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Dissertation presented at Uppsala University to be publicly examined in the Lecture Hall, Växtekologen, Villavägen 14, Uppsala, Monday, April 16, 2007 at 13:00 for the degree of Doctor of Philosophy. The examination will be conducted in Swedish.

Abstract


The decrease in number and area of managed hay-meadows over the last century, in combination with the reduction of traditional management, threatens the biodiversity connected to these habitats. I experimented how management intensity affected meadow characteristics and long-term population viability of three vascular plant species in wooded hay-meadows on the Swedish island of Gotland in the Baltic Sea. I discovered that intensified management (extra raking and/or extra mowing) reduced the amount of litter and biomass, even in well-managed meadows.

The effects of intensified management on population growth rate varied among species. Deterministic demographic models revealed that intensified management increased population growth rate in Succisa pratensis. Stochastic modelling confirmed this, all meadows displayed larger projected population sizes 50 years into the future with intensified management. Polygala amarella responded with lower growth rates in raked plots, a consequence of the plant’s morphology, which makes it prone to being pulled out by raking. Hypochoris maculata had population growth rates close to unity, and showed no response to an increase in management. Examination of the life-history characteristics of Polygala amarella showed that the species’ strategy is aimed at reproduction and fast growth, which is in contrast to the other two species, with their success relying on the survival of older plants. The species-specific responses to management show that several species should be considered when evaluating management practices for conservation of semi-natural grasslands. Furthermore, I suggest that data on stage distributions alone may not be sufficient for identifying threatened populations.

In a study of artificial dispersal between meadows, I found that establishment was twice as successful for planted plug-plants compared to sown seeds. Both methods may be useful for introducing or augmenting meadow populations, depending on access to seed sources and possibilities to nurse plants.

An electronic coordinate measurement device for gathering location data to be used in demographic studies was developed. In the field, the device proved to be a simple and reliable method for locating individuals in permanent plots.

Keywords: coordinates, demographic model, dispersal, hay-meadow, Hypochoris maculata, litter, management, Polygala amarella, stochastic modelling, Succisa pratensis

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List of papers

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals.


II. Wallin, L. & Svensson, B. M. Intensified management affects population growth differently in the two perennial herbs *Hypochoeris maculata* and *Polygala amarella*. Manuscript.

III. Wallin, L., Svensson, B. M. & Lönn, M. Artificial dispersal as a restoration tool in meadows: sowing or planting? Submitted manuscript.

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Introduction

Since the domestication of livestock, humans have relied on semi-natural grasslands to provide fodder. Since the climate cooled in northern Europe around 2000 years ago stores of fodder have been needed when the animals had to be kept inside over winter. The tradition of mowing for hay was therefore introduced (Ekstam et al. 1988). In areas around the southern Baltic Sea, e.g., on Gotland, the wooded hay-meadow was the most common form of fodder grassland up until the beginning of the 20th century (Figure 1, from Kukk & Kull 1997). At this point changes in agricultural practices led to a drastic decrease in area of unfertilised grasslands (Ekstam and Forshed 1996; Martinsson 1999; Ohlsson 2006). Traditional management of these meadows consists of four distinct components throughout the year: raking, mowing for hay, aftermath grazing and pollarding for leaf fodder (Ekstam et al. 1988; Anonymous 1992; Martinsson 1999).

Figure 1. Historical distribution of wooded hay-meadows in Europe. The shaded areas indicate the presence of hay-meadows in the beginning of the 20th century (from Kukk & Kull 1997).

The importance of management

Because semi-natural grasslands can harbour a high biodiversity (Kull & Zobel 1991; Anonymous 1994; Pärtel & Zobel 1999), they are important not
only when considering a cultural and historical legacy, but also from a species conservation point of view (Poschlod & WallisDeVries 2002).

Over the course of the 20th century, most of the traditional meadows in Western Europe have been transformed into heavily fertilised crop fields, turned into coniferous forest plantations or overgrown into broadleaf forests, and management efforts have decreased in many of the remaining meadows. Of the 1.2 million hectares of traditionally managed hay-meadows in Sweden at the end of the 19th century, only about 3000 hectares remain (Anonymous 1994; Martinsson 1999), and these are often small and isolated.

The reason for the high species richness in meadows has been attributed to the constant disturbance and low nutrient levels caused by vegetation removal and grazing, making it impossible for strong competitors to out-compete small or light-demanding species (Kull & Zobel 1991; Zobel 1992; Berendse 1999). Consequently, the need for a management that can preserve the biodiversity of the few remaining meadows is crucial (Oostermeijer et al. 1994; Berlin et al. 2000; Bühler & Schmid 2001; Lennartsson & Oostermeijer 2001; Wahlman & Milberg 2002; Jacquemyn et al. 2003; Brys et al. 2004).

The change in management motivation from the historic fodder production to the present conservation efforts, coupled with the increase in aerial nitrogen deposition over northern Europe, suggest that the current management intensity may not be sufficient to maintain optimal habitats to support the long-term survival of meadow plant species.

A particular concern is increasing nutrient levels, which favour competitive broad-leaved grasses and other nitrogen-demanding species, which in turn leads to increasing litter production (Berendse 1999). This accumulation of biomass and litter increases the difficulties for seeds to both germinate and establish, particularly so when aftermath grazing is abandoned (Bullock et al. 1994; Ekstam & Forshed 1997; Grime 2001; Franzen & Eriksson 2003; Rook et al. 2003).

Population responses in perennial plants to changes in management of semi-natural grasslands

Many studies have concluded that mowing is one of the most favourable management methods for preserving species-richness and viable plant populations in semi-natural grasslands (Tamm 1956; Kotiluoto 1998; Hansson & Fogelfors 2000; Lennartsson 2000; Jensen & Meyer 2001; Lennartsson & Oostermeijer 2001; Stammel et al. 2003), but additional grazing is also very important to keep nutrient levels down (Jacquemyn et al. 2003). As the number of meadows has decreased dramatically, the need for suitable man-
agement to preserve the species richness harboured in the few remaining meadows has become crucial. It is therefore important to know how any decrease in management intensity will affect plant populations with regard to survival, growth and reproduction. Some studies have found differences in population age structure in plant populations growing in different habitat types (Oostermeijer et al. 1994), with populations in habitats with more open vegetation and bare soil displaying higher proportions of seedlings in the population. Conversely, populations in more closed habitats consisted of a majority of old individuals, and have been termed senile.

With increased isolation between meadows, populations also run a risk of never being able to naturally disperse propagules between populations (Primack & Miao 1992; Soons & Heil 2002; Soons et al. 2005). Dispersal is important to maintain genetic diversity, enabling evolutionary responses to changing environmental conditions and decreasing the risks of inbreeding and genetic drift (Ellstrand and Elam 1993; Fischer and Matthies 1997; Edenhamn et al. 1999; Smulders et al. 2000; Eriksson & Ehrén 2001).

A demographic study of a population will give an overall representation of how the individuals in the population contribute to the long-term population growth rate ($\lambda$) through differing levels of survival, growth and reproduction (Caswell 2001). Analytical tools can provide answers to questions concerning how the population is performing after, for example, a change in management and the demographic approach can reveal where the change will have greatest effect. Some life-cycle stages can be more susceptible to management changes, and since financial constraints limit what conservation effects can be realistically achieved, the ability to pinpoint the parts of the population that respond and contribute most to a restoration effort can prove to be valuable (Caswell et al. 1998).

Aims with the thesis

My major aims with this thesis were to investigate whether it was possible to improve the conditions for vascular plant species living in wooded haymeadows, and to develop methods for facilitating dispersal between meadows. I also wanted to evaluate two different approaches when doing a viability analysis, namely a crude but quick stage distribution analysis and a more time-consuming demographic analysis, involving both prospective and retrospective analyses as well as deterministic and stochastic modelling. Demographic modelling is an important tool for investigating the response of plant populations to environmental processes, whether natural or experimentally induced. Using a demographic model, one relies on gathering data on individual plant performance over several years. In an attempt to increase the speed and accuracy of this laborious work, I wanted to develop a simple and
reliable method of tracking individuals between field seasons without using permanent markers.

I was particularly interested in investigating the effects intensified raking and mowing would have on litter accumulation and biomass production in seemingly well-managed hay-meadows (Paper I). I was also interested in how population growth rates ($\lambda$) would be affected by intensified raking and mowing (Papers I and II). If the plant populations respond to intensified management, I wanted to know which demographic transitions contributed most to the differences in population growth rate (Papers I and II). Because habitat isolation and limited dispersal are problems for many meadow species, I examined if the dispersal process could be assisted artificially by sowing seeds and planting plug-plants (Paper III). Finally, to increase the speed and accuracy of demographic data gathering, I partook in the development of an electronic coordinate measurement device (Paper IV).
Methods

Study sites

Five wooded hay-meadows (Bölske, Fardhem, Kullands, Linde and Mullvalds) situated on the southern part of the Baltic island of Gotland, Sweden, were used in the different studies (Figure 2). The meadows are situated between 3 and 55 kilometres apart and are all actively managed meadows. Bölske, Kullands and Mullvalds have a similar management history, with all having a long management history, similar moisture levels and high species richness. Fardhem, which is a newly restored meadow with comparatively lower species richness, was also included in the study since I wanted to test growth and survival in a re-introduction study. Linde was used as seed donor of *Hypochoeris maculata* seeds.

![Figure 2. Study sites on the southern part of the Baltic island of Gotland, east of mainland Sweden.](image)
Study species

The study species (Figure 3) were chosen based on the criteria that they should be herbaceous, perennial, non-threatened meadow plants that signal continuous management and must also be easy to identify, even as seedlings.

*Hypochoeris maculata* L. (Asteraceae) has a basal rosette with leaves that usually press down the vegetation around it. It is insect-pollinated, hermaphroditic and strictly out-crossing (Wells 1976). The fruits of *H. maculata* are wind-dispersed with a pappus. It can be clonal and form several rosettes originating from one individual. It is fairly common in southern and middle Sweden on dry, open sandy soils and a characteristic species in managed semi-natural grasslands (Hultén & Fries 1986; Mossberg & Stenberg 2003).

*Polygala amarella* Cr. (Polygalaceae) is a low-growing herb that mainly occurs on calcareous grasslands. The plant has several leafy stems branching out from a rosette of basal leaves, with a tender stem below attaching it to the ground. It is insect-pollinated, hermaphroditic and self-compatible. The seeds are ant dispersed (Mossberg & Stenberg 2003).

*Succisa pratensis* Moench. (Dipsacaceae) has a rosette of leaves in opposite pairs, all merged at the base of the plant. It is insect-pollinated, hermaphroditic and can produce self-seed, but the self-seed has been shown to be less viable than out-crossed seeds (Adams 1955, Vergeer et al. 2003). It has been found to be slightly clonal, as it is able to sometimes produce side-rosettes attached for the first years to the main plant. The seeds are borne in a hairy capsule, which can attach to furry animals for dispersal (Adams 1955; Römermann et al. 2005), but the hairy fruits have also been classified as wind-dispersed, albeit for rather short distances (Soons & Heil 2002). *Succisa pratensis* is rather common throughout southern Sweden on nutrient-poor soils and occurs in meadows and other semi-natural grasslands (Hultén & Fries 1986). However, it has been found to be in decline in meadows on Gotland in the last decade (Anonymous 2004).

![Figure 3. The study species, from left, *Hypochoeris maculata*, *Polygala amarella* and *Succisa pratensis*. (Photo: Lotta Wallin)](image)
Management intensification

The effects of different management intensities on the populations of *Hypocheris maculata*, *Polygala amarella* and *Succisa pratensis* were investigated during four growing seasons, from 2003 to 2006.

In 2002, I positioned 2–5 transects, with permanent plots measuring 0.71 \( \times \) 0.71 m (0.5 m\(^2\)), with a 0.29 m border zone between plots, in open areas in Böliske, Kullands and Mullvalds meadows. To these, four treatments were applied in a factorial design, with the treatments randomly ordered adjacent to each other within four-plot blocks along each transect, resulting in 12–14 replicate blocks per meadow. The treatments were: extra raking (R), extra mowing (M), extra raking and mowing (RM) and no extra treatment (control, C). The treatments were applied in addition to the usual meadow management and each individual plot received the same treatment over the entire study period.

The intensified management treatments were applied annually in May and October, starting May 2003. The raking treatment consisted of thoroughly raking the plot with a steel garden rake in spring after the normal raking, with the litter collected, dried at 70°C for 48 hours and weighed. The extra mowing treatment in October consisted of cutting the vegetation in the plot with grass shears to a maximum vegetation height of 5 cm. The cut material was collected, dried and weighed as for the raking treatment.

Because the distance between control plots and treatment plots within four-plot replicate blocks could be up to three metres, I evaluated the effect of management in the final year of the experiment by raking and mowing an additional control plot perpendicularly bordering each treatment plot. This enabled a pair-wise comparison of treatment effects (for clarity, these additional control plots will be referred to as the ‘2006 control plots’ to differentiate them from the control plots within the transects).

I measured average vegetation height in the plots using a vegetation ruler (Ekstam & Forshed 1996) each year in July before mowing.

Demographic study

Matrix analyses and population dynamics

In the first season of the study, all study plots were censused for all individuals (seedlings as well as mature plants) of *Succisa pratensis*, *Hypocheris maculata* and *Polygala amarella*. In plots containing more than 15 adult individuals of *Succisa pratensis*, a random sample of 15 individuals was selected. For each individual several parameters were recorded, from which stage classifications could be derived. The parameters measured yearly on
Succisa pratensis were the number of leaves, the width of the longest leaf, the number of fruits and the width of each fruit. For Hypochoeris maculata I measured the width and length of the longest leaf in June, and counted the number of fruits in July. For Polygala amarella I counted the number of stems and the length of the fruit racemes.

Each year in May (after applying the raking treatment) all plants were censused for survival and all new seedlings were recorded and added to the dataset.

Individuals were classified into the following stages for Hypochoeris maculata and Succisa pratensis: seedlings, juveniles, small vegetative, large vegetative, small flowering and large flowering plants (Figure 4a). For Polygala amarella the individuals were similarly classified except for the absence of the juvenile stage (Figure 4b).

![Life cycle graphs](image)

*Figure 4.* Life cycle graphs of Hypochoeris maculata and Succisa pratensis (a) and Polygala amarella (b). Arrows denote possible transitions, $a_{ij}$, where $a$ denote transition probabilities or fecundity and $i$ is the stage in year $t+1$ and $j$ is the stage in year $t$. 
I analysed the demographic data using population matrix modelling (Caswell 2001, Morris & Doak 2002). Using the fate of the individuals from each different stage (where transition probabilities were calculated by combining the underlying vital rates growth and survival) between each year, I constructed transition matrices for the different treatments, pooling the years.

I investigated the total effect of treatments on population growth rate ($\lambda$) by comparing each of the three treatments’ $\lambda$’s with the control $\lambda$. I calculated 95% bias-corrected, confidence intervals using 10 000 bootstrapped projection matrices (Caswell 2001) which were generated by randomly sampling individuals with replacement within stage classes. I used a non-parametric randomisation test (Levin et al. 1996; Caswell 2001) to assess the significance of difference in $\lambda$ between treatments. I compared the treated $\lambda$ with the control $\lambda$ pair-wise, by calculating the difference between them ($\theta_{\text{obs}}$):

$$\theta_{\text{obs}} = \left| \lambda^{(\text{treatment})} - \lambda^{(\text{control})} \right|$$

A test statistic ($\theta_{\text{test}}$) was then calculated from the fates of the individuals in the two treatments being compared by randomly permuting individuals from the combined data set with their history, maintaining the sample sizes. From the permuted data set, the difference between the randomly calculated $\lambda$’s formed the test statistic ($\theta_{\text{test}}$). A total of 2000 permutations were performed. To account for multiple testing, I Bonferroni-adjusted the level of significance ($\alpha$) (Quinn & Keough 2002).

I used a life-table response experiment (LTRE, fixed design, Caswell 2001) to find the transitions that contributed most to the differences in $\lambda$ between the control and treatment matrices. I used the control matrix as a baseline and compared the transition values pair-wise with the three treatment matrices. I decomposed the effect into contributions from each transition value ($c_{ij}$):

$$c_{ij} = \left[ a_{ij}^{(\text{control})} - a_{ij}^{(\text{treatment})} \right] \left( \frac{\partial \lambda}{\partial a_{ij}} \right) A_m$$

where $A_m$ is the mean matrix between the control and the three treatment matrices, respectively (Caswell 1996, 2001). The demographic analyses were done in Matlab ver. 5.2 and 6.3 (MathWorks, South Natick, Massachusetts) using adjusted scripts from Caswell (2001) and Morris & Doak (2002).

I used stochastic simulations on four transition matrices from the different management intensities (2003–2006) in three meadows for *Succisa pratensis* to get long-term stochastic $\lambda$ and the population sizes projected 50 years into the future. All matrices were selected with equal probability (Morris and Doak 2002).
Artificial dispersal

The effectiveness of artificial dispersal of *Succisa pratensis* and *Hypochoeris maculata* using seed sowing or plug-planting was examined by comparing the establishment success of the two introduction methods after two seasons.

The seeds and plug-plants were introduced into three traditionally managed hay-meadows (Bölske, Kullands and Mullvalds). In Kullands both species were already present, in Bölske only *S. pratensis* occurred, and in Fardhem neither of the species initially occurred. Seeds of both species from three different donor sites (Kullands, Mullvalds and Linde (*H. maculata*, or Bölske (*S. pratensis*)) were germinated in the greenhouse at Uppsala University Botanical Garden, and planted as plug-plants in May 2004.

In each of the three recipient sites, eight 0.5 m$^2$ plots were established along transects. Each permanent plot was subdivided into 16 subplots (180 × 180 mm), which, in turn, were divided into two quadrats that each received 50 seeds of each species (October 2003) and two plug-plants (May 2004) of the two species from all donor sites. The average number of emerging seedlings from the two sub-plots was used in the later analyses of donor site importance. For the establishment comparison between plug-planting and seed-sowing, I judged a plot as successfully established if there was at least one surviving plug-plant or seedling after two growing seasons.

Before sowing, I randomly chose half of the 0.5 m$^2$ plots and thoroughly raked the plots with a steel rake to investigate if removal of litter would improve establishment and survival of seedlings.

For the sown seeds, I counted emerging seedlings in May 2004 (emergence in the first growing season) and the number still alive in October 2005 (survival after two growing seasons). I recorded the survival of the planted plug-plants after 18 months, i.e., in October 2005 (survival after two growing seasons).

Ultra-sound positioning system

The demographic study component of my research required that I tracked several thousand individuals over five years. As the meadows are managed using raking, mowing and aftermath grazing, it was not possible to permanently tag each individual, so I needed to find each one at the beginning of each field season. Initially I used a tape measure to record the location of the individuals, but this proved to be error prone and time-consuming and a more accurate and speedy technique was required.

As it was not possible to find any low-cost readily-available solutions for rapidly recording large numbers of coordinates in small plots, I partook in the development of a custom-made electronic pantograph that could accu-
rately measure the location of a measurement stylus within a defined boundary by using ultra-sound travel times.

To assess the impact on measurement error in the dataset, I compared the number of errors in the data in the first field season (when the tape measure method was used) with the within-season errors when using only the electronic pantograph. Only errors exceeding 2 cm were considered because this margin was considered to be sufficiently accurate to identify the individuals, given the movement of the soil during winter and that the movements of the plants themselves were estimated to be of this magnitude.

The accuracy of the instrument was determined by recording the location of the stylus when placed within a 0.5 m² plot, using a grid with $10 \times 10$ known points. The test recordings were performed in a meadow with an average vegetation height of 5 cm. Two operators took four measurements at each grid point to give a total of 400 measurements, from which the deviation from the true coordinates could be determined.
Results and Discussion

Intensified management decreases biomass accumulation

Dry weights of raked litter and mowed biomass were reduced in treated plots compared to the 2006 control plots after four years of intensified management in two of three meadows. This is a sign of biomass accumulation in these meadows, supporting my concern that present-day management is insufficient. The reason for this accumulation may be a combination of the reduction in management intensity and the increased nutrient accumulation from aerial nitrogen deposition (Foster & Gross 1998; Berendse 1999). Regardless of the underlying reason, this has serious implications for seedling germination and establishment (Bullock et al. 1994; Jensen & Meyer 2001).

Most of the management work is presently performed by either local interest groups or volunteers, and represents heavy work for a relatively small economical compensation. Therefore, increased financial incentives may have to be considered in conservation budgets from local councils and the European Union to ensure that the required increase in management intensity levels is achieved.

Higher population growth rates following management intensification

Population growth rates in *Succisa pratensis* differed between the treated and the control plots all three meadows. The permutation tests revealed that both the mowing and the combined raking and mowing treatments resulted in higher population growth rates compared to the control plots. Increased management has been shown to increase population growth rates and persistence in other long-lived perennial species as well (Lennartsson & Oostermeijer 2001; Jacquemyn et al. 2003; Brys et al. 2005; Ehrlén et al. 2005; Colling & Matthies 2006).

*Polygala amarella* displayed a population growth rate that varied considerably among treatments and was below unity for all treatments and control
plots. *P. amarella* had an especially low growth rate for the treatments where raking was included, which can be explained by the plant’s morphology: older individuals have a branched growth form with a basal leaf rosette, below which only a thin stem connects them to the ground, making them vulnerable to being snagged by the rake and pulled out, a phenomenon I observed in the field.

*Hypochoeris maculata* had a population growth rate of around unity, with very little variation among treatments and showed no response to an increase in management. The rosette of the plant is probably able to press down the surrounding vegetation to create an open space to capture sufficient light, Increasing the level of management will therefore not substantially improve the competitive ability of this species. Seedlings may, however, be favoured by increased management intensity, but reproduction was rarely observed in the field during my study. Other studies on perennial plant species living in semi-natural grasslands have generally shown a positive effect of higher management intensity (Bühler & Schmid 2001; Ehrlén et al. 2005). However, Jongejans & De Kroon (2005) found that three different species responded differently to the same environmental factors even though they share similar life-history traits. Therefore one has to be cautious in concluding general responses to, for example, management, drawn from results from just one species, as I have shown by the different responses to an increase in management in my studied species.

Since LTRE analysis is a retrospective method of decomposing the effects of a treatment compared to a control, it cannot be used to forecast the effects of specific management changes (Caswell 1996, 2000). However, LTRE it is very useful for elucidating the reasons for any differences found. I conclude that the reason for differences in population growth rate between treatment and control plots for *Succisa pratensis* in Bölske was that there were higher proportions of juveniles growing into small vegetative plants, as well as a higher proportion of large vegetative plants growing to large flowering plants in the treated plots. The increased management intensity may have made these transitions easier by reducing competition from the surrounding vegetation. The sensitivities of the fecundity values in the matrices were generally not large in any of the meadows or treatments. Instead, I found most of the high sensitivity values for transitions where adult individuals stay in the same stage or grow. There is a slight difference between meadows though, with Bölske having higher sensitivities in the older stages and Kullands and Mullvals having higher sensitivities in the younger stages. In essence this follows Silvertown et al. (1993) and Crone (2001) who suggested that proportional changes in survival in adult stages are more important than fecundity for population fitness in perennial species.

For *Polygala amarella* the LTRE analysis revealed that raking mainly affected transitions of juveniles to older stages negatively, again supporting that this species will not be favoured by intensified raking.
Stochastic simulations demonstrate larger population sizes

The stochastic modelling showed positive effects on *Succisa pratensis* of an increase in management; all meadows displayed larger projected population sizes 50 years into the future with intensified management compared with the control. Although none of the populations in Bölske, including the control, displayed a population growth rate under unity, there was a large difference between the control and the raking plus mowing treatment, showing that population sizes clearly increase with intensified management.

Population structure can possibly reveal population viability

Long-term population growth rates were around unity in all populations of *Succisa pratensis*, even though the population structures were quite different in Bölske, Kullands and Mullvalds, with Bölske having a high proportion of old individuals and few seedlings, and the other two sites having a higher proportion of seedlings. The negligent difference in population growth rate indicates that it is possible for a population to have a stage distribution with a majority of old individuals and yet not shrink. Perhaps we can anticipate a future decline of a population with a skewed distribution. Therefore, it seems wise to judge population viability by combining population growth rate estimates with observations of the population structure (Oostermeijer et al. 1994; Eriksson 1996). Also, since the stochastic simulation revealed larger population sizes following intensified management, it is likely that there is a negative trend not displayed by the deterministic model.

Artificial dispersal successful for establishment of meadow plants

Establishment was twice as successful for planted plug-plants compared to sown seeds. The low germination rate and subsequent survival after one and two growing seasons after sowing is a concern for the long-term survival of the introduced individuals. The seedlings that established from seed were still quite small after two seasons; I observed that the average leaf width was 5 mm for *Succisa pratensis* and 2 mm for *Hypochoeris maculata*. Their small sizes decrease the chances for their long-term survival, as they are still very vulnerable to competition. This is readily apparent in the mortality of more than half of the seedlings of both species between seasons one and two. Both seed sowing and plug-planting have been used in introduction experi-
ments (Walker et al. 2004) but successful long-term establishment of the introduction can be varying (Primack & Miao 1992; Turnbull et al. 2000).

Seedling establishment was affected by donor site. Since the *Succisa pratensis* seeds from the different sources were differing in weight this may well be the overriding determinant for seedling germination. Heavier seeds, with more resources, generally have a greater germination ability compared to lighter seeds (Westoby et al. 1996). In my study, the lightest seeds of *S. pratensis* came from the donor site Bölske, and these seeds failed to germinate both in the greenhouse and in the field.

Coordinate measuring device increases speed and accuracy of data gathering

The two measurement sets taken with the tape-measure system contained 293 measurements with coordinate differences exceeding 2 cm, from a total number of 2496 recordings (12%). The distribution of these errors was roughly even over the size of the plot. The same comparison was performed on two censuses measured with the electronic system, where there were 72 measurements with coordinate differences exceeding 2 cm from a total of 2927 recordings (2.5%). Of these errors, over half had a difference of less than 6 cm.

The results clearly demonstrate the advantages of automating the measuring process. The errors remaining in the measurements reveal two important points: that the concentration of errors below 6 cm indicates that the between-season movement of the plants may be larger than estimated and that the remaining errors above 6 cm must be due to transcription errors; this provides an error baseline that can be subtracted from the tape-measure results to determine the errors directly arising from the manual measurement process.

The precision of the measurement device was ±1.8 cm, which is acceptable in the study system. Even though seedlings occasionally grew in tightly clustered groups, the device was still effective because previous measurements of the relative positions of individuals within a seedling cluster proved sufficient for tracking the same individuals in subsequent seasons.

For demographic studies that use large numbers of tracked individuals, the automation of coordinate measurement can result in an improvement to data reliability and a substantial reduction in the time needed for finding individuals in the field.
Conclusions and Management Implications

I have shown that intensified management (extra raking and/or extra mowing) can reduce the amount of litter and biomass even in meadows that are considered well-managed. Therefore, an increase in the present management intensity level may be necessary to maintain the habitat characteristics that are the basis for preserving long-term viable populations of meadow plants in the future.

In the meadows that showed litter and biomass accumulation I found that intensified management had a positive effect on *Succisa pratensis*, with a combination of raking and mowing increasing the long-term population growth rate compared to the control plots that had just the normal management. For *Hypochoeris maculata*, there was no response to management in population growth rate, but this species was only studied in a meadow in which the levels of biomass accumulation were not affected by an increase in management intensity. *Polygala amarella* responded negatively in the same meadow to any management that involved extra raking due to the structure of the plant – too vigorous raking resulted in pulling the plants out of the ground.

These results suggest that species with differing life-history characteristics and morphologies will react individually to management intensification. I nevertheless advise that if the amount of accumulated litter and vegetation biomass in a meadow is moderate, a more intense management will be needed, even though some species may initially react negatively. Since *Polygala amarella* displayed very dynamic population changes, with a capability for fast growth, large disturbances may not be detrimental to its survival.

Artificial dispersal between meadows can be achieved either by seed sowing or plug-planting. Successful establishment was accomplished by both methods using *Hypochoeris maculata* and *Succisa pratensis* as model species. After two seasons, plug-planting had a higher establishment degree than seed sowing, making the first method especially suitable if seed sources are scarce or if the recipient habitat is highly competitive with, for example, low light levels leading to high seedling mortality.

For demographic studies where large amounts of individual data are gathered over several seasons from permanent study plots, more reliable location data and a speedier acquisition time can be attained by using an electronic coordinate measuring device.
Finally, I want to point to the danger of merely studying the present-day distribution of stages and using this for assessing population viabilities. I have shown that even if a species is common and has a population distribution that appears healthy (i.e., many young individuals, many flowering plants and a high seed production), we can find other populations of the same species with a distribution consisting of mainly of old individuals that displays the same population growth rate. To gain the full picture, more data are required, preferably collected over several years, and stochastic simulations seem to be the most reliable tool when projecting the fate of a population.
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The future is wide open now – like it always was, but without a thesis lingering in the back of my head, the horizon looks a lot clearer!

För ska det va
nån nytta med vår flora
så får den faktiskt inte växa
som den vill....

Allan Edwall
Växtpopulationers dynamik och naturvård i lövbärande ängar – effekter av ökad hävd

Den viktiga hävden

Ångshävd har funnits i Sverige ända sedan järnåldern och skapade ett unikt landskap med en mycket hög rikedom på arter. På ängarna producerades det foder som gjorde att kreaturen kunde överleva vinterinomhus innan de fick komma ut i skogen igen på sommarbete. Vinterfodret var indirekt också väldigt viktigt för åkerbruket, då de stallade djuren producerade gödsel som spreds på åkrarna, därav uttrycket ”äng är åkers moder”.


Sensommaren var också en period då lövtäkt, så kallad hamling eller –på Gotland – klappning kunde äga rum i lövbärande ängar. Eftersom behovet av vinterfodder ofta var stort drygade man ut det genom att skörda lövade grenar från framförallt alm och ask. Detta innebar att mer ljus nådde till markvegetationen, men också att de trädrotsen som dog och förmutade till följd av att grenar togs bort, kunde ge en gödslingseffekt som var gynnsam för gräsväx-
ten. Under vintermånaderna städades det i ängarna, man plockade nedfallna grenar och gallrade i buskar och träd.

Alla komponenter i hävdcyklens skapade tillsammans den näringsfattiga och ljusrika naturtyp där många arter kunde samsas på en begränsad yta. Den mänskliga hävdens skapar alltså förutsättningar för många växter att samexistera genom att snabbväxande och kvävande (det vill säga starkt konkurrenskraftiga) arter inte tillåts ta över.


Ökad hävd ger mindre förna och biomassa

Ett ökat atmosfäriskt kvävenedfall över Nordeuropa och Sverige under de senaste femtiotäta åren har lett till en höjning av näringsnivåerna i de naturligt så näringsfattiga ängsmarkerna. Detta kan leda till en ökad gräsväxt och en ökning av förekomsten av konkurrenskraftiga arter, såsom hundkäx – en av ängshävdare illa sedd art. Eftersom det idag inte finns någon ekonomisk avkastning för ängshö är den mesta av hävden bekostad av olika ekonomiska bidrag från EU och landets länsstyrelser. Den arbetsinsats som krävs för att genomföra alla delar av ängskötseln täcks ofta inte av bidragen. Kombinationen ökade näringsnivåer i ängarna och en svagare hävd tror jag kan leda till att dagens skötelnivå inte är tillräckligt intensiv för att bevara ängarnas höga artrikedom.

Genom att under fyra säsonger experimentellt öka hävdintensiteten i ängar som är välhävdade med dagens mått mätt, kunde jag undersöka om det blev någon skillnad mot den naturliga hävden. Jag använde fasta provrutor, där jag antingen räfsade extra noga på våren, klippte ner vegetationen till lägre än 5 cm på hösten, både räfsade noga och klippte, eller lämnade utan förstärkt hävd, det vill säga dessa provrutor fick den hävd som resten av ängen fick. Jag undersökte hur mängden ihopräfsad förna på våren samt mängden vegetation klippt på hösten påverkades av den extra intensiva hävden. Jag fann att förmångendén minskade i en av ängarna och vegetationsmängden minskade i två av tre undersökta ängar, vilket styrkte min misstänke om att hävden i dagens ängar kan vara för svag.
Växtpopulationer reagerar på ökad hävdintensitet


Artificiell spridning

I och med att ängarna idag är få och ofta ligger långt från varandra kan frö-spridning mellan lokaler vara svårt. Spridning är viktigt för att populationerna ska kunna bibehålla en genetisk variation som är grunden för evolution och anpassning till förändrade miljöförhållanden. Eftersom många ängsväxter inte kan sprida sig längre sträckor, måste vi hjälpa dem för att populatio-
nerna inte ska isoleras. Jag testade att artificiellt sprida slåtterfibbla och ängsvädd med hjälp av två metoder, frösådd och plantering av småplantor. Båda sätten fungerade väl, men metoden med småplantor gav en högre etableringsgrad två säsonger efter introduktionen. Troligtvis är detta en säkrare metod i och med att växterna har hunnit växa till sig i en konkurrensfri miljö (i mitt fall i växthus), medan de plantor som ska etablera sig från frö startar i en mycket hårdare miljö. Om man vill vara säker på att få etablering ska man alltså välja att introducera större plantor.

Enklare mätningar med hjälp av elektroniskt instrument

Eftersom min demografiska undersökning krävde att jag följde samma individ under flera växtsäsonger, innebar det att jag behövde en metod som gjorde att jag enkelt och snabbt kunde hitta tillbaka till rätt individ. Jag kunde inte märka plantan (exempelvis med en färgad tråd), och heller inte lämna markeringar i jorden, eftersom jag var tvungen att avlägsna all spår efter undersökningen innan slättern och efterbetet. Genom att utveckla ett elektroniskt mätinstrument som med hjälp av ultraljud kunde mäta koordinater i mina fasta provrutor, kunde jag göra mätproceduren snabbare och samtidigt minimera antalet felmätta koordinater. Instrumentet kallar jag för ”plantastic”!


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