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Seed dispersal by mowing machinery in a Dutch brook valley system

R. J. STRYKSTRA, G. L. VERWEIJ and J. P. BAKKER

Department of Plant Biology, Laboratory of Plant Ecology, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

SUMMARY

Seed dispersal by mowing machinery was investigated within a grassland reserve. Transported seed numbers amounted to hundreds of thousands. Seeds of 26 species were found on the machinery, including species that play an important role in succession during vegetation restoration (*Holcus lanatus, Rhinanthus angustifolius, Anthoxanthum odoratum*). Species occurrence was related to field abundance, but not to plant size, seed size or month of first flowering. Species seed amounts were also positively correlated only to their abundance within fields. Several abundant species were not found because they carried no seeds at the cutting date (*Caltha palustris, Juncus acutiflorus*). There was a difference in species composition within material accumulating in two machinery parts, which was related to their height above ground level. It was concluded that dispersal by mowing machinery is moderately selective towards and against certain species. Seeds were transported from species-rich fields into species-poor fields and vice versa. The seeds transported after mowing a field were partially deposited in the next field. Dispersal by machinery may have a larger impact on the speed of succession in the hay-fields of the Drentse A reserve than any other form of dispersal and establishment from the seed bank. Therefore, it is important for vegetation restoration in practice. However, machinery does not always connect seed sources with restoration areas. Large-scale machinery movement also creates a new form of vegetation dynamics compared to the days of former, more primitive, agricultural use. Both factors have to be considered when attempts are made to restore species-rich vegetation types. It is probable that new methods will not produce the vegetation that once existed.

Key-words: anthropochory, mowing machinery, restoration, seed dispersal, species establishment, succession.

INTRODUCTION

The dispersal of seeds by vehicles is a common form of anthropochory. Seeds of many species are transported by cars or trains (Clifford 1959; Arnold, 1981; Schmidt 1989; Lonsdale & Lane 1994), which is considered to contribute to the geographical expansion of several species, for instance to the inland dispersal of salt-tolerant seashore species in road verges (Scott & Davison 1985). In agriculture, harvesting machinery is also known to disperse many plant species, arable weeds in particular, which can cause large economic damage (Panetta & Scanlan 1995). In nature conservation, however, it has been suggested that hay-making machinery may play a positive role in the dispersal of hay-field species (De Hullu *et al.* 1985; Ter Borg 1985; Bakker 1989). When hay-making by machinery is carried out to maintain or restore semi-natural grassland vegetation (Green 1980; Bakker 1989), seed transport by vehicles may be important for the re-establishment of rare species.

In The Netherlands, in order to impoverish soils for the restoration of species-rich communities, grasslands are managed by hay-making without fertilizer application (Bakker 1989; Olff & Bakker 1991; Bakker & Olff 1995). Hay-making takes place in the period June–August using common hay-making machinery such as tractor–disk mower combinations. Because of this practice the standing crop declines gradually, which allows species from species-rich communities to re-establish, if propagules are available (Oomes 1990; Olff & Bakker 1991; Berendse *et al.* 1992). One of the areas in which this type of management is practised is a nature reserve in the catchment area of the Drentse A rivulet. In this area, new fields are frequently added to the reserve by the owner, the State Forestry Commission. Within these fields predictable succession takes place, involving the establishment of species not occurring in the fields at the time they were acquired (Olff & Bakker 1991; Bakker & Olff 1995).

The role of the seed bank in the establishment of new species during grassland restoration is considered small (Thompson & Grime 1979; Pfadenhauer & Maas 1987; Grime *et al.* 1988; Bakker 1989; Bakker *et al.* 1996). Therefore, most of the re-establishment of species will be the result of seed dispersal. Although seed sources of most late successional species can be found within the reserve, relatively close to newly acquired fields, the distances that have to be covered are still large, up to hundreds of metres. The naturally occurring dispersal agents, such as wind, water and small animals, seldom lead to fast dispersal over distances of this order of magnitude (Willson 1993). There are no large grazing animals in the reserve that could provide long-range dispersal (Poschlod *et al.* 1996). The results of earlier studies in the Drentse A reserve suggested that seed transport by machinery might provide for long-range seed dispersal within and between fields. In particular this has been shown for *Rhinanthus angustifolius*, which is a characteristic dominant annual in an early successional stage (De Hullu *et al.* 1985; Ter Borg 1985; Strykstra *et al.* 1996).

The aim of this paper is to investigate how important mowing machinery may be as a dispersal agent in the Drentse A reserve. Could it indeed influence the speed and direction of vegetation succession by transporting large amounts of seeds of the most significant species in this succession, such as *Caltha palustris*, *Rhinanthus angustifolius*, *Anthoxanthum odoratum*, *Plantago lanceolata* and *Juncus acutiflorus*?

Therefore, an attempt is made to answer the following questions.

(i) Which species are transported and in what amounts?
(ii) Is a high field abundance indicative of a high seed transportation by machinery?
(iii) To what extent does the machinery favour the dispersal of species with a certain flowering period, seed size or plant size?
(iv) Does the machinery select certain species mechanically during mowing: does a high machinery part transport other species than a low machinery part?
(v) Are seeds, gathered by the machinery in one field deposited in other fields?

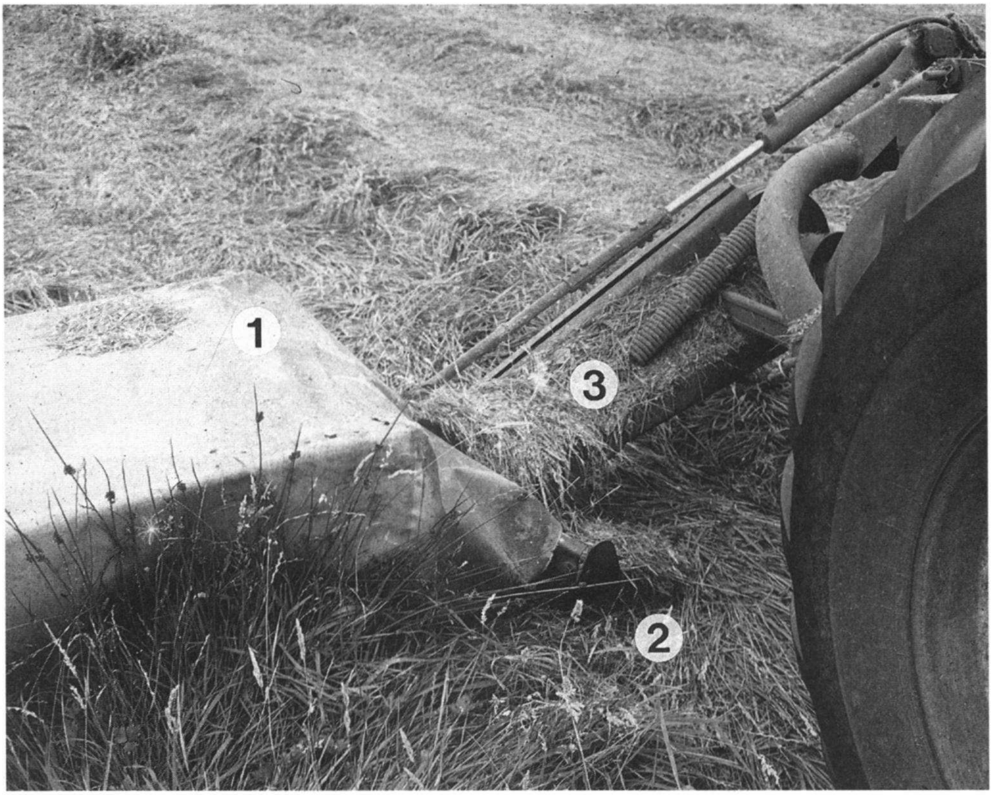

Fig. 1. Parts of the disk mower from which the samples were taken: 1, safety skirt; 2, skid disk; 3, beam. Beam and skid disk are referred to as skid disk and treated as a single sampling site.

METHODS

The study area included seven hay-fields bordering the brooklet Anloër diepje in the Drentse A nature reserve in the northern part of The Netherlands (6°41'E 53°03'N). Six fields had not been fertilized for 20–25 years, were species-rich (up to 30 species per 4 m^2 relevée) and stable in vegetation composition. One field (B2, see below) had not been fertilized for 6 years and was species-poor. In each field, species abundance estimates were made using the Tansley scale. For data analysis this scale was transformed into a simple three-class scale: the Tansley classes 'rare' and 'occasional' were assigned to class 1, 'frequent' and 'abundant' to class 2 and 'dominant' to class 3.

Mowing of the experimental area took place on 4 August 1992. During mowing, most plant material accumulated on the safety skirt (1), the beam (3) and the skid disk (2) of the disk mower (Fig. 1). During the experiment, samples were taken only from these parts. Because of the similarity in height above ground level beam and skid disk were considered as one machinery part, referred to as 'skid disk'. Skid disk and safety skirt are different in their method of seed transport. Accumulated plant material remains on the skid disk until it is wiped off by vegetation. The material on the safety skirt, however, drops off when the machinery leaves a field on moving to another, when the disk mower is lifted into vertical position. As a result, seeds on the skid disk are

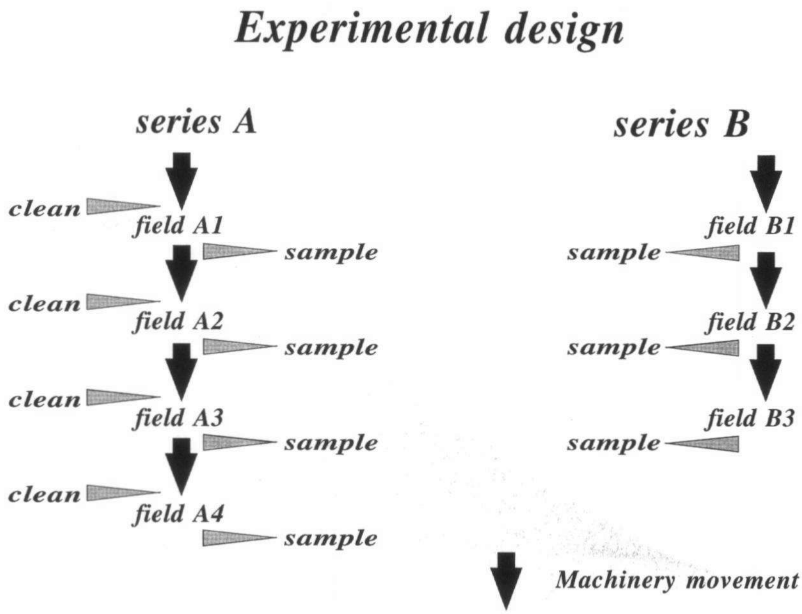

Fig. 2. Experimental design (cf. Methods).

transported within and between fields, whereas the seeds on the safety skirt are only transported within fields.

The mowing of the fields was done in two separate series (Fig. 2): series A was carried out to investigate which species were present on skid disk and safety skirt and in what amounts, series B to investigate the seed transportation between fields. Series A included four species-rich fields (A1–A4). Each time the machinery entered a new field all adhering plant material was brushed off. A single sample of the plant material that accumulated on the machine was taken after mowing each individual field. In series B, which consisted of three fields, the machinery was not cleaned between the fields. The machine started mowing in a species-rich field (B1), then moved into the species-poor field (B2), and finally into a second species-rich field (B3). After mowing each individual field, a single sample was taken.

After collection, the samples were dried and made homogeneous. After that, from each sample one small subsample was taken for seed identification and counting. Seed numbers per gram dry weight were calculated.

The plant species observed in the field were divided into two groups according to the mean of minimal and maximal height values given by the CBS (1987). Species having a mean height larger than 15 cm are referred to as tall, species having a mean height smaller than or equal to 15 cm are referred to as small. As a measure for flowering time, the month of the start of flowering according to the Dutch Botanical Data Base was taken. Five seed size groups were distinguished according to Grime *et al.* (1988).

Differences in the chance of appearance on the machinery between groups of species differing in field abundance, plant size, seed size and month of first flowering were investigated as follows.

The total group of species, found in the established vegetation in all four fields of series A, was divided into a group of species found once or more on the machinery and a group that was never found. Both groups were split up according to abundance, month of first flowering, plant size and seed size. As a measure of abundance the maximal field abundance, reached in series A, was used. To test the significance of differences between the numbers of 'found' and 'not found' species, a Chi-square test was used. Dependence between field abundance, plant size, seed size and month of first flowering was also tested using a Chi-square test.

In series A, every seed amount (number/g) of one species in any of the four fields was regarded as a single observation. Consequently, observations of the same species, but in different fields, were considered to be independent scores. The observations were used for testing differences in seed amounts between species belonging to different classes of abundance, month of first flowering, plant size and seed size. This was done for both the safety skirt and the skid disk to establish differences between machinery parts. Testing was done using one-way analysis of variance for abundance score, seed size and month of first flowering. To distinguish significant differences between classes, the Tukey-test was used. Student's t-test was used for testing plant size. The number of seeds per gram was logarithmically transformed to obtain homogeneous variances.

All statistical calculation was performed using SPSS-PC.

RESULTS

Seed amounts on the machinery

The amount of accumulated plant material was observed to vary highly and irregularly during the mowing of each field. Thick layers of plant material were transported on both safety skirt and skid disk, containing many seeds. During mowing, seeds that had accumulated on the safety skirt occasionally fell off in large numbers when the machine hit irregularities. The top layer of the material on the skid disk was constantly replaced.

The exact amount of accumulated plant material was not quantified. It was estimated that on the safety skirt several tens of grams dry weight were transported. On the skid disk this was estimated to be several hundreds of grams dry weight. The seed numbers per gram dry weight of the sample per field are given in Table 1. Up to 2000 seeds per gram sample dry weight were counted.

Species transport

A total of 52 species was recorded in the established vegetation in the fields of series A, 27 of which were found in the samples taken from the machinery (Tables 2, 3). Species that may reach dominance in advanced stages of the common hay-field succession in the Drentse A reserve were found on the machinery, for instance *Dactylus glomerata*, *Rhinanthus angustifolius*, *Anthoxanthum odoratum*, *Plantago lanceolata*, *Festuca rubra*, *Deschampsia cespitosa* and *Cynosurus cristatus*. Several species were not found in the samples although they showed abundance scores of 2 or 3. These species were *Caltha palustris*, *Ranunculus repens*, *Ranunculus acris* and *Juncus acutiflorus*. The first three species flower early in the season and no longer carried seeds. *Juncus acutiflorus* carried no seeds at the time of cutting. *Juncus effusus*, a rare species in the established vegetation, was over-represented in the samples (Table 2).

The proportion of the total number of species that was found in the samples was significantly related to the species abundance in the established vegetation ($P<0{\cdot}025$).

Table 1. Number of seeds per gram dry weight in the sample taken after mowing fields in series A and B

	Safety skirt	Skid disk
	No. of seeds/g dry weight	No. of seeds/g dry weight
Series A		
Field A1	743	1805
Field A2	715	153
Field A3	1499	1337
Field A4	1164	763
Series B		
Field B1	—	1616
Field B2	—	2007
Field B3	—	650

Most of the abundant species were found in the samples, whereas only a few of the rarer species (class 1) were found (Fig. 3). There was no significant relation to plant size or seed size. There was no significant relationship to month of first flowering, although the highest proportion was found of species starting in May. Most species started flowering in May and June (22 and 17, respectively). A few species started in April (9) and July (4). Abundance, plant size, seed size and month of first flowering were independent.

Seed amounts in the samples

The number of seeds of individual species in the samples was significantly related to their abundance in the established vegetation. On the skid disk the two higher abundance classes have significantly higher seed numbers ($P<0{\cdot}001$, see Fig. 4) than the lowest one. On the safety skirt all three abundance classes differ significantly and seed numbers increase with abundance ($P<0{\cdot}001$, see Fig. 4).

On the skid disk, seed proportions were not related to size class. On the safety skirt, however, a larger proportion of seeds of taller species were found than of smaller species (Fig. 4, $P<0{\cdot}001$). Tall species that consistently had larger proportions of seeds on the safety skirt than on the skid disk were *Dactylis glomerata*, *Festuca pratensis* and *Cynosurus cristatus* (Table 2). No significant difference in mean seed number was found between seed size classes (Fig. 4). Although the mean values of seed numbers are suggestive, no significant influence of month of first flowering on the seed numbers was found, probably caused by the large variance of the seed numbers of plants flowering in April, due to the low number of species (Fig. 4).

Transport from species-rich into species-poor fields and vice versa

Table 4 shows the vegetation composition of the three fields and the results of the seed counting in series B. Vegetation composition within field B2 differs considerably from that within the fields B1 and B3. Field B2 is dominated by *Holcus lanatus* only, whereas in the fields B1 and B3 there are many more abundant species of which *Anthoxanthum odoratum*, *Plantago lanceolata* and *Rhinanthus angustifolius* were not found in field B2. The differences in vegetation composition between field B1 and B2 and between field B2

Table 2. Series A: seed transportation. Percentage of the total amount of seeds per species occurring in the fields of series A, within the samples taken from safety skirt and skid disk after mowing each field. Species characteristics: Seed size (S) according to Grime *et al.* (1988): 1=smaller than 0·21 mg, 2=0·21–0·5 mg, 3=0·51–1·00 mg, 4=1·01–2·00 mg, 5=2·01–size class (H): s=small: mean height <=15 cm; t=tall: mean height >15 cm; cf. Methods) and month of first flowering (M): 4=April, 5=May, 6=June, 7=July). Abundance class (simplified scale, cf. Methods) of the species within each field and percentages of seeds

				Field A1			Field A2			Field A3			Field A4		
					Safety skirt	Skid disk		Safety skirt	Skid disk		Safety skirt	Skid disk		Safety skirt	Skid disk
Species:	S	H	M	A	%	%	A	%	%	A	%	%	A	%	%
Agrostis sp.	1	S	6	2	1·1	0·4	2	0·5	4·7	2	0·9	0·7	3	22·2	59·5
Alopecurus pratensis	2	T	4	1	0·4	—	1	0·1	—	1	—	—			
Anthoxanthum odoratum	2	T	4	3	1·3	1·0	3	4·3	4·0	3	1·3	1·8	2	0·3	0·5
Anthriscus sylvestris	5	T	5	1	0·6	—	1	2·7	1·1	1	0·7	0·9	1	1·7	0·2
Carex aquatilis	3	T	5	1	—	0·1									
Cynosurus cristatus	2	T	6	2	20·9	7·7	2	12·3	7·5	2	1·1	0·1	1	1·3	—
Dactylis glomerata	3	T	5	1	3·1	—	2	24·1	4·5	1	7·5	—	2	37·4	3·6
Dactylorhiza majalis	0	S	5	1	0·9	<0·1	1	0·9	4·0	1	0·4	7·4			
Deschampsia cespitosa	2	T	6	1	0·1	—	1	0·8	0·4	2	10·3	7·0	1	1·3	0·4
Festuca pratensis	4	T	6	1	1·5	—	1	2·1	0·9	1	1·7	—			
Festuca rubra	3	S	5	2	1·5	0·3	2	—	—	1	—	—	3	16·7	13·6
Galeopsis tetrahit	5	S	6							1	<0·1	—	1	0·3	0·1
Galium aparine	5	T	6							1	—	<0·1			
Holcus lanatus	2	T	5	3	50·1	53·1	3	26·7	21·7	3	20·8	13·4	3	12·2	17·2
Hypochaeris radicata	3	S	6	1	<0·1	<0·1							1	—	—
Juncus effusus	1	T	5	1	6·5	21·2	1	8·3	4·8	2	52·4	64·1	1	2·3	0·5
Leontodon autumnalis	3	S	7				1	—	—	1	<0·1	<0·1			
Myosotis palustris	2	S	5							1	—	<0·1			
Plantago lanceolata	4	S	5	3	2·7	3·3	3	10·0	3·6	3	0·3	0·7	1	0·1	0·2
Poa sp.	2	T	5	1	1·0	0·2	1	0·3	2·7	2	0·1	0·8	2	1·0	0·2
Ranunculus acris	4	T	4	2	0·6	0·8	2	—	—	2	—	—	2	0·0	<0·1
Ranunculus repens	5	S	5	2	—	—	2	0·8	0·2	3	0·1	<0·1	2	<0·1	—
Rhinanthus angustifolius	5	S	5	3	6·9	11·0	3	2·9	34·5	3	1·2	2·7	1	0·1	<0·1
Rumex acetosa	3	T	5	2	0·7	0·5	2	2·1	4·0	1	0·3	0·1	2	0·9	<0·1
Rumex obtusifolius	4	T	6	1	—	<0·1	2	1·1	—	1	0·9	<0·1	2	2·1	3·8
Stellaria graminea	2	S	5	1	<0·1	0·2	1	0·1	1·3	1	—	0·2	1	0·1	<0·1
Veronica sp.	1	S	4	1	<0·1	0·1				1	0·2	<0·1			

Table 3. Series A: species not found on the machinery. Species characteristics: Seed size (S) according to Grime *et al.* (1988): 1=smaller than 0·21 mg; 2=0·21–0·5 mg; 3=0·51–1·00 mg; 4=1·01–2·00 mg; 5=2·01–size class (H): S=small: mean height <=15 cm; T=tall: mean height >15 cm; cf. Methods) and month of first flowering (M): 4=April, 5=May, 6=June, 7=July). Abundance class (simplified scale, cf. Methods) of the species within each field and percentages of seeds

				Field			
				A1	A2	A3	A4
Species:	S	H	M	Abundance			
Achillea millefolium	1	S	6				1
Achillea ptarmica	2	T	7		1	1	1
Bellis perennis	1	S	4			1	
Caltha palustris	3	S	4	2		2	
Cardamine pratensis	3	S	4		1	1	
Carex ovalis	2	T	5			1	
Cerastium fontanum	1	S	4	1	1	1	1
Cirsium palustre	4	T	6	1	1	2	
Epilobium sp.	1	S	6			1	
Filipendula ulmaria	3	T	6	1	1	1	
Galium palustre	3	S	5	1	1	1	
Glechoma hederacea	3	S	5				1
Glyceria fluitans	4	T	5			1	
Juncus acutiflorus	1	T	7	3	3	1	
Juncus articulatus	1	T	6			1	
Juncus conglomeratus	1	T	5	2		1	
Lotus corniculatus	4	S	7				1
Lotus uliginosus	2	T	6	1	1	1	
Lychnis flos-cuculi	2	T	5	1		1	
Lythrum salicaria	1	T	6	1		1	
Mentha aquatica	1	T	6	1		1	
Ranunculus flammula	2	S	6	2		1	
Taraxacum sp.	3	S	4		1	1	1
Trifolium pratense	3	S	5	1	1	1	
Trifolium repens	4	S	5	1	1	1	

and B3 are reflected in changes in seed proportions in the samples taken after leaving B2 and B3 (Table 4). In the sample taken after leaving B2, the dominant species in the sample after leaving field B1, *Anthoxanthum odoratum*, *Rhinanthus angustifolius* and *Juncus effusus*, have become less abundant and the dominant species within B2, *Holcus lanatus*, has become dominant. Most species from B1 which were not recorded within field B2 were still found in the sample. Consequently, only part of the accumulated material on the skid disk from field B1 was replaced by material from field B2. The same type of change in sample composition is found after mowing field B3. Seed proportions of a number of abundant species in field B3, for instance *Dactylis glomerata*, *Rhinanthus angustifolius*, *Festuca pratensis* and *Anthriscus sylvestris*, increase in seed number or appear in the sample, whereas the proportion of seeds of *Holcus lanatus* was less then after leaving field B2. Not all changes in seed proportions were related to differences in abundance, for instance for *Juncus effusus*, indicating that chance processes also play an important role.

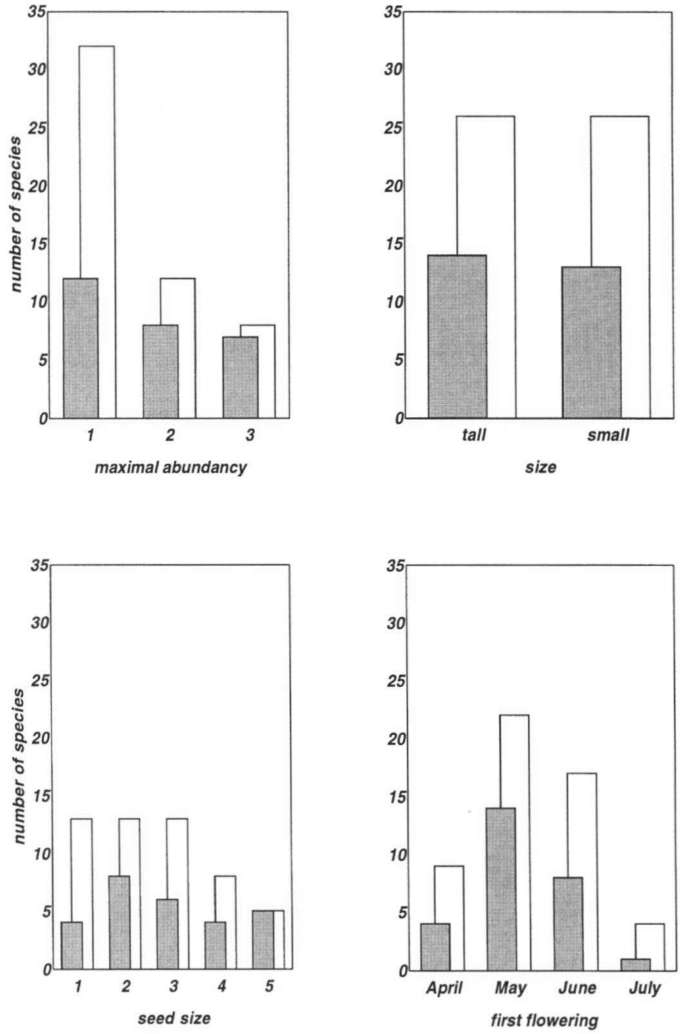

Fig. 3. Series A: total number of species (white bars) and number of species found on the machinery (dark bars) within classes of abundance, plant size, seed size and month of first flowering.

DISCUSSION

The results of this study suggest an important role of machinery in seed dispersal in the Drentse A reserve.

The results show that mowing machinery transports seeds of a wide variety of species. It is estimated that hundreds of thousands of seeds can be transported within and between fields. A number of important species in hay-field succession, such as *Cynosurus cristatus*, *Holcus lanatus*, *Rhinanthus angustifolius* and *Juncus effusus*, are transported in large numbers. This confirms that mowing machinery may be the most important dispersal agent within and between the fields in the Drentse A reserve and may initiate the establishment of less common species in newly acquired fields. This has been suggested in other studies within the Drentse A area (Bakker 1989, Bakker & Olff 1995). Mowing machinery behaves like other vehicles in this respect. The occurrence of a large

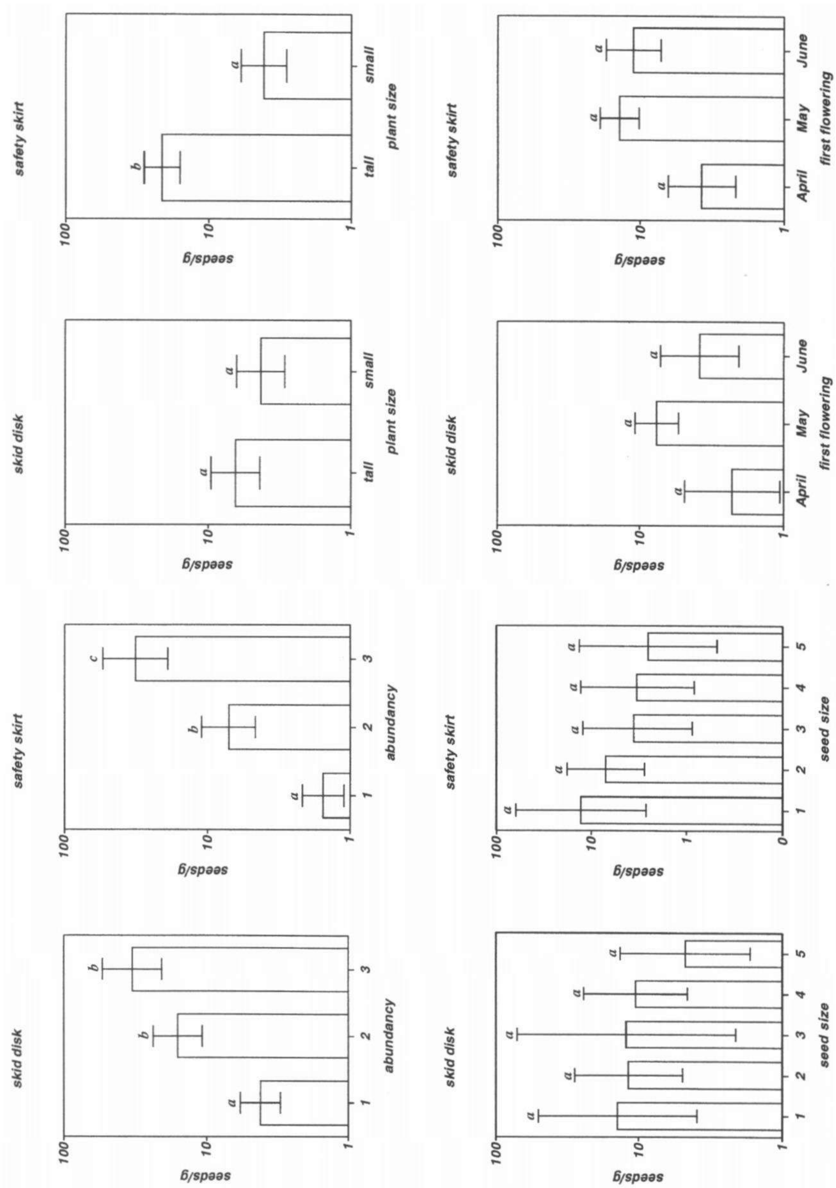

Fig. 4. Mean seed number per gram sample dry weight of the species characteristics abundance, plant size, seed size and months of flowering start on safety skirt and skid disk. Differences between classes of a characteristic on safety skirt and skid disk are tested using one-way analysis of variance. Groups indicated by a different letter are significantly different ($P<0{\cdot}05$) as indicated by the Tukey-test. For plant size Student's *t*-test was used.

Table 4. Seed transportation in series B. Abundance of the species within each field of series B (cf. Methods) and percentages of seeds within the samples taken from the skid disk after mowing each of these fields. Species of which no seeds were found in the samples, and not reach an abundance score in the established vegetation higher than 1 in either of the fields, are omitted from the table. Species are sorted by the seed proportion after mowing field B1

	Field B1		Field B2		Field B3	
Species	A	%	A	%	A	%
Juncus effusus	2	62·0	2	3·6	2	28·4
Holcus lanatus	3	7·8	3	89·4	3	21·0
Rhinanthus angustifolius	3	6·1	—	0·5	3	12·6
Deschampsia cespitosa	2	3·0	—	0·7		
Anthoxanthum odoratum	3	2·7	—	0·2	2	0·3
Festuca pratensis	1	2·4	—	0·2	2	5·3
Plantago lanceolata	3	1·3	—	0·9	2	0·9
Alopecurus pratensis	1	1·1	—	0·1	1	0·2
Poa trivialis	2	1·0	—	1·0	2	2·7
Anthriscus sylvestris	1	0·5	—	<0·1	3	2·0
Cynosurus cristatus	2	0·5	1	0·6	2	1·1
Rumex obtusifolius	1	0·5	1	1·3	2	4·1
Rumex acetosa	1	0·3	2	0·7	3	1·0
Agrostis cappillaris	2	0·2			2	3·5
Dactylorhiza majalis	1	0·1	—	0·1	1	—
Leontodon autumnalis	1	0·1			1	<0·1
Ranunculus flammula	1	0·1				
Ranunculus repens	3	0·1	2	0·2	3	2·5
Veronica sp.	1	0·1	—	0·1	1	—
Festuca rubra	1	<0·1	—	0·2	1	0·4
Alnus glutinosa	—	<0·1				
Caltha palustris	2	—			1	—
Cirsium palustre	2	—	1	—	1	—
Equisetum palustre	2	—				
Ranunculus acris	2	—				
Dactylis glomerata	1	—	1	0·2	2	12·7
Filipendula ulmaria	1	—			2	—
Stellaria graminea	1	—	—	0·1	1	0·5
Trifolium pratense	1	—			2	—
Holcus mollis			1	—	2	—
Bromus mollis					2	—
Lolium perenne					2	—

variety of transported species and the large seed numbers is similar to the results from studies on dispersal of seeds by cars (Clifford 1959; Lonsdale & Lane 1990) and harvesting machinery (Mesa-Garcia *et al.* 1986; Maxwell & Ghersa 1992; Mortimer *et al.* 1993; Howard *et al.* 1993; Ghersa *et al.* 1993).

The amount of seeds on the machinery is related to the species abundance in the vegetation. This corresponds to seed dispersal by cars, which also involves the more common road verge species (Clifford 1959). Seeds of many sizes are transported in the material on the mowing machinery. No selection was found towards any seed size. This is a difference from, for instance, the transportation of seeds imbedded in soil or dirt adhering to cars. These seeds tend to be small (Clifford 1959, Schmidt 1989). Both the relation of seed number with species abundance and the variety of seed sizes suggest that dispersal by machinery is an unselective process.

On the other hand, however, there are several marked exceptions where negative selection does take place. For instance, even among species with a high abundance in the established vegetation, some are not dispersed by machinery at all because they do not fructify at the time of mowing. The most prominent are the late successional species *Caltha palustris* and *Juncus acutiflorus*. Machinery dispersal selects against these species. Nevertheless, both species may appear and become abundant during succession (Olff & Bakker 1991.) *Juncus acutiflorus* may establish from a long-term persistent seed bank deriving from the time before intensifying land use (Thompson *et al.* 1997), which started about 50 years ago (Bakker & Olff 1995). *Caltha palustris*, however, has no long-term persistent seed bank and must be dispersed in another, still unknown way.

Some differences between the transportation of individual species were also found relating to machine structure. On the safety skirt, seeds of tall species were positively selected. This may lead to a certain advantage for larger species regarding within-field dispersal since the safety skirt only contributes to within-field dispersal. The dispersal between fields is not selective in this regard. How important these particular differences are in an ecological sense is unclear, but it shows that the way mowing machinery is built may influence seed dispersal of certain species by positive or negative selection. Differences in the ability to disperse seeds in arable fields, related to machinery structure, have been also found between different types of harvesting machinery (Ballare *et al.* 1987; Wesolowski & Kacuga 1990).

Considering the potentially large capability to disperse seeds and the (moderate) selectiveness towards certain species, it is likely that machinery influences not only seed dispersal but vegetation dynamics as a whole within the fields in the Drentse A reserve. In general, models predict that dispersal plays an important role in species coexistence (Van der Maarel & Sykes 1993; Tilman 1994). Mowing machinery collects seeds from source populations and exports them into new areas. For most grassland species, dispersal distance is considered much smaller than the possible distance potentially covered by mowing machinery (Willson 1993). This means that dispersal by machinery, as a component of the ecosystem, probably influences speed and pathway of succession within newly acquired hay-fields more than any other way of dispersal. Considering the often large distances between seed sources and target area, many species will depend on machinery dispersal for establishment.

Within hay-fields, species may even ‘adjust’ their reproduction cycle to the hay-making practice. For instance, most species recorded in the vegetation start flowering in May and June. It is likely that the hay-making practice influences the occurrence of these species in a positive way, because they complete their reproductive cycle just before cutting, which allows efficient seed dispersal. When cutting date remains the same over a longer period, these species may be more competitive for ‘new’ space (for instance gaps, derived from disturbance in the vegetation by soil perturbations) than species with early or late seed production. In the end this could lead to an equilibrium situation in which the seed production is ‘adjusted’ to a certain extent to the hay-making.

Seed dispersal plays an important role in hay-field restoration. Differences in dispersal processes may lead to different vegetation dynamics. In hay-field reserves the species-rich vegetation of around 1900 often serves as a reference for restoration management. Although no direct comparison can be made between present and historical seed dispersal patterns, there are large differences between the modern management practice and that of earlier days.

On the nutrient-poor sandy soils of the Drenthian plateau, where the brook valley system of the Drentse A is situated, an adapted agricultural system has evolved since the Middle Ages. This system stayed almost intact until the beginning of the 20th century (Bakker, 1989). The grounds around the villages were used as arable land, the grounds away from the villages, mostly nutrient-poor heathland, for common sheep grazing and sod-cutting. The sods were mixed with sheep dung in stables and spread as manure on the arable land. The species-rich brook valley grasslands were used for grazing of cattle, sod-cutting and hay-making. They were also used as common ground. Due to this agricultural use, the vegetation of the Drenthian plateau was heavily influenced by man's activities, not only because of physical management and man-induced nutrient fluxes, but also by seed transport by the grazing animals. Sheep and cattle are known to transport seeds in large quantities in grazed ecosystems (Bakker *et al.* 1996; Fischer *et al.* 1996), mostly in fixed patterns; for instance, along migration routes. As in other common field systems, the distances covered by the animals were large and therefore there was a large potential for seed dispersal (Bakker *et al.* 1996). The species-rich grasslands evolved in this setting (Poschlod *et al.* 1996).

During the 19th and 20th centuries, the agricultural system changed (Bakker, 1989). The common fields were divided into many private properties and artificial fertilizer was introduced. Sheep and cattle herds vanished from the landscape. With the moving herds, much of the potential transport of seeds between similar vegetation types probably also vanished. Most heathlands were converted into arable land. However, brook valley grasslands remained species-rich until they were destroyed by the use of artificial fertilizer in combination with drainage (Bakker, 1989; Olff & Bakker, 1995).

Nowadays, the brook valley grassland system functions again in a totally different way from the past. It is no longer part of an integrated agricultural system, with heathland and arable lands as described above; nor is it divided into private properties. It now forms a system of its own. Current seed dispersal processes are different from those of the past. Almost no connections with other brook valleys or heathland areas exist today. The machinery used in the Drentse A area is used only there. The potential dispersal between fields within the reserve, however, has become larger than in the recent past of multiple ownership, but is limited when compared to the times that large herds were moving through the landscape. The total change in management leads to a change in environmental dynamics, including seed dispersal, which is bound to have effects on vegetation dynamics. For instance, in the latter days of the old agricultural system, separate fields were owned by one farmer. Nowadays they are all owned by one organization. The separate farmers would cut the fields in a 'natural' way, when the production was optimal, waiting until the weather was right. The whole of the present reserve area was sometimes cut within several days. The current management organization has limited manpower, and the reserve is now managed as a single entity. The area that has to be harvested is so large (the Drentse A reserve is about 3000 ha) that it sometimes takes as much as 6 weeks to do this. This naturally has consequences for the phenological stage of plant species when cut.

The lack of connections between seed sources and 'target areas' and different phenology stages at the time of cutting, will lead to favouring certain species and repressing others in their dispersal. It is highly unlikely that the species that benefit at present will be the same species that benefited in the past, since the pattern of seed dispersal in grassland reserves today, both on a small community scale and on a larger landscape scale, is very different from that of the past. This may lead to the development of communities which are different from 'historical' communities, even if it were possible to recreate the same abiotic conditions. Naturally, this does not imply that modern agricultural methods or any different management methods in particular are unsuitable for conservation and restoration purposes. In hay-field management it is almost impossible to return to the old agricultural practice, even on a very small scale. Moreover, the developments which take place under modern management are actually very valuable from a nature conservation point of view. However, it is wise not to expect too much when the aim of restoration is derived from historical references.

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