Grazing Regimes and Plant Reproduction in Semi-Natural Grasslands

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Abstract

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The dominating grazing regime in semi-natural grasslands today is continuous grazing throughout the season, and a high grazing pressure is often advised in order to avoid litter accumulation. Traditional management, on the other hand, included late mowing and grazing, which favoured plant flowering and seed production. This thesis studies the effects of alternative grazing regimes that may ecologically mimic traditional management. The ingoing papers examines: 1) Plant reproduction under late onset of grazing compared to continuous grazing; 2) The tradeoff between disturbance and competition for plant seed production and establishment; 3) Effects of increased flower density in late grazed grasslands on pollinator abundance, visitation rate, and pollen limitation; 4) The impact of landscape, habitat, population, and management on pollination, reproduction, and population structure of *Primula veris*. The studies were performed by using grazing and pollination experiments combined with estimates of habitat and landscape properties. Late grazing enhanced the fruit set without increasing the litter depth. The management effect for individual plant species depended mainly on the species' phenology of reproduction. Late grazing and 1-yr grazing interruption increased seed production linearly, but reduced seedling establishment as a threshold function. The net effect was an increased seedling density and, after six years, species density. Increased flower density in late grazing attracted more pollinators, but resulted in competition for pollinators among flowers. No pollen limitation was, however, found in two experimental species. Direct grazing of reproductive organs outweighed indirect effects on plant reproduction through effects on pollination. Reproduction and population structure of *P. veris* was mainly controlled by seedling establishment, pollen limitation, and direct grazing of fruits. No constant landscape effects were found. Grazed populations had high proportions of seedlings and juveniles due to high recruitment and mortality of adult plants, whereas ungrazed populations had higher proportions of adult plants due to low recruitment. The net effect was similar densities of young plants in grazed and ungrazed populations. Management regimes such as less intense grazing, late summer grazing, or late summer mowing would increase both seed production and establishment, thereby favouring populations of *P. veris*.

Keywords: flower density, fruit set, grassland conservation, litter, management, phenology, pollination, *Primula veris*, seed set, seedling recruitment

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Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Wissman, J., Lennartsson, T. & Jansson, H.-M. Timing of grazing and plant reproduction in semi-natural grasslands. *Submitted manuscript.*

II. Wissman, J. & Lennartsson, T. Grazing and plant recruitment in semi-natural grasslands - a tradeoff between competition and disturbance. *Manuscript.*

III. Wissman, J., Lennartsson, T. & Sjödin, N.E. Floral density and the facilitation of pollination – an empirical study. *Submitted manuscript.*

IV. Wissman, J. Reproduction and population structure of *Primula veris* L. (Primulaceae) in semi-natural grasslands – a landscape and management perspective. *Manuscript.*

As first author, for each paper I contributed with major parts of study set up, field work, data analysis, and preparing of the papers

Introduction

Background

A majority of the red listed flowering plants in Sweden and Europe are confined to the agricultural landscape, especially semi-natural grasslands i.e., unfertilized, uncultivated pastures and hay-meadows (Gärdenfors, 2000). Ceased (Fuller, 1987; Karlsson, 1984; Stanners & Bourdeau, 1995; Wolkinger & Plank, 1981) and/or suboptimal management (Brys *et al*., 2005; Ehrlén *et al*., 2005; Lennartsson & Oostermeijer, 2001) of semi-natural grasslands have been identified as the main threats to grassland species. Negative trends in grassland management are often results of intensified farming, leading to reduced agricultural activity and reduced use of grasslands in less productive regions (Bakker, 1989; Fuller, 1987; Kumm, 2002; Tamm, 1956). In order to preserve biodiversity and to maintain the traditionally managed landscape, governmental subsidies are granted for the farmers' management of unfertilised pastures and hay-meadows.

There is an increasing need to identify factors responsible for negative trends in species richness and to assess evidence-based management tools to prevent further decreases of threatened species in the agricultural as well as other landscape types (Pullin *et al*., 2004; Stewart *et al*., 2005). The recently (2003) founded Centre For Evidence-Based Conservation at the University of Birmingham (Great Britain) demonstrates that this is not an isolated issue to single countries but should be of general interest to conservationists (Pullin & Knight, 2001). For agricultural landscapes, further knowledge is needed concerning management criterions for plants and effects of different managements on plant interacting species, such as pollinators, insect herbivores, seed predators etc.

In this thesis I address some gaps in the knowledge of biodiversity conservation in semi-natural grasslands. I focus on the effects of different kinds of grazing regimes on plants and pollinating insects. Four different studies are presented. Paper I examines the effects on seed production of an alternative grazing regime (late grazing) which in contrast to the most common and recommended grazing regime (continuous grazing throughout the season), imply an ungrazed period in the first half of the season. This grazing regime to some extent imitates the traditional management of hay meadows. Paper II compares the effects of increased seed production with reduced establishment of seedlings due to increase in litter depth in three grazing regimes (continuous grazing, late grazing, and grazing with ungrazed years included). Paper III examines the effects of floral richness on pollination in late and continuous grazing, In Paper IV, finally, I study how population structure, reproduction and

recruitment in *Primula veris* L. are dependent of landscape parameters, differences between populations, and management.

The studies in the thesis are part of the cross-disciplinary project HagmarksMISTRA (Emanuelsson *et al*., 2001; Emanuelsson *et al*., 2003).

Objectives

Most European semi-natural grasslands depend on some kind of human-induced disturbance that prevent succession towards bush vegetation and eventually forest (Hansson & Fogelfors, 2000). Today, this disturbance is cattle grazing in c. 98 % of Sweden's semi-natural grasslands (Gustafson & Ahlén, 1996). Traditionally, however, most of the presently grazed grasslands were managed by mowing. In Sweden, the area of mowed grasslands decreased from 1,5 million to 2 500 hectares from year 1900 to 1995 (Gustafson & Ahlén, 1996; Morell, 2001). Since the late 18th century the total amount of area covered by semi-natural grasslands has decreased by about 90% (Hansson & Fogelfors, 2000).

Several studies have questioned the use of intense continuous grazing in species-rich grasslands that in many cases have a historical use as hay-meadows (Ehrlén *et al*., 2005; Garcia, 1992; Hansson & Fogelfors, 2000; Kruess & Tscharntke, 2002; Lennartsson, 2000; Lennartsson & Oostermeijer, 2001; Simán & Lennartsson, 1998). At ceased management, semi-natural grasslands inevitably turn into forest or shrubland and therefore, continuous grazing is better for grassland biodiversity than no grazing at all (Ekstam & Forshed, 1997; Pavlů *et al*., 2006; Pykälä *et al*., 2005). The consequences of the intense management regime that is prevailing today, is however much less known.

In management of semi-natural grasslands there are two main, opposing factors that determine the positive or negative effects on plant reproduction. The first is litter depth (e.g. Ekstam & Forshed, 1997; Huhta *et al*., 2001), which in most cases is negatively correlated with the germination of seeds and the establishment of seedlings (Hansson & Fogelfors, 2000; Jensen & Meyer, 2001; Jutila, 2003; Lennartsson & Oostermeijer, 2001). Litter depth in grassland is a result of the vegetation height, thus a low and intensively grazed vegetation supports germination (Endels *et al*., 2004; Hayes & Holl, 2003; Rebollo *et al*., 2001; Tilman, 1993). With decreasing vegetation height, the effect of the second factor, disturbance increases. Reduction of vegetation height and litter depth by intense grazing disturbance, necessarily leads to removal of reproductive parts (Ehrlén *et al*., 2005; Huhta *et al*., 2001).

The tradeoff between disturbance (establishment) and vegetation height/litter depth (seed production) is strongly depending on the

timing of disturbance in relation to the plants' phenology of reproduction (Akhalkatsi & Wagner, 1996; Simán & Lennartsson, 1998). Mowing in late July is an intense disturbance, but may allow higher seed production than equally intense grazing from May (Lennartsson & Oostermeijer, 2001). The use of cattle is naturally less expensive and time consuming than mowing, and will therefore probably remain as the major tool for grassland management. This raises the question: how can we use grazing animals in an optimal way to preserve biodiversity in the few semi-natural grasslands that are left?

Managed grasslands

Studies on grassland diversity seem surprisingly unanimous in ranking mowing as the most favourable management regime for biodiversity in nutrient-poor, semi-natural grasslands (Hansson & Fogelfors, 2000; Jensen & Meyer, 2001; Klimes & Klimesova, 2001; Kotiluoto, 1998; Krahulec *et al*., 2001; Lennartsson & Oostermeijer, 2001; Siman & Lennartsson, 1998; Stammel *et al*., 2003; Tamm, 1956). The second most favourable management method in several studies is grazing (Hansson & Fogelfors, 2000; Hellstrom *et al*., 2003; Kotiluoto, 1998; Krahulec *et al*., 2001; Olff & Ritchie, 1998; Stammel *et al*., 2003). Other management regimes are e.g. removal of lignified species and fire (Hansson & Fogelfors, 2000; Kotiluoto, 1998; Moog *et al*., 2002). Below, the first two types of disturbance, mowing and grazing, are discussed.

Mowing

Mowing suppresses tall-growing highly competitive species (Klimes & Klimesova, 2001), and thus has a positive effect on smaller plant species. This effect is due to both the removal of nutrients and the disturbance per se. Tall-growing species lose a larger proportion of their stalk and leafs than small plants when mowed (Tamm, 1956). Thus, both tall species that reproduce before the mowing time and low-growing, poorly competitive species can survive under this management. In addition, since seedlings always are low-growing, removal of vegetation favours the seedling establishment, which is especially important for biennial and annual seed-dispersed species (Lennartsson & Oostermeijer, 2001).

The predictability of the mowing management offers plants good opportunities to adapt to the disturbance (Crawley, 1987; Lennartsson *et al*., 1998). In the modern agricultural landscape it is still possible to find relict populations of plant species with special adaptations for mowing, usually early flowering. Traits that make plants less attractive to herbivores, such as unpalatability, are not

functional in mowing, whereas escape traits, such as rosette growth, may be adaptive in both management regimes.

Grazing

Grazing as disturbance differs from mowing by being more extended in time, usually being earlier in the season, and by less predictable but more selective. The disturbance is affected by a combination of plant adaptations to grazing and the foraging preferences by the grazers (Crawley, 1983). Additionally, grazers may affect the vegetation in pastures by uneven habitat utilisation which creates recruitment gaps (Rook *et al*., 2004; Wallis de Vries *et al*., 1998) and by dunging, urinating and trampling (Bokdam, 2003; Wallis de Vries *et al*., 1998).

Adaptations to grazing

This thesis and many of the recent studies of conservation in semi-natural grasslands concern grasslands in which human-induced management has driven the system for several hundred years. Even if natural herbivores are present (Edwards & Crawley, 1999), their effects are assumed to be small compared to the large impact of grazing cattle. Nevertheless, a large part of the knowledge about the mechanisms of animal-plant interactions and defence strategies in grassland plants is based on studies of defoliation and seed predation of insects and slugs rater than on grazing by larger mammals (Breadmore & Kirk, 1998; Hulme, 1996). As a consequence, much of the knowledge of plant adaptations and vegetation responses to herbivory is somewhat biased towards invertebrate herbivory.

It is often assumed that plant species either have evolved traits to tolerate disturbances (Damhoureyeh & Hartnett, 2002; Tiffin, 2000) or to be resistant against disturbances (Milchunas & Noy-Meir, 2002; Pilson, 2000; Sarmiento, 1992). Tolerance reduces the negative effects of damage once it occurs (Freeman *et al*., 2003; Juenger *et al*., 2000; Juenger & Lennartsson, 2000). Resistance, on the other hand, reduces the levels of damage, and may be divided in two sub-groups. Defence involves chemicals, spines, and thorns to make the plant unpalatable and to reduce herbivory (Fraser & Grime, 1999). Escape from damage can be achieved either by escaping in time (Veenendaal *et al*., 1996, timing of growth and reproduction matches periods with low risk of damage) or by escaping in space as e.g. low-growing rosettes (Juenger & Lennartsson, 2000; Diaz *et al*., 2001; Fernandez *et al*., 1993; Noymeir *et al*., 1989).

Timing of disturbance in relation to plant reproductive phenology is studied in Paper I. Phenology is strictly speaking – "…the study of periodic biological events; in practice often applied to periodic phenomena themselves, such as the lifetime pattern in an organism

of growth, development and reproduction in relation to the seasons" (Begon *et al*., 1996).

The plant phenology is under selection for several traits (Akhalkatsi & Wagner, 1996; Augspurger, 1981; Bishop & Schemske, 1998; Brody, 1997; Lennartsson, 1997a; Ollerton & Lack, 1998; Post *et al*., 2001). Several studies have described selection or adaptations as responses to e.g. seed predation (Bishop & Schemske, 1998; Englishloeb & Karban, 1992; Zimmerman, 1980a), pollination (Gross & Werner P.A., 1983; Kudo, 1993; Ollerton & Lack, 1998; Zimmerman, 1980b), the interaction between pollination and seed predation (Augspurger, 1981; Biere & Honders, 1996; Brody, 1997; Ollerton & Lack, 1998; Zimmerman, 1984), different kinds of disturbance (Fernandez *et al*., 1993; Lennartsson *et al*., 1997), and abiotic factors (Akhalkatsi & Wagner, 1996; Bishop & Schemske, 1998; Galen & Stanton, 1991).

In grazed grasslands the phenology of reproduction determines during how long time a reproductive plant is exposed to the risky environments before fulfilling reproduction (Lennartsson, 1997b). Stanton *et al*. (2000) show that *Sinapis arvensis* L. evolved towards an earlier flowering phenology and faster seed maturation when growing in non-favourable environments. They concluded that this was an evolutionary avoidance strategy to minimise the time in stress. Likewise, Juenger & Bergelson (1997) observed a selection for earlier flowering time in an experiment mimicking grazing by clipping of *Ipomopsis aggregata* (Pursh) V. Grant.

In a study of *Gentianella caucasea* Holub., Akhalkatsi & Wagner (1996) found that four populations growing within eight kilometres from each other developed different flowering times. The differences in flowering time between the populations were concluded to depend on both differences in the duration of the snow cover at different sites, but also to be the result of a directional selection for early flowering time in hay-meadows.

Another type of escape is poorly competing species that have developed an early flowering time to complete their reproduction before the surrounding vegetation grows tall (Klimes & Klimesova, 2001; Schindler *et al*., 2003).

Pollination in grasslands

The pollination of plants is both ecologically and economically important. In many regions, semi-natural grasslands are particularly important pollen and nectar sources in the landscape (Kruess & Tscharntke, 2002; Westrich, 1996) and may therefore indirectly affect the pollination of economically important crops (De Marco & Coelho, 2004; Ghazoul, 2005a; Ghazoul, 2005b; Klein *et al*., 2003; Steffan-Dewenter *et al*., 2005).

An increase of floral richness have been suggested as conservation tool for preserving specific pollinators, e.g. rare bee species (Westrich, 1996), pollen-limited plant species (e.g. Kwak & Bergman, 1996; Van Treuren *et al*., 1993), and to enhance pollination as ecosystem services (Allen-Wardell *et al*., 1998; Kearns *et al*., 1998). The increase of pollination in these cases is due to that higher flower richness can support higher numbers of pollinators. However, if pollination also increases in flower dense patches because they attract more pollinators (facilitation) or if flower density increases the competition for pollinators among flowers is poorly studied. Facilitation of pollination occurs when plants receive higher pollination rates when co-occurring with other flowering species and when increased pollination rates outweigh negative effects of competition for resources (Feldman *et al*., 2004; Laverty, 1992; Rathcke, 1988; Schemske, 1981; Sih & Baltus, 1987; Thomson, 1978). Pollination of plants can be facilitated by the presence of other species (Johnson *et al*., 2003) or by high densities of the species itself (Kearns *et al*., 1998; Sih & Baltus, 1987). The different grazing regimes studied in this thesis can be assumed to strongly influence the floral richness and thereby the pollination of the grassland plants.

Methods

The field work in paper I, II and III was performed in two grasslands, Harpsund (59°23'N 16°29'E) and Pustnäs (59°48'N 17°40'E) both in south-central Sweden. The vegetation at both sites is mainly of dry–mesic herb-rich *Agrostis capillaris* meadow type (Påhlsson, 1994). To examine effects of different grazing regimes the two grasslands were divided into one continuously grazed area (grazed from May to early October) and one late grazed area (grazed from mid-July to early October). Continuous and late grazing treatments were separated by fences until July 20, when the fences were opened and the cattle were allowed to move freely between the two treatments. Additionally, in paper III, metal cages were used to create ungrazed plots in Pustnäs whereas ungrazed years in Harpsund were created by altering grazing between two full-scale pastures, thus, areas remained ungrazed every second year.

Data collected at one site are in fact merely two random samples from two different areas, being treated in two different ways. Due to this, and due to the differences in data sampling design between the two grasslands, all analyses were performed for each grassland separately. Furthermore, the results must be interpreted acknowledging the possibility that the observed differences are area

effects rather than treatment effects. Large treatment areas are, on the other hand, necessary if we want to study natural grazing effects of the cattle.

In paper IV, the field work was performed in an 11 km^2 study landscape consisting of a mosaic of arable fields, pastures (old pastures and meadows), and forests. The landscape is situated on the western part of the island Selaön in Lake Mälaren, south-central Sweden (59°23'N 17°09'E). Reproduction and regeneration in terms of seed set and population properties of *Primula veris* L. was studied in 27 populations and two years in both grazed and ungrazed grasslands.

Summary of papers

Paper I. Timing of grazing and plant reproduction in semi-natural grasslands

The first study in the thesis aims at answering the following questions: How is plant fruit set and fruit production affected by traditional late management (from mid–July) of semi-natural grasslands compared to continuous grazing May to early October, which is the prevailing management in Sweden today? Can variation in fruit set be attributed to certain functional plant traits, e.g. phenology of reproduction?

The results illustrate that fruit production of vascular plants in semi-natural grasslands may be considerably enhanced by delaying the onset of grazing to late July, a more traditional management time in previously mowed grasslands (Figure 1). The fruit set was increased about four times in late grazing compared to continuous grazing. While fruit density increased during the season until the onset of grazing, the fruit density was kept low by a continuous removal of reproductive parts in the continuously grazed areas (Figure 1). The vegetation in the late grazed areas was grazed to approximately the same height as in continuous grazing by the end of the season. Thus, late grazing in this study had most likely no ecological significance in terms of litter accumulation.

Fruit production varied largely between species in the late grazing regime. This was mainly depending on each species' phenology of reproduction. Species having an early reproduction were more favoured by late grazing than late-flowering species. This is similar to the proposed effects of mowing on plants with different phenology (Simán & Lennartsson, 1998). Thus, the difference in grazing effect was not an effect of reproductive shoots escaping completely from

grazing, but of reproductive parts escaping long enough to set seeds. Early flowering has been suggested to be an adaptation to predictably late disturbances such as mowing (Wettstein, 1895; Warwick and Briggs, 1979; Karlsson, 1984; Zopfi, 1993), and this study proves the trait to be functional also under late grazing.

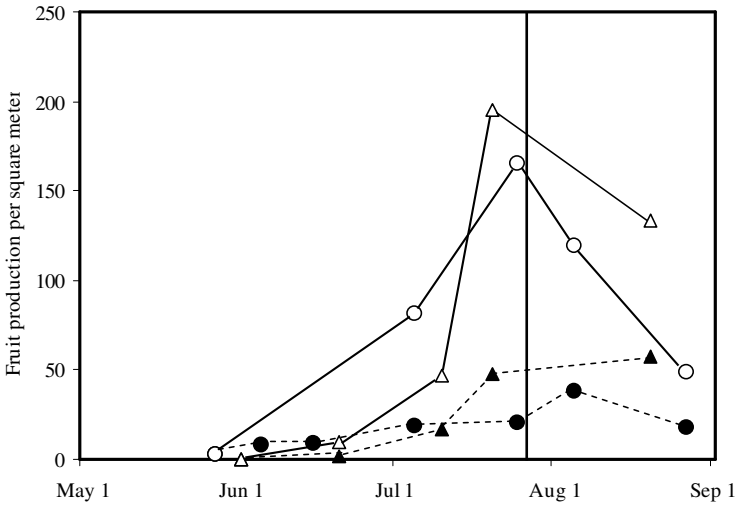

Figure 1. The total fruit production in continuously (closed symbols) and late grazed (open symbols) treatments in Harpsund 2002 (circles) and Pustnäs 2001 (triangles). Vertical line represents the onset of late grazing (onset of continuous gracing was in mid-May).

Tall vegetation before late onset of grazing can be expected to affect the reproduction of small plant species negatively, through competition for light (Jutila and Grace, 2002; Jutila, 2003). However, no such effect was found, as plant height was not correlated with relative fruit production. Neither were any correlation with Ellenberg light index found (Ellenberg *et al.,* 2001), which would have been expected if fruit set was affected by competition for light.

The results indicate that the most common management regime in Swedish semi-natural grasslands (intense, continuous grazing from May to September) considerably reduces plant reproduction. Further, late grazing can significantly increase fruit set, without any obvious negative effects in terms of competition and litter accumulation. Apart from the increased fruit set, the undisturbed early summer can be assumed to have positive effects on the diversity of phytophagous insects as well as nectar and pollen feeders. Poor supplies of pollen and nectar resources have been suggested to be an important threat to, for example, wild bees, of which several species are red listed (Pekkarinen, 1998; Pekkarinen, 1999; Gärdenfors, 2000; Linkowski *et al.,* 2004). The study indicates that the widespread shift from

traditional late management to modern continuous management may lead to considerable changes of vegetation composition and plant population viability in semi-natural grasslands, and that not only management method, but also timing of management is a significant component of this management change. Hence, the use of annual intense grazing as prescribed by subsidiary regulations should be used with care, in favour of more traditional timing and intensity of grazing.

Paper II. Grazing and plant recruitment in semi-natural grasslands – a trade-off between competition and disturbance

The second paper examines the relation between seed production and seedling establishment in three different grazing regimes; continuous grazing, late grazing and ungrazed years (every second year grazing). In the paper plant reproduction is assumed to be a tradeoff between seed production and seedling establishment, in turn a tradeoff between competition and disturbance. The study consists of three parts.

The first part focuses on fruit production and seedling density in three grazing regimes, representing different levels of competition and disturbance. The grazing regimes were: continuous grazing May–October (low competition, high disturbance, thin litter layer), one-year interruptions of grazing (high competition, no disturbance, thick litter layer), and grazing mid-July–October (high competition, late disturbance, moderate litter layer).

Specifically, we address the following questions: (1) To what extent can the fruit production be increased by alternative grazing regimes that reduce grazing intensity, but increase competition? (2) How much is the thickness of the litter layer increased by increasing the vegetation height, and how is the litter layer affecting the establishment of seedlings? (3) What is the net effect on seedling density of the potentially increased fruit production but reduced establishment in the alternative grazing regimes compared to continuous grazing?

The second study compares two of the management regimes, continuous grazing and late grazing, and addresses the following question: (4) How is the abundance of different plant species, and the species density in general, affected by six years of experimental grazing?

The third study is a clipping and sowing experiment on one model species, and addresses the questions: (5) What is the general relationship between damage intensity and (a) seed production (as an effect of competition and herbivory of reproductive organs), and (b) establishment of seedlings (as an effect of litter layer)?

In continuous grazing from May to October, c. 60 (in Pustnäs) and c. 50 (in Harpsund) mature fruits per m^2 were produced (see paper II for definition of mature reproductive units for specific species). Compared to continuous grazing, the fruit production was increased about seven times in Pustnäs by excluding the grassland from grazing during one season, and about 14 times in Harpsund. Also, by delaying the onset of grazing until late July, the fruit production was considerably increased, about five times in Pustnäs and four times in Harpsund. The litter layer was thicker in the alternative grazing regimes compared to the continuous grazing. Despite this, the net effect was an, about five times, increased seedling density in both alternative grazing regimes in Pustnäs and about three times in Harpsund, compared to continuous grazing.

Reduced and delayed disturbance intensity in late grazing thus enhanced plant reproduction compared to continuous grazing, showing that negative effects of disturbance were more important than negative effects of competition in the studied grasslands. After six years this had significantly increased the species richness in late grazing treatment. A number of species showed significantly increased frequencies, whereas no species had been significantly less common in late grazing.

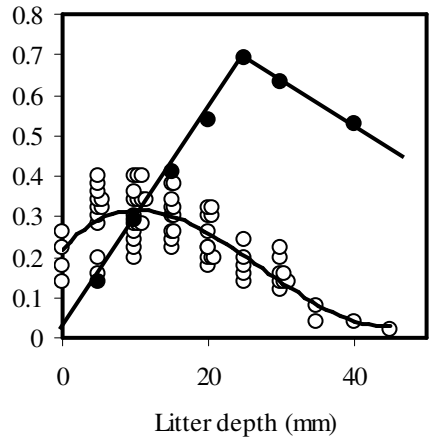

Figure 2. The probability of seedling establishment (open circles) and plant seed set (closed circles) as a function of litter depth in *Gentianella campestris*.

The detailed study of the relationship between disturbance and competition showed that disturbance was more important than competition for seed production of the model species, *Gentianella campestris* (Figure 2). In weak disturbance, the positive effects of reduced damage to the plants outweighed the negative effects of increased competition. The probability of seedling establishment was, on the other hand, only affected (negatively) by competition, in

terms of thicker litter layer (Figure 2). When disturbance was intense enough to damage the plants (vegetation height below the height of *G. campestris* plants), seed production followed a linearly decreasing function of the disturbance intensity. Seedling establishment, in contrast, was a threshold function of the disturbance intensity: the probability of establishment was not affected by the disturbance intensity (litter layer) until the disturbance was weak enough to produce a litter layer of 20–25 mm (Figure 2). Thus, for *G. campestris*, the seed production can be increased by reducing the grazing intensity up to 10–15 cm (resulting in 20–25 mm litter depth) before fruit maturation, without any effects on the probability of seedling establishment (Figure 2).

The three parts of the study explicitly show that plant reproduction can be increased by the two alternative grazing regimes, both reducing the disturbance intensity. It is not likely that the tested types of management have contrasting effects in other vegetation types, as long as litter is not accumulated to a thickness that inhibits seedling establishment.

Paper III. Floral density and facilitation of pollination – an empirical study

As concluded in the two papers above it is possible to enhance the floral richness in semi-natural grasslands by alternative grazing regimes. An enhancement of floral density leads naturally to a higher resource for pollinators. This may either lead to more visits per flower (facilitation) or fewer visits because the flowers compete for pollinators (competition).

Facilitation of pollination has been predicted by theoretical models and demonstrated in some empirical studies, all dealing with systems containing only two or very few species. The occurrence of facilitation in species-rich natural habitats remains more or less hypothetical, and recent theoretical models have suggested that narrow prerequisites may restrict the occurrence of such facilitation in nature. This paper studies how pollinator abundance, pollinator activity, and visitation rate studied responded to flower density in species rich semi-natural grasslands. The flower resources were manipulated by regulating the timing of grazing in the grassland.

Both pollinator abundance and pollinator activity increased with flower density, whereas the visitation rate per flower, i.e. the pollination frequency, showed a neutral or competitional response. Hence, no facilitation of pollination was detected in response to the overall flower density, neither in total nor for single species. Some species showed, however, a tendency of autofacilitation, i.e. increased visitation rate as response to con-specific flower density. The effect of flower density on local pollinator abundance and

visitation rate was not more pronounced at dates with low flower resource per pollinator.

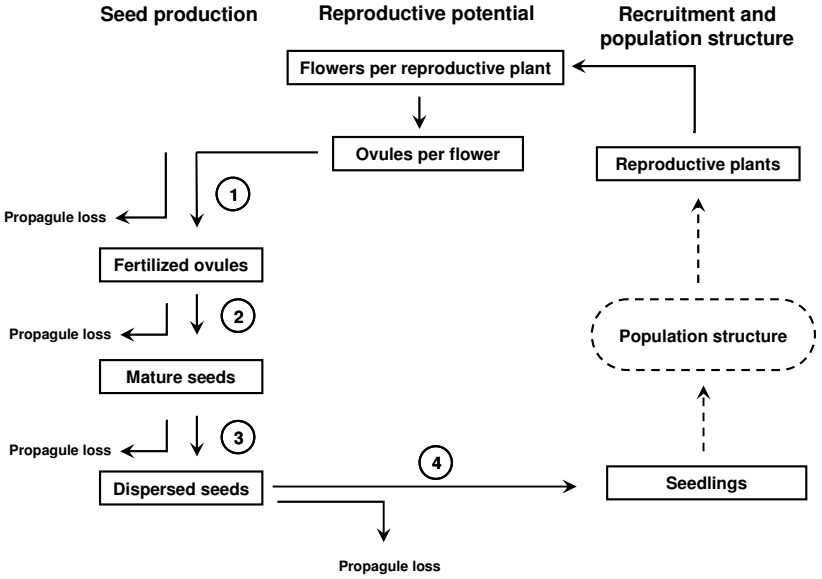

Figure 3. The life cycle of *Primula veris.* Number 1–4 represents transitions between life cycle stages. Propagule losses in each step are (1) insufficient pollination, (2) abortion of young seeds, (3) damage by grazers and herbivores, and (4) death of seeds after dispersal (due to e.g. seed predators or fungus infestations) or poor germination of seeds.

The flower resource increased when delaying the onset of grazing until mid-July, which increased local pollinator abundance, but had no effect on pollinator activity or visitation rate. Fruit set of two experimental species was not pollen limited in any of the grazing regimes, indicating full pollination independent of visitation rate. Fruit production was, however, strongly affected by grazing of reproductive organs, and such direct effects of grazing far outweighed indirect effects on plant reproduction through effects on pollination.

Paper IV. Reproduction and population structure of *Primula veris* L. (Primulaceae) in semi-natural grasslands – a landscape and management perspective

The fourth paper studies the transitions between a number of life stages related to seed production and recruitment of *Primula veris* L. (Figure 3). For each transition, the effects of grazing management, landscape and population characteristics were tested e.g. grazing regime, vegetation height, mean distance to other populations, quantity of adjacent grassland, and surrounding floral richness before

and during *P. veris* flowering. Life stages related to seed production were studied in 31 and 28 populations during 2003 and 2004. Recruitment of seedlings and population structure were examined in 11 populations in one year.

The transition of seedling recruitment (from dispersed seeds to seedlings) accounted for most of the propagule loss in the life cycle. This transition was mainly affected by litter depth. Relatively large propagule losses were also due to pollination limitation and direct grazing of fruits. The quantity of grasslands within 500 meters influenced pollination in 2004, but no landscape parameter was significantly influencing pollination in 2003. Thus, the landscape effect was not constant over time.

The population structure (the proportions of juveniles, vegetative adults and reproductive plants) was affected by management. Populations in grazed areas had high proportions of seedlings and juveniles due to high recruitment and mortality of adult plants, whereas ungrazed areas had higher proportions of adult plants due to low recruitment. The net effect was evened out between treatments and neither density of seedlings nor density of juveniles differed between grazed and ungrazed populations. However, the density of reproductive and vegetative plants was higher in ungrazed areas.

P. veris is decreasing in many parts of Europe (Brys *et al*., 2004; Kery *et al*., 2000). The decrease is often attributed to habitat destruction through ceased management. This study suggests that intense grazing may have similar net effects on *P. veris* populations as ceased management, as long as the grassland persists (Luoto *et al*., 2003; Pykälä *et al*., 2005). Grazed populations suffered from low seed set and high mortality of established plants, whereas ungrazed populations suffered from low recruitment. The phenology of *P. veris* indicates that the species is adapted to late summer mowing. Similar to other studies of grassland plants (e.g. Brys *et al*., 2005; Ehrlén *et al*., 2005; Eriksson & Ehrlén, 1992; Lennartsson & Oostermeijer, 2001) this study suggests that the most favourable management regimes for *P. veris* are those that remove litter but favour seed set, for example years without grazing, extensive grazing regimes, delayed grazing (late summer grazing), late summer mowing, or mixtures of the suggested regimes. Such extensive or delayed management regimes would also favour other grassland organisms depending on nectar, pollen, seeds, or undamaged plants.

Conclusions for conservation

All four studies indicate that intense continuous grazing, which is a common management regime today, may not be optimal for plant species diversity. This is explained both by the ecology of plant reproduction, and by historical management. The management of grasslands has for hundreds of years involved mowing, and in former hay meadows we often find the highest grassland biodiversity. In this thesis the use of alternative grazing regimes, late grazing and years without grazing are shown to have positive effects on grassland plants compared to continuous grazing, and can therefore be recommended as a substitute to mowing in those places where late season mowing is not possible. The effects are particularly strong for early reproducing plants. Late grazing increased the flower richness, which lead to increased pollinator density. This effect was, however, probably more important for the pollinators than for the plants, since no effects on visitation or pollen limitation were found. There is a tradeoff between seed production and establishment. The subsidiary system for grazing management aims at decreasing the litter layer and controlling that grazing is intense enough. However, in grasslands grazed to 5–10 cm of height already in July, plants are seed limited rather than recruitment limited. Weaker or later grazing would increase seed production without negative effects on recruitment, as long as the litter is not accumulated in a thick layer. For the plant species studied here, the threshold was 2–4 cm of litter.

In a historical perspective of grassland management the alternative management regimes in these studies are by no means odd or controversial. Continuous grazing of old may meadows is a young and non-historical management that may in many cases be suboptimal for biodiversity. Instead, site and vegetation type specific management is needed. The proposed grazing regimes in this thesis may not be useful for all types of vegetation or all regions, but the mechanisms and the important connection to the historical management may be general.

This thesis challenges the, in northern Europe, general use of intense and litter removing focused grassland managements and question if the managements are appropriate and positive for species diversity in these grasslands. To preserve or enhance grassland diversity conservationists have to acknowledge the processes that shaped the species rich semi-natural grasslands, thus managements that both reduces litter but also support seed production.

Svensk populärvetenskaplig sammanfattning

Gräsmarker har under hundratals år värderats högt för dess produktion av foder till betesdjuren. Allt eftersom intensifieringen av jordbruket ökat har brukningsregimen ändrats på nästan hela Sveriges gräsmarksareal. Generellt sett har den huvudsakliga betesmarken (utmarken) slutat betas och övergått till att vara skog, åkerholmar som betades på sensommaren efter att åkrarna skördades har övergivits och ängsmarken har övergått till åker, skog eller betesmark. Ängen har från att ha varit den vanligaste gräsmarkstypen, nästan försvunnit och uppgår nu till endast ca 2% av de ogödslade gräsmarkerna. Flera studier visar att slåtter är den brukningsmetod som är mest gynnsam för den biologiska mångfalden av kärlväxter, men den är också arbetskrävande. Detta är en av orsakerna till att produktionen av vinterfoder numer nästan uteslutande sker på åkermark (vallodling). Generellt sett är det på ängar eller marker som tidigare använts som slåttermark där man fortfarande hittar höga naturvärden knutna till gräsmark. Man kan fråga sig om man egentligen kan förvänta sig att bevara eller öka den biologiska mångfalden i gräsmarker utan att ta hänsyn till den tidigare hävden som skapat förutsättningar för de arter som man kan se idag.

Denna avhandling har som huvudmål att undersöka olika alternativa betesregimer och jämföra dem med ett relativt intensivt bete under hela säsongen (vilket är den vanligaste betesregimen idag). Generellt sett är den rådande skötselstrategin för betesmarker att ta bort så mycket vegetation som möjligt under säsongen för att på så sätt minska ansamling av förna som kan kväva vegetation och motverka att frön gror. Men, flera studier visar att många växtarter inte klarar sig så bra i denna typ av skötsel på grund av den minskade frösättningen. Bland dessa arter finns flera som är gynnade av slåtter, vilka i ängar kan blomma och producera frön tidigt på säsongen men i betade marker blir avbetade innan så sker).

De undersökta alternativa betesbehandlingarna är sent bete (efterliknar slåtter) samt betesfria år. I de olika studierna undersöks: I) Om frösättningen ökas i marker med sent betespåsläpp, vilka arter som gynnas av detta samt vilka egenskaper dessa växter har med avseende på blomningstidpunkt. II) Om antalet pollinatörer ökar när mängden blommor ökar och vad detta har för effekt på växterna. III) Om den ökade frösättningen i de alternativa betesregimerna (sent bete och betesfria år) också resulterar i fler nya groddplantor jämfört med kontinuerligt bete, eller om förnatjockleken i de alternativa betesregimerna ökar så mycket att nya plantor ändå inte kan bildas. Slutligen, vilka betningsintensiteter är gynnsamma för exempelarten fältgentiana (*Gentianella campestris*). IV) Vilka livsstadier hos populationer av gullviva (*Primula veris*) som är viktigast för dess

reproduktion, vad som påverkar dessa stadier och vilken betydelse för plantor av *P. veris* det har om de växer i betade eller obetade gräsmarker.

Studierna visar att frösättningen ökar avsevärt när man släpper på bete sent istället för tidigt på våren och att den positiva effekten av den alternativa behandlingen på enskilda arter är beroende av när de blommar. Tidigblommande växter gynnas mer av behandlingen än senblommande. Detta överensstämmer med vad man man får i traditionell slåtter där alla blommor slås av i mitten–slutet av juli. Vegetationshöjden vid säsongen var, trots det sena påsläppet, endast en cm högre i den sena betesbehandlingen vilket ur biologisk synvinkel knappast kan göra någon skillnad (se studie II).

Den andra studien visar att den ökade frösättningen också ger upphov till fler groddplantor. Det visade sig att fler grodplantor bildades ju mer frön som producerades. Detta var också fallet på ytor som var helt obetade. Vissa arter ökade på grund av den ökade frösättningen i de alternativa betesbehandlingarna (sent och betesfria år), medan det inte fanns några arter som signifikant minskade i de alternativa behandlingarna. Ett experiment med olika beteshöjder (vegetationen klipptes till olika höjder) visade att en ökning av frösättningen var viktigare för etableringen av groddplantor hos *G. campestris* än en reducering av förnadjupet. En vegetationshöjd över 10–15 cm resulterade dock i att etableringen minskade.

När blomningen ökar ökar också behovet av pollinatörer. I den tredje studien undersöktes hur antalet besök av pollinerande insekter och antalet pollinationsbesök per blomma är beroende av blomtätheten, både av enskilda arter och av alla arter. Antalet besökare per kvadratmeter ökade med blomtätheten i försöksrutorna vilket resulterade i att antalet besök per blomma inte skilde sig mellan rutorna. När effekten av pollination och bete jämfördes visade det sig att avbetningen av reproduktiva delar påverkade sannolikheten att en växt skall lyckas producera frukter i mycket större utsträckning än pollinationen i dessa marker.

Den fjärde studien visade att det finns flera viktiga skeenden i gräsmarksväxten *P. veris* livsstadier som har stor påverkan på möjligheterna för att ett fröämne skall utvecklas till en ny fullt utbildad växt. De skeenden där flest reproduktiva enheter (som kan ge upphov till en ny planta) försvann var vid pollination, avbetning av frukter och frööverlevnad efter spridning (frö till groddplanta). Antalet groddplantor per frö var starkt beroende av förnadjupet. När populationer i betade och obetade områden jämfördes hade de samma täthet av groddplantor och unga plantor. Detta beror på att negativa och positiva effekter av frösättning och vegetationshöjd (som resulterar i förna) tar ut varandra. Ett lågintensivt betestryck, bete sent på säsongen eller betesfria år föreslås som skötsel för att

förena positiva effekter av både hög frösättning och minskat förnadjup.

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