

## Research Article

# The Effect of Timing of Grassland Management on Plant Reproduction

**Tommy Lennartsson, Jörgen Wissman, and Hanna-Märtha Bergström**

*Swedish Biodiversity Centre, Swedish University of Agricultural Sciences, P.O. Box 7007, 750 07 Uppsala, Sweden*

Correspondence should be addressed to Tommy Lennartsson, tommy.lennartsson@slu.se

Received 15 August 2011; Accepted 4 December 2011

Academic Editor: Andrew Denham

Copyright © 2012 Tommy Lennartsson et al. This is an open access article distributed under the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Seminatural grasslands are maintained by regular anthropogenic disturbance, usually grazing or mowing. Management action late in the growing season was historically more common than today. Two experimental grazing regimes, continuous stocking from May to September and late-onset grazing from mid-July, were compared in two Swedish grasslands. Effects on flowering and fruit production were studied and related to plant functional traits. Change in vegetation composition over six years was analysed in one grassland. Delayed onset of grazing enhanced fruit production up to four times. Phenology of reproduction was the most important plant trait explaining differences in reproduction among species. Diversity of vascular plant species was higher after six years of late-onset grazing. No differences in vegetation height or proportion of grazed shoots were found by the end of the season. The results suggest that early reproduction may function as an escape from damage and that late onset of grazing may be used as a substitute for labour-intensive traditional mowing.

## 1. Introduction

Nonwooded habitats harbour a large proportion of the biodiversity in many temperate regions. High light influx favours small species of plants and species-rich vegetation [1, 2]. This vegetation together with favourable microclimate forms a rich fauna of invertebrates, and both the vegetation and the lower fauna serve as a resource base for higher animals. One group of nonwooded habitats, particularly important to biodiversity, is semi-natural grasslands, that is, unfertilized, uncultivated grasslands, in which anthropogenic disturbances, usually grazing or mowing, are essential or important for keeping the habitats open [3]. In the historical landscape, such grasslands constituted a necessary nutrient base for agriculture and were managed for production of hay and pasture. In the modern landscape, they are usually managed for conservation purposes.

Abandonment of semi-natural grasslands has been identified as a major threat to the European flora and fauna [4, 5]. Most countries in Western Europe have lost more than 95% of their original grassland areas, for example, Sweden [6] and the UK [7]. The unfavourable conservation status of

semi-natural grasslands is indicated by the high numbers of red-listed species confined to such ecosystems [8]. Grassland species are threatened both by ceased management and by insufficient management quality. The latter is partly due to the fact that the present management methods differ considerably from the historical management that has formed the rich grassland biodiversity, for example, in terms of type, timing, and intensity of management [9]. While cessation of management has been generally acknowledged as an important cause of the decline of grassland biodiversity [4], suboptimal management of the remaining grasslands has attracted less attention [10]. An increased focus on management quality may be motivated since as grassland areas become reduced and fragmented, it becomes increasingly important to optimise management of the remaining patches.

In order to obtain such optimal management, we can manipulate the type, timing, and intensity of management, and to some extent the abundance of certain spatial habitat structures which affect the disturbance and the vegetation, for example, shrubs and trees. In this study, we focus on one of these management tools, the timing of management,

and we investigate its importance for plant reproduction in Swedish semi-natural grasslands.

Historically, large grassland areas in Europe were left undisturbed until late in the growing season (July–September) when mowing or late grazing took place [9]. The use of late management in the remaining grassland patches has however been reduced drastically, being replaced by grazing during most of the season [11, 12]. For production reasons, grazing is today often started as early as possible because the nutrient content of the pasture is highest early in the summer [13, 14]. The shift from late to early management has been shown to have strong, usually negative, effects on grassland biodiversity [15, 16], especially when grazing is intense [17, 18]. The timing of management strongly affects the reproduction of plants, which in turn affects both plant population viability and the resource for populations of pollen eaters, nectar eaters, seed predators, and several invertebrate herbivores.

In ecological terms, grazing and mowing exert disturbance and stress to the vegetation by damaging plants and removing biomass. This disturbance is necessary for grassland ecosystems since it maintains openness and counteracts succession towards tall vegetation dominated by few competitive species. Plants in grassland habitats are adapted to the disturbance, for example, by mechanisms related to palatability and mechanical defence [19, 20], growth form [21], and phenology of reproduction [22–24]. Phenology can be assumed to be a particularly important trait in mown and other late managed habitats since it determines whether a plant can produce seeds before the vegetation is disturbed [25].

In this study we experimentally compared two cattle grazing regimes, continuous stocking from May to September and late onset of grazing (grazing from mid-July to September) in terms of effects on plant reproduction. Late onset of grazing was chosen as an alternative to the prevailing continuous stocking regime both because it is a traditional grazing regime and because it may potentially function as a more practical substitute for labour-intense traditional mowing. The study addresses the following questions: (1) what are the differences between continuously and late grazed pastures in terms of production of flowers and mature fruits? (2) How is plant reproductive success affected by species-specific traits such as phenology of reproduction? (3) Can cattle graze the old vegetation late in the summer, or does late-onset grazing have potentially negative effects in terms of ungrazed vegetation by the end of the season? (4) Is late grazing a possible substitute for labour-intense mowing for conservation management?

## 2. Methods

**2.1. Study System and Experimental Setup.** Two, slightly different grazing experiments are analysed in this study. Both were performed in semi-natural grasslands in south-central Sweden, normally grazed annually by 12–18-month-old steers from mid-May to late September. One grassland (Harpsund) is situated in the county of Södermanland ( $59^{\circ}05' N$   $16^{\circ}29' E$ ), the other (Pustnäs) in the county of

Uppland ( $59^{\circ}48' N$   $17^{\circ}40' E$ ), in south-central Sweden. Both sites are flat and without notable slope and have nutrient-poor soils as the result of long history of grazing without fertilisation other than the reallocation of nutrient through dung and urine from the grazers. The vegetation at both sites is mainly of dry-mesic herb-rich *Agrostis capillaris* meadow type [26]. Particularly common species are shown in Table 2 for Harpsund, and the same dominant species are found in Pustnäs. The late and continuously stocked areas in Harpsund were 4 and 6 hectares, resp., and in Pustnäs 1 and 3 hectares, respectively.

Within each grassland, one area was separated from the continuously stocked pasture by fencing until 20 July, when the fence was opened and the cattle were allowed to move freely between the two treatment areas. The grazing pressure was c. 1.8 steers (12 months of age in May) per hectare, corresponding to c. 630 kg live-weight per hectare. When the pasture area increased at late onset of grazing, the stocking density was maintained by adding extra steers. In Pustnäs three exclosure cages per treatment were used in order to examine if the plant reproduction differed between treatment areas independently of treatment.

The use of two large treatment areas per site, instead of a number of small, interspersed areas, may raise statistical problems [27, 28]. Due to this, and as a result of the differences in data sampling design between the two grasslands, all analyses were performed for each grassland separately. The results are interpreted acknowledging the possible area effects. Large treatment areas are, on the other hand, necessary to study natural grazing effects of the cattle. The grazing protected cages in Pustnäs were treated as two random samples, controlling for treatment area.

**2.2. Data Sampling.** The sampling design differs slightly between the two grasslands. Data on four main response variables were collected: (1) production, development, and grazing of reproductive units (see below) during the grazing season (both sites); (2) height and grazing of vegetation during the season (both sites); (3) frequency of grazed shoots of vascular plants in mid-August (Harpsund); (4) number of vascular plant species (Pustnäs). The experiments started in 1997 in Pustnäs and in 2001 in Harpsund.

A reproductive unit was defined for each species as the smallest unit of reproductive organs (buds, flowers, fruits) that could be readily recognized and counted in the field. For most herbs, the reproductive unit was defined as a single bud, flower, and fruit (gynoecium). In *Asteraceae* a reproductive unit was defined as a flower head, and in *Plantago*, spike-forming grasses and sedges were defined as a spike. In small-flowered herbs and in sedges with panicles, cymes, or composed umbels or racemes, reproductive units were defined as the smallest possible assemblage of reproductive organs, usually the second- or third-level branch in the inflorescence. In grasses with panicles, spikelets were used as reproductive units.

Production and development of reproductive units, from bud to mature fruit, were monitored in twenty randomly distributed  $1 \times 1$  m plots per grazing regime in Harpsund, and in seven  $50 \times 50$  cm plots per grazing regime in Pustnäs.

The plots were examined 5–7 times during the season at c. 20-day intervals (see Figure 2 for exact dates). At each occasion the reproductive units of each occurring species were counted and assigned to one of the following classes: grazed (grazed reproductive shoot or branch), bud, flowering, postflowering, immature fruit, and mature/dehisced fruit. For composite reproductive units (see above), the unit was assigned to a certain class if approximately 75% of the flowers in the reproductive unit belonged to that class. Thus, reproduction was measured at the level of reproductive unit, with no estimates of seed production.

The height of the vegetation in the plots was measured eight times from May 24 to September 17 using a rising plate meter [29]. The vegetation height provides an estimate of the grazing intensity. In Harpsund, grazing intensity was estimated also by counting the numbers of grazed and ungrazed shoots 20 days after late onset of grazing in 2001 and 2002, in 25 0.1 × 0.1 m plots per grazing regime, located in a fixed pattern in one 0.5 × 25 m area per grazing regime.

In Pustnäs, three 1 × 2 m coarse-grid metal net cages were randomly located in each treatment in order to indicate area-specific differences between the two treatment areas, in absence of the grazing effect. Data on vegetation height and the production and development of reproductive units were collected as described above.

Plant reproduction was estimated as relative fruit production, defined as the proportion of the reproductive units that developed mature fruits. This estimate was calculated per species in Harpsund, for all species that occurred in a minimum of five plots per grazing treatment. The species were analyzed in order to investigate if some species-specific traits could explain how different species responded to the grazing regimes. This analysis was done by correlating relative fruit production with three species-specific plant traits, with two estimates of species-specific preference by the grazers, and with spontaneous abortion of reproductive units during the growing season. The following plant traits were analyzed: plant height according to Lid [30], Ellenberg light index according to Ellenberg et al. [31], and date of fruit maturation (the approximate date when 50% of the fruits had reached mature stage in late grazing). As estimates of species-specific grazing preference, we used the proportion of reproductive units that were grazed during the first three weeks of grazing, and during the entire season. The level of herbivory during the first weeks of grazing indicates whether the plant species is a “first choice” of the grazers, or whether it is less preferred. Species experiencing low herbivory during the entire season can be regarded as low-preference species [32]. Spontaneous abortion of reproductive units, finally, indicates whether fruit set of the species is restricted by other factors than herbivory, for example, competition in tall vegetation. Twenty-eight species occurred in a minimum of five plots per grazing treatment (see Table 2) and were used in comparison of relative fruit production between grazing treatments.

In Pustnäs the frequencies of all species present in 20 randomly distributed 0.5 × 0.5 m plots were monitored to examine species change over time. This was initiated in 1997, and the same plots were reinventoried in 2003 (except

two plots in both treatments which were not found). The taxonomic nomenclature follows Mossberg and Stenberg [33].

**2.3. Statistical Treatment.** Since most of the data deviated considerably from the normal distribution and in most cases were count data, Spearman's rank correlation, Mann-Whitney *U*-test, and Poisson's regressions were used [34]. Differences in the number of grazed shoots between grazing regimes and years, diversity indexes, and species number per plot were however approximately normally distributed and were therefore analyzed using repeated measures in ANOVA (SAS mixed models procedure) and *t*-tests, respectively. Analysis of differences in the relative fruit production between grazing regimes at different dates was performed using repeated measures in generalized linear models, Poisson's distribution, and log link function (SAS Genmod procedure, GEE-analysis). Bonferroni's corrections of multiple comparisons among species in the two grazing regimes were not necessary since only the number of significance was discussed, not the single cases.

The change of vegetation during six years of grazing experiment was estimated using the Shannon diversity index *H* [35] in Pustnäs in 1997, the initial year of the experiment, and again in 2003.

### 3. Results

The number of species did not differ significantly between the two treatment areas in any of the two grassland sites. In Harpsund, on average 26.0 species of vascular plants occurred per m<sup>2</sup> plot in the continuously stocked and 28.6 species in the late grazed area (Mann-Whitney *U* = 132, *N* = 40, *P* = 0.07). In Pustnäs, each 50 × 50 cm plot had on average 13.4 species with continuous stocking and 12.3 species in late-onset grazing (Mann-Whitney *U* = 13, *N* = 14, *P* = 0.12).

**3.1. Reproduction.** Grazing regime strongly affected plant reproduction, the average production of reproductive units, both in total and in terms of mature reproductive units (Figure 1). Also the average relative fruit production was higher in late grazing compared to continuous stocking, both at plot level and at species level (Figure 1).

The mean density of reproductive units was higher in the late grazing treatment compared to continuous stocking at all observation dates except for the first date in spring (*P* < 0.05, generalized linear model, Poisson's errors, and log link function, with individual plots as repeated measures between observation dates, *df* = 1 for all analyses).

The enclosure cages in Pustnäs showed that no significant differences between treatment areas were found, neither for production of reproductive units (Mann-Whitney *U* = 2.0, *N* = 6, *P* = 0.28) nor for maturation (*U* = 3.5, *N* = 6, *P* = 0.66). Ungrazed plots inside the cages produced on average 451 reproductive units per square meter in the continuously stocked area and 442 in the late grazed area. Of these reproductive units, 401 ± 33 (89 ± 1.6 per cent) matured

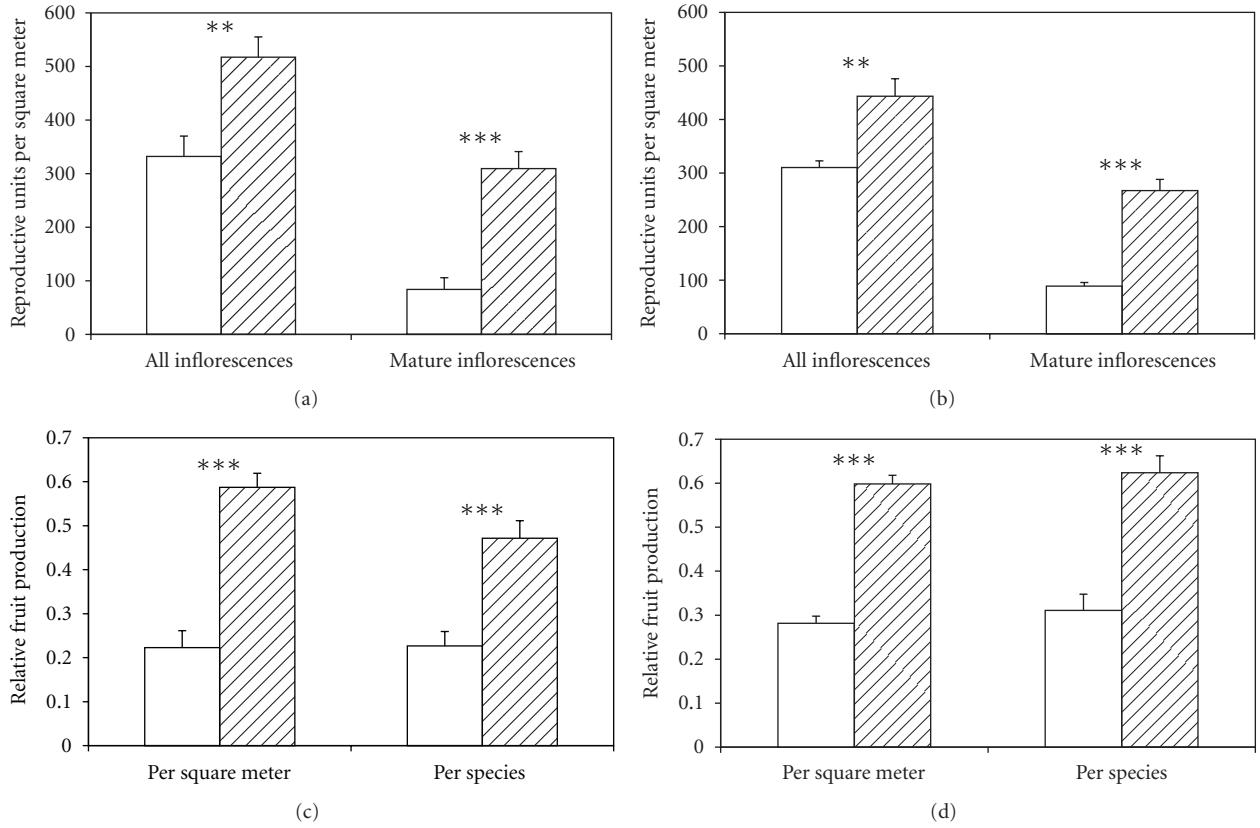


FIGURE 1: Mean production of reproductive units (see text for explanation) in two grazed semi-natural grasslands, Harpsund (a) and Pustnäs (b), and mean (per  $m^2$  and per species) relative fruit production (proportion of inflorescences developing to mature fruit stage) in Harpsund (c) and Pustnäs (d). Two grazing regimes were compared, continuous stocking from mid-May to early October (white bars) and late onset of grazing (grazing from mid-July to early October, dashed bars). Error bars show one SE. Asterisks indicate significant differences between grazing regimes within site (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , Mann-Whitney  $U$ -test,  $N$  (Harpsund) = 20 per grazing regime,  $N$  (Pustnäs) = 7 per grazing regime).

to fruit stage in the continuously stocked area and  $401 \pm 61$  ( $91 \pm 2.0$  per cent) in the late grazed area.

**3.2. Species-Specific Responses.** In Harpsund, relative fruit production was significantly higher in late grazing compared to continuous stocking for 15 of 28 analyzed plant species. No species had higher relative fruit production in continuous stocking (Figure 2, Table 2). Six species produced no mature fruits at all in the 20 plots in continuous stocking, compared to one species in late grazing.

In Pustnäs, there were too few sampling plots to allow for testing of species-specific differences between grazing regimes. Sixteen species occurred in three plots or more per treatment. For seven of the 16 species, relative fruit production in late grazing exceeded that of continuous stocking by a factor  $> 2$ . No species had higher fruit set in continuous stocking.

The mean relative fruit production of single species was negatively correlated with date of fruit maturation for the species. This effect was more prominent in late grazing (Figure 3).

Grazing preference, in terms of degree of herbivory (see Methods), had no significant effect on species-specific

relative fruit production, because the relative fruit production was not correlated with the species-specific herbivory of all reproductive units, neither over the entire season (Spearman's rank correlation  $P > 0.10$ ) nor during the first weeks of grazing ( $P > 0.15$ ). No correlation was found between relative fruit production and any of the other tested species-specific parameters: the Ellenberg light index, plant height, or abortion of reproductive units.

Grasses reached significantly higher relative fruit production than herbs and sedges both in late grazing (Mann-Whitney  $U = 47$ ,  $N = 34$ ,  $P = 0.002$ ) and continuous stocking ( $U = 33$ ,  $N = 26$ ,  $P = 0.013$ , Figure 3).

**3.3. Diversity and Species Richness.** The  $H$  (the Shannon diversity index, [34]) in plots of the vegetation change experiment in Pustnäs did not differ between treatments in 1997, the initial year of the experiment (mean for continuous stocking and late grazing, 1.37 and 1.39,  $t$ -test,  $t = -60$ ,  $df = 38$ ,  $P = 0.555$ ). In 2003, after six years, the diversity in late grazed plots had increased compared to the continuously stocked plots (mean for continuous stocking and late grazing, 1.41 and 1.58, resp.,  $t$ -test,  $t = -6.68$ ,  $df = 36$ ,  $P = < 0.001$ ).  $H$ -indices were not significantly different between

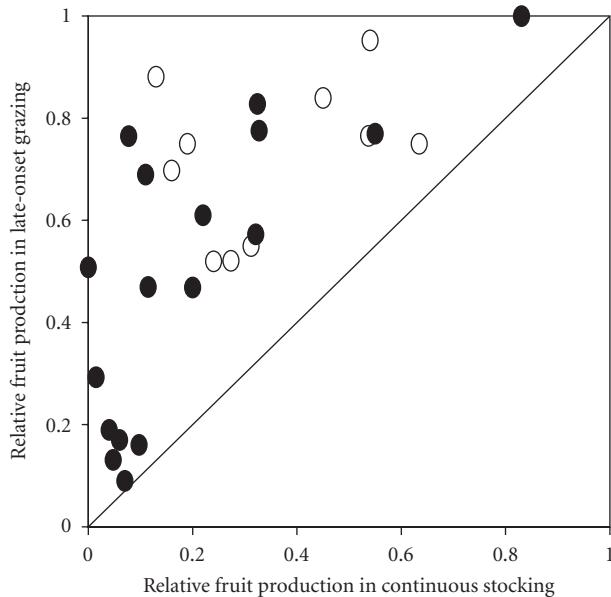


FIGURE 2: Mean per-species relative fruit production (proportion of inflorescences developing to mature fruit stage) of 27 plant species of grasses (open circles) and herbs/sedges (filled circles) in two grazing regimes, late onset of grazing (grazing from mid-July to early October), and continuous stocking (grazing from mid-May to early October), in a semi-natural grassland at Harpsund, see text for explanations.

years in continuous stocking ( $t$ -test,  $t = -1.53$ ,  $df = 36$ ,  $P = 0.134$ ).

The number of species per plot showed a similar pattern. The mean number of species per plot was initially 15.1 in continuous stocking and 14.9 in late grazing ( $t$ -test,  $t = 0.16$ ,  $df = 37$ ,  $P = 0.875$ ). After six years, species number was 14.9 in continuous stocking compared to an increase to 19.4 species per plot in late grazing ( $t$ -test,  $t = -4.53$ ,  $df = 34$ ,  $P = < 0.001$ ).

**3.4. Vegetation Height and Grazing of Shoots.** Grazing regime affected the vegetation height during the early part of the season, but the difference was negligible in late summer and autumn (Figure 4). In continuous stocking, the average vegetation height was low throughout the season, with a slight decrease from c. 4.5 to c. 2.5 cm (Figure 4). Late-onset grazing allowed the vegetation to grow to a maximum average of 8.8 and 8.5 cm of height in Harpsund and Pustnäs, respectively, before the onset of grazing in mid-July. After one month, the late grazed vegetation was reduced to on average 3.5 cm in both grasslands, that is, 1.2 cm taller vegetation than in continuous stocking in Harpsund (Mann-Whitney  $U = 119.0$ ,  $n = 20$ ,  $P = 0.025$ ) and 0.3 cm taller in Pustnäs ( $P = 0.32$ , Figure 4). Inside the exclosure cages in Pustnäs, the vegetation height never differed significantly between the two treatment areas ( $P > 0.35$ ).

The proportion of grazed shoots was measured in mid-August, that is, one month after the onset of late grazing (Table 1). In Harpsund, the proportion of grazed shoots was affected by year (ANOVA, repeated measures:  $df = 1$ ,  $\chi^2 =$

TABLE 1: The mean proportion of grazed shoots in mid-August in two grazing regimes (continuous stocking May–September and late grazing mid-July to September), at two sites (Harpsund and Pustnäs), over two years, 2001 and 2002.  $N = 20$  plots per grazing regime in Harpsund and  $N = 7$  in Pustnäs.

Year	Site	Grazing regime	Mean proportion of grazed shoots (S.E.)
2001	Harpsund	Continuous	0.83 (0.033)
		Late	0.71 (0.050)
	Pustnäs	Continuous	0.98 (0.009)
		Late	0.82 (0.036)
2002	Harpsund	Continuous	0.40 (0.022)
		Late	0.46 (0.055)
	Pustnäs	Continuous	0.46 (0.018)
		Late	0.49 (0.019)

8.1,  $P = 0.006$ ) but not of grazing regime ( $P = 0.862$ ) or the interaction between grazing regime and year ( $P = 0.069$ ), whereas the proportion of grazed shoots in Pustnäs was affected by the interaction ( $\chi^2 = 6.7$ ,  $P = 0.011$ ) but neither by grazing regime ( $P = 0.084$ ) nor year ( $P = 0.140$ ).

#### 4. Discussion

This study shows that the timing of grassland management, here grazing, strongly affects the fruit production of vascular plants which may affect the viability of populations of both plants and other organisms depending on plant reproduction, for example, insects depending on nectar and pollen. The response to the grazing regime, in terms of relative fruit production, varied between species, mainly depending on each species' phenology of reproduction. The plant species diversity increased over time with the grazing regime tested here, late-onset grazing. Late onset of grazing carried no obvious costs in terms of ungrazed vegetation by the end of the season.

In the two studied semi-natural pastures subject to continuous stocking from May to September, the vegetation height was kept almost constantly low throughout the season. As a consequence, the production of fruits was reduced to a fifth compared to undisturbed conditions. By delaying the onset of grazing from mid-May to 20 July, the production of buds and flowers was increased 2–2.7 times compared to continuous stocking and the production of mature fruits c. 4 times. The results were very similar in the two studied grasslands. The increased plant reproduction in late grazing was not an effect of more shoots and reproductive organs escaping herbivory completely, but of more shoots escaping herbivory long enough to produce mature fruits. No difference in number of grazed shoots was found between treatments by the end of the season, but the vegetation was on average 0.3–1.2 cm taller in late than in continuous stocking. The difference of 1.2 cm was statistically significant, but most likely has no ecological significance, for example, in terms of litter accumulation [36].

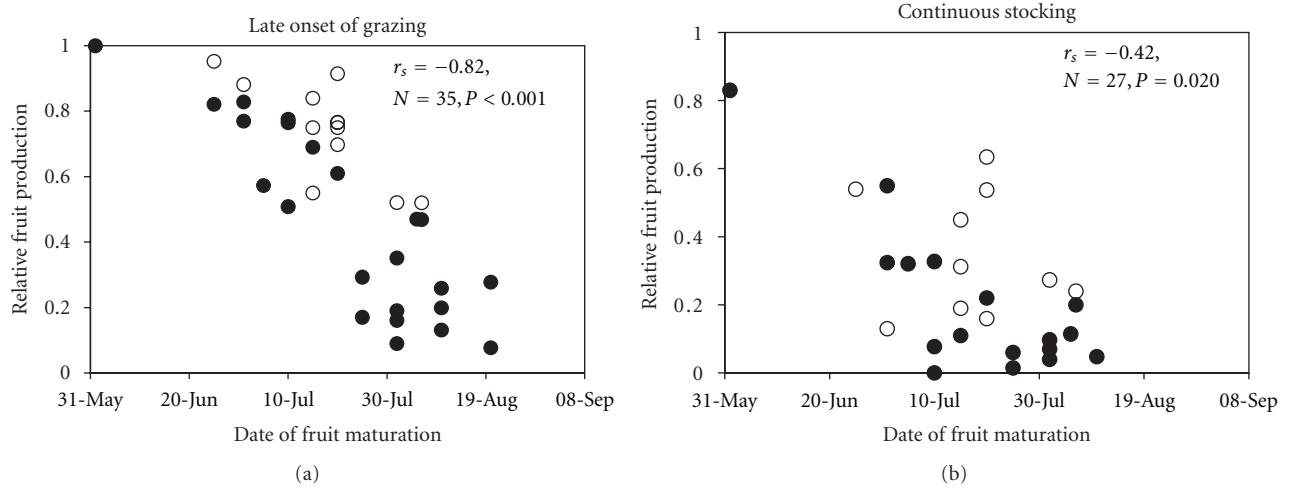


FIGURE 3: Mean per-species relative fruit production (proportion of inflorescences developing to mature fruit stage) of grasses (open circles) and herbs/sedges (filled circles), as a function of each species' date of fruit maturation (see text for explanation). Two grazing regimes were compared, late onset of grazing (grazing from mid-July to early October), and continuous stocking (grazing from mid-May to early October) in a semi-natural grassland at Harpsund, see text for explanations. Spearman's rank correlation coefficients,  $r_s$ , are shown, together with significance tests. For clarity, no error bars are shown.

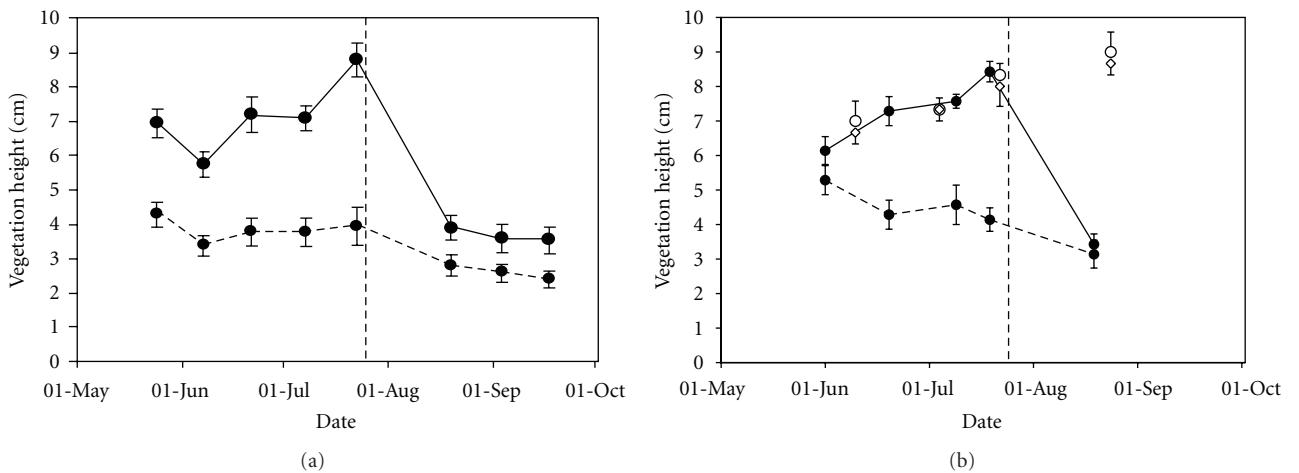


FIGURE 4: Average vegetation height during the growing season in continuously stocked (dashed line) and late (solid line) grazed areas, in two semi-natural grasslands, Harpsund (a) and Pustnäs (b). Vegetation height inside exclosure cages in Pustnäs is shown by open circles (cages in continuous stocking) and open diamonds (cages in late grazing). Error bars show 1 standard error. Onset of late grazing is indicated with a vertical dotted line.  $N = 20$  plots per treatment in Harpsund, 7 in Pustnäs; 3 exclosure cages per treatment in Pustnäs. A dry period in early June caused a temporal drop in turgor and therefore also in the measure of vegetation height.

Tall vegetation before late onset of grazing can be expected to affect the reproduction of small plant species negatively, through competition for light [37]. However, no such effects were found, as plant height was not correlated with relative fruit production, neither was the Ellenberg light index [31], which would have been expected if fruit set was affected by competition for light. Furthermore, the abortion of reproductive units was not correlated with relative fruit production, neither at species nor plot levels. This indicates that effects of spontaneous abortion due to, for example, competition did not contribute significantly to the differences in relative fruit production between species and grazing regimes.

In both grazing regimes, comparison of species showed that relative fruit production was positively correlated with early reproduction. Early flowering has been suggested to be an adaptation to predictably late disturbances such as mowing [24, 38, 39]. This study shows that also late onset of grazing favoured early reproducing vascular plants in a similar way. By 20 July approximately half of the most abundant species had 50% or more of their fruits mature. Although the vegetation was rapidly grazed after onset of grazing in 20 July, some fruits also successfully matured after that date, and a total of 50–100% (median 77%) of the reproductive units of early reproducing species produced mature fruits. In the other, later reproducing half of the species,

TABLE 2: Mean relative fruit production of 28 species occurring in five or more plots per the two grazing regimes: continuous stocking and late grazing, in the grassland Harpsund, see text for details. Differences between grazing regimes are tested using the Mann-Whitney  $U$ -test.  $N$ -values show the number of plots in which the species were present.

Species	Continuous		Late		$U$	$P$
	$N$	Mean (SE)	$N$	Mean (SE)		
<i>Agrostis capillaris</i>	19	0.24 (0.07)	20	0.52 (0.06)	91.0	0.005
<i>Alchemilla</i> sp.	9	0.01 (0.01)	13	0.29 (0.09)	24.0	0.014
<i>Anthoxanthum odoratum</i>	9	0.54 (0.15)	20	0.95 (0.04)	48.0	0.048
<i>Helictotrichon pubescens</i>	14	0.54 (0.09)	13	0.77 (0.11)	50.5	0.048
<i>Carex caryophyllea</i>	5	0.11 (0.07)	8	0.49 (0.25)	12.5	0.250
<i>Cerastium fontanum</i>	15	0.08 (0.04)	16	0.77 (0.11)	29.5	<0.001
<i>Dactylis glomerata</i>	5	0.27 (0.12)	9	0.52 (0.15)	15.0	0.310
<i>Deschampsia caespitosa</i>	5	0.31 (0.14)	5	0.55 (0.20)	8.50	0.400
<i>Festuca pratensis</i>	12	0.45 (0.13)	13	0.84 (0.14)	45.5	0.073
<i>Festuca rubra</i>	19	0.19 (0.05)	19	0.75 (0.086)	50.5	<0.001
<i>Filipendula vulgaris</i>	7	0.20 (0.14)	6	0.47 (0.18)	13.5	0.260
<i>Lotus corniculatus</i>	14	0.04 (0.02)	18	0.19 (0.059)	74.0	0.039
<i>Luzula campestris</i>	15	0.55 (0.10)	19	0.77 (0.04)	99.5	0.140
<i>Phleum pratense</i>	9	0.63 (0.15)	10	0.75 (0.09)	40.5	0.710
<i>Plantago lanceolata</i>	16	0.22 (0.07)	20	0.61 (0.05)	37.0	<0.001
<i>Poa pratensis</i>	20	0.16 (0.06)	11	0.70 (0.10)	31.0	0.001
<i>Potentilla erecta</i>	6	0.05 (0.05)	17	0.13 (0.04)	30.0	0.120
<i>Primula veris</i>	5	0 (0)	10	0.51 (0.13)	7.50	0.020
<i>Ranunculus auricomus</i>	13	0.32 (0.11)	8	0.57 (0.17)	33.0	0.160
<i>Ranunculus polyanthemos</i>	17	0.33 (0.09)	14	0.78 (0.08)	39.0	0.001
<i>Rumex acetosa</i>	16	0.32 (0.10)	12	0.83 (0.09)	40.0	0.008
<i>Stellaria graminea</i>	16	0.08 (0.04)	7	0 (0)	38.5	0.100
<i>Taraxacum</i> sp.	9	0.83 (0.11)	6	1.00 (0)	6.0	0.013
<i>Trifolium medium</i>	8	0.11 (0.06)	17	0.47 (0.09)	28.5	0.018
<i>Trifolium pratense</i>	17	0.11 (0.04)	20	0.69 (0.07)	23.0	<0.001
<i>Trifolium repens</i>	17	0.07 (0.02)	18	0.09 (0.03)	148.0	0.860
<i>Veronica chamaedrys</i>	19	0.06 (0.23)	17	0.17 (0.06)	128.5	0.230
<i>Vicia cracca</i>	6	0.10 (0.06)	8	0.16 (0.12)	23.0	0.870

a median of 26% of the reproductive units produced mature fruits. In comparison with late grazing, mowing in mid-July would have considerably reduced fruit set of all species except for the very early ones. This is because mowing results in immediate removal of reproductive organs, whereas removal by grazing is more extended in time. Much of the fruit maturation in the studied grasslands took place during 20 July–5 August, which suggests that a few days difference in mowing time or onset of grazing would make a large difference in plant fruit set.

Early reproduction may also be an adaptation to more continuous disturbance such as grazing, since the risk of reproductive organs being grazed before fruit maturation is proportional to the time a plant is exposed to a grazed environment [40]. In continuous stocking, the early reproducing half of the species produced a median of 0.32 mature fruits per reproductive unit, compared to 0.08 in the late reproducing species.

Escape from herbivory may also be achieved by mechanisms related to grazing preference [41, 42] or growth-form

[43]. Grasses had higher fruit set than herbs and sedges in both grazing regimes, partly as an effect of early reproduction, but to some extent also as an effect of less herbivory on grasses. The degree of herbivory experienced by a species is an estimate of species-specific grazing preference. Here, preference was not correlated with species-specific fruit set, indicating that differences in preference explains little of the variation in fruit set between species in this system. Plant traits that affect preference may however be a more important mechanism under less intensive grazing, because opportunities for herbivore selection between plant species increase with decreasing grazing intensity [44]. No obvious growth-form-related defence mechanisms, such as thorns, occurred among the analyzed species. Low-growing plants can be expected to be able to escape cattle herbivory to some extent [22], but plant height was not correlated with fruit set in this study.

The species diversity increased during six years of late grazing treatment while the diversity in the continuously stocked plots remained at a constant level. Also, the species

number increased by 30 per cent in late grazing, but remained constant after six years in continuous stocking. Similar observations are made by, for example, Pavlů et al. [45], who reported an increase of forbs in the vegetation after delayed onset of grazing on old leys. An increase of seed production in late grazed areas was pointed out as one of the possible explanations.

In full-scale grazing experiments, the different treatments will always be located in adjacent areas because of the otherwise biased effects of fences (e.g., [45]). Yet, this may cause problems in separating treatment effects from area effects. In this study, however, several factors indicate that the observed differences between grazing regimes were not area effects. Firstly, the two grasslands showed very similar differences between grazing regimes, which indicates a grazing regime effect rather than a site effect. Secondly, the control cages protected from grazing in Pustnäs did not differ between treatment areas in any measured parameter. Thirdly, similarity between treatment areas was indicated by similar number of species. Finally, the differences in plant reproduction between treatments were large and could clearly be attributed to observed grazing of shoots and reproductive organs.

Apart from the increased fruit set and plant species diversity, the undisturbed period in early summer can also be assumed to be positive for phytophagous, nectar- and pollen-feeding insects. Low amounts of pollen and nectar resources have been suggested to be an important threat to, for example, wild bees [46–48] and lepidopterans [49], of which several species are red listed [8].

Acknowledging that only two grasslands were studied, the results clearly indicate that if continuous stocking from spring to autumn is applied in grasslands with a history of late management, plant species diversity can be assumed to decrease as well as the resource for organisms depending on plant reproduction. This is alarming since continuous stocking from May to September is the most common management regime in Swedish and northern European semi-natural grasslands, largely irrespective of their management history [9]. For example, the widespread shift from mowing to grazing may lead to considerable changes of vegetation composition and plant population viability in semi-natural grasslands. The study suggests an increased use of analyses of management history in grassland conservation and management, which would most likely result in an increased use of late management. The study also shows that late onset of grazing may well function as a substitute for labour-intense mowing of semi-natural grassland.

## Acknowledgments

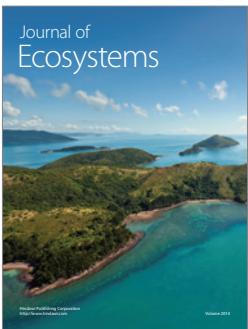
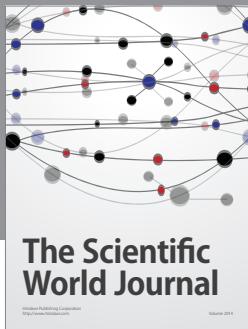
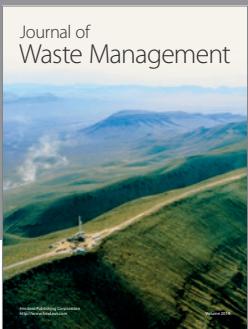
The authors thank J. Bengtsson, Å. Berg, and C. Glynn for discussions, K. Lehtlä, A. Denham, and two anonymous reviewers for comments on the manuscript, S. Overud and E. Sjödin for valuable discussions and help with the field work, and E. Spörndly for being responsible for cattle handling. They further thank Per Rudengren and the Harpsund farm and the Kungsängen experimental farm at SLU for putting their land and grazers at our disposal. The study

was funded by the Foundation for Strategic Environmental Research (HagmarksMISTRA) and the Swedish Council for Forestry and Agricultural Research (Award 34.0297/98 to T. Lennartsson).

## References

- [1] H. Sjörs, *Ekologisk Botanik. Biologi 10*, Almqvist & Wiksell, Uppsala, Sweden, 1971.
- [2] M. Pärtel and M. Zobel, "Small-scale plant species richness in calcareous grasslands determined by the species pool, community age and shoot density," *Ecography*, vol. 22, no. 2, pp. 153–159, 1999.
- [3] U. Emanuelsson, *The Rural Landscapes of Europe—How man has Shaped Europe's Nature*, Formas, 2009.
- [4] R. M. Fuller, "The changing extent and conservation interest of lowland grasslands in England and Wales: a review of grassland surveys 1930–1984," *Biological Conservation*, vol. 40, no. 4, pp. 281–300, 1987.
- [5] D. Stanners and P. Bourdeau, *Europe's Environment. The Dobris Assessment*, European Environment Agency, Copenhagen, Denmark, 1995.
- [6] Statistics Sweden, "Betasmarker—historiska data," Statistiska Meddelanden 36:9001, Statistics Sweden, Borås, Sweden, 1990.
- [7] Nature Conservancy Council, *Nature Conservation in Great Britain*, Nature Conservancy Council, Peterborough, UK, 1984.
- [8] U. Gärdenfors, *The 2010 Red List of Swedish Species*, ArtData-banken, Uppsala, Sweden, 2010.
- [9] E. Gustavsson, A. Dahlström, M. Emanuelsson, J. Wissman, and T. Lennartsson, "Combining historical and ecological knowledge to optimise biodiversity conservation in semi-natural grasslands," in *The Importance of Biological Interactions in the Study of Biodiversity*, J. L. Pujol, Ed., pp. 173–196, 2011.
- [10] G. L. A. Fry, "Conservation in agricultural ecosystems," in *The Scientific Management of Temperate Communities for Conservation*, I. F. Spellerberg, F. B. Goldsmith, and M. G. Morris, Eds., pp. 415–443, Blackwell, London, UK, 1991.
- [11] G. Beaufoy, D. Baldock, and J. Clark, *The Nature of Farming. Low Intensity Farming Systems in Nine European Countries*, Institute for European Environmental Policy, London, UK, 1995.
- [12] A. García, "Conserving the species-rich meadows of Europe," *Agriculture, Ecosystems and Environment*, vol. 40, no. 1–4, pp. 219–232, 1992.
- [13] K. H. Patriksson, *Skötselhandbok för Gårdens Natur-och Kulturvärden*, Swedish Board of Agriculture, Jönköping, Sweden, 1998.
- [14] I. Pehrson, *Bete och Betesdjur*, Swedish Board of Agriculture, Jönköping, Sweden, 2001.
- [15] T. Lennartsson and J. G. B. Oostermeijer, "Demographic variation and population viability in *Gentianella campestris*: effects of grassland management and environmental stochasticity," *Journal of Ecology*, vol. 89, no. 3, pp. 451–463, 2001.
- [16] A. C. Linusson, G. A. I. Berlin, and E. G. A. Olsson, "Reduced community diversity in semi-natural meadows in southern Sweden, 1965–1990," *Plant Ecology*, vol. 136, no. 1, pp. 77–94, 1998.
- [17] E. M. Veenendaal, W. H. O. Ernst, and G. S. Modise, "Reproductive effort and phenology of seed production of savanna grasses with different growth form and life history," *Vegetatio*, vol. 123, no. 1, pp. 91–100, 1996.
- [18] B. Dumont, A. Farruggia, J. P. Garel, P. Bachelard, E. Boitier, and M. Frain, "How does grazing intensity influence the

- diversity of plants and insects in a species-rich upland grassland on basalt soils?" *Grass and Forage Science*, vol. 64, no. 1, pp. 92–105, 2009.
- [19] R. M. Callaway, Z. Kikvidze, and D. Kikodze, "Facilitation by unpalatable weeds may conserve plant diversity in overgrazed meadows in the Caucasus Mountains," *Oikos*, vol. 89, no. 2, pp. 275–282, 2000.
- [20] L. H. Fraser and J. P. Grime, "Interacting effects of herbivory and fertility on a synthesized plant community," *Journal of Ecology*, vol. 87, no. 3, pp. 514–525, 1999.
- [21] I. Noymeir, M. Gutman, and Y. Kaplan, "Responses of Mediterranean grassland plants to grazing and protection," *Journal of Ecology*, vol. 77, no. 1, pp. 290–310, 1989.
- [22] R. Fernandez Ales, J. M. Laffarga, and F. Ortega, "Strategies in Mediterranean grassland annuals in relation to stress and disturbance," *Journal of Vegetation Science*, vol. 4, no. 3, pp. 313–322, 1993.
- [23] T. Lennartsson, P. Nilsson, and J. Tuomi, "Induction of overcompensation in the field gentian, *Gentianella campestris*," *Ecology*, vol. 79, no. 3, pp. 1061–1072, 1998.
- [24] H. J. Zopfi, "Ecotypic variation in *Rhinanthus alectorolophus* (Scopoli) Pollich (Scrophulariaceae) in relation to grassland management. I. Morphological delimitations and habitats of seasonal ecotypes," *Flora*, vol. 188, no. 1, pp. 15–39, 1993.
- [25] M. Akhalkatsi and J. Wagner, "Reproductive phenology and seed development of *Gentianella caucasea* in different habitats in the Central Caucasus," *Flora*, vol. 191, no. 2, pp. 161–168, 1996.
- [26] L. Pahlsson, *Vegetationstyper i Norden*, Nordic Council of Ministers, Copenhagen, Denmark, 1994.
- [27] S. H. Hurlbert, "Pseudoreplication and the design of ecological field experiments," *Ecological Monographs*, vol. 54, pp. 187–211, 1984.
- [28] L. Oksanen, "Logic of experiments in ecology: is pseudoreplication a pseudoissue?" *Oikos*, vol. 94, no. 1, pp. 27–38, 2001.
- [29] M. E. Castle, "A simple disc instrument for estimating herbage yield," *Journal of the British Grassland Society*, vol. 31, pp. 37–40, 1976.
- [30] J. Lid, *Norsk og Svensk Flora*, Det Norske Samlaget, Oslo, Norway, 1979.
- [31] H. Ellenberg, H. E. Weber, R. Düll, V. Wirth, and W. Werner, *Zeigerwerte von Pflanzen in Mitteleuropa*, Scripta Geobotanica, Göttingen, Germany, 2001.
- [32] V. G. Allen, C. Batello, E. J. Berretta et al., "An international terminology for grazing lands and grazing animals," *Grass and Forage Science*, vol. 66, no. 1, pp. 2–28, 2011.
- [33] B. Mossberg and L. Stenberg, *Den Nya Nordiska Floran*, Wahlström & Widstrand, Stockholm, Sweden, 2003.
- [34] G. P. Quinn and M. J. Keough, *Experimental Design and Data Analysis for Biologists*, Cambridge University Press, Cambridge, UK, 2002.
- [35] M. Begon, J. L. Harper, and C. R. Townsend, *Ecology*, Blackwell Science, London, UK, 3rd edition, 1996.
- [36] J. Wissman, *Grazing regimes and plant reproduction in semi-natural grasslands*, Ph.D. thesis, Swedish University of Agricultural Sciences, 2006.
- [37] H. M. Jutila and J. B. Grace, "Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis," *Journal of Ecology*, vol. 90, no. 2, pp. 291–302, 2002.
- [38] T. Karlsson, "Early-flowering taxa of *Euphrasia* (Scrophulariaceae) on Gotland, Sweden," *Nordic Journal of Botany*, vol. 4, pp. 303–326, 1984.
- [39] I. S. Warwick and D. Briggs, "The genecology of lawn weeds. III. Cultivation experiments with *Achillea millefolium* L., *Bellis perennis* L., *Plantago lanceolata* L., *Plantago major* L. and *Prunella vulgaris* L. collected from lawns and contrasting grassland habitats," *New Phytologist*, vol. 83, pp. 509–536, 1979.
- [40] T. Lennartsson, *Demography, reproductive biology and adaptive traits in Gentianella campestris and G. amarella—evaluating grassland management for conservation by using indicator plant species*, Ph.D. thesis, Swedish University of Agricultural Sciences, 1997.
- [41] J. M. Bullock and C. A. Marriot, "Plant responses to grazing and opportunities for manipulation," in *Grazing Management*, A. J. Rook and P. D. Penning, Eds., pp. 17–26, British Grassland Society, London, UK, 2000.
- [42] M. Fenner, M. E. Hanley, and R. Lawrence, "Comparison of seedling and adult palatability in annual and perennial plants," *Functional Ecology*, vol. 13, no. 4, pp. 546–551, 1999.
- [43] P. Tiffin, "Mechanisms of tolerance to herbivore damage: what do we know?" *Evolutionary Ecology*, vol. 14, no. 4–6, pp. 523–536, 2000.
- [44] L. Jerling and M. Andersson, "Effects of selective grazing by cattle on the reproduction of *Plantago maritima*," *Holarctic Ecology*, vol. 5, no. 4, pp. 405–411, 1982.
- [45] V. Pavlů, M. Hejčman, L. Pavlů, J. Gaisler, P. Nežerková, and L. Meneses, "Changes in plant densities in a mesic species-rich grassland after imposing different grazing management treatments," *Grass and Forage Science*, vol. 61, no. 1, pp. 42–51, 2006.
- [46] W. I. Linkowski, B. Cederberg, and L. A. Nilsson, *Vildbin och Fragmentering*, Swedish Board of Agriculture, Jönköping, Sweden, 2004.
- [47] A. Pekkarinen, "Oligolectic bee species and their decline in Finland (Hymenoptera: Apoidea)," in *Proceedings of the Proceedings of the 24th Nordic Congress of Entomology*, pp. 151–156, 1999.
- [48] M. Franzén and S. G. Nilsson, "How can we preserve and restore species richness of pollinating insects on agricultural land?" *Ecography*, vol. 31, no. 6, pp. 698–708, 2008.
- [49] C. Sarin and K. O. Bergman, "Habitat utilisation of burnet moths (*Zygaena* spp.) in southern Sweden: a multi-scale and multi-stage perspective," *Insect Conservation and Diversity*, vol. 3, no. 3, pp. 180–193, 2010.



**Hindawi**

Submit your manuscripts at  
<http://www.hindawi.com>

