

Population structure of the threatened perennial *Serratula tinctoria* in relation to vegetation and management

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Abstract

Question: How does vegetation and management affect the population stage structure of *Serratula tinctoria*, a species indicative of highly endangered and species-rich flood-plain meadows? Are different management regimes suitable to support viable populations of *S. tinctoria*?

Location: Flood-plain of the northern Upper Rhine, Germany.

Methods: We analysed the population structure of *S. tinctoria* at 24 meadow sites which differed in vegetation and management. In this comparative study the investigated meadows were either (1) late mown in September; (2) early mown in June or (3) mown in June and then grazed by sheep.

Results: The structure of the surrounding vegetation had a clear effect on the population structure of *S. tinctoria*. The percentage of bare soil, as well as the cover of bryophytes, were positively related, whereas the Ellenberg N-value of the established vegetation was negatively related to the density and proportion of seedlings. Generally, we found only slight differences between the population structure of *S. tinctoria* in early and late mown meadows. Both management regimes had high densities of seedlings. In contrast, the meadow pastures supported significantly lower densities of seedlings and generative adults but relatively high densities of juveniles and vegetative adults, indicating a greater importance of clonal propagation under grazing pressure.

Conclusions: Our results clearly showed that viable populations of *S. tinctoria* may occur in all of the studied management regimes. Although *S. tinctoria* was considered to be highly sensitive to early mowing, our findings suggest a facilitation of the species at more nutrient-rich sites by mowing in June, which is also a benefit for the integration of management in farming systems.

Keywords: Conservation; Demography; Flood-plain meadow; Grazing; Long-lived perennial; Mowing; Recruitment.

Abbreviation: PAR = Photosynthetically active radiation.

Introduction

The persistence of many plant species in semi-natural grasslands depends on regular and appropriate management. Mowing and grazing are important factors for the maintenance and restoration of high species richness in grasslands (Bakker 1989; Güsewell et al. 2000; Grime 2002). Management regimes have a major impact on the availability of seeds and of suitable safe sites (Harper 1977), which are key factors for reproduction and successful recruitment in plant populations (Eriksson & Ehrlén 1992). Grazing is known to create gaps in the sward that facilitate seedling recruitment (Watt & Gibson 1988; Bullock et al. 1994), whereas mowing can prevent asymmetric light competition (Lepš 1999) but may also hamper seed production (Coulson et al. 2001). Additionally, grassland species are characterized by different mowing and grazing compatibilities, which may be affected by livestock feeding preference and the capacity for regeneration after disturbance (Briemle et al. 2002).

These examples indicate that management regimes can differently affect the dynamics and composition of plant communities and individual plant species. Therefore, the investigation of plant population dynamics in relation to management and environmental variation is of major interest in the successful conservation of threatened plant species. Traditional management regimes often contradict the demands of modern agriculture. In particular, it is difficult to incorporate biomass from late mown meadows in existing farming systems without high compensation payments. Consequently, there is often an urgent need to assess the suitability of alternative management options in maintaining target communities (Bühler & Schmid 2001; Hegland et al. 2001).

The analysis of life stages of perennial plants can provide information for the improvement of conservation and management strategies (Oostermeijer et al. 1994). In contrast to detailed individual-based demographic investigations, the analysis of the population stage structure is less laborious, which has the advantage of better representation since more replicates can

be sampled. Although only a single census per population is conducted, several studies confirmed the usefulness and appropriateness of this method (Oostermeijer et al. 1994; Bühler & Schmid 2001; Hegland et al. 2001; Colling et al. 2002). In the present study we used this approach to assess the suitability of different management regimes for the preservation of highly endangered species-rich flood-meadows along the northern upper Rhine in Germany. *Serratula tinctoria*, characteristic of species-rich flood-meadows (Hölzel 1999), was chosen as a model species. We studied the demographic structure of this species in 24 populations with respect to management, site conditions and vegetation.

The main objectives of the study were (1) to assess the impact of site conditions, vegetation structure and species composition on population stage structure and (2) to evaluate management options for the sustainable conservation of *S. tinctoria* populations and species-rich flood-meadows in general.

Methods

Study species

Serratula tinctoria is a long-lived herbaceous perennial plant, which predominantly occurs in fen meadows and alluvial grasslands on base-rich soils, but also in open deciduous forests, along forest edges and in heathlands (Hegi 1987). The species is considered to be a character species of late mown, nutrient-poor *Molinion* grasslands (Oberdorfer 1983). In our study area and in other parts of central Europe *S. tinctoria* occurs widely in more nutrient-rich flood-meadows of the alliance *Cnidion* (Burkart 1998; Hölzel 1999), which were traditionally used for hay-making. These meadows are characterized by a high variability in soil water potential. While winter, spring and early summer may bring floods, summers are often characterized by periods of drought. *S. tinctoria* is known as a species particularly well adapted to highly variable soil moisture conditions.

Germination of the relatively large seeds occurs in autumn directly after shedding or in the next spring (Hölzel & Otte 2004a) and there is no indication of a long-term persistent seed bank (Hölzel & Otte 2004b). This iteroparous species flowers from July until October. The flowers are pollinated by various insects (*Hymenoptera*, *Diptera*, *Lepidoptera*) and the diaspores are adapted to wind dispersal (Müller-Schneider 1986; Bischoff 2002). *S. tinctoria* can also propagate clonally by forming daughter rosettes at the end of short stolons (Klimeš et al. 1997).

Due to the central European core area of the species, Germany has a high responsibility for the worldwide preservation of *S. tinctoria* (Welk 2002).

Study area and sampling

In the Hessian portion of the Holocene flood-plain of the northern upper Rhine, between the Neckar and Main tributaries, 24 study sites in flood-meadows were selected. The investigated meadows are subject to the following management regimes:

1. Mowing once in September (late mowing) ($n = 8$).
2. Mid-June mowing (early mowing). These meadows were used for hay-making and only in years of high precipitation is a second cut conducted ($n = 9$).
3. Meadow mown in June and grazed in late summer or autumn by a free-ranging flock of sheep ($n = 7$).

All sites are in nature reserves and the current management regimes have been applied for ca. 20 yr.

In August and September 2002, in each population, two randomly selected 1-m² plots (in one population just one plot) were analysed, yielding a total of 47 samples. The total number of individuals in each plot was counted. Although clonal propagation was also possible, each rosette was considered as an individual. For the classification of life stage classes in each individual the total height, total length of the longest leaf, length and width of the longest leaf blade and the number of leaves per rosette were measured. In generative plants the number of flowerheads and stalks was also counted.

To describe species composition, the abundance of all vascular plant species was estimated using a modified Braun-Blanquet scale (van der Maarel 1979). We estimated total vegetation cover, the coverage of mosses, plant litter, the percentage of bare soil surface and mean vegetation height as indicators of vegetation structure. Light intensity penetrating to the ground was measured using a 1-m long Line Quantum Sensor (LI-COR: LI-191SA). We recorded photosynthetically active radiation (PAR, 400 - 700 nm) simultaneously at ground level and in full light above the canopy. Light penetration was expressed as a percentage of the latter value. Light measurements were performed in August and were repeated four times at random in each plot. To determine population size, we counted all flowering plants in small populations. In large populations (> 500 individuals) we used the mean number of reproductive plants per m² and extrapolated it to a value for the total population area. The number of flowering plants per population ranged between 25 and 5000.

Classification of life stages

Based on our field observations of 7055 individuals we distinguished four different life stages, which were defined by leaf number, leaf size and the presence or absence of flowers. To evaluate the appropriateness of the chosen classification and to clarify critical cases we

also applied the method of *k*-means clustering (Legendre & Legendre 1998). The final life stage classes were defined as follows:

1. Seedlings (s) had cotyledons and up to three primary leaves (maximum length of the longest leaf 10 cm, mean length of leaf blade 1.7 cm).
2. Juveniles (j) had mostly four leaves with a maximum length of the longest leaf of 20 cm.
3. Vegetative adults (vA) were characterized by a rosette with between 5 and 11 leaves. The leaves were coarsely serrate, more solid and the texture was more structured than the leaves of the juveniles.
4. Generative adults (gA) normally had one, and in the early mown meadows up to four, flowering stalks. Rosettes whose flowering stalks had been grazed were also considered as generative adults.

Data analysis

For each population the density per m² and the relative proportion of the different life stage classes was calculated.

To assess compositional gradients in the vegetation of the study plots we used Detrended Correspondence Analysis (DCA) on square root transformed cover data (species with less than three occurrences excluded). Axis 1 had a gradient length of 3.023 standard deviation units and thus showed some unimodality (Legendre & Legendre 1998; ter Braak & Šmilauer 1998). The vegetation data were also used to calculate cover weighted means of the Ellenberg indicator values for moisture, light and nutrients (Ellenberg et al. 1992). Correlations between axes scores and habitat variables were analysed using the Pearson correlation coefficient.

The relationship between habitat variables and the density or proportion of each life stage was investigated by simple and multiple regression analysis. Spearman rank correlation coefficients between predictor variables were examined to detect collinearity (Quinn & Keough 2002). Intercorrelated variables were omitted, which resulted in four remaining habitat variables (cover of bryophytes, open soil, relative light intensity, Ellenberg N) and these were chosen as predictor variables in the multiple regression model. We applied the more robust stepwise backward selection procedure (Zar 1999). Proportions were angular transformed and the remaining predictor variables square root transformed prior to regression analyses to meet the normality assumption.

To analyse the counts of individuals per plot and to test for differences in the demographic status of *S. tinctoria* between management regimes, we conducted univariate two-way ANOVA with the densities of each life stage as dependent variable and management type

as well as population as factors. Population was used as a nested random factor within the management regimes. In one population only one plot was analysed so we omitted this population from the analysis, yielding 23 populations in total. To test for the overall effect of management and population we applied a MANOVA. Out of the four common MANOVA statistics we chose the recommended, more robust Pillai's trace for interpretation of results (Quinn & Keough 2002). Prior to analysis the frequencies were log-transformed ($x + 1$) and we achieved normally distributed residuals and homogeneous variances. In case of significance, the analysis was followed by a Tukey's test for unequal sample sizes. The differences in number of flowerheads between management regimes were also analysed by two-way ANOVA and followed by a Tukey's test.

Detrended Correspondence Analysis ordination was performed using the software package PC-ORD 4.14 (McCune & Mefford 1999). Regression analysis was carried out with the General Linear Model module of STATISTICA 6.0 (Anon. 2002). ANOVA, MANOVA and associated tests were calculated with SAS for Windows (Anon. 1999).

Results

Comparison of species composition and site variables

The DCA ordination revealed a clear floristic gradient between early and late mown meadows with *S. tinctoria*. Whereas late mown stands had a high floristic variation along the first axis, early mown meadows and the meadow pastures were more uniform, which is indicated by a clumped distribution in the lower left corner of the ordination graph (Fig. 1).

The first axis showed a positive correlation with the Ellenberg indicator value for light ($r = 0.62$; $P < 0.05$) and a negative correlation with the Ellenberg nutrient value ($r = -0.54$; $P < 0.05$) and the percentage of vegetation cover ($r = -0.50$; $P < 0.05$). The second axis displayed a positive correlation with vegetation height ($r = 0.48$; $P < 0.05$). All other variables were not significantly correlated with the DCA axes.

Relationships between vegetation structure, species composition and population structure

Multiple regression analyses confirmed a clear relationship between the structure and floristic composition of the surrounding vegetation and some life stage classes of the studied populations. In the regression model, the cover of bryophytes and percentage of bare soil were positively correlated with seedling density, whereas the

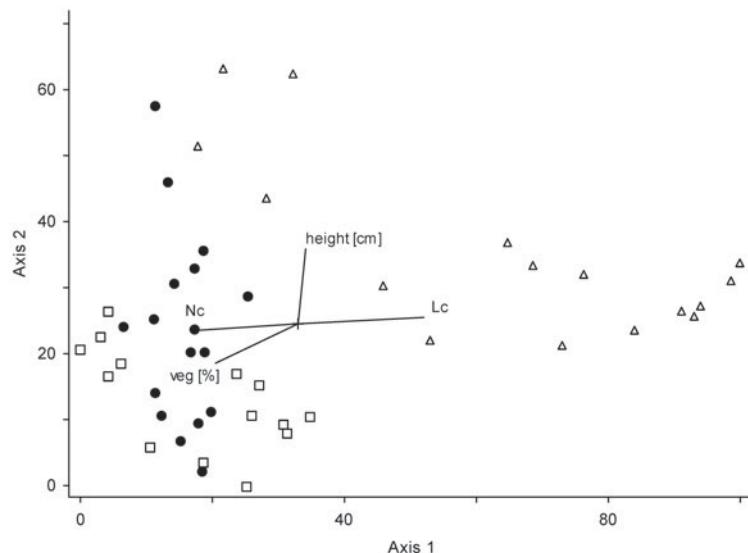


Fig. 1. Joint plot based on Detrended Correspondence Analysis of 47 plots in differently managed meadows with respect to site variables. \triangle = late mown meadows; \bullet = early mown meadows; \square = meadow-pastures. Lc = Ellenberg indicator value for light; Nc = Ellenberg indicator value for nitrogen; height (cm) = measured canopy height; veg (%) = percentage cover of the vegetation.

Ellenberg nutrient value was negatively correlated with seedling density (Table 1). Similarly, in the proportion of seedlings a large part of variance (52%) was explained by habitat variables. Besides the above mentioned variables, relative light intensity was additionally retained as a significant predictor of the proportion of seedlings. Furthermore, the density of generative adults also showed a positive correlation with the cover of bryophytes and a negative correlation with the Ellenberg nutrient value. Conversely, the proportion of vegetative adults was negatively correlated with the cover of bryophytes and the percentage of open soil and positively with the Ellenberg nutrient value.

We also found significant positive correlations of the density and the proportion of seedlings with the estimated population size ($R^2 = 0.390$; $df = 22$; $P < 0.001$; $R^2 = 0.357$; $df = 22$; $P = 0.001$).

Impact of management on population structure

Univariate two-way ANOVA of the mean density of *S. tinctoria* life stages revealed significant differences between management regimes for the seedling and generative adult stage class (Table 2). Significant differences between the density of populations were found in all life stage classes with the exception of vegetative adults. Despite the high variability between populations (Pillai's Trace < 0.0001), MANOVA of all life stage classes resulted in an overall significant management effect (Pillai's Trace 0.0003).

As shown in Fig. 2 the densities of seedlings and generative adults significantly differed between management regimes while juveniles and vegetative adults showed no differences in their densities. The *post-hoc* test confirmed that the meadow pastures had significantly

	Predictor variable	β	t	P
a. Densities				
Seedlings (ind. m^{-2})		$R^2 = 0.326$		
	Cover bryophytes (%)	0.461	2.421	0.025
	Open soil (%)	0.572	2.921	0.008
	Ellenberg N	-0.427	-2.394	0.027
Generative adults (ind. m^{-2})		$R^2 = 0.316$		
	Cover bryophytes (%)	0.367	2.105	0.047
	Ellenberg N	-0.439	-2.520	0.020
b. Proportion of plants				
Seedlings (%)		$R^2 = 0.522$		
	Cover bryophytes (%)	0.664	3.906	<0.001
	Open soil (%)	0.709	4.214	<0.001
	Light (%)	0.364	2.336	0.031
	Ellenberg N	-0.364	-2.381	0.028
Vegetative adults (%)		$R^2 = 0.454$		
	Cover bryophytes (%)	-0.452	-2.639	0.016
	Open soil (%)	-0.589	-3.335	0.003
	Ellenberg N	0.561	3.497	0.002

Table 1. Stepwise multiple regression of the relationship between the density or proportion of four life stage classes of *Serratula tinctoria* and habitat characteristics on the population level ($n = 24$). For the full model four predictor variables were chosen (see text). Backward selection of variables was used ($P < 0.05$). R^2 = adjusted coefficient of determination; β = standardized regression coefficient; t = t -test for the deviation of β from zero.

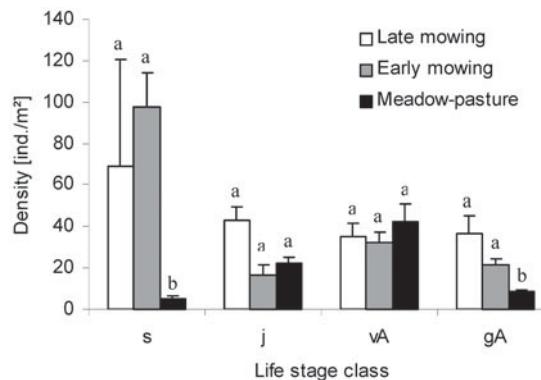


Fig. 2. Mean densities of life stage classes of 24 populations of *Serratula tinctoria* with respect to different management regimes. Letters indicate if means differ significantly in life stage class at $\alpha < 0.05$ (Tukey's test). s = seedling; j = juvenile; vA = vegetative adult; gA = generative adult.

lower densities of seedlings than the late or early mown meadows (Fig. 2). Similarly, the mean density of generative adults was also significantly higher in early and late mown meadows than in meadow pastures. Generally, there were only slight differences between early and late mown meadows, whereas the meadow pastures were characterized by a divergent population structure. Although the meadow pastures had a lower density of seedlings and generative adults, the density of juveniles was comparable and the density of vegetative adults was even slightly higher than in the other management regimes.

The number of flowerheads per population was significantly higher in both late and early mown meadows than in meadow pastures (Fig. 3). The same was true for the mean number of flowerheads per plant and population, which was significantly higher in early mown meadows than in meadow pastures ($\alpha = 0.05$, Tukey's test).

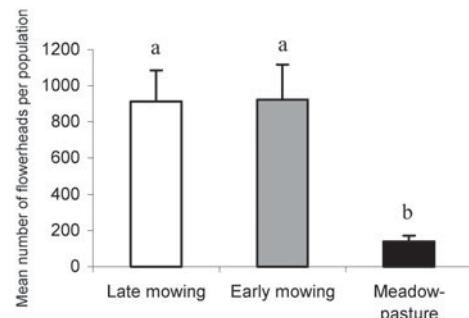


Fig. 3. Mean number of flowerheads per population of *Serratula tinctoria* and s.e. with respect to three different management regimes. Letters indicate if means differ significantly at $\alpha < 0.05$ (Tukey's test).

Discussion

Effects of habitat conditions on population structure

The structure and composition of the surrounding vegetation had a strong effect on the population structure of *Serratula tinctoria*. For seedlings, the main variables of influence were cover of bryophytes, open soil and Ellenberg N-value. The percentage of bare soil was positively correlated with the density and proportion of seedlings, which confirms earlier evidence that gaps provide particularly suitable conditions for germination and seedling recruitment in grasslands (Grubb 1977; Silvertown 1981; Křenová & Lepš 1996; Kotorová & Lepš 1999).

The positive relationship between cover of bryophytes and density or proportion of seedlings may be interpreted as a protective effect of the moss layer on

Table 2. Univariate two-way ANOVA of the density of life stage classes of 23 *Serratula tinctoria* populations in three management regimes. Population was used as a nested random factor within the management regimes. Prior to analysis the frequencies were log-transformed ($x + 1$). MS = mean squares.

Source of variation		df	MS	F	P
Seedlings	Management	2	4.208	6.41	0.007
	Population (Management)	20	0.656	9.17	< 0.001
	Error	23	0.072		
Juveniles	Management	2	0.249	0.70	0.507
	Population (Management)	20	0.354	2.09	0.046
	Error	23	0.170		
Vegetative adults	Management	2	0.095	0.68	0.518
	Population (Management)	20	0.139	0.87	0.622
	Error	23	0.160		
Generative adults	Management	2	1.491	7.96	0.003
	Population (Management)	20	0.187	5.99	< 0.001
	Error	23	0.031		

seed germination. These results agree with findings of Ryser (1993) and Oostermeijer et al. (1994). The latter hypothesized that the moss layer reduces winter mortality of seedlings. The bryophyte layer may also provide protection against seed predation (van Tooren 1988) or prevent desiccation of seedlings (Špačková et al. 1998). During & van Tooren (1990) emphasized that the protective role of the moss layer is more important in communities with high summer drought or temporal desiccation, which is in line with the environmental situation in the studied flood-meadows. In contrast, several authors found inhibiting effects of the bryophyte layer on seedling recruitment in permanently wet meadows (Špačková et al. 1998; Kotorová & Lepš 1999; Eckstein et al. 2004).

Higher nutrient availability, indicated by Ellenberg nutrient values, also led to a decrease in the number and proportion of *S. tinctoria* seedlings which corresponds with the findings of Rusch & Fernández-Palacios (1995) and Lepš (1999). Similarly, the percentage of light reaching the soil surface was positively related to the proportion of *S. tinctoria* seedlings, which was also found by other authors as a major factor controlling recruitment (Jensen & Meyer 2001; Jutila & Grace 2002).

In contrast, vegetative adults were negatively related to the cover of bryophytes and open soil and positively correlated with the Ellenberg nutrient value. This showed that vegetative adults predominantly occurred in habitats with different vegetation structure and floristic composition than seedlings. As confirmed by the other results (Fig. 2), the more nutrient-rich meadow pastures are characterized by high densities of vegetative adults.

Effects of late and early mowing

As shown in Fig. 3, viable populations of *S. tinctoria*, suggested by high numbers of seedlings, occurred in early as well as in late mown meadows. The mean density of seedlings in early mown meadows was even higher than in late mown meadows. This indicated, that although these meadows were cut in June, germination and early establishment were successful. The rosette species *S. tinctoria* rarely flowered before mid-June and was able to recover rapidly after cutting, which is a general character of many rosette species (Briemle & Ellenberg 1994). Even if the plant already had a stem with buds it responded to cutting by a rapid re-growth of two or more generative stems (pers. obs.). Similar results were obtained by Lennartsson & Oostermeijer (2001) who showed that *Gentianella campestris* had a high capacity for compensatory seed production after mid-July mowing. After mowing in June, *S. tinctoria* flowers from early August onwards and sets seed in September or October. This also applies to other target species of

flood-meadows, such as *Sanguisorba officinalis*, *Silaum silaus*, *Inula salicina*, *Allium angulosum* and *Cnidium dubium* (Joyce 1998; Hölzel et al. 2002). These species may benefit from competitive release after hay-making in early June inducing a higher availability of light. For flood-meadows along the Elbe River, Leyer (2002) found that early mowing prevents species-rich stands forming a dense litter layer and weakens competitors with predominantly vegetative propagation such as *Elymus repens* or *Phalaris arundinacea*.

Our results clearly suggest a facilitation of *S. tinctoria* by early mowing in relatively nutrient-rich *Cnidion* meadows. This contrasts with other authors who have reported sensitivity to early mowing (Briemle & Ellenberg 1994; Briemle et al. 2002). However, in the case of early mowing no, or a very late, second cut in autumn appears to be of crucial importance. An early second cut in August or September, would probably lead to a failure of seed production due to immature seeds at the time of mowing (Hölzel 1999) and thus negatively affect the viability of *S. tinctoria* populations in the long-term. As pointed out in many other studies (e.g. Hegland et al. 2001; Overbeck et al. 2003) management regimes have to respect the phenology of seed production to assure the potential for dispersal and non-clonal regeneration.

Effects of grazing

In contrast to early or late mown populations, the meadow pastures were characterized by low densities of seedlings and generative adults, but relatively high densities of juveniles and vegetative adults. The low number of seedlings is most likely an effect of the damage to adult plants and their seeds by subsequent grazing, which reduces the potential for the recruitment of new individuals (Bastrenta 1991; Bühler & Schmid 2001; Lennartsson & Oostermeijer 2001). This is also illustrated by a significantly lower number of flowerheads in the meadow pastures. As indicated by the relatively high proportion of vegetative adults, the reduced generative reproduction under grazing pressure seems to be at least partly compensated by a raised importance of clonal propagation.

More suitable conditions for establishment of *S. tinctoria* in the meadow pastures due to trampled gaps (Bullock et al. 1995; Lennartsson & Oostermeijer 2001) were not detected, which was also reported for coastal grasslands by Jutila (2003). In contrast, mowing alone creates moderate sward disturbance through hay-making machinery (Bakker et al. 1980) which provides a sufficiently high number of regeneration niches, which is quite often found in relatively large-seeded meadow species (Kotorová & Lepš 1999).

Based on the results of the DCA ordination (Fig. 1) one may at first argue that the effects of different management regimes are a result of differences in site conditions indicated by the nutrient gradient along the first axis, which separates early mown meadows and meadow pastures on the one hand from late mown meadows on the other. However, contrary to this expectation, major differences in stage structure were not found between late and early mown meadows but between these two and meadow pastures. The overall significance of management effects could also be confirmed by MANOVA.

Conclusions

Our results clearly showed that viable populations of *S. tinctoria* may occur in early as well as in late mown meadows and even in meadow pastures, which have received this type of management for more than 20 years. Contrary to traditional beliefs, there is no urgent need for late mowing, which considerably widens the options of agricultural use. Hay from early mown flood-meadows may be easily incorporated as basic fodder in feeding systems for cattle and horses (Donath et al. in press). In accordance with other studies, our results suggest that the analysis of population structure of long-lived perennials such as *S. tinctoria* is a particularly useful tool to evaluate the suitability of different management options for the preservation of endangered semi-natural grassland species (Bühler & Schmid 2001; Hegland et al. 2001; Colling et al. 2002).

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