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Restoration of ditch bank plant diversity : the interaction between spatiotemporal patterns and agri-environmental management

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Chapter 6

Effects of mowing date on the opportunities of seed dispersal of ditch bank plant species under different management regimes

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To be submitted

Abstract

Mowing and plant removal is a traditional practice in low-intensity farming and likely to lead to high plant species richness. Even today, scientific knowledge on the impact of mowing on seed availability is still very limited. We studied whether the seed availability of ditch bank plant species was affected by the timing of mowing and, if so, whether the effect varied according to management regime (nature reserve, agri-environment scheme (AES) with long-term management, AES with short-term management, conventional management). Our focus was on seed availability for transportation, because restoration of ditch bank vegetation is known to be limited by seed dispersal. The presence and seed-setting of 25 target species in 384 plots were recorded at the mowing date, under four management regimes. A Hierarchical Generalized Linear Model (HGLM) was used to analyze the effects of mowing date and management on the number of species setting seed. It suggests that when the mowing is twice annually, mowing on July 1st and on Sept. 1st will result in a maximum number of species of which the seeds are available for transportation and, therefore, create largest opportunities for seed dispersal on ditch banks in the western peat area of the Netherlands. The effect of mowing date differs among species, with certain rare species like *Caltha palustris* and *Lythrum salicaria* in particular differing from the commoner species. A flexible mowing regime varying from year to year would therefore help to protect these rare species. The later peak in seed-setting found in nature reserves and long-term AES suggest a postponed mowing compared to conventionally management and short-term AES.

Introduction

With loss of biodiversity continuing apace, the restoration, development and conservation of endangered plant communities have become important aims of nature conservation authorities (Edwards et al., 2007; Ozinga et al., 2009). The success of such efforts depends very much on the ability to provide suitable site conditions and seed sources (Pywell et al., 2002; Donath et al., 2007). Mowing, with subsequent removal of cuttings, is a traditional practice in low-intensity farming and likely to lead to high plant species richness (Huhta and Rautio, 1998). In recent years it has been discussed as a possible restoration measure and its practicability tested in a range of ecosystem including fens, meadows, semi-natural grassland and field margins (Hansson and Fogelfors, 2000; Stammel et al., 2003; Middleton et al., 2006; Musters et al., 2009).

On the one hand, it is postulated that mowing promotes favourable site conditions. It extends the space available for plant establishment by increasing light availability at ground level (Schaffers, 2002; Billeter et al., 2007). It also mitigates the negative effects of nutrient enrichment on plant species diversity by removing accumulated litter from the system (Hovd and Skogen, 2005). On the other hand, the mowing equipment may function as a vector for long-range seed dispersal within and between fields and is therefore thought to be important for the re-establishment of rare species (Strykstra et al., 1997). Until now, many studies have examined the influence of mowing on changes in site conditions that favour target species (Stampfli and Zeiter, 1999; Maron and Jeffries, 2001; Stammel et al., 2003; Billeter et al., 2007). However, only a handful of studies have directly compared the effect of mowing on seed dispersal (Strykstra et al., 1997; Coulson et al., 2001).

Mowing before species have set seeds strongly diminishes the seed sources for re-establishment (Kleijn et al., 2004; Geertsema, 2005; Leng et al., 2009). Appropriate timing and intensity of mowing may therefore have a substantial effect on seed availability at the location. However, it also affects the amount of seeds available for transportation by mowing equipment. It is possible to explore the effect of mowing time on seed availability for transportation by investigating the number of seed-setting species and the percentage seed set per species at the moment of mowing. We illustrate the pattern of number of seed-setting species and its consequences of seed availability in Fig. 1. We assumed that the number of seed-setting species would increase in time until it reached a maximum. The number will then decrease due to shedding of seed in certain species (Fig. 1a). Accordingly, the seed availability for both the location and transportation will increase up to the maximum number of seed-setting species. After the maximum, the seed availability

on the location will be constant (seeds in the plants plus seeds on the ground), but the seed availability for transportation will decrease as seeds in the plants decrease (Fig. 1b). The percentage seed set per species will show a similar pattern as the number of seed-setting species.

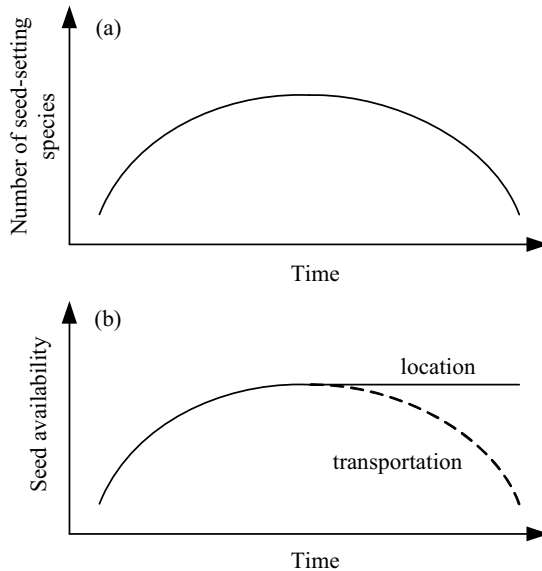


Fig. 1. Concept of the pattern of number of seed-setting species **(a)** and seed availability for the location and transportation **(b)**.

In landscapes dominated by agriculture, ditch banks provide an important refuge for plant species in terms of survival and diversity (Smart et al., 2006). Over the past 30 years, however, the species diversity of ditch banks has been in decline (McNeely et al., 1995; Blomqvist et al., 2003). One of the main policy initiatives to conserve the plant diversity of ditch banks has been the introduction of agri-environment schemes (AES), which were first implemented in England, Germany and the Netherlands in 1987. Earlier Dutch AES comprised a regime of zero fertilizer inputs, extensive grazing and later initial mowing and grazing at the start of the season. The latest schemes continue to recommend nutrient reduction, but impose few restrictions on the timing of mowing or grazing (DLG, 2000). The effectiveness of AES, however, is still being questioned (Kleijn and van Langevelde, 2006; Blomqvist et al., 2009). Seed limitation might be an important factor of variation in species richness (Zobel et al., 2000; Blomqvist et al., 2003; Leng et al., 2009). It is therefore important to test a range of mowing strategies, which might influence the seed availability for transport to establish the regime most effective for increasing the chances of plant dispersal.

In this paper we report a comprehensive study of the number of seed-setting species and the percentage seed set per species of ditch banks at the time of mowing under different management regimes. Mowing is at least twice a year in our study

area. We hypothesized that the number of seed-setting species and seeds per species would increase with postponement of first mowing to later in the growing season. We further hypothesized that the number of seed-setting species and seeds per species would increase as the time between first and second mowing was extended. Finally, we hypothesized that the effects of mowing treatments would be different under different management regimes, because of differences in environmental conditions such as nutrient availability between nature conservation and agricultural areas. Because seed dispersal seems crucial for restoration of ditch bank plant diversity, we are looking for the combination of first and second mowing time that optimizes the opportunities for seed transportation, i.e. on the highest sum of the first and second mowing time number of seed-setting species and seeds per species, while the seeds are still in the plants (Fig. 1).

Materials and methods

Study site and species

The study took place from May to October 2008 on a network of ditch banks at Krimpenerwaard (province of South Holland, The Netherlands) in an area of farmland used as pasture for dairy cattle and sheep. The soils here are mainly peat or peat with clay. The ditch banks are 0.8-1.5 m wide, with slopes ranging from 15° to 20°. The vegetation is dominated by *Agrostis stolonifera*, *Holcus lanatus*, *Glyceria maxima*, *Glyceria fluitans* and *Cardamine pratensis* (Blomqvist et al., 2009).

As experimental sites, ditch banks under four types of management were chosen, nature conservation, AES with long-term management, AES with short-term management and conventional management (control). The nature conservation strategy in this area aims to conserve biodiversity such as plants and meadow birds by providing relatively nutrient-poor conditions and limited grazing intensity. For AES with long-term management we chose sites where AES had been in place for more than 16 years, and for AES with short-term management sites initiated less than 6 years ago. In AES, a ‘no cure, no pay’ system is in force whereby farmers are free in their choice of management regime, but are recommended to apply the following treatments: first mowing at the end of June or beginning of July, zero fertilizer inputs, low stocking rate and deposition of dredged material on the top of ditch banks (van Strien, 1991). Conventional management is the regime implemented by farmers when choosing freely. The first mowing is usually around June 1st, second mowing around Aug. 1st and fertilizer inputs, ditch sediment deposition are applied on ditch banks (personal observation).

We used a set of 25 target species of dual interest, species deemed to be valuable ditch bank plants under Dutch government policy, on the one hand, and species the presence of which are used as criteria for rewarding farmers implementing AES, on the other. A list of the species along with their salient characteristics which might be related to the seed-setting is provided in Table 1.

Table 1. Overview of target species with their characteristics. Lumped taxa * *Myosotis arvensis* and *Myosotis discolor*. Nature value, Clausman and van Wijngaarden (1984). Minimum light requirement (L), Nutrient requirement (N) from Ellenberg et al., (1992); Hill et al., (1999), shade tolerant(6), intermediate(7), light demanding(8); N, indifferent(×), oligotrophic(1-4), mesotrophic(5-6), eutrophic(7-9). Flowering period, month number. All other characteristics from Biobase (CBS, 2003).

Species name	Nature value	Germination period	L	N	Mean plant height	Begin flowering	End flowering
<i>Achillea ptarmica</i>	42	Spring	8	2	60	7	8
<i>Caltha palustris</i>	36	Late spring	7	×	32.5	4	11
<i>Centaurea jacea</i>	35	Late Summer	7	×	65	6	9
<i>Cirsium palustre</i>	37	Early summer	7	2	105	6	8
<i>Filipendula ulmaria</i>	31	Late spring	7	4	90	6	8
<i>Galium palustre</i>	35	Autumn	6	4	27.5	5	9
<i>Hydrocotyle vulgaris</i>	40	Spring	7	2	15	7	9
<i>Hypericum perforatum</i>	31	Spring	7	3	50	6	8
<i>Iris pseudacorus</i>	40	Early summer	7	7	80	5	9
<i>Lathyrus pratensis</i>	32	Autumn	7	6	75	6	7
<i>Leucanthemum vulgare</i>	39	Late summer	7	3	45	5	8
<i>Lotus uliginosus</i>	40	Spring	7	4	65	6	9
<i>Lychnis flos-cuculi</i>	44	Direct	7	×	60	5	11
<i>Lycopus europaeus</i>	29	Early summer	7	7	60	6	10
<i>Lysimachia thyrsoiflora</i>	37	Late spring	7	3	45	5	9
<i>Lythrum salicaria</i>	31	Spring	7	×	90	6	7
<i>Mentha arvensis</i>	37	Late spring	7	×	30	7	7
<i>Myosotis*</i>	40	Spring	7	6	25	5	9
<i>Pedicularis palustris</i>	60	Late spring	8	2	32.5	5	11
<i>Potentilla palustris</i>	41	Late spring	8	2	60	6	11
<i>Prunella vulgaris</i>	31	Early autumn	7	×	26	5	9
<i>Ranunculus flammula</i>	43	Direct	7	2	27.5	6	8
<i>Rhinanthus angustifolium</i>	44	Spring	7	2	45	5	7
<i>Veronica beccabunga</i>	39	Late spring	7	6	37.5	5	11
<i>Vicia cracca</i>	25	Direct	7	×	115	6	10

Experimental design

In order to include a wide range of ditch banks in our study, for each of the four management regimes six ditch banks were selected in different polders. Each of these banks was assigned to 16 plots on which four different first-time mowing treatments (FT I - FT IV) and four second-time mowing treatments (ST I - ST IV) were combined in all permutations (Fig. 2). A total of 384 plots were thus investigated. Each plot was 10 m long, with its width depending on the steepness of the ditch bank (average, $0.96 \text{ m} \pm 0.12 \text{ m}$).

Just before each mowing, biomass samples were clipped. In each plot, two replicates were sampled by cutting the vegetation in a $20 \times 50 \text{ cm}$ square (0.1 m^2) 3 cm above grade. These were dried at $70 \text{ }^\circ\text{C}$ for 72 h and weighed. Biomass calculated as g dry weight/ m^2 was then used as a measure of productivity. Habitat variables of potential influence on ditch-bank vegetation were measured, including ditch bank width, slope angle and ditch water table (van Strien, 1991). In each plot, both the presence of the species and the species with ripe seeds in all the individual target species were recorded just before mowing.

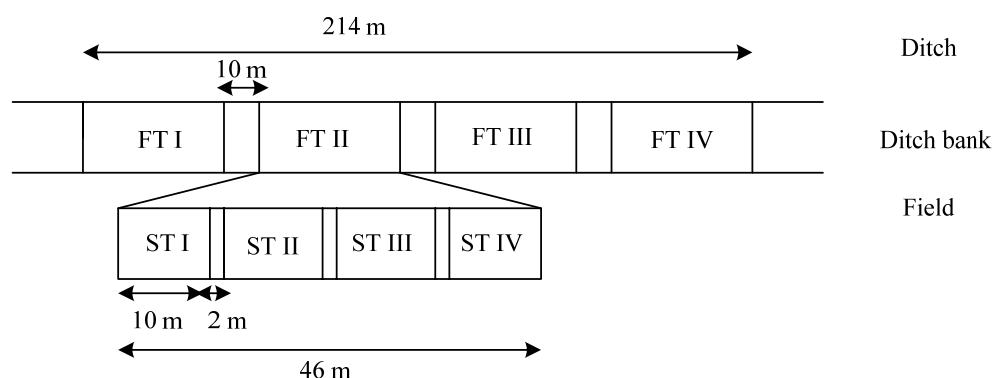


Fig. 2. Experimental set-up comprising sixteen plots on each ditch bank (FT I - FT IV= experimental first mowing; ST I - ST IV= experimental second mowing).

We applied double mowing regimes on each plot. Both the first and second mowing date was categorized as four mowing treatments with regular intervals of two weeks from May 15th to July 1st and Aug. 1st to Sept. 15th individually. Mowing was carried out with a brush-cutter, the action of which is equivalent to typical cutting with a disc mower. The vegetation was mown to a height of 5-10 cm. All the cut plant material was removed immediately after mowing and throughout the experimental period no deposition of ditch sediment was permitted.

Data analysis

To analyze the effects of treatments and management regimes on total target species, we used a Hierarchical Generalized Linear Model (HGLM), taking as dependent variables the total number of species setting seed and the percentage of species with seed at both first and second mowing time. HGLM was used because the two dependent variables in the sampled plot are assumed to have a normal distribution and the sample locations were assumed to be a random sample of all possible locations (Lee and Nelder, 2001). The time of first mowing, the time of second mowing, their interaction, the management regime and variables of potential influence on ditch-bank vegetation were included in the fixed model. We considered our study locations as random samples of all ditch banks, therefore ditch-bank was treated as the random model. A normal distribution and an identity link function were used. Additionally, we used T-test to compare the number of seed-setting species under different mowing time and used Mann-Whitney U-test to test species characteristics differences among species.

To investigate the effect of four different managements on number of seed-setting species, Mann-Whitney U-test was again applied to compare biomass, species richness under different management regimes. The HGLM was run using the statistical program GENSTAT 11.0, while all other calculations were performed with SPSS 16.

Results

Seed set at first and second mowing time

The average number of species per location setting seed at the first mowing time rose significantly as the time of first mowing was delayed (Fig. 3a). Figure 4a shows that on May 15th *C. palustris* was the only species seeding. On June 1st or June 15th this was the case for seven species and the percentage seed set per species tended to be greatest on July 1st except for *Cirsium palustre*. *Galium palustre*, *Lathyrus pratensis*, *Lotus uliginosus* and *Vicia cracca* had seed set by July 1st, while no seeds of *Lythrum salicaria* were found at first mowing, regardless of mowing date.

The average number of species with seed at second mowing was highest when first mowing was on May 15th and second mowing on Sept. 1st (Fig. 3b). At the species level, seven out of 11 species showed maximum seed set when first mowing was on May 15th, while the percentage seed set for these 11 species differed

considerably at the second mowing date (Fig. 4b). *C. palustris* and *Rhinanthus angustifolius* had no seed set at second mowing.

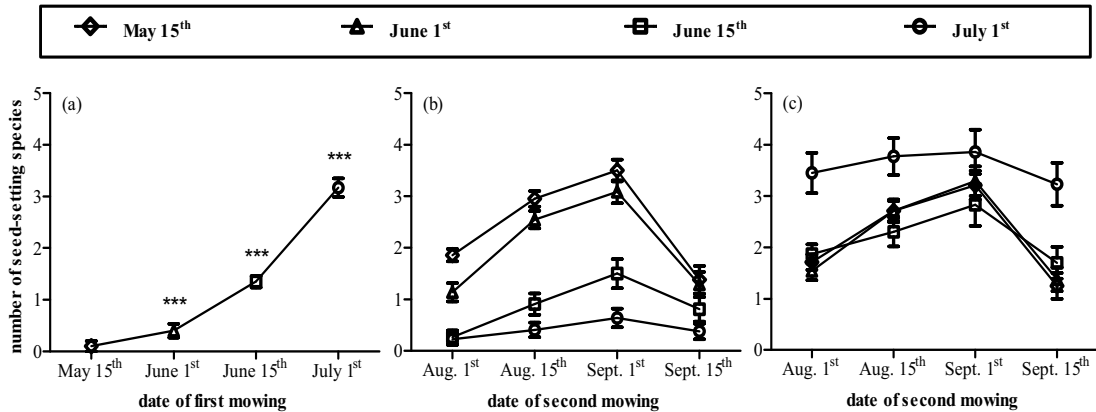


Fig. 3. Number of species setting seed at first (a), second (b) mowing and under double mowing regimes (c). Significant differences between May 15th and other first mowing dates on number of seed-setting species are indicated by asterisks (***) = $p < 0.001$, T-test). Vertical bars are standard errors.

Seed set under double mowing regimes

A significant relationship was found between mowing date and total number of seed-setting species at mowing under double mowing regimes (Table 2). Considerably higher numbers were observed with first mowing on July 1st and second mowing on Aug. 15th or Sept. 1st. The greatest number of seed-setting species was found when mowing was on July 1st and Sept. 1st (Fig. 3c). The average number (3.86 ± 0.43) was 126% higher than the number of seed-setting species when mowing on June 1st and Aug. 1st, the conventional mowing regime (1.71 ± 0.15). None of the habitat variables was found to have a significant effect on the relationship between mowing date and number of seed-setting species.

There are large inter-species differences with respect to percentage seed set under double mowing regimes. Generally speaking, species can be assigned to one of five groups, the first three of which have been reported on in Figure 4. Group A comprises those species in which the peak in the percentage plants with seeds is independent of second mowing date. The six species in this category are *C. palustris*, *G. palustre*, *Iris pseudacorus*, *L. flos-cuculi*, *R. angustifolius* and *V. cracca*. With the exception of *C. palustris*, all these species had the highest percentage seed set on July 1st. Group B are those species in which maximum seed set occurs during a prolonged interval between the first and second mowing. In *L. pratensis* and *L.*

uliginosus this maximum occurred over a period of 10 to 12 weeks, while in *Lysimachia thyrsoflora* and *L. salicaria* it was 16 weeks. Group C comprises species in which maximum seed set occur during a short interval between the two mowing dates. In *C. palustre*, *Myosotis* and *Ranunculus flammula* maximum seed set was recorded over a 6-week period. Group D are those species that were present but in which no seeding was observed, such as *Filipendula ulmaria*, *Hydrocotyle vulgaris*, *Lycopus europaeus* and *Mentha arvensis*. Group E, finally, comprises the eight species of the 25 target species that were not found. They are *Achillea ptarmica*, *Centaurea jacea*, *Hypericum perforatum*, *Leucanthemum vulgare*, *Pedicularis palustris*, *Potentilla palustris*, *Prunella vulgaris*, *Veronica beccabunga*. When compared species characteristic differences in all possible combination of pairwise species group, only group A and group D showed significant first flowering time differences ($P=0.02$, Mann-Whitney U-Test).

Table 2. Results of HGLM analysis of impact of first and second mowing date, their interaction, management regimes and habitat variables on total number of seed-setting species and percentage of species with seed under double mowing regimes. * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$.

	Total number		Percentage	
	Estimate	t	Estimate	T
Constant	5.54	1.99	-0.05	-0.13
June 1 st	-0.33	-0.91	-0.12	-1.79
June 15 th	0.04	0.11	-0.06	-0.93
July 1 st	1.64	4.57***	0.24	3.69***
Aug. 15 th	1.09	3.02**	0.13	1.98*
Sept. 1 st	1.63	4.55***	0.16	2.51*
Sept. 15 th	-0.38	-1.05	-0.15	-2.33*
June 1 st * Aug. 15 th	0.16	0.34	0.11	1.09
June 1 st * Sept. 1 st	0.32	0.63	0.09	1.01
June 1 st * Sept. 15 th	0.41	0.79	0.13	1.41
June 15 th * Aug. 15 th	-0.59	-1.16	-0.04	-0.48
June 15 th * Sept. 1 st	-0.59	-1.16	-0.06	-0.67
June 15 th * Sept. 15 th	0.24	0.47	0.12	1.28
July 1 st * Aug. 15 th	-0.77	-1.52	-0.07	-0.74
July 1 st * Sept. 1 st	-1.22	-2.41*	-0.21	-2.21*
July 1 st * Sept. 15 th	0.08	0.16	0.03	0.36
AES, short-term	0.25	0.77	-0.11	-1.46
AES, long-term	0.01	0.02	-0.05	-0.74
Nature reserve	0.75	2.02*	0.02	0.25
Ditch-bank width	-1.48	-1.57	0.04	0.29
Ditch-water level	1.54	0.56	-0.06	-0.23
Ditch-bank slope	-0.13	-1.71	0.03	1.44
<i>Estimates of parameters</i>				
Phi	0.25	3.35	-3.16	-42.37
Lambda ditch-bank	-1.59	-3.88	-7.82	-7.87

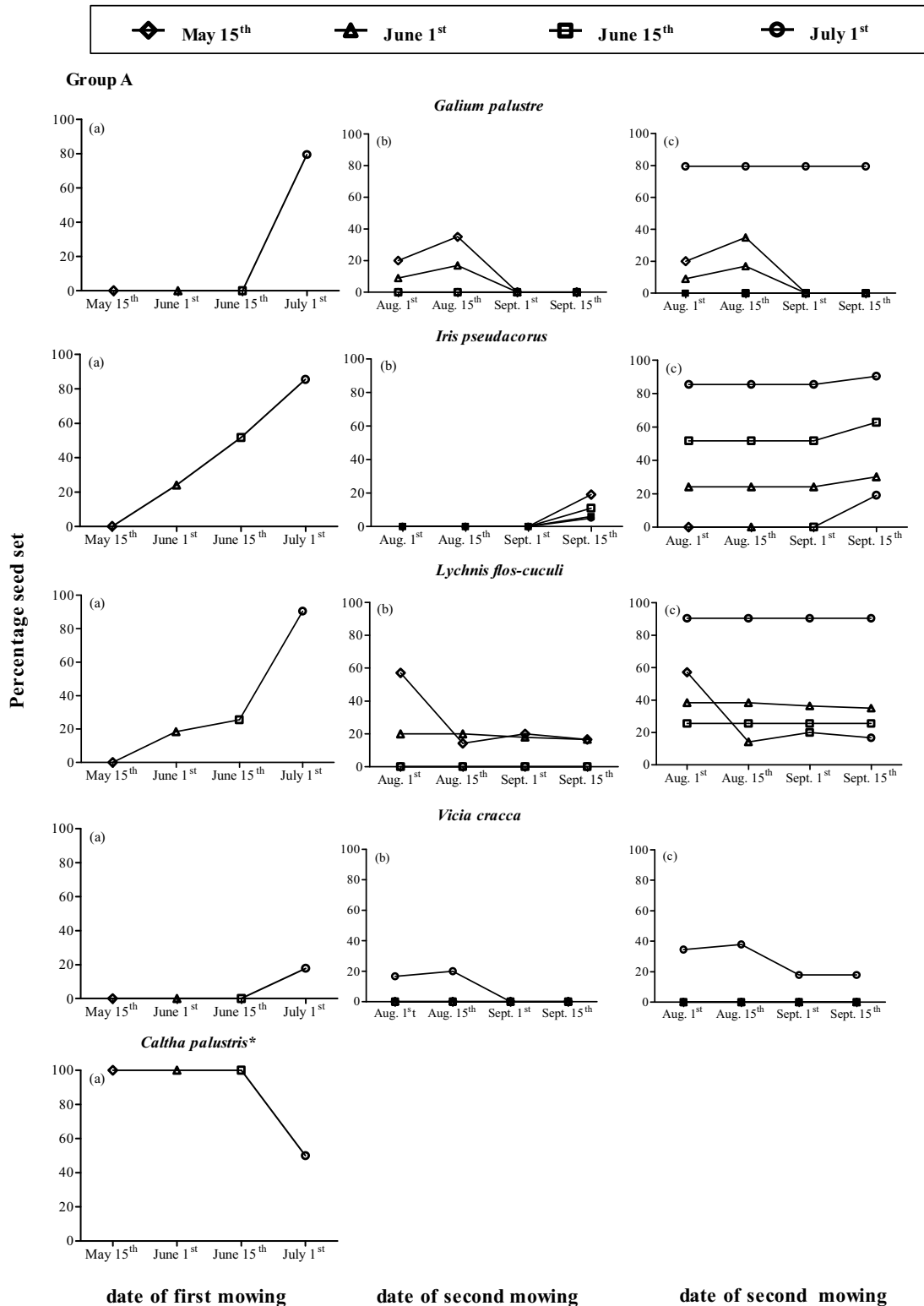


Fig. 4. Percentage seed set per species at first (a) and second (b) mowing and under double mowing regimes (c). * species found only at first or at second mowing. The species not shown in the figure were those that did not produce seeds.

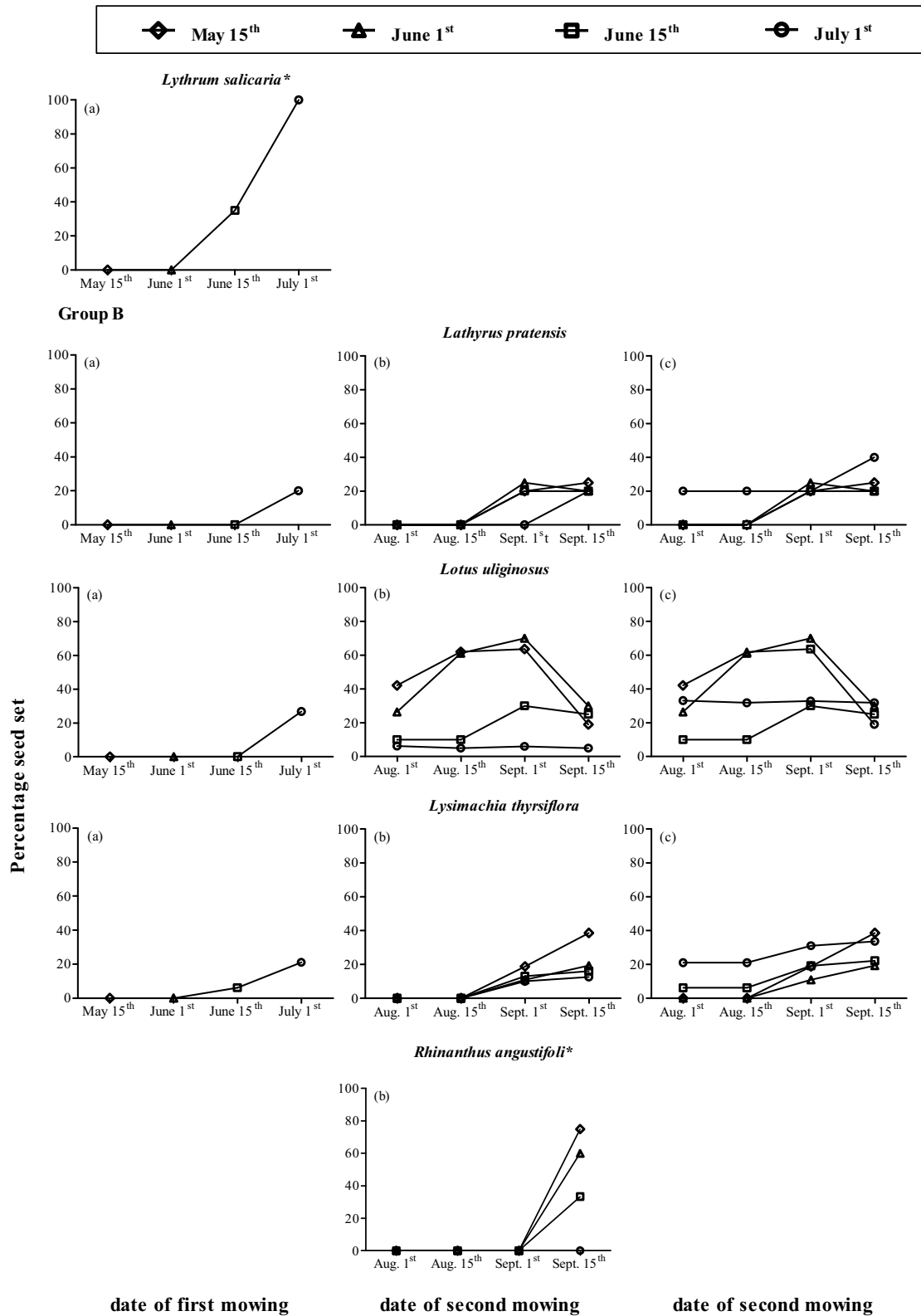


Fig. 4. Continued.

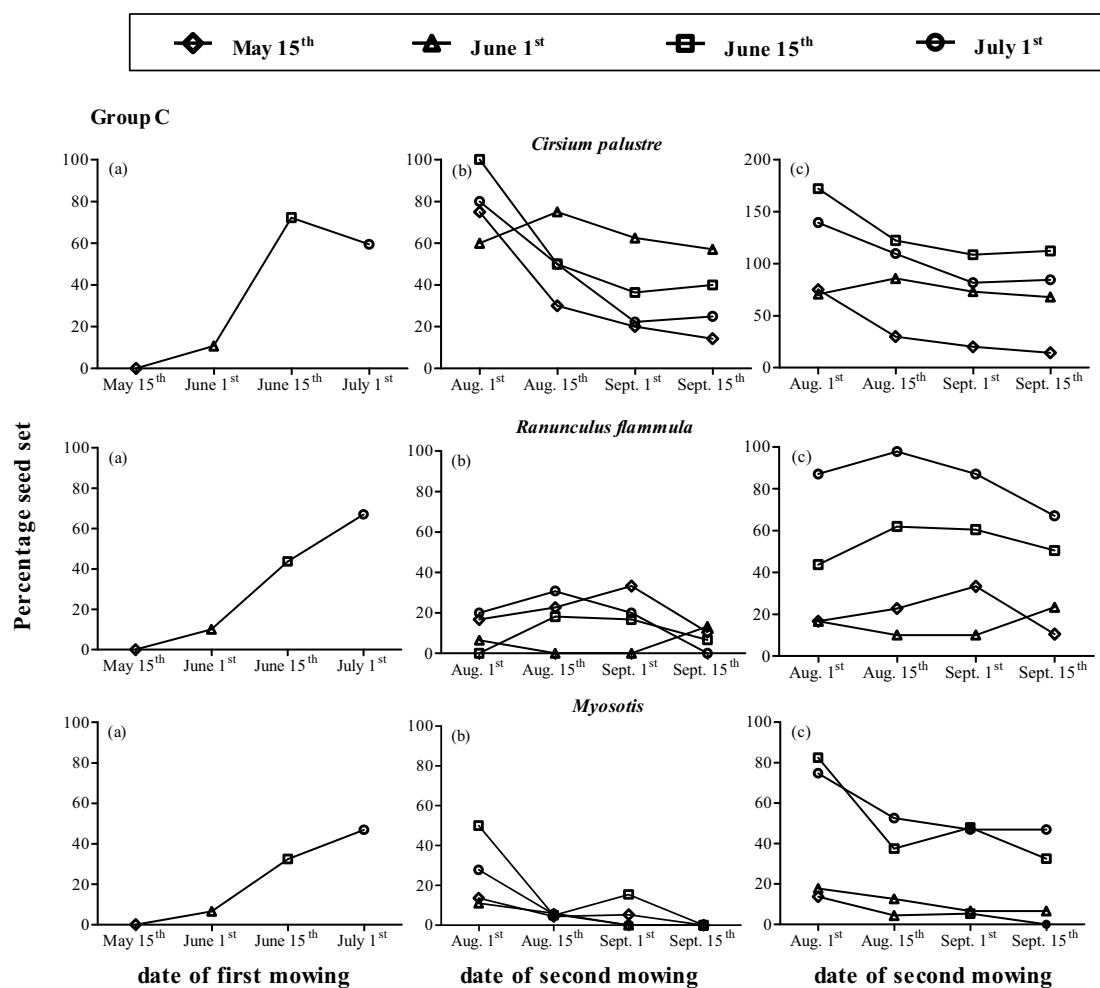


Fig. 4. Continued.

In 12 out of 13 species, the highest percentage seed set was at least twice compared to mowing on June 1st and Aug. 1st, the conventional mowing regime (Fig. 4c). Five species, such as *L. pratensis*, *L. thyrsoiflora*, *L. salicaria*, *R. angustifolius* and *V. cracca*, can not be found setting seeds when mowing first on June 1st and later on Aug. 1st.

Effect of management

Biomass varied depending on management regime and was highest on plots under conventional management and lowest in nature reserves. On the other hand, species richness was lowest under conventional management and significantly higher in nature reserves (Fig. 5).

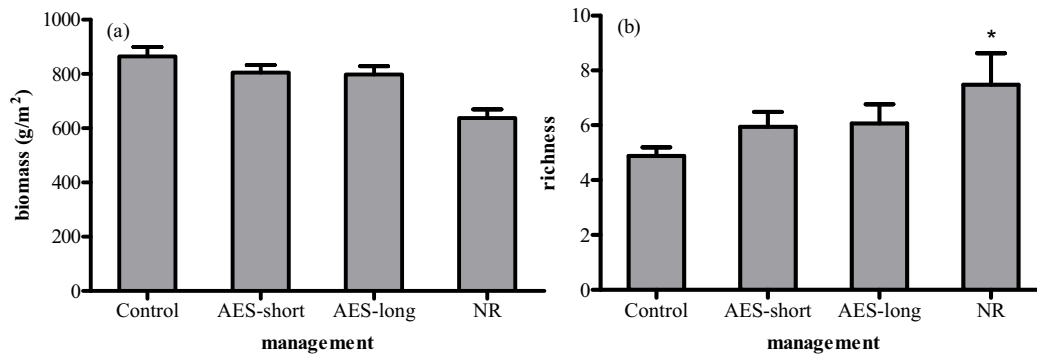


Fig. 5. Total biomass production (a) and species richness (b) under different management regimes. Significant differences between conventional management and other regimes are indicated by an asterisk (* = $p < 0.05$, Mann-Whitney U-test). Vertical bars are standard errors.

The HGLM analysis showed a significant effect of management on the total number of species setting seed, with significantly higher numbers being found in nature reserves compared with conventionally managed plots (Table 2). No difference in percentage of species with seed was found between conventionally managed and other plots. On plots under short-term AES and on conventionally managed plots, seed set peaked on Aug 15th, while in nature reserves and on long-term AES plots this was on Sept. 1st (Fig. 6).

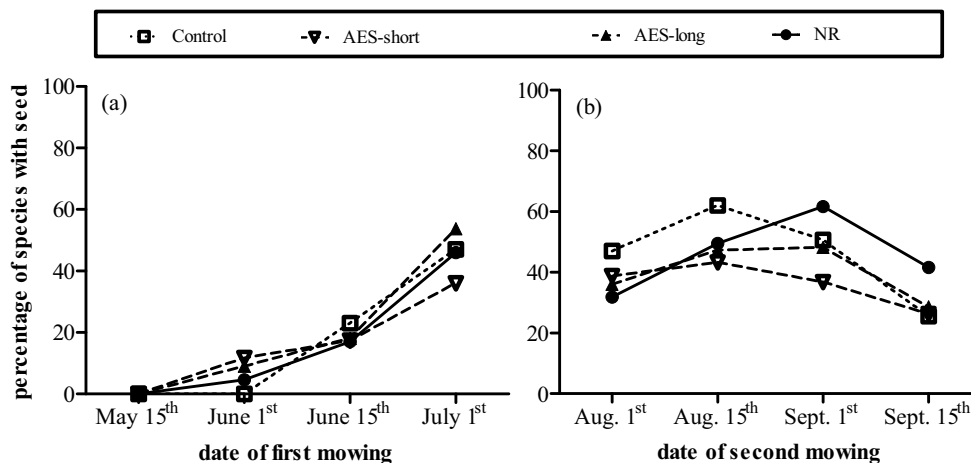


Fig. 6. Percentage of species with seed on date of first (a) and second (b) mowing under different management regimes.

Discussion

Seed set at first and second mowing time

Our first hypothesis, that higher number of seed-setting would correlate positively with later mowing date, was supported by the results. As first mowing was delayed, the number of species setting seed rose. The target species considered in our study vary widely in terms of seed-setting phenology and later first mowing would give many species like *G. palustre*, *L. pratensis*, *L. uliginosus* and *V. cracca* an opportunity to set seed prior to mowing.

Our second hypothesis, that the number of seed-setting would be enhanced by extending the interval between first and second mowing, was also supported by the results. That the highest number of seed-setting species was recorded with the first mowing on May 15th and a late second mowing on Sept. 1st is in line with Blomqvist et al. (2006) who found enhanced species reproduction with May and autumn mowing. Seven species showed maximum percentage seed set at the second mowing when the first mowing was on May 15th and *G. palustre*, for instance, had seeds at the second mowing only if first mowing was on May 15th or June 1st. This result indicates that in some species earlier first mowing might enhance flowering and seed-setting opportunities in the period prior to second mowing. For eleven of the target species, the percentage seed set at the time of second mowing differed considerably. When aggregated, however, the total number of species setting seed was found to peak on Sept. 1st, regardless of the date of first mowing. After September the number of species with seed declined, which can be attributed to the shedding of seeds during this period. This is further confirmed by investigations in the field, where in most common species (*G. palustre* and *Myosotis*) no seed-setting individuals were found after September.

Effect of mowing date on seed set under double mowing regime

The highest total number of seed-setting species was found with a combination of first mowing on July 1st and second mowing on Sept. 1st. Moreover, it has a 126% higher number of seed-setting species compared to mowing under conventional mowing regime, a combination of June 1st and Aug. 1st. As a consequence, under a twice mowing regime, mowing on July 1st and Sept. 1st would result in a maximum seed availability for transportation, and therefore in maximum opportunity for seed dispersal. Although it is possible that earlier first mowing might enhance target-species seed-setting by reducing competition (Collins et al., 1998; Hovd and Skogen,

2005; Williams et al., 2007), this potential effect seem to be outweighed by the positive effect of late first mowing on late seed-setting species. That half the target species exhibited maximum seed set when first mowing was on July 1st also corroborated the importance of a later date for first mowing. None of the habitat variables deemed to potentially affect plant diversity proved to influence the effect of mowing date on the number of seed-setting species.

At the species level, the six species in group A showed no impact of second mowing on maximum seed set. Some species like *L. flos-cuculi* have low germination rates or have difficulty establishing, especially under high-biomass ditch banks according to Blomqvist et al. (2006), and in *C. palustris* and *R. angustifolius* no seeds at all were observed after first mowing. For these species, then, the appropriate mowing regime should be a single mowing at the occurrence of maximum seed set to obtain highest seed availability for transportation or a single mowing later on to achieve highest seed availability for the location. The species in group B and C that showed an impact of both first and second mowing on maximum seed set were categorized based on the interval between the two mowing dates. In group B, maximum seed set was recorded over an interval of over 10 weeks between mowing. A later date for second mowing is therefore needed to obtain a high percentage of seed-setting individuals. *L. salicaria*, for instance, should be mown in September if viable seeds are to be formed to get highest seed availability for transportation and mown after September for the location. The species in group C showed maximum percentage seed set over a 6-week period, with the timing of second mowing seemingly not that important, compared with group B. All the species in group C were found to belong to the commonest species considered in our study. In this group, moreover, the time between the beginning and end of flowering (3 to 6 months) is much longer than in group B (2 to 3 months). This suggests that the mechanism behind the effect of second mowing date might lie in the duration of flowering. For species in this group, a combination of later date for first mowing and earlier date for second mowing is necessary to obtain maximum seed availability for transportation and a single later date for first mowing is needed to obtain maximum seed availability for the location. In the species in group D no seed set was observed and significant differences in the start of flowering were found compared with group A. Most of the species in group A begin flowering in May, while those in group D do not start flowering until June. This indicates that first mowing should take place later for group D than for group A and that in the present study mowing too early may be one explanation for the lack of seed set in the species of group D.

When comparing the percentage seed set differences between optimal and conventional mowing regime, we found that 12 out of 13 species have more than two

times higher percentage seed set and 5 species can only be found under optimal mowing regime. This means that mowing regime in conventional management seriously hampers seed availability for plant species in ditch banks, both for transportation and for the location.

Effect of management (nutrient availability) on number of seed-setting species

Our final hypothesis was that the number of species setting seed is influenced by differences in nutrient availability among management regimes. Although the number of seed-setting species found on conventionally managed plots was considerably lower than in nature reserves, there was no difference in the percentage seed set per species. The relatively low species richness on conventionally managed plots leads to fewer species setting seed compared to nature reserves. This possibility lends support to earlier findings that species diversity in grassland tends to decline when total annual biomass production exceeds 600-700 g/m² (Oomes, 1992). The hypothesis is further supported by the earlier timing of the peak in seed set on conventionally managed plots compared with nature reserves. With greater nutrient availability, species are presumed to grow faster.

Implications for conservation

Current management in ditch banks does not address the issue of seed availability for transportation, and, therefore, ignores the opportunities for seed dispersion by mowing equipment. This study showed clearly that seed availability for transportation, measured as percentage seed set per individual species as well as number of seed-setting species, was significantly lower under a conventional mowing regime compared to the optimal one. Land managers and farmers therefore need to select appropriate mowing times for increasing opportunities for dispersal of the species being targeted. Our result shows that when mowing twice annually, on July 1st and on September 1st, respectively, may in principle be a useful strategy for maximizing seed transportation by mowing equipment on ditch banks in the western peat area of the Netherlands. For increasing seed availability at the location, mowing on July 1st and not before September 1st would be helpful.

The impact of mowing date differs from species to species. Certain species like *C. palustris* and *L. salicaria*, in particular, are thought to be affected by early mowing via germination and competition (Blomqvist et al., 2006; Williams et al., 2007). From this perspective early mowing might be good for certain species. To

protect these rare and internationally valued species it would therefore be useful to establish flexible mowing regimes that vary from year to year.

The higher number of seed-setting species found in nature reserves combined with the later peak in seed-setting highlights the need to take different management into consideration. Our results suggest it may be necessary to mow later in nature reserves and long-term AES than on conventionally managed and short-term AES plots. At the same time, though, this conflicts with the idea that the higher number of species producing seed in nature reserves, and mowing machines as dispersal vectors, make it possible to enlarge opportunities for species dispersal outside nature reserves by first mowing in nature reserves and then, using the same equipment, mow the agricultural surroundings.

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