing the effects of withdrawal and re-introduction of management on grasslands. The aim of the community-level survey was to explore the effects of abandonment, mowing and grazing on semi-natural meadows in northern Finland. At the species level, the aim was to evaluate the responses of three monocarpic meadow species to various degrees of simulated grazing under natural growth conditions.

The community-level studies suggest that strongly competitive grass species with rapid vegetative growth, especially those forming tussocks, are able to retain or increase their cover in abandoned meadows. However, most species are able to persist in a meadow for a long time after abandonment, even when a group of immigrants arrive. This leads to a temporary increase in species diversity, and it may therefore be used as an indicator of ongoing succession. Nevertheless, abandonment is harmful for the rare archaeophytic species in the long run. Late mowing does not have extensive short-term impacts on grass-dominated semi-natural meadows. Therefore, it is neither an efficient nor a substitutional way of management when the goal is to restore a formerly grazed pasture. Mowing executed early in the season may, however, be a more appropriate way of inducing changes in species composition and enhancing species richness.

According to the results of the species-level studies, *Erysimum strictum* and *Rhinanthus minor* tolerate well minor apical damage, while more severe damage has a detrimental impact on the performance of both species. The observed differences in regrowth responses between the two species are presumably due to their different habitat requirements in relation to competition. The species-level experiment with two late-flowering populations of field gentian *Gentianella campestris* ssp. *campestris* revealed that the southern, Swedish population that has been regularly grazed and mown overcompensated for the intermediate (50%) damage level, whereas the northern, Finnish field gentians growing in unmanaged habitats showed at best partial or full compensation. Regular grazing and mowing have presumably favoured grazing-tolerant plant species, i.e. species with a good regrowth capacity.

Herbivory reshapes grassland plant communities in two ways: directly by affecting the survival and reproductive success of individual plants and indirectly by changing the competitive environment. Tall and competitive perennial species suffer relatively more from damage than true grassland species, i.e. small herbs and grasses, which are better able to tolerate regular tissue losses and respond to damage within the ongoing growing season. As a result, certain species benefit from grazing and mowing in the sense that they may gain more through competitive relaxation than they lose in defoliation.

Keywords: regrowth capacity, secondary succession, simulated herbivory, vegetation management

To my family

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Oulu, March 2001

A-P. Huhta

List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I Huhta, A-P (1996) Vegetation changes in semi-natural meadows after abandonment in coastal northern Finland. *Nord J Bot* 16: 457-472.
- II Huhta, A-P & Rautio, P (1998) Evaluating the impacts of mowing: a case study comparing managed and abandoned meadow patches. *Ann Bot Fenn* 35: 85-99.
- III Huhta, A-P, Rautio, P, Tuomi, J & Laine, K (2001) Restorative mowing in recently abandoned semi-natural meadow: short-term effects and long-term predictions on plant community structure. Manuscript, submitted.
- IV Huhta, A-P, Tuomi, J & Rautio, P (2000) Cost of apical dominance in two monocarpic herbs, *Erysimum strictum* and *Rhinanthus minor*. *Can J Bot* 78: 591-599.
- V Huhta, A-P, Lennartsson, T, Tuomi, J, Rautio, P & Laine, K (2000) Tolerance of *Gentianella campestris* in relation to damage intensity: an interplay between apical dominance and herbivory. *Evol Ecol*, in press.

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1 Introduction

1.1 Abandonment, restoration and plant strategies

The use of semi-natural meadows as pastures for livestock was the basis for traditional agriculture in Finland. As recently as the beginning of the 20th century, one of the main tasks of stock raising was to produce dung to fertilize the small patches of cultivated fields surrounding villages. No manure was spared for the outlying meadows, although they provided winter forage for the cattle (Anonymous 1993). Today, the abandonment of traditionally managed meadows has reduced the number of species in these formerly species-rich plant communities (Aronsson 1991).

The increasing interest in the conservation of semi-natural grasslands has produced research projects where the aim has been, besides providing basic knowledge about grassland dynamics, also to find new ways for restoration practices. The vast majority of studies dealing with grassland dynamics and restoration have been carried out in the nemoral and boreonemoral vegetation zones in Central Europe (e.g. Willems 1983, Oomes 1990, Stampfli 1992, 1999, Zobel *et al.* 1996, Muller *et al.* 1998, Pärtel *et al.* 1998) and, compared to Finland, in even more exotic vegetation zones (e.g. Miles 1987, der Heer 1991, Tilman & El Haddi 1992, Díaz *et al.* 1994, Kindscher & Wells 1995), while such studies are still quite scarce in the boreal zone, particularly Finland (cf. Hægström 1990, Malkamäki & Hægström 1997, Kotiluoto 1998, Jutila 1997, 1998, 1999, Tikka 2001).

Grassland dynamics and restoration may be studied from various standpoints, ranging from the species level (cf. e.g. Lennartsson 1997, Zopfi 1998) to the habitat and community levels (cf. Schaminée & Meertens 1992, Rodriguez *et al.* 1995). One way to evaluate the state of a meadow, or to ascertain whether management has been successful, is to examine the abundance of plants of different origin. Due to centuries of human impact, meadows have received species from various habitats. These species coexist with indigenous but hemerophilic (apophytic) species. Archaeophytes were introduced to Finland before the early 17th century (Sukopp & Hejný 1990, Suominen & Hämet-Ahti 1993). A high abundance of archaeophytes in a Finnish semi-natural meadow is an indirect indication of the fairly “good“ state of the habitat, whereas a high number of

neophytes implies weediness caused by attempts to improve the vegetation stands by additional sowing or fertilization. Another, and even more popular way to estimate the state of a meadow is to classify the species into categories representing different life-history strategies. In general, life-history strategy is an important indicator of the vulnerability of a species (Noss 1983), but it may also help to evaluate the state and the need for restoration of a habitat. Evaluation of the proportion of r and K strategists (MacArthur & Wilson 1967), the grazing tolerance strategies according to Oksanen and Ranta (1992), or alternatively, the plant strategies of the competitive - stress-tolerant - ruderal (CSR) model (Grime 1977, 1979) may reveal the state of the meadow in relation to the intensity of management well before there are any apparent changes in habitat physiognomy.

A third way of evaluating management success is simply to observe the responses of selected species or groups of meadow species to grazing and/or cutting and to free succession. In principle, there are three ways that plants may use to avoid consumption or at least to minimize the effects of tissue loss in case of herbivory: (1) escape in time or space (e.g. Janzen 1970, Feeny 1976), (2) defence mechanisms (thorns, spines and secondary substances, see Grubb 1992, Karban & Baldwin 1997, Tollrian & Harvell 1999), and (3) compensatory capacity or tolerance, i.e. an ability to regrow after damage. Grassland plants seem to have at least moderate tolerance to tissue losses caused by grazing or mowing (McNaughton 1979). The documented cases from northern Europe indicate that herbaceous plants with a high compensatory capacity seem to be, with certain exceptions, archaeophytes (Lennartsson *et al.* 1997) and, more importantly, monocarps, i.e. plants that produce offspring only once in their lifetime (Verkaar *et al.* 1986, Hendrix & Trapp 1989, Prins *et al.* 1989, Reichman & Smith 1991). When management is discontinued, archaeophytes are gradually replaced, usually by native perennials with poor tolerance to frequent damage (Irwin & Aarssen 1996, Venecz & Aarssen 1998, but see also Lehtilä & Syrjänen 1995). Thus, from the manager's point of view, the abundance of species with different life-history strategies or, perhaps more significantly, plants with good compensatory capacity may be used as an indicator of the condition of a grassland community (Lennartsson & Svensson 1996).

1.2 Effects of herbivory and competition on plant architecture

Defoliation does not have the same impact on all plants. Plants with low growth forms or rosettes recover better than those with erect growth forms (Parr & Way 1988, Mitchley & Willems 1995). In addition, plants that have tough, narrow, finely lobate or scale-like leaves recover relatively better from herbivory compared to plants with broad and mesomorphic leaves, which are often prone to desiccation and contamination (Oksanen & Virtanen 1995). The regrowth after herbivory takes place in two zones of intense growth: apical and leaf meristems. In grasses, the leaf meristem is situated at the base of the lamina, while the apical meristem is enwrapped by the leaves. Further, when the apical meristem is pressed close to the ground, the consequent twofold protection makes grasses resistant against herbivores (Prins *et al.* 1980). In contrast, typical grassland herbs have an exposed apical meristem and leaf meristems placed quite diffusely next to the leaf

(Prins *et al.* 1980), and they are thus less protected against grazing. There are some exceptions to this rule. In *Plantago maritima*, 80% of the growth takes place at the base of the leaves, and the old leaves envelop the apical meristem. This enables partially consumed leaves to regrow (Prins *et al.* 1980). Other species with an extremely good compensatory ability include *Ipomopsis aggregata* (Paige & Whitham 1987) and *Gentianella campestris* (Lennartsson *et al.* 1997, 1998), which owe their good capacity for regeneration to their “bud bank“ situated at the base and nodes of the stalk (Lehtilä 1999).

Injury of a plant by a herbivore usually leads to the loss of apical dominance, i.e. the interruption in correlative inhibition, whereupon the auxin production of the leading shoot tips ceases. This, in turn, enhances the production of new lateral branches and inflorescence (Cline 1991). Repeated herbivore attacks result in highly branched, bush-like growth forms (McNaughton 1984). Apical dominance is generally considered an adaptation to competition for light, because rapidly growing, unbranched individuals are more likely to be successful in the competition for light compared to ones that allocate resources away from vertical growth to branches close to the ground (Irwin & Aarssen 1991, 1996, Bonser & Aarssen 1996). If the phenotype before damage is already very branched, indicating weak apical dominance, the removal of apical dominance may have only marginal effects on branching intensity (Järemo *et al.* 1996).

Even though the area of photosynthetically active tissue decreases due to herbivory, this may lead to increased light availability for the remaining, previously shaded leaves. This, in turn, will increase their photosynthetic capacity (McNaughton 1979). The five main traits associated with high tolerance to herbivory after damage are 1) an increased net photosynthetic rate, 2) a high relative growth rate, 3) increased branching or tillering after release from apical dominance, 4) mobilization of the pre-existing high levels of carbon storage in roots for allocation to above-ground reproduction, and 5) an ability to move the carbon stores from roots to shoots (Strauss & Agrawal 1999). However, there is usually a breakdown point, after which the plant is unable to fully recover from damage. When the decrease of leaf area or the loss of nutrients exceeds this point, the potential positive responses cannot compensate for the negative impacts of herbivory (Crawley 1997).

1.3 Effects of herbivory on competitive interactions and species diversity

Generally, grazing and mowing tend to decrease above-ground competition, at least in moderately humid areas (Milchunas & Lauenroth 1993). However, the situation may be quite different in more arid conditions. In the Serengeti short-grass steppe, grazing markedly promotes sprouting and spreading by runners and rhizomes. This is in stark contrast to the predictions that grazing will relax competition (McNaughton 1983, 1984). Although grazing may not have any major impact on above-ground competition in communities adapted to grazing, it may intensify competition for below-ground resources. The degree of intensification depends on the grazing intensity, the proportions of grasses with different statures, and the abundance of grazing-tolerant and intolerant

plants (Milchunas *et al.* 1988). In contrast, the regrowth responses of communities consisting of grazing-intolerant plants are less well developed. In those communities, rhizomatous and tillering plants are less abundant, and when grazing or mowing is introduced to such habitats, competitive interactions undergo major changes.

Usually, generalist herbivores do not graze selectively on individual plants, but rather cut off patches containing several plants. The impact of grazing on the growth of a single plant is therefore connected to the fates of the neighbouring plants. The indirect influence, including increased light availability and reduced competition for nutrients, may sometimes be equally important as are the direct one. Thus, some species may become more abundant because they gain relatively more by the competitive release for light than they lose in defoliation compared to other species (Brown & Allen 1989, McNaughton 1986b, but see Bergelson & Crawley 1992a, b).

It has been reported that grazing increases diversity (e.g. Gibson *et al.* 1987, Belsky 1992, Pettit *et al.* 1995), and when grazed areas are abandoned, the number of species present declines (Rodenburg 1967, During & Willems 1984). On the other hand, intensive grazing in a limited area may also decrease the number of species (Olf & Ritchie 1998). Generally, moderately intense grazing leads to enrichment in species composition in conditions where the competitively dominant plants suffer, but subordinate species face no substantial detrimental effects (Harper 1977). In this case, both competitive and less competitive species may co-exist, which results in species-rich vegetation stands. This is the cornerstone of the intermediate disturbance hypothesis (Grime 1973, Huston 1979, Milchunas *et al.* 1988). According to Crawley (1997), if there is a link between herbivory and species diversity, it is most likely to be connected with the competitive ability, palatability or grazing tolerance of the plant species. If herbivores prefer palatable dominant species, diversity increases. On the other hand, diversity may be low under high grazing pressure if there is only a limited number of grazing-tolerant species (Crawley 1997).

Grazing and mowing are suggested to alleviate the successive establishment of “true“ grassland species (cf. Zobel *et al.* 1996). These are commonly short and grazing-tolerant plant species (Milchunas *et al.* 1988). Mowing and grazing may not, however, alone be sufficient to restore the former species richness, due to limitations on seed dispersal and seedling establishment (Davies *et al.* 1999, Stampfli & Zeiter 1999). Thus, the availability of seeds may become a bottleneck in meadow restoration (Stampfli & Zeiter 1999), especially when abandonment and consequent species decline occur simultaneously over large geographical areas (cf. Eriksson *et al.* 1995).

1.4 Plant defence and tolerance to herbivory

Tolerance refers to the ability of a plant to maintain its fitness through growth and reproduction after herbivore damage (Rosenthal & Kotanen 1994). The published physiological and ecological studies indicate that the mechanisms involved in tolerance are numerous and variable (Lehtilä 1999). According to Rosenthal and Kotanen (1994), some of the plant traits may reflect selection driven by herbivory, whereas others are merely by-products of other selective factors, e.g. growth forms. Similarly, certain

tolerance mechanisms may be involved in defence trade-offs, while others are not. Regardless of its evolutive origin, tolerance may often influence community composition and the evolution of plant defence (Rosenthal & Kotanen 1994).

As mentioned above, moderately intense herbivory may increase diversity, if the level of defence correlates negatively with the competitive ability. The reason for this is that herbivory prevents preferentially the species that would otherwise dominate the community (Rosenthal & Kotanen 1994). From the manager's point of view, this may also have side effects: when grazing suppresses competitively strong species, it may concomitantly allow the establishment of spiny, thorny or poisonous species into otherwise invasion-resistant grassland community (Crawley 1983). Similarly, the negative correlation between tolerance and competitive ability may result in increased diversity regardless of unselective grazing. Accordingly, if defence and competitive ability are positively correlated, herbivory may reduce diversity. Tolerance to herbivory is also determined by the external growth conditions. Habitats that are rich in resources and characterized by a low level of competition and stress should allow greater tolerance, because herbivory damage could be repaired at a lower cost (Maschinski & Whitham 1989, Rosenthal & Kotanen 1994).

It is often assumed that defence and tolerance could be regarded as alternative evolutionary traits for coping with herbivory (van der Meijden *et al.* 1988, Belsky *et al.* (1993), which does not, however, mean that they would be mutually exclusive. Both theoretical considerations (Pacala & Crawley 1992) and empirical studies (Mauricio *et al.* 1997) suggest that tolerant and defensive plants should succeed equally in grazed grasslands. Thus, natural selection may simultaneously favour both greater defence and tolerance. However, they may involve different costs and constraints. For example, in habitats grazed by unselective herbivores, grazing pressure may be so severe that it is impossible for even the worst tasting genotype to avoid serious injuries (Westoby 1989). In such a case, tolerance may still be a viable strategy. This is the most plausible explanation for the fact that grasslands with a long grazing history tend to be dominated by grazing-tolerant plants, whereas the vegetation in areas with low grazing pressure tends to be sensitive to domesticated herbivores (Rosenthal & Kotanen 1994).

1.5 Aims of the study

The studies presented below were carried out both at the community level and at the level of individual species and aim to provide useful perspectives into the dynamics and restoration of semi-natural grasslands. I have studied the impacts of discontinued management, mowing and/or grazing on grassland communities (I-III). At the community level, my purpose was to find out the outcomes of both abandonment or re-introduced management on semi-natural meadow vegetation. Secondly, I have studied the grazing tolerance of a few grassland herbs (IV-V) with the general aim of finding out whether the compensation capacities of the study species reflect adaptation to competition for light (Aarssen & Irwin 1991) or, alternatively, to herbivory or, more generally, to predictable damage (McNaughton 1979, Paige & Whitham 1987, Tuomi *et al.* 1994, Crawley 1997).

Finally, I will discuss the role of mowing as a tool of restorative management of semi-natural grasslands.

2 Material and methods

2.1 Community-scale evaluation of meadows

The data in the first paper (I) were collected in 1989 from 22 meadow sites, 12 of which were still being grazed or mown, while 10 were abandoned. Some of them had been cultivated, although it had been several years since the last ploughing or sowing had taken place. Many of the investigated meadows were known to have had species-rich flora before they had been abandoned (pers. obs. from a databank supplied by the Botanical Museum of Oulu). The time of abandonment for each meadow was determined by interviewing the landowners. At each site, cover projections of five to twelve circular ($r = 1$ m) sample plots were analysed by recording each plant's cover projection.

The sample plots were located systematically along transects crossing the meadow lengthwise. The starting point of the first line was chosen subjectively from a site regarded as typical of each site. The study sites varied considerably in area from a few square meters to several hectares. The distance between the sample plots was five metres, except in the smallest meadow patches, where it was shortened to three metres. The distance between the transects in a meadow smaller than one hectare was 20 meters, while at sites larger than one hectare it was 40 meters. Vegetation was classified using TWINSpan clustering (Hill 1979), and compositional gradients of the whole data set were investigated using Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) (Ter Braak 1987).

In the second work (II), the data was collected during one season (1995) from two intensively mown and two abandoned meadow patches. The compared adjacent habitat patches were remnants of a larger meadow area, and the differentiated management regimes were responsible for the structure of the vegetation. The physical conditions between the habitats were studied first by an analysis of nutrient concentrations and the thickness of the organic layer within each site. Species inhabiting differently managed sites were categorised using two competing theories for plant strategies, the MacArthur-Fretwell scheme as outlined by Oksanen and Ranta (1992) and the CSR model (Grime 1979, Grime *et al.* 1988). Ordination was performed with the Canonical Correspondence

Analysis (CCA). Additionally, the characteristics of the habitats were considered by categorising the species into woody, herbaceous perennials, annuals and biennials and also into natives, archaeophytes and aliens. Finally, the commonly used diversity measures, such as Simpson and Shannon indices and the evenness index, were calculated for each site.

In the third study (III), mowing was introduced into the Kiiminki Haaraoja meadow, which was a former cattle pasture. After a survey of the overall species composition of two adjacent meadow ridges, thirty-nine permanent quadrats were assigned along the ridges, using stratified random sampling (Økland 1990). Ten quadrats were left unmown (=references), and mowing was started in the remaining 29 quadrats (0.25 m² each). The projection percentage cover of each field and ground layer species occurring in each quadrat was recorded yearly. Field survey and mowing were executed at the same phenological stage each year, vegetation sampling at the end of June, and mowing with scythes in mid- to late August. The study lasted for six years, including the starting year 1993. Temporal changes were tested with repeated-measures analysis of variance (ANOVAR). The expected long-term effects of abandonment and restorative mowing were analysed by calculating the transition probabilities of tall and small herbs and grasses for unmown and mown plots and simulating the course of succession by transition matrix models (e.g. Usher 1987, Calder *et al.* 1992). Finally, the monthly and daily ground surface temperatures of the mown and unmown plots were studied with four temperature data loggers during the summers 1997-98.

2.2 Compensation studies

Grasslands are dominated by monocarpic species, especially annuals, biennials and short-lived perennials that have good ability to recover after shoot damage (Verkaar *et al.* 1986, Paige & Whitham 1987, Reichman & Smith 1991, Paige 1992). They are also particularly suitable for studying life-time fitness of plants (Marquis 1992). Tall wormseed mustard, *Erysimum strictum* P. Gaertn., B. Mey. and Scherb. (Brassicaceae) used in the fourth (IV) paper and field gentian, *Gentianella campestris* ssp. *campestris* (L.), Börner, used in the fifth (V), are biennial herbs. Their seeds germinate in spring and develop into a rosette-stage during the first summer, and flower during the second. *Rhinanthus minor* L. (Scrophulariaceae), used in the fourth (IV) paper is annual, hemiparasitic herb. *Gentianella campestris* is known to have a very good compensatory capacity, including overcompensation in some populations (Lennartsson *et al.* 1997, 1998, Juenger *et al.* submitted). The compensation capacity of *Erysimum strictum* and *Rhinanthus minor* has not been documented earlier. In spite of some differences in their life-history, habitat preference and growth habit I expected that these species provide suitable study objects in order to reveal possible response patterns of monocarpic herbs in semi-natural meadows subjected to various intensities of simulated grazing.

In general, the treatments in the studies IV-V were similar: the chosen target plants were subjected to different clipping levels simulating minor, intermediate and major damage caused by herbivores or mowing. In the clipping treatments, 0% (control), 10%, 50% or 75% of the main stem was removed. Replicates with comparable initial plant

sizes were chosen, and the clipping point in each case was determined by the prevailing height. The control and clipped plants were collected when the fruits were fully ripened, usually after the first frosts. Several direct and indirect performance parameters were measured from the plants, including height, above- and below-ground biomasses, number of branches, nodes and fruits, seed weight and, if possible, number of seeds and unfertilized ovulae per fruit. The degree of compensation was evaluated as undercompensation, exact compensation and overcompensation. According to Belsky (1986), a plant undercompensates when the production of biomass or seeds by clipped plants is smaller than that by unclipped control plants. Correspondingly, equal performance of clipped and unclipped plants indicates full or exact compensation, and clipped plants showing overcompensation perform better than the controls. All the compensation experiments were carried out during the year 1998.

2.3 Study area and species

All study areas, except the one in the paper V, were located in the middle boreal vegetation zone (Ahti *et al.* 1968). The meadows studied in the first paper (I) were situated on the northern coast of the Gulf of Bothnia. The municipality of Keminmaa, from where the material for the second (II) community level paper has been collected, was located in the province of Lapland on the northern coast of Gulf of Bothnia (65°45'N, 24°30'E). The population of *Rhinanthus minor* (IV) and the Finnish population of *Gentianella campestris* (V) were also located in the same area. The other *G. campestris* population studied was located in Björnvad, central Sweden (59°20'N, 16°51'E). The meadows of Keminmaa resemble common bent meadows described by Pålsson (1994), and were dominated by the following grass and herb species: *Achillea millefolium*, *Agrostis capillaris*, *Galium verum*, *Pimpinella saxifraga* and *Poa pratensis*. The hemiboreal meadows of Björnvad, in turn, are characterised by *Avenula pratensis* and *Festuca rubra* and they resemble herb-rich *Agrostis capillaris* meadows (cf. Pålsson, 1994). The meadow of Haaraoja in Kiiminki (III) is located in the province of Oulu (65°10'N, 25°50'E) 100 km south from Keminmaa area. The vegetation resembles *Festuca rubra* - *Bistorta vivipara* and *Geranium sylvaticum* type meadows described by Pålsson (1994).

3 Results

3.1 Succession patterns in northern Finnish meadows

According to the survey carried out in northern Finland (I), particularly the driest and the moistest meadows resemble the previously described vegetation types in northern Finland (cf. Cajander 1909, Teräsvuori 1926, 1927). The results suggested that drought may delay the invasion of tall, broad-leaved species. The results also supported the idea that abandoned meadows of comparable moisture gradients begin to resemble one another in the later stages of succession.

The results on ordination suggested that the succession stage was clearly reflected in the resulting data matrix, while the former management type was not. Because the most abundant species were present in every sample group, more precise categorization of the sample groups was bound to be based on the less abundant indicator species. However, the assessment of the moisture conditions using indicator species was rather unsuccessful. The results also suggested only a weak correlation between age and the dryness of the sample plots. This was probably due to an uneven distribution of dry and moist sample plots in the data set rather than being a real tendency of the succession. It is more likely that soil moisture increases gradually after abandonment, particularly in grasslands of peaty origin.

In general, secondary succession seemed to be considerably slower in dry conditions on sandy substrates than on moister soil types. Mesic meadows are invaded by species with strong vegetative growth, particularly *Deschampsia cespitosa*, a bunch grass that effectively suppresses invasions by less competitive species. *D. cespitosa* was found to be abundantly present in both currently used and abandoned meadows. Thus, when a meadow is left unmanaged, this species has an advantage compared to other mid- to late-successional species, and it increases rapidly along with some other generalist species. Furthermore, the results suggested that *D. cespitosa* is a rather poor indicator of the successional stage of a meadow because it occurs abundantly in both managed and abandoned meadows.

3.2 Effects of mowing and abandonment on grassland communities

Continuous management strongly affected species composition in the Keminmaa meadow patches (II). The plant communities under continuous management consisted of species able to tolerate regular disturbance, in this case mowing. In contrast, the abandoned habitats around the Keminmaa churches included species with variable life-history strategies. The species composition was more variable in unmanaged than in managed meadows, because the managed sites were colonized by a small group of species with similar growth strategies. According to diversity indices, the species diversity was higher in abandoned meadow patches than in managed ones. However, the evenness values of abandoned and managed meadows suggested that the species dominance patterns were quite similar under both management practices.

The proportions of species origin, growth forms and life-history strategies varied between the habitats. Perhaps the most marked difference was seen in the comparison of two plant strategy theories, namely MacArthur-Fretwell's scheme and Grime's (1977, 1979) triangular strategy (CSR) theory. The proportion of grazing-tolerant plants (see Oksanen & Ranta 1992) was found to be larger in managed lawns than in abandoned meadows. Correspondingly, more K strategists inhabited abandoned meadows. Species representing the S and SR strategies (cf. Grime *et al.* 1988) did well on managed sites. The average cover value of ruderal species, which require open patches for regeneration, was low. At mown sites the ground layer was occupied by a thick cover of mosses, whereas at abandoned sites the closed field layer canopy did not allow ruderal species to regenerate.

The six-year study in Kiiminki (III) suggested that mowing late in the season causes only a few changes in grass-dominated meadows. The results showed that the average field cover decreased during the study period, and that the change was parallel in both mown and unmown plots of the meadow. According to matrix simulations, the cover of small herbs is expected to decrease in unmown plots and increase in mown plots, provided that the transition probabilities remain unchanged during the course of succession. Tall herbs are predicted to increase in both unmown and mown plots. During the simulation period of 30 years, the cover of grasses first declined and then remained unchanged in both unmown and mown plots. In all cases, the asymptotic stable distributions of cover classes corresponded well to the actual distributions observed in 1998.

3.3 Effects of simulated grazing on plant growth and reproduction

The experiments with two monocarps, *Erysimum strictum* and *Rhinanthus minor* (IV), suggest that both species tolerate well small damage of shoot apices, while more severe shoot damage tends to have detrimental effects on the performance of both species, especially *R. minor*.

The *Erysimum* individuals that experienced 10% clipping were taller and had more nodes than the control plants. Furthermore, nearly all of the control plants remained unbranched, whereas the 10% clipped plants branched vigorously and produced more

fruits than the controls. The more severely damaged plants also produced more branches than the controls, but they compensated only partially or, at best, exactly in all the other performance parameters. As a whole, clipping delayed the time of flowering and, as a consequence, lowered significantly the estimated fruit maturity. The clipped *Erysimum* plants produced more seeds per plant than the unclipped controls. However, on the basis of a germination experiment, the viability of seeds in the control plants was significantly higher compared to the clipped plants. Thus, the total fecundity, in terms of viable seeds, of the unclipped controls was higher compared to the clipped plants.

A major difference between *R. minor* and *E. strictum* was that the apical damage did not induce any vigorous branching in the former species. *Rhinanthus* also tolerated poorly the highest damage levels. The 50% clipped *Rhinanthus* plants were shorter and produced fewer branches, less above-ground biomass, fewer fruits and lighter seeds than the control plants. *R. minor* was unable to compensate at all for 75% shoot damage; no regrowth was observed and only short stalks with small root stocks were found at the end of the experiment.

In work V, field gentians in the northern population of Keminmaa showed at best exact compensation in response to simulated herbivory, whereas plants in the Swedish population of Björnvd overcompensated in terms of most performance parameters. Shoot damage affected the shoot architecture of *Gentianella campestris* by stimulating branch growth along the main stem. In Björnvd, clipping induced the growth of new branches, especially from the lower stem nodes. The response was most conspicuous after 50% clipping. The highest damage levels (50-75%) also induced the growth of secondary branches. In Keminmaa, only primary branches were produced, and mainly at the upper stem nodes, in both undamaged and damaged plants. The biomass compensation was considerably better among the southern field gentians than in the northern population. In Björnvd, all damage levels induced full or overcompensation. On an average, 10% and 50% clippings increased the above-ground biomass 1.6- and 2.8-fold, respectively, compared to the control plants. Even after the 75% clipping, the plants were able to compensate almost fully for the lost above-ground biomass. In the Keminmaa population, full compensation was achieved after 10% and 50% clippings, but not after 75% clipping. The impact on fruit and seed production in Björnvd was parallel to that on vegetative biomass. Overcompensation in the number of fruits and seeds was found after both 10% and 50% biomass removals. Plant performance showed a strong nonlinear relationship between the damage level and the compensation. In Björnvd, the 10% and 50% damage levels increased the number of fruits 1.7- and 2.3-fold, respectively, as compared to the control plants, whereas 75% biomass removal resulted in exact compensation. In Keminmaa, no overcompensation was observed, and the number of fruits and seeds decreased with increasing damage intensity. Damage levels of 10% and 50% induced full compensation, while the highest damage level of 75% strongly reduced fruit and seed production. The compensatory responses in the number of seeds per plant in relation to damage level showed a quadratic pattern in Björnvd and a decreasing linear pattern in Keminmaa.

4 Discussion

4.1 Static and dynamic aspects of grassland communities

The results of the first paper suggested that some species, including *Deschampsia cespitosa*, may attain secondary succession through an inhibitive pathway (Connell & Slatyer 1977). Succession after abandonment includes continuous litter accumulation and thickening of humus with a concomitant increase in moisture retention. Eventually, the change in moisture conditions leads to an increase in primary production and promotes slow, but steadily, changes in vegetation composition, even in the driest types of meadow. Litter accumulation, on the other hand, prevents seedling establishment effectively (Facelli & Facelli 1993). A dense litter layer also reduces the solar radiation reaching the ground surface and decreases the temperature fluctuation during the growing season (Huhta, unpublished data), and hence affects the seed germination conditions and seedling recruitment in the long run.

After abandonment, the invasion rate of late seral species, particularly tall and broad-leaved herbs, varies greatly, depending on the latest type of management. However, tall herbs may occur scarcely also in regularly managed meadows (cf. Calder *et al.* 1992). Later in succession, their competitive dominance reduces the abundance of low-growing, grazing-tolerant species. Ultimately, this leads to a reduction in vegetation stratification. The most recent manner of management is an important determinant of vegetation development during the first years of secondary succession.

According to the Keminmaa case study (II), diversity measures and determination of the proportions of plants representing different life-history strategies help to evaluate the stage of succession of a meadow (cf. Brown & Southwood 1987) and thus to facilitate decision-making as to whether and when management practices should be initiated.

The results of the Kiiminki follow-up study (III) show that the proportion of tussocky, intermediate-sized grasses is expected to decrease both after abandonment and during late mowing. This is contrary to the prediction that grasses, particularly mesomorphic and tough-leaved xeromorphic grass species, should increase due to consumption at the expense of other growth forms (cf. Owen 1980, Oksanen & Ranta 1992). The results are in accordance with Tamm (1956), who observed that mowing favours herbs - commonly

small or intermediate in size - at the expense of grasses. It seems that mowing does not, at least at the beginning of restoration, have a similar impact on grasses as grazing would have. The reason is that grazing and trampling create regeneration patches more effectively than mowing. In general, grasses are able to overcome intense mowing due to their extensive rhizome systems. For the same reason, grasses also remain abundant during free succession (Stampfli & Zeiter 1999). In contrast, tall herbs suffer, almost without exception, from mowing (Mitchley & Willems 1995). According to the Kiiminki study (III), however, mowing late in the season is not necessarily detrimental for them, either.

Matrix simulations (III) showed somewhat different long-term trends of vegetational change than was expected on the basis of the observed short-term changes. Small herbs are expected to decrease in unmown plots and tall herbs are expected to increase in both unmown and mown plots, although tall herbs tend to be more abundant in unmown plots. Furthermore, tussocky grasses are expected first to decrease and then to remain quite stable in both unmown and mown plots. The overall results of this simulation study are in agreement with a number of grassland succession studies (e.g. Keever 1950, Egler 1952, Pickett 1982, Thalen *et al.* 1987, Ward & Jennings 1990, Belsky 1992, Mitchley & Willems 1995). It is generally expected that the cover of tall herbs will slowly increase in unmown plots, suppressing the small, herbaceous plant species, but they cannot completely conquer the space from grasses. The slight increase of tall herbs in mown plots indicates that one particular tall herb, *Geranium sylvaticum*, is able to remain well represented even in mown plots when mowing occurs late in the season. According to the results of the simulation experiment, the mown plots seemed to be in a sub-climax stage (*sensu* Tansley 1935). None of the plant groups mentioned above are expected to dominate regularly mown stands alone. As a result, a late-mown meadow may remain physiognomically unchanged for decades. This is in accordance with the findings of the first work (I) of this thesis. Species representing various growth forms and showing different successional preferences are able to coexist in a regularly mown meadow (cf. Losvik 1988, Eriksson *et al.* 1995). Mowing is a precondition for the existence and preservation of species-rich grassland habitats, although the enrichment of a grassland community may take a considerably long time (Gibson & Brown 1992). However, the discovered similar short-term changes in both mown and unmown plots were rather surprising. It seems that the short-term changes in vegetation cover in recently abandoned grass-dominated meadows are governed rather by abiotic factors, e.g. the yearly variation in precipitation and thermal sum, than by differences in the type of management. As a visible result, no rapid changes due to overgrowing will take place within the first few years after abandonment.

According to Austin (1977), the interest in successional studies focuses on changes in species composition: “whether recognizable groups persist at a site over time or change, and whether different sites show similar behaviour through time“. Briefly, there are two ways of studying succession, static and dynamic. The static way means that trends are determined by making a cross-sectional analysis of the prevailing condition of a particular habitat and comparing it to the existing knowledge of the successional stages of the area. This ergodic hypothesis (*sensu* Gleason 1927) is based on the assumption that the spatial variation between different-aged habitats is equivalent to the temporal changes at one site (Gibson & Brown 1992). In contrast, the dynamic manner of studying

succession is based on consecutive observations of one site. The former method was applied in the coastal northern Finland and Keminmaa field studies (I-II) and the latter in the Kiiminki study (III). It was expected that the dynamic way of studying changes in meadow vegetation would yield considerably more abundant and more precise information about the development of vegetation in relation to the modes of management compared to the static studies. However, substantially more time and effort were invested in the Kiiminki study compared to the survey studies of northern coastal Finland and Keminmaa. Further, because the *in situ* vegetation responses observed in Kiiminki were smaller than expected, the benefits gained did not fully satisfy the expectations applied to the dynamic method. Thus, the static method has obvious advantages: it is quick to carry out, simple and quite reliable. Static, survey-type research on conservation ecology is still truly needed along with dynamic, experimental studies.

4.2 Tolerance of grassland herbs to simulated grazing

Lately, it has been widely debated whether plant compensation ability can be considered an adaptive response to herbivory. The question is closely connected to the dilemma of whether herbivory is always detrimental for plants or whether there may also be some beneficial effects. Several studies have presented results suggesting that some plant species have notably good regrowth abilities, even to an extent that grazed or artificially damaged individuals produce a greater biomass and have higher fecundity than undamaged control plants. Paige and Whitham (1987) found that a monocarpic herb, scarlet gilia, *Ipomopsis aggregata* (Polemoniaceae), is able to overcompensate, i.e. to produce more vegetative and reproductive biomass compared to ungrazed plants as a response to herbivory. Later, however, their findings have been questioned (Bergelson & Crawley 1992a, b, Belsky *et al.* 1993), and the questions of whether overcompensation really exists as an adaptive trait and whether herbivory may, in some cases, be beneficial for plants are still debated intensively (Tuomi *et al.* 1994, Bergelson *et al.* 1996, Järemo *et al.* 1996, Nilsson *et al.* 1996, Paige 1999, Agrawal 2000, Juenger & Bergelson 1997, 2000). One of the reasons for the dispute is that overcompensation has often been demonstrated in conditions with not much competition and a surplus of nutrients and water (Belsky 1987, Benner 1988, Maschinski & Whitham 1989). Moreover, overcompensation has only occurred as a response to seasonally limited herbivory (Crawley 1997), even though, in theory, overcompensation may be possible even when a plant is repeatedly damaged (Nilsson *et al.* 1996). Recently, Lennartsson *et al.* (1997, 1998) suggested that the capacity of field gentian (*Gentianella campestris*) for overcompensation is likely to be an adaptive trait with an evolutionary history related to habitats with a high and predictable risk of damage.

The ability of a plant to maintain its fecundity after damage depends on its ability to rebuild the lost vegetative and reproductive structures and biomass. The outcome of this may not be identical to the plant's initial appearance. This is where the maintenance or, alternatively, disruption of apical dominance becomes crucial. If the plant branches vigorously after stem damage (i.e. the apical dominance is broken), it may lose the advertising power of the flowers, particularly in highly competitive environments. On the

other hand, if the plant does not branch and tries to maintain its initial single-stem growth form, it does not have much of a chance to compensate for the damage in terms of fecundity. The fourth paper (IV) focused on the regrowth responses of two monocarpic herbs, *Erysimum strictum* and *Rhinanthus minor*, to simulated grazing. According to the results, *Erysimum strictum* performed better than *Rhinanthus* when the plants were clipped. The reason for this may lie in the differing habitat preferences of the species. *Erysimum* prefers open and half-open vegetation stands, and the cost of apical dominance may therefore be higher (i.e. branching would be more profitable than being unbranched, cf. Aarssen 1995) contrary to the hemiparasitic *Rhinanthus minor*, which prefers denser vegetation with many potential hosts (van Hulst *et al.* 1987). However, the sward surrounding *Rhinanthus* should not be so tall as to prevent successful presentation of flowers, a demand which is best fulfilled in managed short-grass meadows. Despite the fact that the apical damage (10%) on *Erysimum* resulted in only a slight delay in flowering, the germination ability of seeds was low compared to undamaged controls. This suggests that clipping-induced changes in plant performance are utterly detrimental in spite of the increase in total seed production. Whether this is an indication of a failure in pollination or of some other, as yet unknown, factor remains to be studied. In a common garden experiment, *Erysimum* overcompensated for apical damage (10% clipping) with no difference in the germination success of unclipped and clipped plants, when the seeds were cold-treated at -20°C (Huhta *et al.*, in press). Consequently, no final conclusions can be drawn about the effects of clipping on the seed viability of *Erysimum*.

According to the fifth paper (V), field gentians in the northern population of Keminmaa compensated fully as a response to simulated herbivory, whereas plants in the southern population of Björnvad overcompensated in most aspects of measured performance. In general, the compensatory responses of *G. campestris* in relation to the degree of damage showed parallel patterns in both populations. Plant performance was reduced at the highest damage level compared to the intermediate damage level (Björnvad) or to unclipped controls (Keminmaa). In Björnvad, furthermore, the intermediate damage level induced higher compensatory growth than the lowest level of damage. The linearly decreasing compensation response of the Keminmaa population to an increasing level of damage is consistent with the general view that herbivory is, without exception, detrimental to plants (e.g. Belsky 1986, Bergelson & Crawley 1992a, Belsky *et al.* 1993, Bergelson *et al.* 1996, Crawley 1997). In contrast, the compensation response of Björnvad plants was strongly nonlinear, resulting in overcompensation both in vegetative and fecundity performance. This suggests that herbivory or other induced damage may sometimes improve the reproductive performance of grassland plants.

The compensation responses of grassland plants in relation to damage intensity seem to be highly species- and population-specific. Presumably, 50% cutting represents an optimal level for *G. campestris* populations originating from habitats with sustained grazing and/or mowing. The particular cutting intensity for this species leaves a sufficient number of meristems and photosynthetic tissue intact for regrowth but, on the other hand, is efficient enough to remove apical dominance and trigger compensatory growth (V). A prerequisite for overcompensation is that, after the damaging event, regardless whether it was caused by mowing or grazing, the injured main stalk is replaced by several side-stalks or branches, and none of the stems gains advantage over the others. The situation reminds us of the story of the battle between Hercules and Hydra, where Hercules' sword

does not kill the beast, but instead several new heads grow to replace the lost one, making the beast or in this case the plant - even more vigorous (cf. Graves 1980). Branching may therefore be a visible morphological sign of compensatory capacity. Architectural changes will be further reflected in the vegetative and reproductive performance, depending on the fate of the activated meristems (Geber 1990). Fecundity may correlate with architecture (e.g. Preston 1998), provided that the activated meristems produce flowers or inflorescences, and that there are sufficient resources to support the development and maturation of seeds. Obviously, low- and intermediate-level damage did not cause any serious source limitation among the plants used in the Björnvad population of *G. campestris*, and both fruit and seed production occasionally even increased following clipping.

4.3 Mowing and grazing in grassland restoration

The damage caused by mowing, in particular, affects equally all species with similar architecture and the same phenological state. However, some species are able to replace the lost biomass more quickly and thus suffer relatively less than the others. In Finnish managed grasslands, the losers are typically tall competitors for light, often perennial forest species with a wide ecological amplitude. Tall perennials and tree saplings invade meadow vegetation during irregular or temporary breaks in management. Even if these competitors and/or stress tolerators could compensate for lost tissue by, for instance, postponing their reproductive effort to the following year, the difference compared to species able to tolerate regular tissue losses and to respond to damage within the ongoing growth period is sufficient to maintain the dominance of true grassland species (cf. Owen & Wiegert 1981, Tolvanen *et al.* 1992, 1994, Wegener & Odasz 1997). Thus, species with a good compensatory capacity indirectly gain from being injured, provided that other species within the community are simultaneously also damaged. When management discontinues, this slight advantage in favour of meadow species disappears and typical meadow species are replaced by ones representing later seral stages.

The situation in regularly mown grasslands is not completely analogous to grazed ones. Mowing affects all species beyond certain height, and only a few species with low-creeping shoots or rosettes pressed tightly against the ground avoid damage (Losvik 1988). Moreover, some plants may escape damage by flowering and setting seed before or after mowing has taken place (Lennartsson *et al.* 1997, Crawley 1997). However, grazing and mowing also have many parallel effects on grassland vegetation. The greatest differences appear in their effects on the patchiness of vegetation and the properties of soil. The effects of grazing and different types of mowing on certain community characteristics are shown as summarized from a number of references in Table 1.

Table 1. Effects of grazing and early- and late mowing on grassland vegetation

Parameter	Grazing	Mowing and raking	References
Stature	Unevenly degrading	Early: evenly and strongly degrading Late: evenly degrading	Tamm 1956, Andersen <i>et al.</i> 1990, Bakker & de Vries 1992
Shoot density	Stimulating	Stimulating	Valentine <i>et al.</i> 1997
Biomass production	Highly stimulating	Early: stimulating Late: stimulating (up to certain threshold)	Prins <i>et al.</i> 1980, McNaughton 1984, 1986a, Westoby 1989, Hik & Jefferies 1990, Cargill & Jefferies 1984,
Species diversity	Increasing	Early: increasing or decreasing	During & Willems 1984, van Andel & van der Bergh 1987, Losvik 1991, Belsky 1992, Eriksson <i>et al.</i> 1995, Zobel <i>et al.</i> 1996, Gusewell <i>et al.</i> 1998, Linusson <i>et al.</i> 1998, Stampfli & Zeiter 1999, Smith <i>et al.</i> 2000
Colonization of new species	Stimulating	Moderately stimulating	Hertz 1934, Willems 1983, Milchunas <i>et al.</i> 1992, Gibson <i>et al.</i> 1993, Diaz <i>et al.</i> 1994, Stampfli & Zeiter 1999
Litter layer	Scatteredly decreasing with increasing light and radiation	Early: decreasing with evenly increasing light and radiation Late: moderately decreasing with evenly increasing light and radiation	Facelli & Facelli 1993, Carson & Peterson 1990, Humphrey & Patterson 2000
Patchiness	Highly stimulating	Moderately stimulating	Rodriquez <i>et al.</i> 1995, Malkamäki & Hæggröm 1997
Soil porosity	Highly compacting	Compacting or indifferent	Malkamäki & Hæggröm 1997
Soil nutrient level	Stabilizing or increasing	Early: decreasing Late: slowly decreasing or stabilizing	McNaughton 1979, Spatz 1980, van Duuren <i>et al.</i> 1981, Bakker 1987, Pegtel 1987, van Andel & van der Bergh 1987, Parr & Way 1988, Oomes 1990, Mathews <i>et al.</i> 1994, Pettit <i>et al.</i> 1995

Tamm (1956) already noticed that some species were common in regularly mown areas, but rare or absent in grazed ones. Furthermore, certain species seemed to favour grazed pastures and occurred scarcely also in mown meadows. According to Tamm (1956), the vegetation sward is shorter in mown meadows and more clearly dominated by herbaceous species, although grasses are also common. Mown and grazed grasslands differ physiognomically. Depending on the intensity of grazing, the vegetation in grazed areas is typically patchy. In mown meadows, the vegetation sward is more uniform (Table 1), even though the species composition between the two may not differ greatly. A similar situation seems to prevail between the mown and abandoned meadows studied here. Particularly grass-dominated meadows seem to remain quite unchanged for a long time.

The most essential difference between mowing and grazing is seen in the frequency and intensity of disturbance (i.e. removal of plant biomass, Grime 1977, 1979). Mowing causes high-intensity disturbance with a low frequency. In contrast, the vegetation in a grazed meadow is exposed to low-intensity and high-frequency disturbance (During & Willems 1984). Unlike mowing, grazing is often selective (Arnthórsdóttir 1994), and certain species are favoured and some avoided by grazers. Grazing favours rosette plants and prostrate growth forms, which leads to the development of dense field and bottom layers. Mowing, on the other hand, favours late-flowering, non-rosette plants and prostrate herbs. The height of the vegetation sward is lower in grazed pastures than in mown meadows (Table 1). Thus, light penetration is greater in pastures than in mown meadows, not to mention abandoned ones. The number of emerging seedlings is greater in grazed than in mown meadows (cf. Losvik 1988, Lennartsson 1997), although many seedlings die due to trampling at early stages. When grazing is replaced by mowing, the multi-layered vertical stratification usually decreases (Losvik 1988, but see Roxburgh *et al.* 1993). According to Losvik (1988), the numbers of short-lived perennials, rosette plants and creeping growth forms diminish because openings are no longer created by grazing and trampling. Finally, they are replaced by more erect species that are less affected by mowing than grazing.

Traditionally, semi-natural meadows were used for mowing and aftermath grazing (Ekstam *et al.* 1988). At present, mowing is more often replaced by grazing than vice versa. In most semi-natural grasslands, it is mowing rather than grazing that has ceased, and these areas are used - if at all - for incidental cattle grazing. Furthermore, they are often only slightly grazed (cf. Vainio & Kekäläinen 1997, Schaminée & Meertens 1992). Unfortunately, there is no data available from the Kiiminki meadow (III) immediately after the management ceased, but only seven years after the abandonment. Therefore, the question of whether mowing alone is enough to replace grazing in this particular case remains open. The seven years before restorative mowing was started may have been enough to cause profound changes in species abundance. Particularly the species that have only a short-term seed bank may have disappeared (O'Connor 1991).

Mowing and grazing also have different impacts on the soil nutrient status (Table 1). Mowing leads to a continuous nutrient loss and even depletion in poor soils (Tamm 1956), whereas in rich soils it may take decades before the soil nutrient status is markedly affected (Berendse *et al.* 1992). If the total nutrient pool in soil is only reduced by 5 % annually, the change does not have any far-reaching effects on the long-term nutrient status, nor is it reflected in the species composition (Pegtel 1987). In contrast to mowing, grazing causes part of the nutrients to be recycled back into soil (Mathews *et al.* 1994). However, intense grazing may erode the humus layer, especially in dry stands (Tamm 1956). Soil fertility may affect both the productivity and the diversity of species in grasslands. Generally, it is assumed that the productivity of grassland communities correlates negatively with species diversity (Silvertown 1980, Bakker 1987). This relationship is not, however, unambiguous. According to Bakker and de Vries (1992), even when the standing crop is equal in both mown and grazed areas, the species diversity is greater in grazed ones. During and Willems (1984) point out that the differences between grazing and mowing become clearer towards higher productivity. Mowing at different times during the growing season results in different amounts of yield, but it also has various effects on the reproduction of different species. Moreover, according to Oomes

(1992), one cannot make very far-reaching conclusions about structurally different vegetation types merely by considering production. However, there is consensus among researchers that mowing and grazing lead to an increase in the number of species in abandoned meadows (During & Willems 1984, Gibson *et al.* 1987). Mowing and particularly grazing create gaps in the vegetation, which is a prerequisite for a great number of species (Pegtel 1987, Lennartsson 1997). According to Bakker (1987), particularly grazing changes the competitive relations in grasslands, which leads to an increased number of species. In contrast, in meadows with a long mowing history, competition for below-ground resources may be more important. According to Vinther (1983), a certain grazing intensity enables the development of a “floristic optimum“, i.e. the maximum number of species that can coexist in a given place. A decrease or increase in grazing intensity causes a decline in the number of species. Thus, it could be claimed that mowing, in habitats where it maintains a high level of diversity and is a “normal component“ of the environment, is not a “negative disturbance factor“ at all (Kull & Zobel 1991).

4.4 Mowing and grazing as selective forces in grasslands

In general, mowing and grazing serve as significant selective factors in grasslands (Fig. 1). Despite their great impact on shaping plant communities, they also strongly influence evolution in plant populations. Many species include subspecies and forms (e.g. seasonal forms) that are adaptations to herbivory or mowing (Zopfi 1993, 1998). For example, van Tienderen and van der Toorn (1991) observed that *Plantago lanceolata* produced a large number of small spikes in grazed grassland to diminish the possibility that all spikes are eaten at once, whereas plants in a mown meadow produced more seeds per spike. In general, many of these adaptations depend on the phenotypic plasticity of plant species (cf. van Tienderen 1990). However, there are documented cases where genetically based differentiation among populations has also occurred in response to different management practices (Till-Bottraud *et al.* 1990). Thus, it seems plausible that the major cultural impacts, grazing by domesticated animals and mowing for winter forage, have affected meadows long enough to give rise to genetically based adaptations in plant species.

According to Edwards and Gillman (1987), under a particular regime of herbivory, some plant genotypes may be favoured over the others, and a change in the regime may sometimes alter very quickly the genetic composition of a plant population. If none of the individuals within a plant population turn out to be tolerant, the plant species will disappear from the community. Hence, in most communities the plant species present and the genetic composition of their populations are, to some extent, products of past herbivory. In stable conditions, the relative abundance of plant species and the genetic make-up of their populations reflect an approximate equilibrium between all the various selective pressures, including herbivory (Edwards & Gillman 1987). Despite the fact that mowing has, from the evolutionary point of view, been carried out only for a short time, there is reason to believe that mowing also acts as a selective force, causing genetically based changes in plant species and, thus, in population structure.

It may also be postulated that some selective factors, in addition to grazing and mowing, may have affected the development of the plant response to damage. In addition to various biotic, community level factors, abiotic ones such as, temperature and water and nutrient availability, influence the plant responses to herbivory (Fig. 1). It is therefore also possible that, at least to some extent, the responses of grassland plants to grazing and mowing may be mere by-products of selective forces other than the cultural impact. According to Andersson and Appelqvist (1991), biotopes that resemble forest pastures, wooded meadows and pastured shrub- and woodlands, have actually existed for millions of years in the boreonemoral zone. Thus, human activities may have only restored and expanded these habitats and helped grassland species by expanding their distribution to human-influenced habitats. However, it has to be admitted that, in the boreal vegetation zone, ungulate herbivores have had less pronounced effects on vegetation, although they may have played a role as breakers of succession. Only a few of the organisms in the boreal zone have adapted exclusively to open, grazed habitats. Instead, many the species have adapted to stages of secondary succession after forest fires (Andersson & Appelqvist 1991).

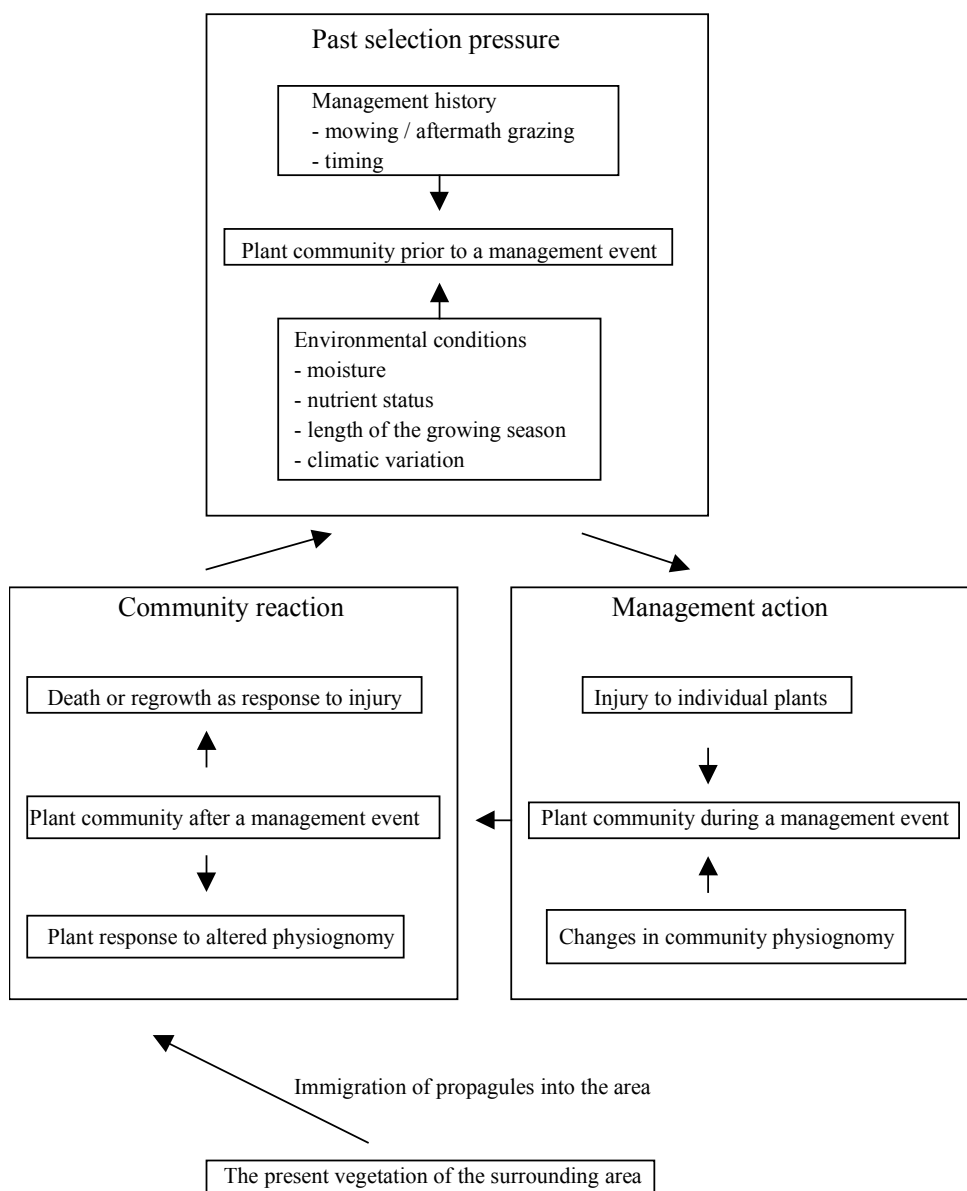


Fig. 1. Illustration of the forces and responses shaping semi-natural grasslands. The impact of mowing / grazing may be a mixture of strong and weak effects, depending on the location of the community on an environmental gradient and on the evolutionary history of the mode of management. Modified from Milchunas et al. (1988) and van Hulst (1992).

5 Conclusions

Herbivory and mowing reduce plant performance by removing various amounts of plant tissue. This may lead to the death of an individual or, as is more often the case, to a change in its resource allocation, rate of photosynthesis, morphology and reproduction. At the population level, it is appropriate to ask how the removal of plant tissue, whether through mowing or herbivory by ungulate grazers, affects the abundance and distribution of the species. At the community level, mowing- or grazing-mediated damage affects species composition through the relative competitive abilities of plant species. The negative impact of damage on some species may provide competitive advantage to others.

With restoration, ecosystem-oriented ecologists may attempt to reach a certain level of productivity or species diversity, whereas population ecologists may rather be interested in restoring a given threatened species by preserving favourable habitats (Werner 1987). From a manager's point of view, the abundance of species with different origins, life-history strategies or, perhaps most significantly, compensatory abilities may be used as an indicator of the condition of a grassland community. However, the herbivory- or mowing-mediated changes in a community take a considerably long time and are, due to their complex environmental effects, difficult to predict. Late mowing provides a way to maintain the existing vegetation. The goal of late mowing is thus to eliminate tall herbs and woody growth forms and to keep them away from the area. Compared to early mowing, late mowing allows not only the species to set seed, but also the perennial species to allocate nutrients to their below-ground reserves. Therefore, the effect of late mowing centers on removing the senescent plant material and preventing litter accumulation. This is enough to preserve grassland in a *status quo*, but not enough to accomplish any major short-term changes in community composition. Early mowing may well produce a different response than late mowing, because the flowering and seed-setting of late successional species are delayed or even prevented. This restorative management is likely to have more profound effects on productivity and species composition.

Finally, it must be realized that re-introduction of traditional ways of management is not enough to restore the former species richness in grasslands. If the process of abandonment takes place simultaneously in a large geographical area, such as Finland, the species may not recolonize restored meadows simply because there is not a sufficient

species pool from where propagules could spread (Pärtel *et al.* 1998), or because the distances between populations are too long to allow effective dispersal (Hanski 1999).

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