VARIATION IN GRAZING TOLERANCE AND RESTORATION OF MEADOW PLANT COMMUNITIES

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Abstract

The area of traditionally managed semi-natural meadows is declining throughout Europe. Knowledge of how to restore their species richness is urgently needed. Community manipulations by means of grazing and mowing and, on the other hand, knowledge of species-level responses as well as the responses of functional plant groups to management may help in planning appropriate restoration tools.

The restoration of species richness was studied in two community-level experiments: in a sheep grazing experiment and in a mowing experiment. Three species-level studies were conducted to test the compensatory capacity of monocarpic, herbaceous plants (Gentianella amarella, Erysimum strictum, Euphrasia stricta) to simulated herbivory (10–50% of stem being cut). The perennial Linaria vulgaris was used to study whether there is any benefit of clonal integration in the tolerance of simulated herbivory. This topic was studied in a growth experiment and a 13C tracer study.

In both grazing and mowing experiments, small herbs gained more space, while the dominant tall herbs subsided. The species number increased by 30% on the grazed plots, but mowing did not affect species richness, probably indicating seed limitation. At sites of this kind, seed addition could be used to promote restoration. Functional plant groups appeared to be useful in predicting the effects of grazing on plant communities. Early season grazing and mowing seem to be proper management tools in overgrown/degraded meadows. In species-level studies, all the species had relatively good compensatory capacity to repair small damage. Overcompensation was observed in response to apical damage, especially when the growing conditions were favourable, supporting the compensatory continuum hypothesis. The studied monocarpic plant species may share a common unbranched growth form where incidental apical damage leads to activation of uninitialized meristems and slight overcompensation. These responses may represent consequences of adaptation to above-ground competition, rather than adaptation to predictable herbivory. In Linaria, damaged ramets were not supported, but the neighbouring ramets seemed to compete with each other for root resources. While growing in disturbed habitats, it is more profitable for this species to invest in new ramets.

The present studies showed that, while the appearance and structure of a traditional grassland rich in small-growing herbs can be restored in five years, it is more difficult to increase species diversity by mere mowing or grazing. Knowledge of the tolerance of individual species for herbivory could provide useful information for planning management practices. More studies on the effects of different management tools on different meadow types are urgently needed for the maintenance of the diversity of these valuable environments.

Keywords: compensatory continuum, functional plant groups, herbivory, management, monocarpic species, mowing, restoration, semi-natural meadows, species diversity
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Tiivistelmä


Tämä työ osoitti, että vaikka perinteisen matalakasvuisen lajirikkoon niittyön ulkonäkö ja rakenteen voidaan palauttaa viidessä vuodessa, on vaikeampaa lisätä lajirikkautta pelkän niiton tai laidunnuksen avulla. Tietämässä yksittäisten kasvillehjen vasteista biomassaan menetykseen voi auttaa sopivien hoitojärjestelmien suunnittelussa. Lisää kokeita eri hoitojartojen vaikutuksista ja eri niittityyppeillä tarvitaan pikaisesti näiden arvokaiden elinympäristöjen monimuotoisuuden ylläpitämiseksi.

Asiasanat: herbbioria, kompensaatiokasvu, lajirikkauks, luonnonniityt, monokarppiset lajit, niitto, toiminnalliset kasvyyhteisöt
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Oulu, October 2004

Kalle Hellström
List of original papers

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


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1 Introduction

1.1 Background of meadow restoration

Semi-natural meadows are one of the most species-rich habitats in Europe. Up to 70 vascular plant species may grow in a square metre in an Estonian wooded meadow (Kull & Zobel 1991) or in the meadows of the Carpathian Mountains in the Czech Republic (Klimeš et al. 2000). In Finland, where calcareous meadows are rare, the reported maximum species richness is 46 species per m² (Pykälä 2001). Traditional grazing and mowing have created conditions that promote coexistence of many plant species by reducing interspecific competition. Moderate grazing has been shown to increase species diversity in mesotrophic and eutrophic soil conditions (Bakker 1998).

Unploughed, unfertilised semi-natural meadows formed the basis for traditional agriculture. In northern Europe, hay collected from these meadows enabled cattle to survive over the winter (Vainio et al. 2001). In Finland, the area of semi-natural meadows reached a maximum of 1.6 million hectares in the 1880’s (Soininen 1974). Due to the intensification of agriculture during the past decades, the area of semi-natural meadows has decreased in many European countries, including Britain (Gibson et al. 1987), The Netherlands (Berendse et al. 1992), Switzerland (Stampfli & Zeiter 1999) and Sweden (Eriksson et al. 1995). In Finland, only 18 690 hectares of meadows were found in a national inventory in the 1990s (Salminen & Kekäläinen 2000). Of this area, 56% was still grazed, but only 2% was continuously mown (Vainio et al. 2001). After the inventory in the 1990’s, management has been restarted in several areas. Only 20% of the valuable semi-natural meadows were within the special farming subsidy system. On the other hand, additional 11 470 hectares of grasslands, which were not valued in the inventory, got this subsidy in the late 1990’s (Salminen & Kekäläinen 2000). The ambitious aim is to get 60 000 hectares of semi-natural grasslands into management by 2010. This is a big challenge, as another 40 000 hectares of new semi-natural meadows need to be restored (Salminen & Kekäläinen 2000). The present area of semi-natural meadows is much larger in many European countries than in Finland. For instance, in Great Britain and Ireland it is at least 25-fold, in Germany and Hungary 10-fold and in Sweden 7-fold compared to Finland (Salminen & Kekäläinen 2000). However, the original area of semi-natural
grasslands also seems to have been larger in these countries than in Finland. In Finland, many restoration experiments were started in the 1990’s, and knowledge of semi-natural grassland management is gradually accumulating (Kotiluoto 1998, Jutila 1999, Huhta 2001, Tikka 2001, Jantunen 2003, Pykälä 2003).

Management of semi-natural meadows is important for the preservation of the rich flora and fauna associated with these habitats. As many as half of the vascular plant taxa have been estimated to have benefited from grazing and mowing in Finland (Salminen & Kekäläinen 2000). In the Finnish red listing of 2000, 28% of endangered taxa live in different cultural habitats (Anon. 2001). In addition to conservation of biodiversity, management of meadows is essential for preserving the traditional open landscape, living countryside, cultural history and related traditions, and that they can serve as a source of recreation and sites for education and tourism. We also have international responsibility for the conservation of certain species and habitats (Salminen & Kekäläinen 2000).

1.2 Grazing and mowing as enhancers of species richness in meadows

Grazing is commonly used in restoring species richness in overgrown meadows and areas previously in agricultural use. The effectiveness of reintroduced grazing in increasing species richness depends on the characteristics of each particular community. In western Europe, good results have been achieved by sheep grazing (Gibson et al. 1987, Willems 1983, Bakker 1998). Similarly, tree cutting and sheep grazing were sufficient practices to increase the number of species in an abandoned alvar grassland because target species could spread to the restored area from nearby preserved meadows (Pärtel et al. 1998). In more nutrient-rich areas, on clay soil in England (Snow et al. 1997) as well as in wooded meadows in SW Finland (Kotiluoto 1998), mowing may be needed in addition to grazing. Mowing has been established as an effective tool to increase species richness in dry and mesic meadows (Willems 1983, Fenner & Palmer 1998, Klimeš et al. 2000, Wahlman & Milberg 2002).

Even though reintroduced management often yields good results in restoration, the change may sometimes remain small due to various reasons. Restoration practices may be ineffective in increasing species richness if the local species pool is limited (cf., Treweek et al. 1997, Stampfl & Zeiter 1999, Huhta et al. 2001), or if the seed bank does not contain suitable species (Treweek et al. 1997, Bakker & Berendse 1999, Rosef 2004). Nowadays, mowing is used as an alternative to grazing. In Finland, for instance, mowing may be sometimes easier to organise than grazing because of the lack of grazing cattle in many areas. Traditionally, mowing and grazing were used as complementary management tools. The meadows were mown in late July or early August, and animals were allowed to graze the aftermath for some weeks in August-September (Salminen & Kekäläinen 2000). Other management tools, such as burning or mechanical/chemical removal of woody plants, have been ineffective to preserve the species richness and composition of meadows (Hansson & Fogelfors 2000, Wahlman & Milberg 2002).
1.3 Competition, stress and disturbance

Knowledge of the responses of different functional plant groups, i.e., plants with similar strategies, to grazing may be useful in planning restoration practices on an overgrown meadow. Moderate grazing may affect plant diversity positively, as it prevents competitively superior species from gaining dominance over the weaker ones (Grime 1973, Al-Mufti et al. 1977). Interspecific competition may also be altered because grazers often select their food by eating first the most palatable species (Daubenmire 1968). Several species responses on semi-natural meadows can be understood in the context of the C-S-R-model of plant strategies presented by J. Philip Grime (1977).

According to this model, species can be grouped on the grounds of how well they tolerate stress and disturbance (Fig. 1a). Grazing is considered to cause low-intensity but high-frequency disturbance in vegetation. Ruderals (R-strategy) are species that can withstand frequent and severe disturbance. They are typically annuals or small and fast-growing species with good dispersal ability. Dry meadows are usually inhabited by stress tolerators (S-strategy), which are able to withstand drought and shortage of nutrients. They are slow-growing plants with tough and small leaves that are often highly defended. They may, however, have a poorer capacity to compensate for lost biomass than R-strategists, which are adapted to more nutrient-rich habitats. C-strategists are tall-growing and broad-leaved species that benefit from lack of management. They are well able to compete for light and nutrients, but they are not able to tolerate regular disturbance, such as grazing or mowing (Grime 1977). Therefore, their abundance is expected to decrease when management is reintroduced after abandonment.

Many common meadow species follow the general C-S-R strategy or some of the intermediate strategies: S-R, C-R or S-C strategy (Grime et al. 1988). They have optimal growing conditions in habitats where moderate intensities of disturbance and stress reduce competition, e.g., on unfertilised pastures and meadows (Grime 1977). A model related to the C-S-R strategies is the hump-back model of management intensity proposed by Grime (1973). This model has also been referred to as the intermediate disturbance hypothesis, as it predicts that species diversity will be highest at intermediate levels of management, such as grazing, mowing, burning or trampling. The hypothesis assumes that when productivity is sufficiently high, competitive exclusion will decrease the number of coexisting species at low disturbance levels. Accordingly, at very high disturbance levels, only a small number of ruderal species are able to tolerate such high damage levels (Grime 1973).

Oksanen & Ranta (1992) have proposed an alternative theory to Grime’s triangle of C-S-R strategies. This MacArthur-Fretwell (MAF) scheme is based on MacArthur’s (1972) view of competition and uses his theory on $r$- and $K$-selection. Herbivory is also included in the model in the way introduced by Fretwell (1977). In the MAF scheme, the viable plant strategies are defined by the intensity and frequency of disturbance (Fig. 1b). Low frequency and low intensity of disturbance imply $K$-selection (corresponding to Grime’s C-strategy). Low frequency and high intensity elicit $r$-selection (cf., R-strategy by Grime), while high frequency and low intensity lead to $g$-selection. The latter type of disturbance is caused by selective nibbling by small grazers, for example, and it favours plants that roughly correspond to Grime’s (1977) S-strategists (Oksanen & Ranta 1992).
Another alternative model to Grime’s C-S-R model is the resource ratio hypothesis presented by Tilman (1980). Its main difference compared to Grime’s concept of C-strategy concerns the way plants achieve competitive superiority. Tilman assumes that plants requiring the lowest resource level will win in competition, and that competitive ability is highly dependent on the resources limiting plant growth in a given environment. For the debate that arose, see e.g., Thompson 1987, Tilman 1987, Grace 1991, Wilson & Lee 2000. Furthermore, Taylor and co-authors (1990) presented a model where plants may have four extreme strategies. In this habitat template model of quadrangular space, the axes are defined by $r/K$ selection and, on the other hand, by selection induced by impoverished environmental resources.

To conclude, Grime’s model may well be an oversimplification and difficult to test empirically, but it is still a highly useful theory for community ecology (Wilson & Lee 2000), while both the C-S-R model and the alternative models are usable in restoration studies (e.g., Huhta & Rautio 1998). In the present experiment, I mainly utilised the original C-S-R model.

Fig. 1. The viable plant strategies according to a) Grime’s C-S-R model and b) the MacArthur-Fretwell (MAF) scheme. In the C-S-R model, the intensity of stress and disturbance determine the plant strategies. In the MAF scheme, the strategies are determined by the intensity and frequency of disturbance.

### 1.4 Life-history traits and species responses to management

The use of plant functional traits (i.e., traits that respond to the dominant ecosystem processes) in predicting the responses of different plant groups to management has received increasing attention during the last few years (McIntyre et al. 1995, Huhta & Rautio 1998, Dupré & Diekmann 2001, Diaz et al. 2001, Kahmen et al. 2002). By using functional groups instead of individual species, it is possible to discover more general patterns and to predict the dynamics of plant communities (McIntyre et al. 1995). The
often studied life-history attributes include plant life cycle, Raunkiaer’s life form, plant growth form (canopy structure), regenerative strategy, seed size and plant height. Most of these studies have considered several life-history traits simultaneously.

Grazing-resistant species have been found to be shorter in height and to have smaller, tender leaves with larger specific leaf area (leaf area per leaf mass) than grazing-susceptible species (Díaz et al. 2001). For example, in Australian grasslands, therophytes (annuals) increased with increasing grazing pressure (McIntyre et al. 1995). High grazing levels decreased the proportions of chamaephytes (shrubs), phanerophytes (trees) and hemicyryptophytes. Within hemicyryptophytes, the growth form affected their occurrence at different levels of grazing. With regard to seed morphology, species with adhesive seeds were favoured at moderate grazing levels. The proportion of species with mobile (very small) seeds increased with increasing grazing intensity. The number of species with vegetative reproduction was higher at moderate grazing levels than at low or high levels (McIntyre et al. 1995). In another study conducted in Australia, high grazing pressure was associated with annual grasses, low-growing leafy perennial grasses with small seeds, mat-forming large-seeded herbs as well as low-growing, scrambling, small-seeded herbs (McIntyre & Lavorel 2001). When comparing seven plant life-history traits in Swedish grazed and abandoned meadows, Dupré & Diekmann (2001) found that grazed sites had higher proportions of legumes, therophytes and species with rosette leaves and regeneration by means of a persistent seed bank. Abandoned meadows were characterised by monocots, geophytes and species with vegetative regeneration as well as leafy canopy structure. Leaf anatomy (in relation to humidity) and the mode of seed dispersal were less important indicators of differences in management (Dupré & Diekmann 2001).

Plant growth form may be more important in determining the structure of grasslands than Raunkiaerian life form because most of the species in grasslands are hemicyryptophytes (Mitchley & Willems 1995). Seed size is important for plant survival and competitive ability in many species. For instance, Armstrong & Westoby (1993) found, when comparing survival after 95% biomass loss at the early seedling stage in 20 pairs of phylogenetically close large- and small-seeded species, that large-seeded species showed better survival in 14 out of 16 pairs where there was a difference in survival.

1.5 Grazing tolerance of monocarpic species

Plants can cope with herbivores by at least two means. First, they may resist herbivory by escaping in time, i.e., flower and set seed rapidly when herbivores are absent, or they can prevent herbivore foraging by producing toxic secondary compounds or by mechanical means, such as spines, thorns, tough leaves and waxes (Rosenthal & Kotanen 1994). Both chemical and mechanical traits constitute a basis for plant resistance. These mechanisms are referred to as resistance because they reduce biomass loss to herbivores.

Second, plants may tolerate being grazed. Tolerance is defined as the ability of plants to maintain their fitness in spite of biomass loss to herbivores (e.g., Strauss & Agrawal 1999). Plants repair the lost biomass by producing new leaves, branches or reproductive parts. This requires that they have undifferentiated meristems left in their undamaged parts, e.g., at the base of the stem. This kind of compensation may include several
growth-promoting mechanisms. For example, light availability may increase for the remaining leaf area, water and nutrient availability to the surviving leaves may be improved, senescence of leaves may decrease, floral abortion may be reduced, or photosynthates may be redistributed to the production of new leaves (Crawley 1997). The plant may use all these means to guarantee its growth and reproductive success in the presence of herbivores. Despite the numerous studies conducted during the past decade, many of the mechanisms related to tolerance are still poorly known: how common is overcompensation, how does overcompensation develop in the course of evolution, is there additive genetic variation in compensatory ability in response to herbivory, and is overcompensation related to induced plant defence? (Agrawal 2000). This work aims to shed some light on the first question.

It is often assumed that herbivory generally decreases plant fitness, i.e., plants undercompensate for injuries (Belsky 1986). However, damaged and undamaged plants may perform equally well (exact or full compensation, sensu Belsky 1986). During the last two decades, it has been argued that plants may sometimes even be able to overcompensate for the lost biomass or, in more general terms, for the cost of herbivory. Overcompensation, meaning that damaged plants perform better than their intact neighbours, was first reported in grasses (McNaughton 1979, 1983). Grasses have a good compensatory capacity as their leaf meristems are close to the ground and the apical meristem is enclosed by the leaves (Prins et al. 1980). In herbs (dicots), meristems are more susceptible to damage as they are situated higher along the stem and are usually less well protected. The first evidence of overcompensation in dicots was reported in *Ipomopsis aggregata* by Paige and Whitham (1987). After losing 95% of its biomass, *I. aggregata* produced more biomass, fruits and seeds compared to ungrazed neighbouring plants. This study gave rise to a critical debate on overcompensation (Bergelson & Crawley 1992a,b), but a number of studies have since demonstrated that overcompensation in terms of vegetative biomass in response to herbivory may be fairly common in grasses (Georgiadis et al. 1989, Wegener & Odasz 1997) and monocarpic herbs (Benner 1988, Lennartsson et al. 1997, Mahry & Wayne 1997, Paige 1999, Huhta et al. 2000a,b), but it is sometimes also seen in perennial polycarpic herbs (Escarré et al. 1996, Hendrix & Trapp 1989) as well as in trees (Hjälten et al. 1993). Evidence of overcompensation in seed production is less common, and it has been mostly found in monocarpic plants growing in either cultivated (Benner 1988) or natural populations (Maschinski & Whitham 1989, Paige 1992, 1999, Lennartsson et al. 1998, Huhta et al. 2000b).

Two evolutionary interpretations have been proposed to explain why plants may overcompensate in response to grazing. First, overcompensation may indicate that the plant is well adapted to herbivory (Crawley 1987, Paige & Whitham 1987, Agrawal 2000). This requires that the plant has undifferentiated meristems available, where new growth can begin after a herbivore attack. Undamaged plants are expected to have an unbranched architecture and to be governed by apical dominance. The damage breaks the apical dominance, and the plant develops many lateral branches. Theoretical models have proposed that selection may favour this growth strategy under a high and predictable risk of damage (van der Meijden 1990, Vail 1992, Tuomi et al. 1994, Nilsson et al. 1996a, Lehtilä 1999). In some models, the probability of being damaged has to be over 50% for overcompensation to be favoured. These models assume that the plant has dormant buds
that can be activated when the plant is damaged. Likewise, it is advantageous for the plant to store its resources until the peak of attack risk may be seen as a bet-hedging strategy (Vail 1992, Nilsson et al. 1996a). This interpretation does not explain, however, why undamaged plants do not begin to grow branches when the risk of herbivory has passed (Crawley 1987).

Second, overcompensation may be regarded as a response of plants that have been selected for apical dominance for reasons other than herbivory. For instance, in environments where light competition is intense, selection may favour fast vertical growth and unbranched architecture because the plant has to reach a light gap to survive in competition. An unbranched individual that allocates most of its resources to vertical growth may perform better in tall vegetation than a plant that shares its resources between vertical growth and lateral branches (Aarsen & Irwin 1991). Apical dominance is maintained by auxin, which suppresses the growth of lower lateral meristems. When the topmost meristems are removed by herbivores, for example, the production of auxin ceases, leading to the activation of previously inhibited lateral buds (Phillips 1975). In this context, overcompensation can be seen as an expression of the cost of apical dominance (Aarsen & Irwin 1991). The cost is realised in good growing conditions, e.g., in the absence of competition, where increased branching would be favourable, but apical dominance constrains lateral branching. The plant is released from this constraint when grazing destroys the apical meristems and releases the suppressed meristems from correlative inhibition (Aarsen & Irwin 1991, Aarssen 1995, Huhta et al. 2000b). Plants usually also change their meristem allocation during their development. The proportion of inactive meristems decreases and those of growth and reproductive meristems increase with age and increasing plant size (Bonser & Aarssen 2003). Apical dominance is high in low-resource conditions, especially in light-limited and sometimes nutrient-poor habitats (Bonser & Aarssen 2003). Adaptation to competition and to herbivory may also simultaneously shape the compensatory responses of plants. According to Järemo and co-authors (1996), when the evolutionary history of a plant involves both competition for light and herbivory, the latter will probably be decisive in the evolution of overcompensation.

In addition to the evolutionary interpretations presented above, hypotheses have been put forward to explain how environmental conditions may affect the ability of a plant to tolerate biomass loss. Maschinski and Whitham (1989) proposed that the response of an individual plant may vary from negative (undercompensation) to positive (overcompensation), depending on the local growing conditions. This “compensatory continuum” hypothesis predicts grazing tolerance to be superior when the plant has plenty of water and nutrients available and experiences no competition. Maschinski and Whitham (1989) found support for this hypothesis in Ipomopsis arizonica. They found undercompensation or, at best, exact or full compensation among plants growing in competition with grasses and without supplemental nutrients. Overcompensation was found only among fertilized plants growing free from competition. The results by Benner (1988) on Thlaspi arvense also supported this hypothesis. Some studies, however, have shown that compensation in dicotyledonous herbs is most effective at low resource levels (Hawkes & Sullivan 2001). This is predicted by the growth rate model of Hilbert and colleagues (1981), where plants growing in resource-poor conditions need only a small
increase in their relative growth rate (RGR) to compensate for biomass loss. In resource-rich conditions, plants grow close to their maximal RGR and cannot increase their RGR much more, and compensation is hence expected to remain weak. Competition with taller species may be more crucial for annual species, which are often low-growing and poor competitors for light. Therefore, for example, hemiparasitic *Euphrasia* species grow in habitats where the surrounding vegetation remains low, such as alpine meadows, base-rich fens, seashores, calcareous rocks and grazed/mown meadows (Karlsson 1986). If the vegetation becomes too high and dense, the mortality of hemiparasitic species may rise due to the more intense light competition (van Hulst *et al.* 1987).

### 1.6 Clonal integration and grazing tolerance

Clonal growth is common among plants because it involves many benefits. The potential benefits of clonal integration include more effective use and recycling of scarce resources, division of labour between ramets, sampling of the environment at many micro-sites and regulation of ramet population size by apical dominance (Jónsdóttir & Watson 1997). The intensity of ramet integration varies between species and environments (Pitelka & Ashmun 1985). In many species, the connections between ramets persist for years, e.g., up to 7 years in *Podophyllum peltatum* (de Kroon *et al.* 1991) or as long as over 20 years in *Carex bigelowii* (Jónsdóttir & Watson 1997). Some plants may maintain strong independence of ramets throughout their life. The degree of integration has been studied by radioactive or stable isotope tracers as well as by severing rhizome connections (Pitelka & Ashmun 1985). Various stress factors often increase ramet integration, and undamaged ramets may provide resources to neighbouring damaged ramets (Pitelka & Ashmun 1985). Clonal integration can thus increase plant tolerance to herbivory (Ashmun *et al.* 1982, Schmid *et al.* 1988, Price *et al.* 1992). Damage or stress may lead to reintegration of independent ramets. A spatially and temporally patchy environment favours spreading to new suitable habitats and acropetal transport. In a spatially and temporally stable environment, remaining in one place is favoured over spreading to new sites. An environment of this kind enables persistence and monopolization of the clone in the habitat. Strongest integration is shown by species growing in such environments (Pitelka & Ashmun 1985). In a comparative analysis of species with different successional stages, Tamm *et al.* (2001) found that species growing on open meadows have lower vegetative mobility and shorter ramet life-span than species on overgrown wooded meadows. This leads to a higher turnover rate of ramets, which may enable greater species richness of the former community (Tamm *et al.* 2001).

### 1.7 Aims of the study

The aim of the present thesis was, on the one hand, to find out how grazing and mowing may influence the abundance of different functional plant groups and species diversity in semi-natural meadows (papers I, II) and, on the other hand, to study the variation in the compensatory capacity of some monocarpic meadow species (papers III-V), and whether
the clonal growth form may help meadow herbs to tolerate simulated herbivory; here *Linaria vulgaris* was used as an example (paper VI).

More precisely, the aim of the sheep grazing experiment (I) was to find out whether the responses of different functional plant groups could be used in evaluating the success of restoration of species richness and composition in an overgrown mesic meadow. The functional groups represent different successional stages, and their responses mirror the phase of the restoration process. This information can be used to optimise the management practices. It was expected that the abundance of tall herbs and grasses indicative of rich soil would decrease and the cover of small herbs and graminoids thriving on poorer soil would increase in response to grazing. Besides, it was expected that grazing would increase the number of species as it enables the coexistence of species with various life-histories.

The aim of the mowing experiment (II) was to test how different mowing treatments promote species richness in a hay meadow where traditional (late summer) mowing turned out to be ineffective in increasing species richness (Huhta *et al.* 2001). Early mowing performed in late June was introduced to control the abundance of tall herbs, especially *Geranium sylvaticum*. This treatment was also expected to favour small herbs and grasses, as they get more space when tall dominants are suppressed. Disturbance treatment (late mowing combined with breaking of the soil surface) was used to promote germination from the seed bank. This management may be seen to simulate the mechanical effect of the hoofs of grazing animals on soil surface.

The tolerance of monocarpic plant species for various levels of simulated herbivory was tested in three clipping experiments (III-V). The clipping levels were 0, 10 and 50% of the stem being removed in the experiments III and V and 0, 10, 50 and 75% in the experiment IV. The study with *Erysimum strictum* (III) was designed to test the compensatory continuum hypothesis (see 1.5). Further, the importance of delayed flowering as a potential cost of regrowth was assessed. *Gentianella amarella* (IV) was used to test the compensatory capacity of this species in two natural populations and to compare the results to some earlier results obtained with monocarpic species, namely *Gentianella campestris* (Huhta *et al.* 2000a), *Erysimum strictum* and *Rhinanthus minor* (Huhta *et al.* 2000b). In *Euphrasia stricta* (V), in addition to studying compensation, the effect of surrounding vegetation on the performance of the hemiparasite was explored. Neighbour clipping was expected to have two alternative effects: it could improve the growth of *Euphrasia* by reducing the competition for space and light, or it may decrease the growth and tolerance of *Euphrasia* as the source of host resources is partially removed.

Two experimental approaches were used to study clonal integration in a perennial clonal herb *Linaria vulgaris* (VI). Firstly, a growth experiment was designed to test whether there is a net transfer of benefit between neighbouring ramets when part of the clone is damaged. In this factorial common garden experiment, a target ramet was either defoliated or left intact, the apex was cut or left intact, and neighbouring ramets were either defoliated or left intact. Secondly, based on the results of the growth experiment, a $^{13}$C tracer study was conducted to verify the degree of physiological integration of ramets in terms of carbon.

As a whole, I hope that my thesis contributes to the basic ecology of plant-herbivore interactions as well as to the application of this knowledge to the management of semi-
natural grasslands. Rather little is still known about the prevalence of overcompensation, and there is no consensus as to what mechanisms and environmental factors contribute to high tolerance in different circumstances. Knowledge of the responses of species and plant communities to management by grazing and mowing is needed to plan effective restoration programs. In Finland, restoration programs have been started during the last 10 years, but much more information is still needed on such factors as the effects of different management practices, the effects of management on various organisms, the nutrient status of these environments, the significance of different types of grasslands and the restoration of overgrown habitats (Salminen & Kekäläinen 2000).
2 Material and methods

2.1 Community-level experiments

The sheep grazing experiment (I) was carried out in 1996-2000 on the Nyby farm in the rural community of Ii on the coast of the Bothnian Bay in northern Finland (65° 29’ N, 25° 20’ E). This regionally valuable semi-natural grassland (Vainio & Kekäläinen 1997) had been out of use for at least 10 years. It had been used as a pasture until 1969 and occasionally in the 1980’s. The study plots were established on two meadow patches ca. 50 m apart (later called the E and W sites). At both sites, seven 1 m² permanent plots were located in a 10 m × 10 m grid. Altogether, there were seven ungrazed exclosure plots (fenced) and seven grazed plots. The grazing period was from the 1st of July to the 30th of September. The percentage cover of all vascular plant species and litter was estimated visually on each plot in mid-June every year. The change in vegetation was studied by examining the responses of different functional plant groups: herbs vs. grasses, tall vs. short species, species differing in flowering time, species representing different C-S-R strategies (Grime et al. 1988, Heikkinen & Kalliola 1990) and species indicative of rich vs. poor soil (nitrogen indicator values of species by Ellenberg and co-authors (1992). For the present study, the C-S-R model was considered appropriate in classifying species based on their stress and disturbance tolerance, and no other models were therefore applied (e.g., Tilman 1980, Taylor et al. 1990, Oksanen & Ranta 1992). Grime’s model is considered a good predictor at the species level (Wilson & Lee 2000).

The mowing experiment (II) was performed in 1998-2003 on Kiiminki Haaraoja meadow (65° 10’ N, 25° 50’ E) ca. 20 km from Oulu in northern Finland. This regionally valuable meadow was used as a pasture for cattle until 1985. Management was restarted in 1993 by mowing annually in August. This treatment did not much change the vegetation (Huhta et al. 2001), and new mowing treatments were therefore introduced in 1998. Each of the four treatments was replicated on 10 permanent plots 0.25 m² in size. The treatments were: 1) early mowing in late June, 2) late mowing in August, 3) late mowing + disturbance (breaking the soil surface) and 4) untreated control. The percentage cover of all vascular plant species, mosses, lichens and litter was estimated annually in late June before the early mowing. The mean vegetation height was estimated...
in June 2003 on each plot with a “meadow ruler” (see Ekstam & Forshed 1996). The cover and maximal height of three model species (Geranium sylvaticum, Campanula rotundifolia and Agrostis capillaris) were also measured in June 2003.

Temporal changes in vegetation were analysed in these two studies (I, II) by means of repeated measures ANOVA. In the mowing experiment (II), the values recorded in 1998 were taken as a baseline and the values for 1999-2003 were divided by those of 1998. In the grazing experiment (I), a grazing response index (GRI) was calculated for each functional plant group to estimate the changes taking place in their abundance in response to grazing. GRI was calculated by comparing the relative change (from 1996 to 2000) in the mean cover on grazed plots to the relative change in cover on ungrazed plots. Furthermore, temporal trends in the abundance of individual species were studied by using Spearman’s rank correlations ($r_s$) to follow how the abundance of the species on grazed and ungrazed plots changes over time. Based on these correlation coefficients, the species were classified as ones that increased, decreased or showed no response to grazing (see Table 1 in paper I). The structure of the plant community and the effects of grazing on species composition were studied by performing NMDS ordination following the procedure recommended by Minchin (1987). Ordination was accomplished by using the R program (Ihaka & Gentleman 1996), the isoMDS package MASS (Venables & Ripley 1999) and the VEGAN package by Jari Oksanen (available at http://cran.r-project.org/).

In the mowing experiment (II), the temporal trends of the three model species (G. sylvaticum, C. rotundifolia and A. capillaris) were studied by computing Spearman’s rank correlations between abundance and time in years (1-6) since the beginning of the study separately for the different treatments. The effects of the treatments on the mean vegetation height and the three species were tested with one-way ANOVA, and post hoc tests (control vs. treatments) were carried out with the LSD procedure (Saville 1990). A species turnover index ($T$) was calculated to study the quantitative change in species composition in the different treatments during this 5-yr study. This index was calculated as $T = (A+D)/n$, where $A$ is the number of new species on a plot during the study, $D$ is the number of species that disappeared from the plot, and $n$ is the total number of species at the beginning of the study period (Berlin et al. 2000).

### 2.2 Species-level experiments

The species used in the clipping experiments (III-V) are monocarpic annual or biennial species, while Linaria vulgaris (VI) is a perennial clonal herb. Euphrasia stricta agg. (V) is an annual hemiparasitic species devoted to low-growing vegetation types, such as grazed and mown meadows. Erysimum strictum (III) and Gentianella amarella (IV) are biennial species that form a rosette in the first year and flower during the second growing season. In nature, they grow on half-open habitats, such as rocks and riversides. Human settlement has provided them new habitats, e.g., grazed/mown meadows and road/railway verges. Linaria vulgaris (VI) is a clonal herb that grows on open, often disturbed habitats and has good spreading potential via adventitious roots. The study with G. amarella (IV) was performed in its natural habitats (Paltamo and Kuusamo), whereas the experiments
with *Erysimum* (III), *Euphrasia* (V) and *Linaria* (VI) were carried out in common garden conditions at the Botanical Gardens of the University of Oulu. All the plants in the same treatment within an experiment were provided with similar growing conditions. The surroundings of the plants (within a 10-20 cm radius) growing free of competition were cut to low height or weeded. The individual plants subjected to competition by other species were randomly allotted to different cutting treatments. The plants growing free from competition were also randomly allotted to various cutting regimes (III, V).

The damage levels within the three clipping experiments (III-V) were consistent. They all consisted of: 1) control (0% clipping), 2) removal of the shoot apex (10% clipping), and 3) cutting half of the stem away (50% clipping). The experiment with *G. amarella* also involved 75% clipping because it is known that *Gentianella* species have a good compensatory potential (Lennartsson et al. 1998, Huhta et al. 2000a). Shoot apex removal can be considered to simulate insect damage, whereas the higher damage level intended to mimic injury caused by mammals. The clippings were done with scissors. The plants were clipped 1-2 weeks before flowering: *Erysimum* in mid-June, *Euphrasia* at the end of June and *G. amarella* during the first half of July. Lennartsson and co-authors (1998) defined the term ‘inductive time period’ (ITP), i.e. the period when the plant has physiological potential to repair damage. This period is often short, being ca. 3 weeks in *G. campestris*. The early limit of ITP may be constrained by the resources available for regrowth in the early season and the late limit by the availability of undifferentiated meristems in the late season (Lennartsson et al. 1998). In the present study, the clippings were done within the presumed species-specific limits of ITP. In the experiment with *Erysimum strictum* (III), where the compensatory continuum was tested, part of the plants were fertilized four times during the study with 20 ml of liquid NPK fertilizer. The effect of competition caused by neighbouring plants was tested in two experiments (III, V). In the study of *E. strictum*, the grasses *Poa pratensis* and *Festuca rubra*, which were grown together with *E. strictum*, mainly implied root competition (III), while the sown host species *Trifolium repens* and *Festuca rubra* caused above-ground competition with *Euphrasia* (V). Additional data were collected from natural populations of *Erysimum* and *Euphrasia* to explore their shoot architecture and the effect of mowing in field conditions. The viability of seeds was tested in a germination experiment (III).

The degree of compensation was studied by comparing different performance measures of clipped plants to those of unclipped control plants. The comparison may indicate either under-, exact, or overcompensation (see definitions in introduction). The effects of simulated grazing were studied on several performance parameters: shoot weight, root weight, plant height, number of branches, fruit number and total number of seeds. The number of seed scars was used to estimate seed production in *Erysimum* (III) and *G. amarella* (IV). For *Euphrasia* (V), no reliable measure of seed production was obtained, and fruit number was used as a measure of reproductive success.

The *Linaria* study (VI) consisted of two experiments, the growth experiment was carried out in the summer 2001 and the $^{13}$C tracer study in 2003. The growth experiment was carried out by transplanting 106 clones of *Linaria* from their natural habitat in Oulu into the garden in October 2000 and in June 2001. The clones were allotted into eight treatment combinations: 1) cutting of the apex of one ramet, later called target ramet (yes/no), 2) defoliation of this target ramet (yes/no) and 3) defoliation of all the other
ramets in the same clone (yes/no). Both levels of each treatment were compared with both levels of the other treatments, which resulted in a fully factorial (2 × 2 × 2) design. Apex cutting caused only minor damage, whereas defoliation consisted of removal of about 90% of all leaves. Defoliation was repeated four weeks after the first treatments. The experiment was terminated in October 2001, the plants were dried, and different growth measures were determined.

The 13C tracer study was started in June 2003 by transferring 95 Linaria clones with two young shoots connected to each other via rhizome to the garden. The plants were grown in plastic pots in a mixture of sand and garden soil (1:1). In the treated clones one ramet was treated, whereas in the control pots both of the two ramets were left intact. The treatments were: 1) apex cut and 2) 67% of all leaves removed. Six days after these cutting and defoliation treatments, 13C labelling was performed. One ramet in a clone was sealed into a plastic bag for five hours, and 8.32 mg 13C was released as 13CO2. To enable reciprocal labelling, in half of the treatment pots the damaged ramet was labelled and in the other half of the pots the intact ramet was labelled. After six days the experiment was terminated, the roots were washed clean of any soil, and the plants were dried (48h in +60°C) and milled, and the 13C content of the samples was analysed by EA IRMS at Iso-Analytical Ltd., UK. A background value for 13C was obtained from the 12 Linaria shoots collected at the time of transplantation. The amount of enriched 13C was calculated by subtracting the background value (1.0799%) from the total concentration of 13C in the sample and by multiplying this value by the total amount of carbon (mg) in the sample. The latter value was obtained by multiplying the plant dry weight (mg) by the total carbon concentration in the sample. Initial height was used to estimate initial shoot dry weight (by using other plants, good compatibility between these traits was obtained, regression, r² = 0.53). RGR was calculated as follows: \( \frac{\ln (\text{final weight}) - \ln (\text{average initial weight})}{\text{growth period as days}} \). For roots, the pooled initial root weight of these 17 clones was used to calculate RGR.

The results were analysed with ANOVA using the SPSS software. The design was protected ANOVA with Erysimum (Scheiner 1993, III), two-way factorial ANCOVA with G. amarella (IV) and two-way factorial ANOVA with Euphrasia (V) and Linaria (VI). The protected ANOVA combines MANOVA and ANOVA. In both of them, a three-way factorial design was applied. Pairwise comparisons between the treatments were performed by comparing treatment means with the LSD procedure (III, IV; Saville 1990). In the study with Euphrasia, polynomial contrasts were computed for clipping levels in mown and unmown neighbourhoods (V), and in Linaria contrasts with untreated control were computed (VI). In Erysimum, the effects of the treatments on the phenological state of the plants were tested with G-tests. In Erysimum and Euphrasia, the correlations between the performance parameters were studied by calculating Pearson’s correlation coefficient (r). In the 13C tracer study on Linaria (VI), the effect of the treatments on carbon allocation were analysed by repeated-measures ANOVA. The effect of the treatments on above- and below-ground biomass and relative growth rate (RGR) as well as the root 13C concentration were tested with one-way ANOVA. Multiple comparisons between the treatment means were performed with Tukey’s HSD tests for the amount of root 13C.
3 Results

3.1 Effects of sheep grazing on functional plant groups

After three years of grazing, the mean number of vascular plant species per plot had increased by ca. 30%, which equals an average increase of $4.1 \pm 0.9$ (mean $\pm$ S.E.) species (I). In the exclosures, the number of species had remained the same, ca. 14 species per plot. Most species invading the grazed plots had already been present in the community. Some small herbs increased their cover when grazing removed litter and suppressed the dominant species. The species invading the grazed plots included *Rhinanthus minor*, *Cerastium fontanum*, *Stellaria graminea*, *Trifolium pratense* and *Taraxacum* sp. The most apparent change during the study was the disappearance of litter on the grazed plots. At the end of the experiment there was hardly any litter on the grazed plots when its cover in the exclosures was 31% (Fig. 2).

Examination of the responses of different functional plant groups to grazing made it evident that the plant height, flowering time and soil nutrient indicator value of the species are crucial in predicting the plant response to grazing. Tall herbs comprised a large proportion of the plant cover at the beginning of the experiment (Fig. 2). These species are strong competitors ($C$-strategists), and they had increased their cover during the period of abandonment of over ten years. Grazing suppressed the abundance of early-flowering tall herbs at the less overgrown W site in the third year, but at the E site, which seemed to have been ploughed earlier and where these herbs were more abundant, grazing had no effect. Contrary to the early-flowering tall herbs, late-flowering tall herbs occurred mainly only at the W site. By the end of the study, grazing suppressed their abundance. Small herbs growing on moderately rich soil and representing the general $CSR$ strategy seemed to increase in the course of grazing. Species that increased their cover after grazing included *Cerastium fontanum*, *Ranunculus acris*, *Stellaria graminea* and *Trifolium pratense*. The cover of small herbs indicating poor soil conditions increased slowly on grazed plots. Only one new small herb invaded the grazed plots during the study, namely the $R$-strategist *Rhinanthus minor*. Its cover increased due to grazing. According to the grazing response index (GRI), rich-soil grasses decreased in response to
Fig. 2. The study area of the sheep grazing experiment (I) in June 1996 (left) before grazing was started and after four years grazing in June 2000 (right). Three exclosures are also seen in the figure on the right.

grazing. This was further confirmed by the negative correlation coefficient of *Elymus repens* with time. On the other hand, poor-soil grasses increased strongly in response to grazing. This group was mainly composed of *Agrostis capillaris*. The cover of this species increased over time (a positive correlation coefficient with time).

The above results were reflected in the relative abundances of the different C-S-R strategies. Ungrazed plots moved towards dominance by C-strategists, whereas general CSR-strategists increased in abundance on grazed plots (Fig. 2. in I). Similar trends were also seen in NMDS ordination. Grazed plots moved towards greater abundance of small herbs. There was no clear trend in the response of ungrazed plots. Different plots moved into different directions, and the overall change was small. The differences in species composition between the two sites could clearly be seen in the ordination graph (Fig. 4. in I).

3.2 Minor effects of mowing after five years

The species number did not increase in any of the mowing treatments during five years (II). The number of species per plot tended to slightly decrease on abandoned and late mown plots. Early mowing and late mowing combined with soil disturbance preserved species richness best. These temporal trends did not, however, differ significantly between the treatments (Table 1 in II). Soil disturbance treatment combined with late mowing did not promote germination of new species, as only one new species appeared during the study, namely *Mentha arvensis* in 2001. Seven species disappeared from the plots during the study. The combined turnover index of all plots was 0.14. Turnover on individual plots was higher, the average being 0.58. Treatments had no effect on this index. Late mowing and abandonment seemed to be unfavourable for rosette-forming small herbs, e.g., *Pilosella officinarum*, which disappeared from several plots. Early mowing tended to favour small herbs, such as *Fragaria vesca*, which invaded three new plots.
Mosses and lichens suffered from abandonment, as the litter layer became thicker during the study. Late mowing tended to favour tall-growing herbs, while early mowing as well as late mowing combined with disturbance favoured small herbs, even though the year × treatment interactions were not significant. Treatments had no effect on the cover of grasses, but there was a significant temporal trend. Their cover decreased remarkably during the last two years (2002-2003) irrespective of the treatments. With regard to the three model species, it was found that late mowing favoured the tall herb *Geranium sylvaticum*, while late mowing combined with soil disturbance favoured the small herb *Campanula rotundifolia*. On the other hand, mowing was harmful for the grass *Agrostis capillaris*, especially late mowing combined with soil disturbance. All the mowing treatments performed in 1998-2002 decreased the mean height of the vegetation by the end of the study (2003). The vegetation height on the plots with early mowing or late mowing with disturbance was only half of that on the unmown plots. On the late mown plots, vegetation height was somewhat higher but still lower than on abandoned plots.

### 3.3 Variation in the compensatory ability of monocarpic plants

A common feature seen in all of the three clipping experiments (III-V) was that the plants could compensate for biomass loss up to 50% level, at least when the growing conditions were favourable (Table 1). Overcompensation was found only after 10% clipping in competition-free conditions and after 50% clipping in fertilized *Erysimum*.

In *Erysimum*, clipping increased both shoot and root biomass among fertilized plants growing free from competition (III). In the presence of competition, irrespective of fertilization, clipped plants performed equally well as control plants (Table 1). *Gentianella amarella* could compensate for the lost shoot biomass up to 50% (Paltamo) or even 75% (Kuusamo population) clipping level. The latter population showed a tendency to overcompensation after 10% clipping (IV). There was no indication of reallocation of resources from below-ground parts into shoots, as clipping had no effect on below-ground biomass (Table 1). In *Euphrasia*, the plants compensated relatively well at both damage levels (10% and 50%) during a favourable year 2000, but clipping decreased shoot biomass during the drier summer of 2001 (Table 1).

Final height indicates how well the plants have been able to maintain their vertical growth in spite of clipping. Apical damage of 10% had no adverse effect on vertical growth. Higher damage levels reduced final height in *Gentianella* and *Euphrasia*, while *Erysimum* was able to maintain its vertical growth in spite of 50% clipping, except when fertilization was combined with competition (Table 1).

Plant architecture may critically affect the ability to recover from damage. If a plant loses a large portion of its above-ground parts, it is essential that it has undifferentiated meristems lower along the stem. These meristems can grow new branches that compensate for the lost biomass as well as for the lost reproductive potential. Clipping did not increase branching in *Erysimum strictum* (Table 1). In fact, in favourable conditions (fertilization, no competition), clipping decreased the number of branches compared to untreated control plants (III). Under competition, plants had fewer branches but clipping did not decrease them. However, the number of branches and the number of
Table 1. Tolerance of the studied monocarpic species (III-V) measured as the performance of clipped plants (damage levels 10 and 50%) in relation to the performance of unclipped plants in different populations/environmental conditions. + = improved performance (overcompensation), 0 = equal performance (exact compensation) and - = reduced performance (undercompensation) as compared to undamaged plants. Performance measures: final shoot and root dry weight (wt), final height and total number of branches, fruits and seeds per plant (for Gentianella seeds per capsule).

<table>
<thead>
<tr>
<th></th>
<th>Shoot wt</th>
<th>Root wt</th>
<th>Height</th>
<th>Branches</th>
<th>Fruits</th>
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<td>Control</td>
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<td>Fertilization</td>
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<td><strong>Gentianella (IV)</strong></td>
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<td>Kuusamo</td>
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<td><strong>Euphrasia (V)</strong></td>
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Seeds correlated positively in all treatments in Erysimum, indicating that shoot architecture can be an important determinant of reproductive output in monocarpic plants. Architectural changes were most apparent in Gentianella and Euphrasia (Table 1). In the Paltamo population of G. amarella, control plants and apically damaged plants had hardly any branches, whereas higher damage levels (50 and 75%) induced vigorous branching (IV). In the Kuusamo population, damage did not increase branching significantly. In Euphrasia, apical damage was enough to induce copious branching when the plants grew without competition in a favourable year (IV). When there was competition, 50% clipping decreased the number of branches. In the drier year, branching was weaker but clipping did not decrease it further (V).

Although plants may compensate well and sometimes even overcompensate in terms of biomass, vertical growth or architectural changes, these responses may not always imply a good compensatory ability in terms of reproductive output or life-time reproductive success (Belsky 1986). This is also seen in Table 1, where the plant responses in the number of fruits and seeds do not always correspond to those seen in biomass and architecture. Fruit production is a reliable measure of reproductive output in compensation studies, provided that clipping does not reduce the number of seeds per fruit. In Erysimum, clipping improved fruit yield among fertilized plants, and clipped plants produced as many fruits as control plants even in unfertilized conditions (III). The pattern in the number of seeds per plant was nearly identical to that in the number of fruits (Table 1). Further, seed weight was also measured in Erysimum. In the control
group, 10% clipping increased seed weight, but in the fertilized plants growing with or without competition, both clipping levels reduced seed weight (III). In *G. amarella*, small damage (10%) resulted in full compensation (Paltamo) or slight overcompensation (Kuusamo) in fruit production (Table 1). Higher damage levels decreased the number of fruits. 75% clipping did not decrease the number of fruits any further compared to 50% clipping (IV). In the Paltamo population, 10% clipping had no effect on the number of seeds per capsule, 50% clipping decreased it slightly, and 75% clipping resulted in only one third of the number of seeds produced by control plants. In the Kuusamo population, none of the treatments differed from each other, even though plants with 10% clipping tended to have more seeds per capsule and those with 50% and 75% clippings less than the control plants (IV). In *Euphrasia*, 50% clipped plants produced as many fruits as control plants in 2000. When growing free from competing neighbouring plants, 10% clipped plants showed slight overcompensation. In 2001, fruit production was also poor in control plants, and clipping decreased it drastically (Table 1). In *Euphrasia*, plant fitness was further assessed by multiplying the mean number of fruits per plant by the survival rate of plants in that treatment (V). The response was non-linear in relation to damage intensity in 2000, the highest fitness being shown by the plants with 10% clipping growing without competition. Fitness following 50% clipping was nearly the same as in unclipped plants in a competition-free environment. In 2001, fitness was much lower independent of the treatment and decreased along with increasing clipping intensity. In the presence of 50% clipping with competition, fitness dropped to zero.

Simulated grazing may also have an effect on plant phenology. This may imply a potential cost of compensatory regrowth if compensation delays flowering and fruit maturation and reduces seed viability. This was tested with *Erysimum* (III). Clipping delayed flowering. Among unclipped plants, fertilization also delayed flowering. However, none of the treatments had an effect on the germination success of seeds. On an average, 76 ± 2% of the seeds germinated.

In the two common garden experiments (III, V), additional data were collected from natural populations to compare them with the results gained in garden conditions. All *Erysimum* individuals in the field population from where the plants were moved to the garden were investigated to find out the plant architecture in nature (III). An unbranched architecture seemed to prevail in the population (85% of all individuals). In a random sample of branched and unbranched individuals (n = 15 for both), the former were taller and produced more seeds per fruit as well as more fruits and seeds per plant. Seed production also correlated positively with branching intensity. There were no differences between branched and unbranched plants in their seed weight or seed germination success. In the *Euphrasia* study, data from 7 mown and 7 unmown populations were collected (V). The plants in mown populations tended to have more branches, but were shorter than the plants at unmown sites. At the latter sites, the plants had greater shoot biomass and more fruits than the plants at mown sites, even though the difference was not statistically significant. The correlations between different parameters indicated that plants are able to tolerate better minor damage (number of branches, shoot weight and fruit number correlated positively with cutting height). The height of surrounding vegetation influenced the shoot architecture of *Euphrasia*: the plants were taller, and the lowest branch was situated higher along the stem in the individuals growing in high
vegetation. Most parameters correlated positively with each other both in the garden and in the field.

3.4 Damaged ramets are not supported by neighbours in Linaria

The performance of a shoot (ramet) in Linaria depended on what happened to the neighbours attached to that shoot (VI). Intact ramets did not support damaged ramets in the same clone. The target ramet was better able to compensate (measured as shoot weight) for apex cutting or heavy defoliation (but not both of them) when the other ramets in the clone were defoliated. Instead, when the neighbours were left intact, cutting of the target apex decreased its shoot weight. A rather similar pattern was seen in the number of fruits produced by the target ramet. Target cutting and combined cutting and defoliation were harmful for target fruit production when the other ramets in the clone were left intact. But, when the other ramets were defoliated, neither of these treatments alone had an effect on target fruit yield. In combination, however, they led to very poor fruit set, the average being 76% less than in control plants. Plants were highly branched in nutrient-rich garden conditions. Apex cutting decreased significantly the number of branches in the target ramets. Defoliation of the target ramet had no effect on its branching, but defoliation of the other ramets in the same clone tended to increase target branching.

In the 13C tracer study, 44% of the inserted 13C was recovered in the plants at the end of the experiment. The treatments had a similar total amount of 13C label per pot. In the control clones, an average of 5.7% of the enriched 13C was translocated to the neighbouring ramet, and the treatments did not cause a difference in carbon allocation between the ramets. On the other hand, the treatments affected carbon allocation into the roots. Apex-cut plants allocated more carbon assimilates into the roots than defoliated plants. Plants could not compensate for the lost biomass in 12 days. Apex cutting had an equally large effect on shoot biomass as 67% defoliation. The former decreased shoot biomass by 29%, while the latter reduced it by 25%. Treatments had no effect on the below-ground biomass of the clone. Because the relative growth rate of treated plants was similar to that of controls, damaged plants did not compensate for the lost biomass during the study period.
4 Discussion

4.1 Restoration of meadow communities

4.1.1 Grazing and mowing as management tools

Grazing and mowing had many favourable effects on the composition of the meadows under restoration in the present experiments (I, II). The litter layer nearly vanished, plants were more evenly distributed throughout the area, vegetation height was lower, and small-growing species gained more space after management. The most important response variable in restoration studies is obviously the increase in species number. This seemed to be the most serious problem in the restoration of meadows. Even though species number increased by ca. 30% per plot during the study in response to sheep grazing (I), the rate of change was slow compared to many other grazing and mowing studies (Willems 1983, Gibson et al. 1987, Snow et al. 1997, Pärtel et al. 1998, Wahlman & Milberg 2002). Hardly any new species arrived in the meadows in the present two studies (I, II). An increase of same magnitude was observed in restoring wooded meadows in SW Finland (Kotiluoto 1998). A key factor in this slow response may be seed limitation, see discussion below (chapter 4.1.3). However, the species richness of meadows may be inherently lower in northern Finland than at more southern latitudes, which must be considered when evaluating management goals and success.

The management tools suitable to restore previous species richness vary depending on the type, productivity and species composition of the plant community. Mere low-intensity sheep grazing has been a sufficient tool in the management of hill pastures (Hulme et al. 1999) and chalk grasslands of low productivity (Willems 1983, Gibson et al. 1987, Bakker 1998). At more nutrient-rich sites, additional measures are needed to generate change in vegetation structure and composition. Because, in the present sheep grazing study (I), tall herbs were dominant in the community and the soil was rather fertile, a combination of early mowing followed by grazing would probably have given better results (cf., Snow et al. 1997, Kotiluoto 1998, Mittlacher et al. 2002). Mowing combined with aftermath grazing has been the traditional way of management of wooded
and mesic meadows in northern Europe. Another possibility to reduce the dominance of tall species is to start grazing earlier in the season (in northern Finland in early June). Spring grazing has promoted an increase in species richness in formerly intensively used lowland meadows in the UK (Bullock et al. 2001). Mowing has also been found to be an effective tool in increasing species diversity especially on drier meadows (Willems 1983, Fenner & Palmer 1998, Klimeš et al. 2000, Wahlman & Milberg 2002).

It is also important to specify the target community when the restoration practices are started. This is done by means of the soil properties, present state and species composition of the community as well as the species pool of the region. In the two study areas covered in this thesis, the target community would be a low-productivity meadow with many small herbs and grasses. However, the speed of change is often slow during restoration. It has been estimated that the return of previous species richness after reintroduction of management takes at least the time that has passed since abandonment. For instance, in Öland (Sweden), a wooded meadow resembled the traditional one after 36 years of restoration (Mitlacher et al. 2002), and it has been estimated that the development of a species-rich chalk grassland takes 100 years (Gibson & Brown 1992). A species-rich meadow is often the result of decades of management. New species arrive one by one during the years and gradually establish their presence in the community. The succession in a species-rich meadow may occasionally reach a plagioclimax, where the species composition does not change as long as the conditions remain unchanged (Gibson & Brown 1992). To sum up, restoration practices take time, and it was not unusual that the changes were relatively small in these two five-year studies.

4.1.2 The effects of management depend on plant life-history strategies

The procedure of dividing species into functional plant groups proved to be useful in studying the effects of grazing on plant community change (I). The criteria used in this grouping were life-form (graminoids vs. herbs), plant height, flowering time and soil nutrient requirements. In the mowing experiment (II), the changes in species abundance were smaller, but there were some trends in the temporal dynamics of the three model species (Geranium sylvaticum, Campanula rotundifolia and Agrostis capillaris) and in some of the functional groups.

Grazing had somewhat different effects on early- and late-flowering tall herbs (I). Early-flowering tall herbs Anthriscus sylvestris and Geranium sylvaticum decreased only on the W site. They seemed to thrive better on the E site, which may have been ploughed in the past. The late grazing period may explain this weak response. Both of these species are strong competitors and easily outcompete smaller plants. These species had already flowered and started to reallocate resources into the roots when grazing started in July. These two species increased during the restoration of wooded meadows in SW Finland (Kotiluoto 1998). Late grazing and mowing have been found to promote the formation of side rosettes in Anthriscus (van Mierlo & van Groenendael 1991), which could explain its success in these studies. In the present mowing experiment (II), late mowing also favoured G. sylvaticum. This was further predicted by the previous matrix simulation of vegetation development in this meadow (Huhta et al. 2001). G. sylvaticum has also been
found to thrive well in abandoned meadows but to be absent from intensively mown sites (Huhta & Rautio 1998). Early mowing kept this species in control in the present study (II). In contrast, the late-flowering tall herbs Epilobium angustifolium and Filipendula ulmaria suffered from grazing (I) because the grazing took place at the most sensitive phase of their life-cycle: just before and during flowering. Sheep are known to graze eagerly on Epilobium on wooded meadows (Häggström 1990). Kotiluoto (1998) also found that this species decreased during restoration. Similar responses have been reported elsewhere in response to grazing. Low stocking rate in Australian subtropical pastures was associated with tall height, erect growth and exposed inflorescences (McIntyre & Lavorel 2001). In a comparison of subhumid upland grasslands of Argentina and Israel, Diaz and co-authors (2001) found that nearly 80% of the species suffering from grazing were tall (>40 cm), and that large leaves tended to be associated with a negative response to grazing. This is in accordance with the present study and the predictions of Grime (1977) that tall and broad-leaved C-strategists are most sensitive to grazing.

Small herbs increased in cover when grazing suppressed the dominance of competitively superior tall herbs and grasses and when the litter layer decreased (I). Many species in this group are general CSR-strategists and show widely variable responses to, for example, soil conditions. Adequate space for growth seems to be more important for their success than the soil conditions. In other studies, moderate grazing has also been found to favour smaller and small-leaved species (Díaz et al. 2001), mat-forming or scrambling forbs (McIntyre & Lavorel 2001) or rosette-forming/basal-leaved species (Kahmen et al. 2002, Dupré & Diekmann 2001). An example of scrambling forbs that was also favoured in the present grazing study is Trifolium pratense. Grazing similarly favours species with short life-cycle (Dupré & Diekmann 2001). The only annual species (R-strategist) that increased due to grazing in (I) was Rhinanthus minor. A similar observation was also reported by Kotiluoto (1998). Early mowing and late mowing combined with disturbance tended to favour small herbs, even though this positive effect was not as strong as expected (II). Disturbance treatment was introduced to increase seedling recruitment, but it hardly had that effect. This treatment favoured Campanula rotundifolia. It is a S-strategist (Grime et al. 1988), and it presumably benefited from the very dry June of 2003. This species was also favoured by mowing in other studies (Huhta & Rautio 1998, Kahmen et al. 2002, Wahlman & Milberg 2002). Early mowing further benefits rosette-forming species since, for instance, Pilosella officinarum persisted on early mown plots, but disappeared from many unmown and late mown plots. The study site of the mowing experiment, the Haaraoja meadow, is characterised by many small-growing species indicative of nutrient-poor soil. Nutrients are removed via the mown biomass, and the species of richer soil do not thrive there because the humus layer is thin and exposure to the sun makes it a dry growing place.

Two tall grasses, Alopecurus pratensis and Elymus repens, growing on nutrient-rich soil decreased in response to grazing (I). This is because they are nitrophilous to some extent and are expected to decrease in the long term when management removes nutrients via removed biomass (cf., Oomes 1990), even though grazing does not reduce the soil nutrient pool as effectively as mowing. Willems (1983) also found that grasses with similar growth form decreased due to grazing. Low grazing pressure has been found to favour medium-sized leafy perennial grasses in Australian pastures (McIntyre & Lavorel 2001). In contrast, grazing favoured smaller grasses thriving on more nutrient-poor soil,
such as *Agrostis capillaris*, which is a CSR-strategist and has a good regenerative capacity from basal meristems, as well as *Anthoxanthum odoratum* and *Festuca ovina*, which are stress tolerators (I). The latter two species may have been favoured by the more extreme growing conditions as grazing removed the tall shading vegetation (cf., Haggström 1990, Hulme et al. 1999, Hansson & Fogelfors 2000). In the present mowing experiment (II), there was a general decrease in the cover of grasses, especially during the last two years, due to unfavourable weather conditions (drought). All the mowing treatments tended to decrease the abundance of *Agrostis capillaris*. It has been found to thrive well on meadows abandoned long time ago (Losvik 1999), but it may also decline when tall herbs gain dominance (Huhta & Rautio 1998, Hansson & Fogelfors 2000).

In these studies, I found the C-S-R-model useful in evaluating community changes in response to restoration. However, in the case of grazing and mowing, the MAF model (Oksanen & Ranta 1992) might very well provide further insight with respect to the intensity and frequency of biomass loss. This would require detailed knowledge of the grazing tolerance of meadow plants in response to the degree and frequency of damage, both of which can shape plants’ compensatory responses (e.g., Tuomi et al. 1994, Nilsson et al. 1996b). As stated earlier, the functional approach was found to be useful when studying the responses of different plant groups to management. When the responses of specific functional groups are known, the development in an area intended to be restored can be predicted and the management practices adjusted by sorting out the species composition of the area. The functional approach is a relatively new tool in searching for more general and applicable ways of predicting management impacts on plant communities. The rather similar responses seen in several studies performed in different environments suggest that the method is worth studying in more detail.

### 4.1.3 Obstacles to meadow restoration

Even though there are many good examples of successful restoration trials, the results may sometimes remain poor. Surplus of soil nutrients is a problem in many meadows with intensive previous agricultural use. However, the decline in annual dry matter production due to removal of the mown material does not always guarantee an increase in species diversity. In a 17-year study of a formerly fertilised area in the Netherlands, annual yield dropped to half of what it used to be, but species number declined by 40% per plot when fertilisation was stopped and the site was mown annually (Berendse et al. 1992). On the other hand, seed limitation seems to be a serious problem in meadow restoration in many areas throughout Europe. In their review of seed sowing experiments, Turnbull et al. (2000) found seed limitation in around 50% of the experiments, and it was more common in early successional habitats. The lack of suitable seed sources has slowed down the increase in species richness on Dutch chalk grasslands (Bobbink & Willems 1991), Swiss meadows (Stampfli & Zeiter 1999), calcareous lowland meadows in England (Treweek et al. 1997), overgrown Norwegian grasslands (Rosef 2004) and wooded meadows in the archipelago of SW Finland (Kotiluoto 1998). A lack of propagules may also have restricted the increase in species richness in the two restoration experiments described in this thesis. A species may sometimes emerge from a seed bank,
but most grassland species unfortunately disappear from the seed bank after some years or decades of abandonment (Bakker & Berendse 1999). The key factor is the composition of the local species pool (Zobel 1997). Increase in species richness during restoration is possible only if a large pool of suitable species has been preserved near the site, and if the species are able to spread to the site within a moderate time (e.g., ≤ 5 years). Recently, many seed addition experiments have been carried out with encouraging results in efforts to increase the species diversity of degraded grasslands (Tilman 1997, Stampfli & Zeiter 1999, Zobel et al. 2000, Pywell et al. 2002).

Other problems in maintaining the diversity of semi-natural meadows include eutrophication and isolation. These habitats are inherently characterised by species thriving on rather nutrient-poor soil. Surplus of nutrients leads to a situation where these species are outcompeted by taller species. Grazing management may increase eutrophication if additional fodder is provided to animals, if semi-natural habitats are used only as overnight places, or if they are connected to sown pastures (Pykälä 2001). Atmospheric nitrogen deposition also increases eutrophication. Berlin and co-authors (2000) found in a long-term study that, despite unchanged management, species composition tended to change due to nitrogen deposition and changes in the surrounding areas; for example, grasses became more abundant while the typical grassland species and those favoured by mowing decreased. Isolation, in turn, results from the intensification of agriculture: there are less traditionally managed areas, and the remaining meadows are more distant from each other. In Finland, the area of semi-natural meadows has declined so much and so quickly that isolation is presumably a serious threat to the preservation of their species composition. It has been estimated that the area of managed rural biotopes in Finland should be threefold compared to the situation in the 1990’s to preserve their species composition and species richness (Salminen & Kekäläinen 2000). Due to the isolation of meadows, rare plant species even in managed areas are at risk of extinction, as it was found in Switzerland (Fischer & Stöcklin 1997).

The implication of these previous and present restoration studies is that local species richness can be restored within the limits of the local species pool of the focal meadow as well as the habitats in its immediate vicinity (Fig 3). When grazing (or mowing) is introduced, the species richness of the focal community will slowly increase towards the limit of the local species pool (LSP), but it may not actually reach the level of the LSP because, for instance, a number of species may be lost from the meadow due to their intolerance of grazing, or because not all species included in the LSP have succeeded to invade the focal community within a given time. In Fig. 3, I have assumed that, after a given period of management, local species richness will reach some expected level, say $\text{expLSR} < \text{LSP}$, when mere grazing (or mowing) is used. If the aim is to increase species diversity above the LSP level, addition from the regional species pool (natural dispersal) or propagule addition (sowing) is needed. This also requires that management (grazing or mowing) will be continued because most of the new species would disappear via competitive exclusion if management were dropped.
Local species richness is influenced by the local species pool (LSP) and the regional species pool (RSP). By grazing (or mowing), the local species richness (LSR) could be increased to an expected level (expLSR). Addition from the regional species pool is needed to further increase diversity in the presence of grazing above LSP. For simplicity, I have here assumed that LSP and RSP remain constant over time.

4.2 Variation in grazing tolerance

4.2.1 Herbivory and competition shape compensatory responses

During the last 15 years, ecologists have explored alternative strategies of plant resistance to herbivores (Strauss & Agrawal 1999). It is increasingly considered that tolerance (ability to withstand and repair damage) could operate as an alternative strategy. It has been proposed that resistance and tolerance may represent mutually exclusive strategies in plant responses to herbivory (van der Meijden et al. 1988, Fineblum & Rausher 1995). In some circumstances grazing pressure may be so high that resistance is not a viable strategy, whereas tolerance is. However, in other conditions, natural selection may favour both high resistance and high tolerance at the same time (Rosenthal & Kotanen 1994, Mauricio et al. 1997, Tiffin & Rausher 1999). Both resistance and tolerance involve potential costs (for a review of models, see Lehtilä 1999). High tolerance to herbivory may help meadow plants to survive in managed habitats and gain benefit in relation to
grazing-susceptible taller species. The present findings indicate that many meadow herbs have rather high tolerance to simulated herbivory. The mechanisms behind this are discussed below.

Of the two proposed evolutionary interpretations of overcompensation, i.e., adaptation to predictable damage due to herbivory and adaptation to competition for light, adaptation to frequent and heavy herbivory seems unlikely in the three species of this study (III-V) because the best plant performance was achieved at low damage levels (apical damages, 10% biomass loss). Similarly, in *Brassica rapa*, when folivory by *Pieris rapae* was used, it was found that the best tolerance (reaction norm) was obtained at a 20% damage level (J. Lau, unpubl. data). The level of natural herbivory is possibly so low in these species that maximum tolerance is achieved at 10-20% apical or foliar damage levels. In contrast, plant fitness in overcompensating *Gentianella campestris* populations is maximal at a 50% damage level (IV, Huhta et al. 2000a). *Gentianella* species are dependent on the low sward that is maintained by grazing, for example. Therefore, it is likely that they have developed high tolerance to herbivory. In *Ipomopsis aggregata*, up to 95% biomass loss in the early season by deer browsing leads to overcompensation (Paige & Whitham 1987). Theoretical models suggest that selection favours overcompensation when the risk of being damaged is high, generally 50% or higher (van der Meijden 1990, Vail 1992, Tuomi et al. 1994, Nilsson et al. 1996a). Plants in an overcompensating population are characterised by apical dominance and unbranched architecture before any herbivore attack has taken place. Shoot damage removes apical inhibition, and suppressed meristems start to grow. This pattern has been observed in, for instance, *G. campestris* (Huhta et al. 2000a) and *Ipomopsis aggregata* (Paige & Whitham 1987). There may be occasional herbivory/mowing in most studied populations: low grazing intensity by cattle in *G. amarella* in Paltamo (IV), presumably insect herbivory in *E. strictum* (III) and mowing in *Euphrasia* populations (V). I am inclined to conclude that these infrequent events of damage could not have maintained such a strong selective pressure that they would have given shape to the shoot architecture of these species.

Another reason for overcompensation in the response to damage may be that plants have adapted to the intense above-ground competition for light or pollinator availability that maintains apical dominance and unbranched appearance. Overcompensation may be a manifestation of the cost of apical dominance in plants that are released from correlative inhibition after the removal of apical meristem (Aarssen & Irwin 1991, Aarssen 1995). This interpretation as an explanation for overcompensation is possible in the present species. These monocarpic species may share a common growth form that is characterized by fast vertical growth and unbranched architecture in the early season before the competitive species reach their full height. Plants repair the occasional instances of damage by effective use of uninitialized meristems for reproductive purposes in the upper parts of the stem. This is seen as slight overcompensation at small damage levels. In monocarpic species, overcompensation may also be related to their reproductive tactics (Fig. 4). For instance, strictly biennial species cannot postpone their development beyond the initiation of flowering. Thus, in response to damage, biennial species may, more than polycarpic species, invest the remaining resources and meristems in reproduction to maximize their fitness. Whether the compensatory investment by biennial species leads to over- or undercompensation may depend on the growth
conditions (Fig. 4). Delayed flowering is a potential cost of compensation (see paper III), and it may well be that, for polycarpic species, the best option is to avoid this cost by postponing reproduction to the next season, whereas biennial, as possibly other monocarpic, species do not have this option.

Fig. 4. Hypothetical bet-hedging scenario for compensatory growth in monocarpic species. It is assumed that, in response to grazing at the flowering stage, polycarpic species can postpone their reproductive effort to the next growing season, whereas strictly biennial and other monocarpic species cannot do that. It is also assumed that compensatory regrowth is associated with a potential cost in terms of delayed flowering and seed maturation. In unfavourable years, this may lead to poor reproductive success and undercompensation. In favourable years, the delay in flowering may not have any adverse effects on reproductive success and seed survival.

Plant architecture as well as the number and position of uninitialized meristems also shape the compensatory responses. Herbivores usually change plant architecture by
removing the apical meristem, which leads to the activation of previously suppressed lateral meristems. This is manifested as increased branching and may lead to bushy growth. In perennial woody species, repeated herbivory may result in highly branched, broom-like growth forms (Mopper et al. 1991). Increased branching as a tolerance mechanism has been found in many studies (Benner 1988, Lennartsson et al. 1998, Huhta et al. 2000b, Lortie & Aarssen 2000). In this study, too, clipping increased branching in *G. amarella* (IV) and *Euphrasia* (V). In *Erysimum*, nutrient-rich conditions in the common garden as such increased branching, but clipping did not increase it any further. In fact, when plants were fertilized, clipping decreased the number of branches (III). Meristem allocation is indeed linked to the resource status of the plant. When there are plenty of resources, the plant allocates its resources to growth and reproductive meristems. Accordingly, in resource-poor conditions (such as in severe light competition), the plant saves a part of its resources for later use and maintains many inactive (dormant) meristems (Bonser & Aarssen 2003). High apical dominance in low-resource conditions may arise from the fact that the plant has not enough resources for branching or reproduction (Bonser & Aarssen 2003). This might well explain why most of the individuals were unbranched in the natural population of *Erysimum* (III).

### 4.2.2 Grazing tolerance is dependent on growing conditions

There are two plant-herbivore theories that make conflicting predictions about how resource conditions affect the plant responses to herbivory. The continuum of responses model (or compensatory continuum hypothesis) presented by Maschinski and Whitham (1989) predicts that compensation is highest when there are plenty of resources available and little competition. In contrast, the growth rate model (Hilbert et al. 1981) postulates that plants growing at low resource levels (small relative growth rate) are most likely to be able to compensate for damage.

The results obtained with *Erysimum strictum* clearly supported the compensatory continuum (III). Plant growth and reproduction were improved by fertilization, but decreased by competition. Overcompensation was observed only in fertilized plants growing free of competition (III). This higher tolerance was not due to the reallocation of resources from roots to shoots because plants also overcompensated for root biomass in the absence of competition. In other studies where overcompensation was found, clipping increased both above- and below-ground biomass (Paige & Whitham 1987, Huhta et al. 2000a). The results with *Euphrasia* also supported the compensatory continuum, as slight overcompensation in fruit production was observed in 10% clipping when plants grew free from competing neighbours. Competition decreased plant fitness especially in the second year when all the 50% clipped plants died when growing in high swards (V). Hawkes & Sullivan (2001) suggested in their review that exact and overcompensation are more likely in high-resource conditions for monocots and in the presence of low resources for dicot herbs. In general, plants grow better in the presence of abundant resources or no herbivory, but the interaction of these two factors seems to be more complex (Hawkes & Sullivan 2001). The authors present that self-shading limitation will be greatest in ungrazed monocots growing at high resource levels (cf., McNaughton...
Herbivory decreases self-shading, which increases the amount of light received by the remaining tissues. Hawkes and Sullivan (2001) also proposed that the carbon-nutrient balance hypothesis (Bryant et al. 1983) and the light competition hypothesis (Irwin & Aarssen 1996) may explain better the responses observed in dicot herbs and woody plants than those seen in monocots. Plants growing at nutrient-rich sites are more likely to be carbon-limited, and herbivory is expected to increase carbon limitation. The light competition hypothesis predicts that tolerance will be greatest at intermediate resource levels. At high resource levels plants are more likely to be shaded by their neighbours, and at very low resource levels there may not be enough resources to fuel compensatory growth (Irwin & Aarssen 1996). This is in accordance with the results obtained on *Euphrasia* (V). These hemiparasites need a certain level of host resources but if the vegetation is too high, they are outcompeted for light (cf., van Hulst et al. 1987).

It seems that the compensatory capacities of polycarpic and monocarpic herbs differ in relation to resource availability. Many polycarpic dicot herbs are slow-growing and thrive on rather nutrient-poor soil. Short-term fertilization has, in fact, been observed to reduce the tolerance of three herbaceous perennials growing on poor soil (Hicks & Turkington 1999). Monocarpic herbs, often annuals or biennials, grow frequently at disturbed sites (ruderal strategy), where the soil is often nutrient-rich. The difference between perennial and annual/biennial species may also be linked to their different life-histories. Perennial species may use surplus resources for growth and storage and are not able to mobilize these stored reserves rapidly after damage. Monocarps, in contrast, use at flowering stage all the currently available resources for reproduction, and extra resources are likely to increase their reproduction. In this respect, the results on *Erysimum* supported this idea (III).

### 4.2.3 Ramets compete for resources in *Linaria* clone

In clonal plant species, intact ramets may support damaged ramets (e.g., due to herbivory) in the same clone. This has been observed in, for instance, *Clintonia borealis* (Ashmun et al. 1982), *Solidago canadensis* (Schmid et al. 1988) and *Glechoma hederacea* (Price et al. 1992). Damage can also lead to reintegration of independent ramets (Pitelka & Ashmun 1985). No such support was found in the present *Linaria* experiment, however (VI). This may be due to the growth strategy of the species. *Linaria* grows on habitats where various disturbance factors are common (shores, road verges, ruderal sites). It may be unprofitable for a clone to repair damaged shoots as this species easily forms new shoots via adventitious roots. Its growth strategy resembles that described by Pitelka & Ashmun (1985): in a spatially and temporally patchy environment, spreading to new sites and acropetal transport, i.e., from older parts to younger ramets, are favoured.

Even though intact ramets gave no support to damaged ramets, *L. vulgaris* clones showed clonal integration because ramet fates were not independent. The effects of simulated herbivory depended on what happened to the neighbours of the damaged ramet. Because the damaged target ramet could better compensate for the lost biomass when its neighbours had also encountered damage, sister ramets in a *Linaria* clone
compete for resources. The $^{13}$C tracer study suggested that they do not compete for carbon (at least in these conditions) but for other resources (water, nutrients) in the common root system. In *Solidago altissima*, it has also been found that sister ramets compete for nutrients in the common root system (Abrahamson *et al.* 1991). Similar within-plant competition for resources has also been seen between the branches of Scots pine (*Pinus sylvestris*, Honkanen & Haukioja 1994) as well as between the branches of a pea plant (*Pisum sativum*, hypothesis of branch competition presented by Sachs & Novoplansky 1997).

Defoliation and apex cutting also affect plant physiology. Defoliation increases the root-to-shoot ratio and decreases transpiration through foliage, and because many nutrients are moved by the gradient in the plant water potential (Marschner 1995), it may reduce the transpiratory drive of nutrient uptake. Apex cutting reduces auxin production, and because auxin is an important determinant of sink strength, apex removal decreases sink strength for phloem-transported metabolites, such as amino acids and sucrose. In line with the important role of auxin, the effect of mere apex removal was equally large as that of the removal of 2/3 of all leaves in the present $^{13}$C experiment (VI). Apex cutting increased carbon flow from the cut ramet to the root system. In many perennial plants, the net translocation of assimilated carbon is towards below-ground, where carbon is stored and consumed in the uptake of nutrients and water. Species with strong integration for carbon store large amounts of assimilates in their old rhizome system. Rhizomes also serve as overwintering organs.
5 Conclusions

The general implication of the two community-level experiments was that the structure of an abandoned/degraded meadow can be restored in a few years, but increased species richness may be more difficult to achieve. This is probably due to seed limitation, which can be expected to be common in Finland and many other countries because the remaining meadows are small and scattered in a landscape of modern agriculture, human settlement and forests. Therefore, I suggest that seed addition is needed in these areas to restore the former species diversity. Seeds belonging to the regional species pool, i.e., innate to the area, should be used.

The method and timing of management is vital to the outcome of restoration. Late mowing and late grazing are less effective than early mowing and grazing in changing an overgrown meadow towards a traditional one dominated by small-growing herbs and grasses. In the late summer, many tall-growing dominant herbs have already flowered and transported their resources to the below-ground parts, and hence late management merely serves to maintain the prevailing situation. Sheep grazing seemed to be suitable in the restoration of the present overgrown mesic meadow but some additional practices, e.g., mowing before grazing, might have given even better results. The traditional way to manage mesic meadows was to mow them in late July, after which animals were allowed to graze the aftermath. Grazing and mowing were not here compared in the same experiment, but it seems that both are useful management tools.

Based on simulated herbivory experiments on six species in the present thesis, I am inclined to assume that herbivory is not the primary evolutionary force that has shaped the growth patterns of these species. The studied monocarpic species may share a common growth form that enables effective reproduction in the presence of neighbouring plants. These plants allocate most resources to vertical growth instead of lateral branching. Plants are able to repair incidental damage by activating uninitialized meristems and changing allocation within the canopy. This may sometimes lead to slight overcompensation in terms of seed production. Consequently, the selection of an unbranched architecture in response to above-ground competition or to shortage of soil nutrients may well have contributed to the compensatory capacity of many monocarpic herbs. In other cases, however, adaptation to predictable damage may have been decisive, especially in species which are able to overcompensate in response to extensive shoot
damage and intensive grazing. The situation of perennial species may be more complex. For instance, clonal integration may help them to recover from herbivory. However, the results obtained with *Linaria* showed that a damaged ramet is not supported by intact neighbours in the same clone, but the two competed for below-ground resources. This is also related to the growth strategy of this species: when growing in disturbed habitats, it is more profitable to invest in new ramets and acropetal transport than in the maintenance of old ramets.

The present thesis showed that many small meadow herbs tolerate herbivory fairly well. Under management, they benefit in relation to taller species, which are more susceptible to damage. Grazing and early mowing gave promising results on the restoration of degraded semi-natural grassland habitats. However, we need more studies on the effects of varying degrees of damage and also on the frequency of damage in meadow plants. Such knowledge would be important in understanding the changes that occur in plant communities in response to grazing and mowing, and it would also help in planning and elaborating efficient restoration practices. Seed limitation seems to be an obstacle in restoring species diversity, and it is suggested that this could be overcome by seed addition measures.
References


