

Small-Scale Structures and Grazing Intensity in Semi-Natural Pastures

- Effects on Plants and Insects

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Abstract

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Semi-natural grasslands characterized by nutrient poor soils are among the most species-rich habitats in Europe and they harbour many red-listed species. The area of semi-natural grasslands has decreased drastically due to intensified land use or abandonment of farms. Ceased grazing can lead to encroachment of shrubs and trees and reduced plant species richness. The aim of this thesis is to study the effects of spatial structures and grazing intensity on plant assemblages, plant reproduction and phytophagous insects. Pastures with scattered trees and shrubs grazed by cattle in south central Sweden were used as study sites. The studied spatial structures were two trees: *Betula pendula*, *Pinus sylvestris*, two shrubs: *Juniperus communis*, *Rosa dumalis*, and dung rejects, grazing rejects (ungrazed patches) and grazed patches. Trees and shrubs are long-lived structures and they significantly influenced plant assemblages. For example, *R. dumalis* shrubs had a positive effect on tall, grazing sensitive species and a negative effect on short, less competitive species. Structures that could function as grazing refuges, i.e. shrubs, dung and grazing rejects increased plant reproduction. Grazing intensity also had a strong effect on plant reproduction and intensive grazing decreased the quantity of flowers and fruits. The effect of spatial structures on four plant species of the Fabaceae family and their seed predators was also studied. The four species varied in abundance between the structures but in shrub rejects and dung rejects reproduction was higher than in grazed patches. The available oviposition places, i.e. pods, for seed predators were considerable higher in shrub and dung rejects than in grazed patches. But no clear patterns in predation rate between structures were found. For two species long pods were more predated than short pods indicating oviposition selection at pod level. In conclusion, regulation of grazing intensity and shrub cover are important tools when managing pastures for both plants and phytophagous insects.

Key words: Apion, Bruchus, *Betula pendula*, functional traits, grazing refuge, *Juniperus communis*, *Pinus sylvestris*, reproduction, *Rosa dumalis*, seed predation.

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Contents

Introduction, 7

Background, 7

Effects of Grazing, 8

Shrubs and Trees, 8

Study Areas, 9

Study Species, 9

Objectives, 10

Hypothesis, 10

Summary of Papers, 11

Paper I, 11

Paper II, 12

Paper III, 13

Paper IV, 13

Populärvetenskaplig sammanfattning på svenska, 14

Acknowledgement, 16

References, 17

Appendix

Paper I-IV

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

- I. Pihlgren, A. & Lennartsson, T. Floral resources in semi-natural grasslands - significance of grazing intensity and spatial variation. *Manuscript.*
- II. Pihlgren, A. & Lennartsson, T. Shrub effects on herbs and grasses in semi-natural grasslands - positive, negative or neutral relationships? *Submitted.*
- III. Pihlgren, A. Effects of spatial structures on reproduction and seed predation of four legumes (Fabaceae) in semi-natural pastures. *Manuscript.*
- IV. Lenoir, L. & Pihlgren, A. 2006. Effects of grazing and ant/beetle interaction on seed production in the legume *Vicia sepium* in a seminatural grassland. *Ecological Entomology* 31, 601-607.

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Introduction

Background

To understand the Swedish agricultural landscape of today it is important to know something about traditional land use and how land use has changed throughout the history. From ca 2500BP to late nineteenth century the traditional land use system in Sweden was based on fenced inland with arable fields and fields for hay-making and outland with permanent grazing (Dahlström *et al.*, 2006). Trees and shrubs were often found in meadows and grasslands and they were used for pollarding, coppice and as fruit and berry trees and they were an important part of the traditional agricultural system (Peterson, 2005). During the past 150 years the area of semi-natural grassland in Sweden has decreased drastically due to transformation of hay-meadows into arable fields, plantation with coniferous forests, fertilization, abandonment and encroachment of bushes and deciduous trees (Ihse, 1995; Dahlström *et al.*, 2006). After the Second World War the modification of the agricultural landscape included enlargement of fields due to intensification and changed owner forms, i.e. small farms were aggregated into larger farms (Ihse, 1995). Around 1900 Sweden had approximately 1.5 million ha semi-natural hay-meadows and pastures (Mattson, 1985). In 2002-2004 the Swedish meadows and pastures were inventoried and 228 919 ha of semi-natural pastures and 6 661 ha of meadows were described (Jordbruksverket, 2005). In Europe, the area of semi-natural grasslands has decreased due to intensification of the agricultural land use, which has led to fodder production on arable land instead of in unfertilized grasslands (Hodgson *et al.*, 2005). Semi-natural grasslands characterized by nutrient poor and calcareous soils are among the most species rich habitats in north-western Europe (Kull & Zobel, 1991; Mortimer *et al.*, 1998; Pärtel & Zobel, 1999) and semi-natural grasslands in Sweden harbour a large proportion of the Swedish red-listed species (Gärdenfors, 2005).

The concern over the impact of agriculture on the environment in Europe has led to the introduction of agri-environmental schemes in countries both within and outside the European Union. The schemes vary between countries but the main objectives are to reduce nutrients and pesticides, protect biodiversity, restore landscapes and prevent rural depopulation (Kleijn & Sutherland, 2003). In Sweden there is a new agri-environmental scheme running for 2007-2013. One part concerns semi-natural grasslands, both pastures and hayfields, and farmers can receive payment for managing grasslands. However, the following general requirements have to be fulfilled; no accumulation of litter may occur, all trees and shrubs that indicate encroachment must be removed in the beginning of the period and thereafter be continuously removed until the end of the period. In general pastures shall be grazed every year, for hayfields the hay shall be cut every year and removed (Regeringskansliet, 2006). Grasslands with high conservation values can receive higher payment but then the farmer has to follow specific management requirements, for example what type of animals should be used or at what time grazing and or cutting shall be done (Regeringskansliet, 2006).

Effects of Grazing

Grazing increase plant diversity by consumption of competitive dominant species and by disturbance such as trampling, and thereby allowing smaller and less competitive species to coexist (Belsky, 1992; Crawley, 1997; Milchunas *et al.*, 1988; Olf & Ritchie, 1998; Rambo & Faeth, 1999; Rook *et al.*, 2004). Grazing also decreases the amount of litter in grasslands and thereby increase seedling establishment of species that are hampered by a thick litter layer (Jensen & Gutekunst, 2003). Grazing by large herbivores influence the vegetation dynamics and dietary choices play a major role in shaping the sward structure (Palmer *et al.*, 2004). Natural selection for maximizing the energy intake rate has led to preferences of particular plant species determined by their digestability and nutrient value (Bakker, 1989; Bullock & Marriot, 2000). Thus, cattle can maximize their daily intake by selecting patches with high digestibility (Bakker, 1989). In heterogeneous grasslands cattle avoid areas with low forage quality and alternate among areas with high forage quality, which leads to a mosaic of areas with low grazing pressure and areas with intense grazing (Bailey *et al.*, 1998). Herbivores avoid grazing near their own excreta and leave up to 40 cm of the vegetation near dung pats and thereby create temporal grazing refuges for plant species (Jones & Ratcliff, 1983; Shiyomi *et al.*, 1998). The concentration of nutrients in dung patches may increase growth rate, change survival and alter growth form of plants (Bullock & Marriot, 2000). Moreover, several studies have shown that herbivores avoid grazing near spiny or unpalatable plant species and thereby grazing-sensitive plants can gain protection from herbivory (Callaway, 1995; Callaway *et al.*, 2000; Hjalten & Price, 1997; Rebollo *et al.*, 2002; Olf & Ritchie, 1998; Rousset & Lepart, 2003). Intensive grazing can increase the forage value of grasslands by the creation of swards dominated by species tolerant to grazing (Cingolani *et al.*, 2005).

The relative effect of grazing on vegetation depends on the grazing pressure. At moderate grazing pressure the animals are able to graze selectively, which can lead to maximum biodiversity levels (Rook *et al.*, 2004). At high grazing pressures the possibility to graze selectively decreases compared to lower grazing pressures (Jerling & Andersson, 1982). For example, in salt-marsh vegetation dominated by *Festuca rubra*, small-scale patterns of tall and short *F. rubra* developed at intermediate stocking rate. In heavily grazed areas and in ungrazed areas no such patterns were found, indicating that the highest selectivity occurs at mediate grazing pressures (Berg *et al.*, 1997). Intense grazing can also decrease growth and reproduction of smaller, low-competitive species, like *Plantago maritima* and flowering success can be significantly higher in less grazed areas than in intensively grazed areas (Jerling & Andersson, 1982).

Shrubs and Trees

Abandonment of grasslands, or reduced grazing leads to accumulation of litter, higher abundance of dominant species, establishment of thorny shrubs like *Crataegus* spp., *Juniperus communis*, *Prunus spinosa*, *Rosa* spp. and *Rubus* spp. and eventually forest (Bailey *et al.*, 1998; Vera, 2000). Encroachment of shrubs like *Potentilla fruticosa* and *Juniperus communis*, result in reduced plant species richness (Rejmanek & Rosén, 1992). However, clearing of shrubs combined with reintroduced grazing are successful methods to increase plant species richness again

(Rosén & Bakker, 2005; Barbaro *et al.*, 2001). The effects of shrub encroachment on plant diversity are ambiguous. Some studies have demonstrated negative effect on plant diversity but other studies have shown that trees and shrubs in semi-natural grasslands are correlated with species richness of plants, insects and birds (Söderström *et al.*, 2001; Lindborg & Eriksson, 2004).

Trees and shrubs can influence the soil characters beneath their canopies; they can lower soil temperature and increase soil nutrients (Callaway *et al.*, 1991; Dahlgren *et al.*, 1997; Austad & Losvik, 1998; Chambers, 2001). Pine trees in grasslands can lower soil pH due to acid bark litter (Amiotti *et al.*, 2000) and oak trees and juniper shrubs can increase soil pH under their canopies compared to adjacent grassland (Dahlgren *et al.*, 1997; Chambers, 2001). Pine trees and juniper shrubs can also increase soil water content under their canopies (Chambers, 2001) and under dense canopies the abundance of light-demanding species decrease and are replaced by shade tolerant species (Anthelme *et al.*, 2001).

Study Areas

All study sites were selected in the County of Uppland, south central Sweden (between 59°44'-60°17'N and 17°20'-18°36'E). The mean precipitation in the region is 550 mm per year and the mean temperature is -4° in winter and 16.0° in summer (Vedin, 2005). In total 17 different semi-natural pastures were used as study sites and each pasture were used for one or more studies. The pastures were grazed by meat or dairy cattle and the vegetation was unfertilized and uncultivated. All pastures were inventoried in the "National survey of semi-natural meadows and pastures" during 2002-2004 and classified as valuable pastures (Persson, 2005). The vegetation was characterized as species rich *Agrostis capillaris* type (Påhlson, 1994) and common herbs and grasses were *Achillea millefolium*, *Festuca rubra*, *Galium verum* and *Poa pratensis*. Scattered trees of *Betula pendula*, *Picea abies* and *Pinus sylvestris* and shrubs of *Juniperus communis*, *Prunus spinosa* and *Rosa* spp. occurred in all grasslands. Most pastures included small forested areas and abandoned agricultural fields intermingled with species rich areas, often on hilly and stony parts of the pastures. The pastures probably have a long grazing history and for three sites this was confirmed by historical maps, 1850-60, where the areas were assigned as pastures.

Study Species

To study the effects of spatial structures and grazing intensity on insects, phytophagous insects were chosen since they depend on plants to complete their lifecycle and thereby are more likely to respond to different grazing intensities. We have chosen to work with leguminous plants of the Fabaceae family and their mono- and oligophagous seed predators, since the fruit is easy to collect and search for seed predators. Four legumes that are common in semi-natural pastures in Sweden were selected; *Lathyrus pratensis* L. (meadow vetchling), *Lotus corniculatus* L. (common bird's-foot-trefoil), *Vicia cracca* L. (tufted vetch) and *Vicia sepium* L. (bush vetch). The four species differ in growth forms and occur in slightly different habitats and they can be expected to respond differently to grazing intensity. Both *L. pratensis* and *V. cracca* are climbing herbs and they can occur in both open and shrubby habitats (Mitchley & Willems, 1995). *L. pratensis* flowers and set fruits in June-August and have up to 10 seeds per pod (own data). *V. cracca* flowers in

June-August and the pods have 4-8 seeds (Mossberg & Stenberg 2003). *V. sepium* have tendrils and occur mainly in shrubby habitats and flowers in early summer and the pod ripe with 3-7 seeds (Mossberg & Stenberg, 2003). *V. sepium* possess extra floral nectaries (EFN's) at the base of their leaves and the EFN's are visited by ants (Lenoir & Pihlgren, 2006). *L. corniculatus* occurs mainly in the open habitats and flowers continuously through the summer. The inflorescence has 1-5 flowers and the fruit is a pod with 1-30+ seeds (Ollerton & Lack, 1998). The most common seed predators on these legumes are weevils (*Apion* spp.) and seed beetles (*Bruchus* spp.). Weevils of the *Apion* genus are often host specific, for example *Apion loti* lives almost exclusively on *L. corniculatus* (Gønget, 1997). *Apion cerdo* is oligophagous on *Vicia* species but in Nordic countries *A. cerdo* particularly feed and oviposits on *V. cracca* and sometimes on *L. pratensis* (Gønget, 1997). *Apion craccae* is another seed predator on *V. cracca* and the beetle *Apion subulatum* mainly predate on *L. pratensis* seeds (Gønget, 1997). The seed beetle *Bruchus atomarius* is a generalist and oviposits on *Vicia sepium*, *Lathyrus linifolius* and *Lathyrus vernus* (Freude *et al*, 1981; Östergård & Ehrlen, 2005). In this region *V. sepium* seeds is mainly predated by *Bruchus atomarius* (Lenoir & Pihlgren, 2006). *Bruchus loti* oviposits both on *L. corniculatus* and on *Lathyrus* species (Freude *et al*, 1981).

Adult weevils feed on the host plant and the fertile females search young pods and lay their eggs between the seeds. After 4-6 days the larvae hatch and penetrate a seed which it eats out and then pupates within the seed (Gønget, 1997). When the beetle emerges, it eats its way out of the pod wall. Weevil larva can be parasitized by Hymenoptera.

Objectives

The aim of this thesis is to increase the knowledge about spatial structure like trees, shrubs, dung pats, grazing rejects and grazed patches and how they influence plant assemblages, plant reproduction and phytophagous insects. The purpose is also to study how spatial structures influence grazing selectivity of grazing animals and how grazing in turn form the vegetation. The aim is also to study how grazing intensity affect plant reproduction and the abundance of phytophagous insects.

Hypothesis

Trees and shrubs are long-lived structures compared to dung pats and grazing rejects and can therefore be expected to influence plant assemblages. *R. dumalis* shrubs can also, due to their spiny branches, function as grazing refuges where animals avoid grazing and thereby allowing plant reproduction to be higher than in surrounding grazed patches. Plants with different functional traits such as plant height, growth form or seed weight were expected to respond differently to presence of shrubs and to grazing. Small plants were expected to tolerate grazing better than tall species and tall species were expected to be better competitors than short species.

Trees can not function as grazing refuges and were not expected to increase plant reproduction. Beside long-lived trees and shrubs, there are temporary structures like dung rejects and grazing rejects that can increase plant reproduction.

Temporary structures are not likely to be persistent long enough to alter plant species composition. But temporary grazing rejects are likely to influence plant reproduction. Therefore the temporary structures; dung reject, grazing reject and grazed patch were included in the studies. Beside plant species, insects that are dependent on plant structures such as flowers and seeds for completing their life cycle can have an advantage in grazing refuges (Morris, 1967; Morris, 2000). Therefore phytophagous insects were expected to choose oviposition places in grazing refuges more frequently than in grazed patches.

The quantity of grazing rejects and grazed patches is probably a function of grazing intensity with fewer grazing rejects in intensively grazed pastures than in low-intensively grazed sites. The importance of shrub rejects may also vary with grazing intensity.

Summary of Papers

The effects of trees, shrubs, spatial structures and grazing intensity on plant species composition and plant reproduction were studied in paper I. The effects of *Rosa dumalis* shrubs on plant assemblages were studied in paper II. Effects of spatial structures and grazing on four legumes and their seed predators were studied in paper III. The effects of grazing and ant/seed predator interactions on seed production in *Vicia sepium* were studied in paper IV.

Paper I

Semi-natural grasslands depend on regular disturbance like grazing or mowing to counteract succession towards tall, species poor vegetation, scrubland and eventually forest (Vera, 2000). However, many grass sward plants depend on grazing refuges for reproduction and many insects use flowers and seeds for feeding and oviposition (Morris, 1967; Milchunas & Noy-Meir, 2002). When managing for preservation of biodiversity, the aim must be a disturbance regime that counteract succession but allow reproduction of plants and insect.

Spiny shrubs and dung pats may function as grazing refuges, since grazing animals avoid grazing near their own excreta and near spiny species (Bakker *et al.*, 2004; Rousset & Lepart, 2002). Temporary grazing refuges are created by selective grazing and dietary choices by grazing animals (Rook *et al.*, 2004). Long-lived or permanent structures like trees and shrubs were expected to influence plant species composition but not temporary structures like dung pats, grazing rejects and grazed patches.

The aim of this study was to examine the effect of grazing intensity and density of spatial structure on plant reproduction and species composition.

The study was performed in 14 pastures with different grazing intensities and the studied structures were; *Betula pendula*, *Pinus sylvestris*, *Juniperus communis*, *Rosa dumalis*, dung pats, grazing rejects and grazed patches. Plant abundance and number of reproductive units were counted in 15 plots, 50 x 50 cm, per structure and site. Vegetation height was also measured in each plot. The results showed that vegetation height and number of fertile shoots were correlated and reproduction were higher in grazing rejects, near dung pats and near shrubs than in grazed patches and under trees. This indicates that shrubs, but not trees, can function as partial grazing

refugees. Trees and shrubs also influenced species composition but not temporary structures. The results were used to model the effect of three different grazing intensities with three different shrub covers on plant reproduction. The simulation showed that grazing intensity was more important for plant reproduction than shrub cover due to the strong effect on the quantity of grazing rejects. Trees, shrubs, vegetation height and grazed patches affected plant composition but not dung pats and grazing rejects.

Grazing also affected the proportion of grazed and ungrazed patches in the vegetation and in intensively grazed pastures almost no grazing rejects were present in August.

Paper II

In this study the effects of *R. dumalis* shrubs on plant species composition, plant reproduction and seedling establishment were investigated. Shrubs can function as grazing refugees where cattle avoid grazing and thereby plant reproduction is higher than in the surrounding grassland (Callaway, 1995; Rousset & Lepart, 2003). Shrubs may also have negative effect on grasslands plants due to deeper litter layer and reduced light availability (Jensen & Gutekunst, 2003; Rejmanek & Rosén, 1992; Einarsson & Milberg, 1999). Different plant species were expected to react in a positive, negative or neutral way to shrubs. The relationships between plants and shrubs were tested if they could be attributed to functional traits like plant height, Ellenberg value, growth form, Raunkiaer life form or seed weight (Ellenberg *et al.*, 1991; Müller-Schneider, 1986; Lid, 1985).

The study was performed in three pastures and plant abundance and plant reproduction was estimated in plots placed at different distances from shrubs. Vegetation height and litter depth were measured in all plots. At one locality seedlings of herbs and sedges were counted per plot.

R. dumalis shrubs did not affect plant species richness and between 14-30% of the species showed a positive relationship with shrubs and between 8-16% showed a negative relationship, and most species were neutral to shrubs. The shrubs functioned as grazing refugees with taller vegetation and deeper litter layer than in the open grassland. The reproductive success was highest in shrubs and decreased with distance to shrub. However seedling establishment correlated negatively with litter depth and seedling density peaked between 60 and 90 cm from the shrub. Tall species and grasses were more abundant in shrubs than short species and herbs. No difference in life form or growth form was found between plants with high shrub association and plants with low shrub association. In one pasture light demanding species avoided shrubs and in one pasture species with heavy seed were more common in shrubs.

Many of the species that showed a positive relationship with shrubs are considered to be grazing sensitive, for example, *Anthoxantum odoratum*, *Campanula persicifolia* and *Dechampsia flexuosa* (Svensson & Glimskär, 1990; Hanson & Fogelfors, 2000; Wahlman & Milberg, 2002). Many species that were negatively influenced by shrubs were short species that are less competitive and more grazing resistant than taller species (Diaz *et al.*, 2001). The establishment of seedlings showed a slightly different pattern than the adult plants and the effects of shrubs varied between life stages. Overall, the net effects of *R. dumalis* shrubs on species diversity and species abundance were neutral but the effects on reproduction and seedling density were

positive. The increased flower and fruit production near shrub can also be important for other organisms, like insects feeding on pollen, nectar and seeds (Bergman, 2001; Potts *et al.*, 2003)

Paper III

The effects of four spatial structures, *Rosa dumalis* shrubs, dung pats, grazing rejects and grazed patches, were studied on the abundance, flowering, fruiting and seed-predation for four legumes: *Lathyrus pratensis*, *Lotus corniculatus*, *Vicia cracca* and *Vicia sepium*. The study was performed in seven pastures with different grazing intensities. Abundance and number of flowers and pods was counted in 160 plots per pasture. Each plot was classified as one of the four structures in both June and August and the change in cover was calculated. Vegetation height was measured in each plot. When the pods were mature they were collected, dried and then examined with respect to pod length, number of seeds, aborted seeds and ovules under a compound microscope. Each seed was searched for seed predators and classified as predated or unpredated and the seed predators were determined to species level using Gønget (1997).

In general the four species varied in abundance between structures, and flowering and fruiting were higher in rejects than in grazed patches. *L. pratensis* was more abundant in rejects than in grazed patches and the flowering and fruiting was highest in dung rejects. *L. corniculatus* was most abundant in dung rejects and in grazed patches, and the reproduction was highest in dung rejects. *L. corniculatus* was the only species positively affected by grazed patches and in general short species are more resistant to grazing than tall species (Diaz *et al.*, 2001; Cingolani *et al.*, 2005). *V. cracca* did not differ in abundance between structures but reproduction was higher in rejects than in grazed patches. *V. sepium* occurred almost only in rose shrubs but reproduction did not differ between the structures. The available resources for seed predators were higher in dung pats and rose shrub than in grazing rejects and grazed patches at the end of the summer. Too few pods could be collected in the grazed patches and predation rates were only compared between rejects and predation rate did not differ between rejects. Predation rate was higher in long pods than short pods for *L. pratensis*, but no difference was found for the other species. Furthermore seed set varied with vegetation height for two species and *L. pratensis* had higher seed set in short vegetation and *V. cracca* in tall vegetation. In conclusion, by lowering grazing intensity and/or increase the density of shrubs, plant reproduction and thereby seed predator density can be increased.

Paper IV

In this study the interactions between ants and seed predators and the effect on seed production in *V. sepium* were studied. These interactions were studied in both grazed and ungrazed conditions. It has been shown that ants can protect host plants by preying on arthropods herbivores or by interrupting their oviposition or feeding (Koptur & Lawton, 1988; Oliveira, 1997). We hypothesize that ants are attracted to extra floral nectaris (EFN's) and that ants in return protect *V. sepium* plants from being attacked by seed predators. To test our hypothesis we applied four different treatments on a total of 240 *V. sepium* plants; i) EFN's were removed; ii) ants were prevented from reaching the plant by applying sticky glue on the stalks; iii) both EFN's were removed and sticky glue was added; iv) no treatment was

applied. The experiment was set up in both grazed plots and in cages where grazing was prevented. Plant height was measured and number of buds, flowers and pods were counted for all plants. The number of visiting ants and seed predators were counted twice a week. The effect of *R. dumalis* shrubs on *V. sepium* plants and the interactions between ants and beetles were also studied by comparing plant under *Rosa dumalis* shrubs with plants in grassland plots. The results from the ant experiment showed that ants were attracted to EFN's, but presence of ant did not decrease the predation rate by the main seed predator, *Bruchus atomarius*. Grazing reduced plant height, the number of buds, flowers and pods but seed set was higher in grazed patches than in cages. Ant activity was not influenced by grazing, but ants were most active when the plants were flowering, i.e. early in the summer and lower when pods had developed. *B. atomarius* oviposits on the pods and not on flowers, thus the difference in timing in ant-beetle abundance can be one reason why no effect on seed predation by ants was found. In general, *B. atomarius* selected long pods with many seeds more frequently than short pods with few seeds for oviposition. *V. sepium* plants growing in rose shrubs were taller than plants growing in grasslands plots but no difference in flowering or fruiting was found. However, pods were shorter and had fewer ovules and thereby higher seed set than plants in grassland plots. No difference in predation rate was found between shrubs and grassland plots. The predation rate was overall higher in the experimental plots than in shrub or grassland plots. This may be due to more conspicuous host plant since vegetation was weeded around the experimental plants but not in the shrubs or grassland plots. Interaction between plants and insects are variable and depend on several ecological factors like resource limitation, insect levels and timing. However, it remains to discover if *V. sepium* benefits from EFN's.

Populärvetenskaplig sammanfattning på svenska

Det traditionella jordbruket i Sverige fram till slutet av artonhundratalet bestod av inägor med åkrar och ängar och utmark där djuren betade. Träd och buskar var en viktig del av systemet och de användes bl.a. för lövtäckt, till skottskog och som frukt- och bärträd. Under de senaste 150 åren har andelen naturbetesmark minskat drastiskt p.g.a. intensifierad markanvändning, gödsling, skogsplantering och igenväxning. Naturbetesmarker är näringsfattiga och artrika habitat som hyser många rödlistade arter.

Naturbetesmarker är beroende av störning som bete eller slåtter och betande djur ökar växtrikedomen genom att minska mängden dominanta arter och genom att skapa störning med tramp. Bete minskar mängden förna och ökar därmed etableringen av arter som inte kan gro i tjock förna. Betesdjur påverkar också vegetationen genom att beta vegetation med bra kvalitet och undvika vegetation med dålig kvalitet eller osmakliga arter. Betesdjurens val av föda skapar därmed en blandning av rator och betade fläckar. Betesdjur undviker också att beta nära mockor eller taggiga arter som rosbuskar. Rosbuskar och mockor skapar på så sätt betesrefuger där växter kan blomma och sätta frö. Effekterna av bete beror av betesintensiteten och ett högt betetryck minskar växters möjlighet till reproduktion. Ett svagt bete kan leda till igenväxning av träd och buskar med minskad artrikedom som följd. Men förekomsten av enskilda träd och buskar kan också ha en positiv effekt på växter,

insekter och fåglar.

Studierna har genomförts i flera olika naturbetesmarker som ligger i olika delar av Uppland. Markerna är upptagna i "Ängs- och hagmarksinventeringen" som ogödslade naturbetesmarker med höga floristiska värden.

Syftet med avhandlingen är att studera effekten av rumsliga strukturer som träd och buskar på artsammansättning och reproduktion hos växter. Syftet är också att studera hur rumsliga strukturer i kombination med olika betestryck påverkar vegetationsstrukturen med betade fläckar och rator och därmed också växters och insekters reproduktion.

Som studiearter har fyra ärtväxter valts; gulvial, käringtand, kråkvicker och häckvicker. De fyra arterna skiljer sig åt i växtsätt och var de förekommer i naturbetesmarker. Gulvial, kråkvicker och häckvicker har klängen att klättra med och kan förekomma i buskar. Käringtand förekommer oftast i öppna fläckar i en betesmark. De fyra växterna besöks av olika skalbaggar som vivlar och fröbaggar. De vuxna skalbagarna äter på värdväxten och honorna lägger sina ägg på eller i ärtskidan. Larverna lever av fröna innan de förpuppas och kläcks till nya skalbaggar.

Häckvicker har också nektarier vid bladbasen som utsöndrar nektar. Nektarierna besöks av myror och därför valdes den arten ut för en studie om interaktioner mellan värdväxt, myror och fröpredatorer.

I den första studien studerades hur sju olika rumsliga strukturer; björk, tall, en, nyponros, komockor, rator och betade fläckar påverkade växters förekomst och reproduktion. Resultaten visade att långlivade strukturer som träd och buskar påverkade artsammansättningen i vegetationen men inte temporära strukturer som komockor, rator eller betade fläckar. Blomning och frösättning var högre i strukturer som kan fungera som betesrefuger; buskar, komockor och rator än under träd och i betade fläckar. Växter hade också fler blommor och frukter i hög vegetation än i låg vegetation. Resultaten användes också till en modell som visade att betestryck var viktigare än buskar för växters reproduktion eftersom betesintensitet starkt påverkar mängden rator i en betesmark.

I den andra studien studerades effekten av rosbuskar på artsammansättning, växters reproduktion och groddplantsetablering. Rosbuskar påverkade inte antalet arter, men artsammansättningen skilde sig från öppen gräsmark. Högväxta och beteskänsliga arter som stor blåklocka och ängshavre var vanligare i buskar än i öppen mark och lågväxta och beteståligen arter som röllika, vitklöver och rödven var vanligare i öppna fläckar. Många arter var också lika vanliga i buskar som utanför. Buskarna fungerade som betesrefuger med högre vegetation och mer förna än i betade fläckar. Blomning och fruktsättning var högst i buskar och minskade med avståndet från busken. Etablering av groddplantor påverkades negativt av den tjocka förnan i buskar och flest groddplantor hittades mellan 60-90 cm från buskarna. Som sammanfattning kan man säga att effekten av rosbuskar på artsammansättningen var neutral och effekterna på växters reproduktion var positiv.

I den tredje studien undersöktes hur fyra rumsliga strukturer, rosbuskar, mockor, rator och betade fläckar påverkade förekomst, blomning, frösättning och fröpredation hos fyra ärtväxter. De fyra ärtväxterna var gulvial, häckvicker, kråkvicker och käringtand. Studien genomfördes i sju betesmarker med olika betestryck. Förekomst, antal blommor och antal baljor räknades i 160 rutor per lokal och i varje ruta mättes vegetationshöjden. Varje ruta klassades som en av de fyra

strukturerna. När baljorna var mogna, samlades de in och undersöktes under lupp. Baljlängd och antal frön per balja räknades, liksom antalet frön som var angripna av fröpredatorer. De fyra arterna varierade i förekomst mellan strukturerna och gulvial var vanligast i komocksator och i betade fläckar. Häckvicker var vanligast i rosbuskar och käringtand i betade fläckar och komocksator. Kråkvicker var lika vanlig i alla strukturer. Generellt var antalet blommor och frukter högre i rosor och komocksator än i rator och betade fläckar. Antalet tillgängliga baljor för fröpredatorer var därmed högst i rosor och i komocksator. Dock kunde ingen skillnad i predationsgrad mellan rosor, rator och komockor hittas. Men för gulvial var långa baljor, mer angripna än korta baljor men ingen sådan trend fanns för de andra tre arterna. Sammanfattningsvis var rosor och komockor viktiga för ärtväxternas reproduktion och för att skapa tillgängliga baljor för fröpredatorerna. Genom att reglera betestryck och mängd buskar kan man påverka arters frösättning och därmed även mängden fröpredatorer.

I den sista studien studerades effekten av interaktioner mellan myror och fröpredatorer på fröproduktionen hos häckvicker. Interaktionerna studerades både i betade fläckar och i burar där betesdjuren inte kom åt att beta. För att testa om myror kunde försvara häckvickerplantor från att attackeras av fröbaggar och i belöning få nektar från nektarier i bladvecken så sattes ett experiment med fyra olika behandlingar upp på totalt 240 plantor. Behandlingarna var 1) nektarierna togs bort, 2) myrorna hindrades från att besöka plantorna med hjälp av kladdigt lim, 3) både nektarier togs bort och kladdigt lim sattes dit, 4) ingen behandling. Växthöjd mättes och antal blommor, frukter och antal besökande myror och fröbaggar räknades två gånger i veckan. Resultatet visade att myror besökte nektarierna men de försvarade inte häckvickerplantorna mot fröpredatorer. Det kan förklaras av att myraktiviteten var högst tidigt på sommaren när plantorna blommade och lägre när frukterna hade utvecklats och fröbyggarna lägger sina ägg. Bete hade ingen effekt på interaktionerna men minskade dock mängden blommor och frukter kraftigt. Fröbyggarna lade oftare sina ägg på långa baljor med många frön än på korta baljor med få frön.

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