

# Seed dispersal effectiveness in three adjacent plant communities: xerothermic grassland, brushwood and woodland

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*Received 18 Feb. 2004, revised version received 18 Oct. 2004, accepted 17 Dec. 2004*

Czarnecka, J. 2005: Seed dispersal effectiveness in three adjacent plant communities: xerothermic grassland, brushwood and woodland. — *Ann. Bot. Fennici* 42: 161–171.

This study investigates the dispersal ability of seeds and fruits of plant species in three adjacent plant communities — xerothermic grassland, brushwood and woodland — through analysis of the soil seed bank and its changes at the borders of the communities. I tested the following null hypothesis: effective seed dispersal leads to negligible differences in the richness and structure of the seed bank among these plant communities. However, considerable differences, both quantitative and qualitative, were observed among the seed banks of the neighbouring plant communities. I noted the highest average density of seeds, 32 450 per square metre, within the brushwood, half of that density (14 058) in the grassland seed bank, and less than a tenth of that density (2245) in the woodland bank. Most of the seeds remain in the close vicinity of their parent plants. In the analysed arrangement of plant communities, the most effective methods of seed dispersal seem to be myrmecochoria and endozoochoria. Seeds and fruits of the last type of dispersal are the most abundant in the woodland seed bank, where tree crowns host a lot of birds. Very effective dispersal is also exhibited by *Betula pendula*, an anemochorous pioneer species, and *Hypericum perforatum*.

Key words: brushwood, seed bank, seed dispersability, woodland, xerothermic grassland

## Introduction

Species composition and changes can be attributed to numerous factors, many of which are connected with the characteristics and changes of the habitat. Yet, environmental features are not the only elements responsible for the structure and dynamics of a plant community; some factors are connected with seeds and their dispersability. Both the dispersal ability of diaspores and seed

longevity are responsible for the formation of the soil seed bank. In this view, species composition is the result of demographic processes, such as seed production and dispersal, and also seed and adult longevity and germination characteristics (Van Groenendael *et al.* 2000).

Fruits and seeds of many plant species exhibit various adaptations enabling them to spread over vast distances. Animals, water and wind are most commonly used for the seed dispersal; seeds can

also be actively thrown by plants themselves (Howe & Smallwood 1982). A dispersal distance greater than 100 metres can be covered with the help of animals (eating fruits and subsequently excreting seeds, transporting seeds on hair or feathers) and wind; here, the most important are ascending air currents and storms (Cain *et al.* 2000). In numerous cases long-distance dispersal is connected with human activity: diaspores are transported by cars together with the soil stuck to tyres; important, too, is the transport of garden soil, and the escape of species which can potentially become persistent weeds from crops and gardens (Hodkinson & Thompson 1997). Despite numerous adaptations, however, most seeds tend to remain in the close vicinity of their parent plants (Verkaar *et al.* 1983).

The ability to spread over vast distances is negatively correlated with seed size, however, a big amount of stored food, deposited for example in big-sized cotyledons, increases the probability of seedling survival (Wilson *et al.* 1990, Ehrlén & Eriksson 2000). The principle of trade-off can be observed here: the ability to colonise new territories hardly ever goes hand in hand with the competitive ability. 'Colonisers' make poor 'competitors' (Ehrlén & Van Groenendael 1998).

Plants can exhibit two strategies: dispersal in space, and dispersal in time (dormancy). However the trade-off pattern seems not to be very clear in this case (Ehrlén & van Groenendael 1998). Dormancy is more common in species with smaller and compact seeds lacking morphological adaptations for dispersal (Rees 1993, Hodkinson *et al.* 1998, Funes *et al.* 1999). Smaller seeds are also better dispersers, because of their large surface area to weight ratio (Huges *et al.* 1994, Ehrlén & van Groenendael 1998).

Active dispersal of diaspores, reflecting local vegetation and invasion from surrounding sites, affects the composition of the soil seed bank. In a landscape mosaic of old fields and different types of woodlands intercommunity colonisation can add to the richness of the communities (Beatty 1991). Some studies show that exchange of seeds between neighbouring plant communities is usually ineffective (Dzwonko & Loster 1992, Hutchings & Booth 1996). The slow invasion of seeds from the chalk grassland into

adjacent ex-arable land is the main factor contributing to the poor development of grassland vegetation there (Hutchings & Booth 1996). Primary woods (ancient oak-hornbeam woodlands) cannot play the role of a potential source of seeds for restoration of this type of community on pine wood plantations, either. The migration of many woodland species from primary to secondary woods is very slow (Dzwonko & Loster 1992, Dzwonko 2001).

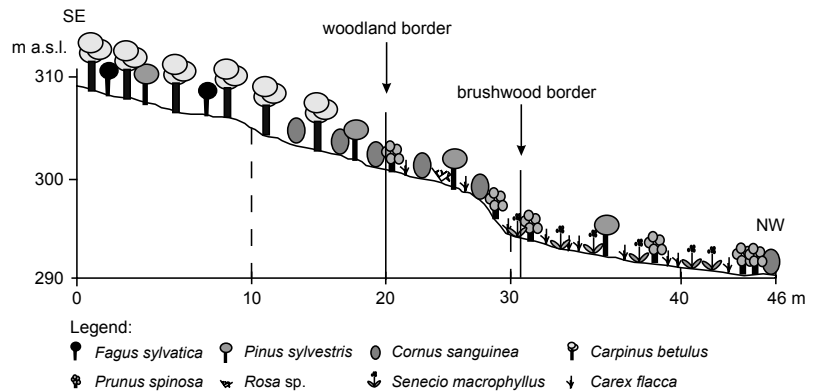
In this paper I will study the dispersal ability of seeds and fruits of some plant species in three adjacent plant communities: xerothermic grassland, brushwood and woodland. This community arrangement, together with the clearly marked borders separating particular zones, allows me to observe which of the diaspores are transported to distances greater than several metres from parent plants. The analysis and conclusions are based on data concerning changes in the composition of the soil seed bank at the borders of the communities.

In this study I tested the null hypothesis that effective seed dispersal should result in small differences in the richness and structure of the seed banks among these particular adjacent communities.

## Material and methods

### Site description

The study area was located on the White Mountain, a hill of the altitude 349 m a.s.l. It is situated in south-eastern Poland in the Central Roztocze Region (50°28'N, 23°29'E). Its soils consist mainly of Cretaceous marls and loess. The largest part of the southern and south-western slopes are overgrown with xerothermic grassland of the alliance *Cirsio-Brachypodium pinnati* Hadač *et* Klika 1944 *em.* Krausch 1961. This grassland is characterised by a mosaic spatial structure. Lower patches of grassland with smaller plant density are characterised by an abundance of the following species: *Aster amellus*, *Teucrium chamaedrys*, *Carex transsilvanica*, *Euphorbia cyparissias* and *Scabiosa ochroleuca*. One species, *Brachypodium pinnatum*, dominates in higher patches, which are also denser.



**Fig. 1.** Scheme of the study site and the vegetation.

*Brachypodium pinnatum* is accompanied by *Linum flavum*, *Salvia verticillata* and *S. pratensis* there (Czarnecka 1994). One species included in “The Polish Red Data Book of Plants” was observed there. It is *Senecio macrophyllus*, with the VU (vulnerable) threat category (Czarnecka & Kucharczyk 2001).

A brushwood of the *Rhamno–Prunetea* Rivas Goday *et* Garb. 1961 class (with dominance of *Prunus spinosa* and *Cornus sanguinea*) forms the border between the grassland and the woodland. It is a belt of vegetation adjacent to the woodland, which is dominated by *Carpinus betulus*, and also contains *Fagus sylvatica*, *Populus tremula*, *Tilia cordata*, *Betula pendula* and *Pinus sylvestris* (Czarnecka 1994, 1995).

The nomenclature of species follows Mirek *et al.* (1995) and the classification of plant communities follows Matuszkiewicz (2001).

## Methods

The study was carried out in November 1997, when seed shedding was finished. I took three soil samples (100 ml, 5 cm deep) per metre along the transect 46 metres long (Fig. 1), which I traced on the north-western slope through xerothermic grassland (15 m), brushwood (11 m) and woodland (20 m). Surface area of soil sampled was 2708 cm<sup>2</sup> (883 in grassland, 648 in brushwood and 1177 in woodland area). I pooled three samples from each metre and I treated separately the pooled samples taken from each particular metre. The volume of the soil samples was reduced by washing and sieving (with a sieve of

a diameter of 0.25 mm). Then, under the magnification of 10× all the seeds were picked out and recorded. Species presence in the seed bank was quantified as the mean number of seeds per square metre.

I employed non-parametric tests to analyse the data because of their deviation from normality. The Kruskal-Wallis test was used to check the significance of the differences among the means (mean number of species, mean densities of seeds, mean proportion of different dispersal modes) calculated for three sets of data (grassland, brushwood and woodland). I used the Mann-Whitney *U*-test when only two sets of data were compared. In some cases I gathered grassland and brushwood species into one category because of the similarities in the species composition of herb layer and abundance of some species of shrubs in the area of grassland.

I classified the species into five commonly used dispersal modes (e.g. Dzwonko & Loster 1992, Dzwonko 2001): anemochores = diaspores with wings or plumes and the smallest seeds with no dispersal adaptations; barochores = bigger seeds with no dispersal adaptations; endozochores = fruits with fleshy pulp, which are eaten by vertebrates, mainly by birds; epizoochore = fruits with hooks and hairs which adhere to fur or feathers; myrmecochore = seeds and fruits with elaiosomes.

I determined seed production by multiplying an average number of units per square metre (flowers, inflorescences or stems, depending on the morphology of a given species) and a mean number of seeds developed per unit. Observa-

tions were carried out during the whole vegetative season. Thirty units per species and 30

quadrats (one m<sup>-2</sup>) in every plant community were surveyed.

**Table 1.** Composition of the seed bank. Species recorded only once are listed below the table. Life forms: H = herb, S = shrub, T = tree. Dispersal mode: A = anemochore, B = barochore, En = endozoochore, Ep = epizoochore, M = myrmecochore.

Taxon	Life form	Dispersal mode	Mean number of seeds per m <sup>2</sup>		
			Grassland	Brushwood	Woodland
<i>Ajuga reptans</i>	H	M	68	46	119
<i>Betula pendula</i>	T	A	385	294	272
<i>Campanula trachelium</i>	H	A	45	93	9
<i>Carex digitata</i>	H	M	408	124	68
<i>Carex flacca</i>	H	B	4760	5780	17
<i>Carex transsilvanica</i>	H	B	1360	46	–
<i>Carpinus betulus</i>	T	A	23	155	486
<i>Chenopodium album</i>	H	B	11	–	9
<i>Cirsium arvense</i>	H	A	11	46	9
<i>Cirsium vulgare</i>	H	A	45	15	17
<i>Clinopodium vulgare</i>	H	B	227	1190	51
<i>Cornus sanguinea</i>	S	En	11	15	145
<i>Coronilla varia</i>	H	B	11	–	17
<i>Daucus carota</i>	H	Ep	11	46	9
<i>Euphorbia cyparissias</i>	H	M	45	62	–
<i>Fallopia convolvulus</i>	H	A	34	77	–
<i>Fragaria viridis</i>	H	En	181	510	43
<i>Galium mollugo</i>	H	A	45	15	–
<i>Hypericum perforatum</i>	H	A	680	788	77
<i>Leucanthemum vulgare</i>	H	A	91	46	9
<i>Linum catharticum</i>	H	A	1133	155	–
<i>Medicago lupulina</i>	H	B	113	124	26
<i>Origanum vulgare</i>	H	A	3241	21204	162
<i>Pimpinella saxifraga</i>	H	B	91	124	9
Poaceae	H	A/B	11	15	–
<i>Polygala vulgaris</i>	H	M	57	–	–
<i>Prunella vulgaris</i>	H	B	34	–	–
<i>Prunus spinosa</i>	S	En	11	15	9
<i>Ranunculus</i> sp.	H	B	57	232	–
<i>Rubus</i> sp.	S	En	–	–	179
<i>Salvia verticillata</i>	H	B	136	355	–
<i>Sambucus ebulus</i>	H	En	34	62	281
<i>Senecio macrophyllus</i>	H	A	306	15	–
<i>Teucrium chamaedrys</i>	H	B	–	31	9
<i>Thymus pulegioides</i>	H	A	11	108	–
<i>Trifolium alpestre</i>	H	B	57	15	–
<i>Urtica dioica</i>	H	A	11	247	–
<i>Verbascum nigrum</i>	H	A	215	15	–
<i>Veronica chamaedrys</i>	H	A	11	155	17
<i>Viola</i> sp.	H	M	11	155	179
Total number of seeds	–	–	14058	32450	2245

Species which were recorded only once (life form; dispersal mode):

- Grassland: *Agrimonia eupatoria* (H; Ep), *Astragalus glycyphyllos* (H; B), *Cichorium intybus* (H; A), *Hieracium pilosella* (H; A), *Sanguisorba minor* (H; B), *Scrophularia nodosa* (H; A);
- Brushwood: *Erigeron annuus* (H; A), *Euphorbia helioscopia* (H; M), *Picris hieracioides* (H; A), *Torilis japonica* (H; Ep), *Valeriana officinalis* (H; A);
- Woodland: *Crataegus monogyna* (S; En), *Rumex acetosella* (H; A).

## Results

The analysed soil samples contained seeds of 53 taxa. I observed the highest diversity within the xerothermic grassland (44 taxa), intermediate diversity in the soil of the brushwood (40 taxa), and the lowest diversity in the woodland (27 taxa) (Table 1). Only 18 taxa showed a frequency higher than 30% in at least one of the communities. I identified most of the seeds at species level; such an identification proved impossible in three genera: *Ranunculus*, *Rubus* and *Viola*. All of the grains of grasses were identified as Poaceae.

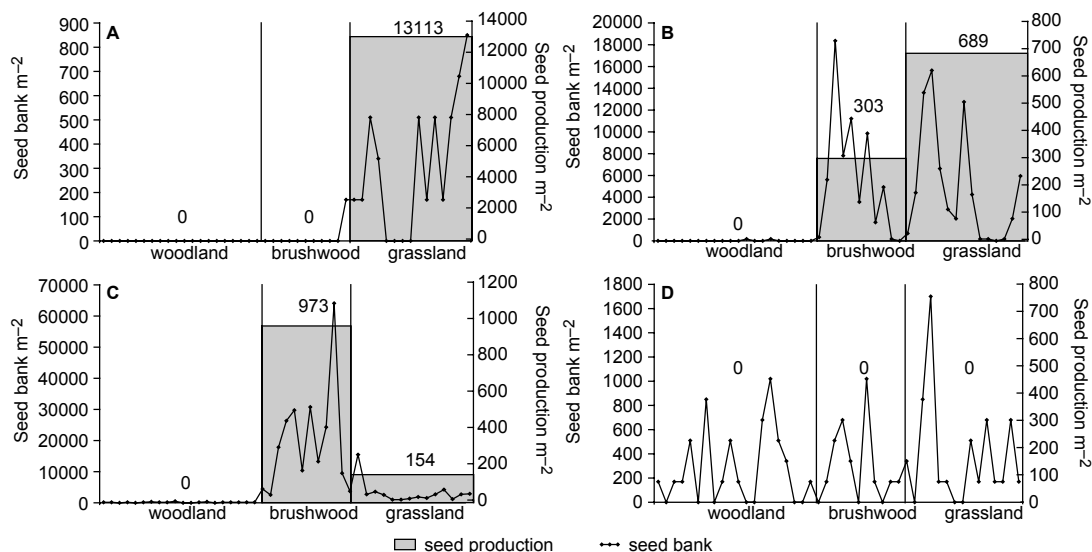
The highest average seed density, reaching 32 450 per square metre, was observed in the soil of the brushwood, half of that density (14 058) in the seed bank of the grassland, and only a tenth of that density (2245) in the seed bank of the woodland.

In addition to these strong quantitative differences, there were striking qualitative differences

in the composition of the soil seed bank in the different communities. Among the most frequent species we may easily define groups with the occurrence centres in different vegetation types (Table 2 and Fig. 2). For all these taxa, except *Betula pendula*, *Carex digitata* and *Medicago lupulina*, differences in average number of seeds among communities were statistically highly significant. The number of seeds of *Carex digitata* in soil of grassland was surprisingly high considering the distance from woodland and brushwood (the area of abundance of the parent plants). It suggests that this myrmecochorous species is a good coloniser. *Betula pendula*, an anemochorous pioneer species, was characterised by a similar average seed number in woodland (where some flowering and fruiting trees were observed at a significant distance from the study area), and in the soil of brushwood and grassland. Moreover, its frequency was high in all these communities (Fig. 2).

**Table 2.** Species composition of the seed bank. Species with higher than 30% frequency in at least one community were recorded (number of seeds per m<sup>2</sup> in parentheses); tested with the Kruskal-Wallis test. Frequency: ● ≤ 10%, ● = 11%–50%, ● > 50%.

Centre of abundance of adult individuals	Frequency and mean number of seeds in soil per m <sup>2</sup>			P
	Grassland	Brushwood	Woodland	
Grassland				
<i>Carex transsilvanica</i>	● (1360)	● (46)	– (0)	< 0.001
<i>Linum catharticum</i>	● (1133)	● (155)	– (0)	< 0.001
<i>Senecio macrophyllus</i>	● (306)	● (15)	– (0)	< 0.001
<i>Verbascum nigrum</i>	● (215)	● (15)	– (0)	< 0.05
<i>Medicago lupulina</i>	● (113)	● (124)	● (26)	n.s.
Brushwood and grassland				
<i>Origanum vulgare</i>	● (3241)	● (21204)	● (162)	< 0.001
<i>Carex flacca</i>	● (5051)	● (5780)	● (17)	< 0.001
<i>Clinopodium vulgare</i>	● (227)	● (1190)	● (51)	< 0.05
<i>Salvia verticillata</i>	● (136)	● (355)	– (0)	< 0.001
<i>Ranunculus</i> sp.	● (57)	● (232)	– (0)	< 0.001
Brushwood				
<i>Hypericum perforatum</i>	● (680)	● (788)	● (77)	< 0.001
<i>Fragaria viridis</i>	● (181)	● (510)	● (43)	< 0.01
<i>Carex digitata</i>	● (408)	● (124)	● (68)	n.s.
Woodland and brushwood				
<i>Cornus sanguinea</i>	● (11)	● (15)	● (145)	< 0.05
Woodland				
<i>Carpinus betulus</i>	● (23)	● (155)	● (486)	< 0.001
<i>Betula pendula</i>	● (385)	● (294)	● (272)	n.s.
<i>Viola</i> sp.	● (11)	● (155)	● (179)	< 0.01
Absent in the border of the study area				
<i>Sambucus ebulus</i>	● (34)	● (62)	● (281)	< 0.05



**Fig. 2.** Relation between the place of development and the number of diaspores and their distribution in soil. — **A:** *Senecio macrophyllus*. — **B:** *Carex flacca*. — **C:** *Origanum vulgare*. — **D:** *Betula pendula*.

Soil seed bank data can be ordered according to many criteria. In this study, taxa were grouped by plant life form, syntaxonomic status and the diaspore dispersal mode (Table 3). The differences in the bank structures of particular types of vegetation are statistically highly significant, in both the average number of species belonging to particular categories, and the average seed number in general. The analysed communities differ not only in the vegetation, but also in the seed bank. The differences observed in their qualitative and quantitative structure resulted from the surprisingly low mobility of seeds leading to lack of diaspore exchange between the communities. In the case of woodland anemochores and myrmecochores, the differences were statistically significant when the best dispersers, *Betula pendula* and *Carex digitata*, were excluded from the analysis. This shows that seed dispersal of the other species from these groups is inefficient.

The woodland seed bank is easily distinguished when we order the samples according to the percentage share of a particular type of seeds (the dispersal mode and type of plant community were taken into consideration) and the mean number of seeds (Figs. 3 and 4). The considerable contribution of woodland anemochores (mainly *Carpinus betulus* and *Betula pendula*) and woodland myrmecochores (*Carex*

*digitata* and *Viola* sp.) was striking here. High numbers of endozoochorous seeds of *Sambucus ebulus* were also found in the woodland seed bank. I found fruiting individuals of *S. ebulus* at a distance exceeding a hundred metres from the study site, which undoubtedly indicates long-distance seed dispersal. The seed banks of grassland and brushwood, however, exhibited considerable similarities (Fig. 4). Yet, these similarities did not seem to result from the effective dispersal of seeds and their exchange between the communities. They rather resulted from the fact that in both plant communities, their species composition of the herb layer was to a large extent similar: within the brushwood I observed a large coverage of the following species, characteristic of the class *Festuco-Brometea* Br. Bl. et R.Tx. 1943 and *Trifolio-Geranietea sanguinei* Müll. 1962: *Salvia verticillata*, *Brachypodium pinnatum*, *Euphorbia cyparissias*, *Teucrium chamaedrys*, *Agrimonia eupatoria*, *Origanum vulgare* and *Clinopodium vulgare*.

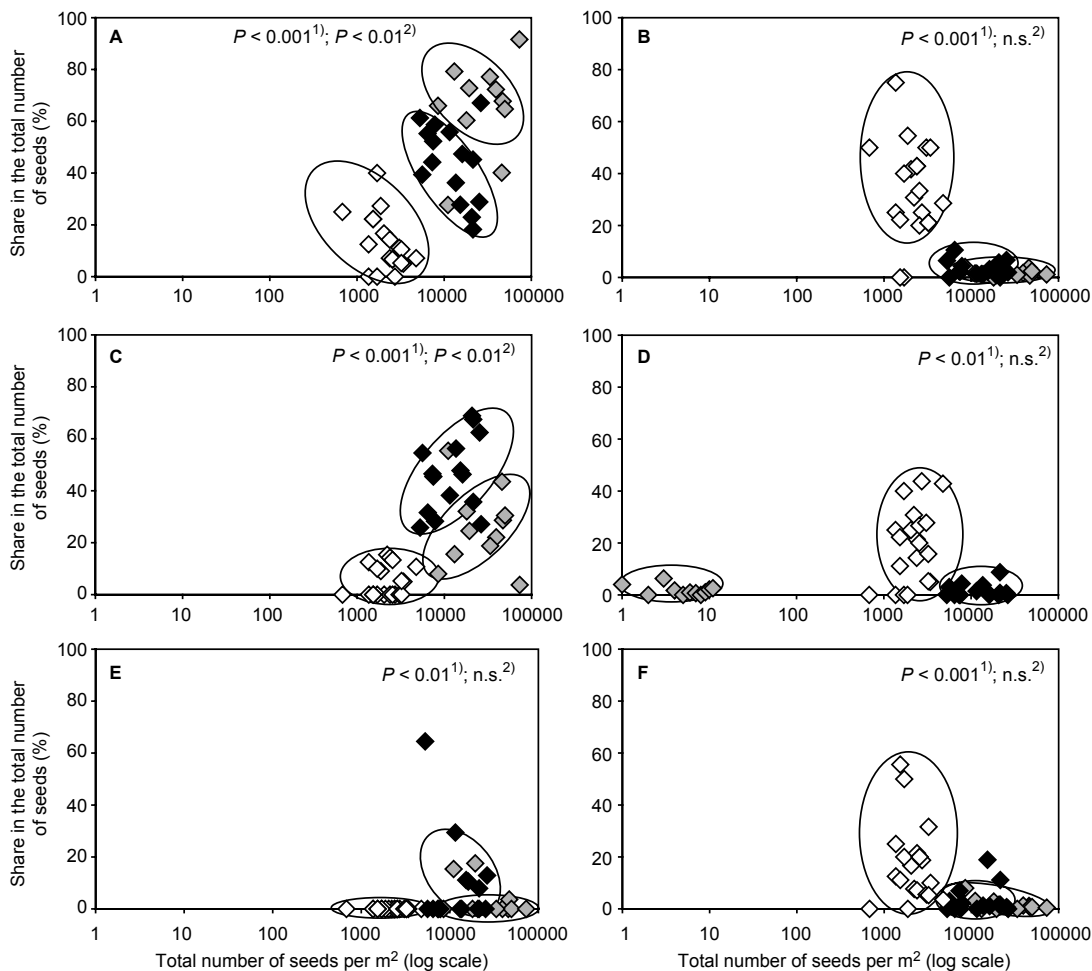
## Discussion

Verkaar *et al.* (1983) observed (and this observation was further confirmed by the research done

**Table 3.** Mean values of seed bank variables for woodland, brushwood and grassland. Differences analysed with the Kruskal-Wallis test. Woodland barochores and endozoochore were not detected.

Variables	Mean number of species in sample			Mean number of seeds per m <sup>2</sup> in sample				P
	Grassland	Brushwood	Woodland	Grassland	Brushwood	Grassland	Brushwood	
1. All species	11.8	12.5	6.4	< 0.001	14058	32450	2245	< 0.001
2. Life form								
Grasses and sedges	2.5	1.6	0.4	< 0.001	6539	5965	85	< 0.001
Dicotyledonous herbs	8.3	9.5	3.8	< 0.001	7095	26010	1054	< 0.001
Trees and shrubs	1.1	1.4	2.2	< 0.01	430	479	1096	< 0.01
3. Syntaxonomic status								
Grassland and brushwood species	9.0	8.3	2.5	< 0.001	12931	30909	587	< 0.001
Woodland species	2.0	2.6	2.8	< 0.05	952	865	1131	n.s.
4. Dispersal mode								
Anemochores								
Grassland and brushwood anemochores	4.6	3.4	1.3	< 0.001	5825	22486	255	< 0.001
Woodland anemochores	1.1	1.5	1.6	n.s.	465	541	765	< 0.05
Woodland anemochores with <i>B. pendula</i> excluded	0.3	0.7	0.9	n.s.	79	247	493	< 0.001
Barochores								
Grassland and brushwood barochores	3.4	3.5	0.5	< 0.001	6777	7774	119	< 0.001
Endozoochores								
Grassland and brushwood endozoochores	0.7	1.0	1.2	n.s.	238	603	485	< 0.05
Myrmecochores								
Grassland and brushwood myrmecochores	0.5	0.3	0.0	< 0.01	102	62	0	< 0.01
Woodland myrmecochores	0.9	1.2	1.3	n.s.	487	325	365	n.s.
Woodland myrmecochores with <i>C. digitata</i> excluded	0.3	0.7	0.9	< 0.05	79	201	320	< 0.05





**Fig. 3.** Relation between total seed number, which is the best variable differentiating three vegetation types (Kruskal-Wallis test:  $P < 0.001$ ), and the type of dispersal of seeds. — **A:** Grassland and brushwood anemochores. — **B:** Woodland anemochores. — **C:** Grassland and brushwood barochores. — **D:** Grassland and brushwood endozoochores. — **E:** Grassland and brushwood myrmecochores. — **F:** Woodland myrmecochores. Woodland barochores and endozoochores were not detected. White: samples from woodland. Grey: samples from brushwood. Black: Samples from grassland. <sup>1)</sup> differences among the three vegetation types analysed with the Kruskal-Wallis test; <sup>2)</sup> differences between brushwood and grassland analysed with the Mann-Whitney *U*-test.

at the White Mountain) that in xerothermic species most of the seeds remain within the range of 0.3 to 3.5 m from a fruiting individual. For some species it is the stem length that determines the distance over which the seeds and fruits are transported (*Scabiosa columbaria*, *Daucus carota*). For others, whose flowers are located low (e.g. *Linum catharticum*), the wind force above the ground level, which depends on plant density, is of primary importance (Verkaar *et al.* 1983). More than 50% of cypselas of *Cir-*

*sium vulgare* remain no further than one metre from the parent plant; only 10% of them reach a distance longer than 32 m, these being the seeds, which have been elevated to considerable heights (Klinkhamer *et al.* 1988).

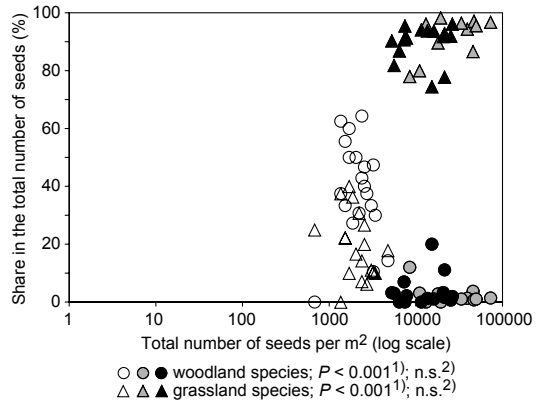
Endozoochorous diaspores, which are transported over long distances by birds, are clearly grouped in the vicinity of trees. This fact confirms the observations of numerous authors (e.g. McClanahan & Wolfe 1987, Debussche & Isenmann 1994, Adamowski & Knopik 1996).



According to Dzwonko and Loster (1992), flying anemochores and endozoochore are the best colonisers. The poorest are heavy anemochores, barochores and myrmecochores. Observations of the distribution of diaspores of *Betula pendula* (anemochore) and *Sambucus ebulus* (endozoochore) in the present study confirm these statements. *Carex digitata* (myrmecochore) appeared to be quite a good coloniser, too.

The trade-off between seed dispersal and dormancy is not very clear here. In *Betula pendula* dispersability is accompanied by seed dormancy (longevity index calculated according to Thompson *et al.* 1998 on the basis of seed bank database (Thompson *et al.* 1997) is 0.8). The efficient dispersal of diaspores of *Carex digitata* compensates for their reduced dormancy (longevity index 0.25; but Thompson *et al.* 1993 join ant dispersal with a persistent seed bank). In the group of poor dispersers there are also species with a persistent (*Origanum vulgare* 0.73; *Linum catharticum* 0.67) and transient seed bank (*Carpinus betulus* 0.0).

Regardless of the plant community type, the most numerous diaspores in the seed banks are usually the ones of the smallest size, most commonly persistent and belonging to pioneer species. These species usually produce many long-lived diaspores, transported over long distances, in contrast to the species characteristic of the climax state. The latter seeds perish quickly if they do not manage to germinate (Thompson & Grime 1979, Baker 1989). There occur a couple of 'cosmopolitan', small-seeded anemochorous species whose diaspores appear in the soil of various plant communities. These are species of the *Betula* and *Hypericum* kinds (Pirożnikow 1983, Bigwood & Inouye 1988, Kjellsson 1992, Milberg & Hansson 1994, Milberg & Persson 1994, Warr *et al.* 1994, Milberg 1995, Bekker *et al.* 1997, Mitchell *et al.* 1998, Jankowska-Błaszczuk 2000). Their seeds were also found in the soil of the examined plant communities. *Hypericum perforatum* is a common element of xerothermic grasslands in south-eastern Poland (e.g. Fijałkowski 1954, 1958, Izdebski & Fijałkowski 1956, Izdebski 1958) and the presence of this species, or its relative *H. maculatum*, in the seed bank of grassland communities seems to be a ubiquitous phenomenon (Milberg 1992, 1995, Milberg & Persson 1994, Willems 1995,



**Fig. 4.** Relation between total seed number and the status of species. White: samples from woodland. Grey: Samples from brushwood. Black: samples from grassland. <sup>1</sup> Differences between the three vegetation types analysed with the Kruskal-Wallis test. <sup>2</sup> Differences between brushwood and grassland analysed with the Mann-Whitney *U*-test.

Kalamees & Zobel 1997). Their diaspores were also present in the soil of other plant communities, e.g. woodland (Jankowska-Błaszczuk 2000). Those observed in the soil of the studied vegetation types come mainly from the adjacent balks and wastelands. Equally effective was the dispersal of another typical pioneer species, *Betula pendula*.

## Conclusions

1. The original null hypothesis was rejected. Considerable differences in the qualitative and quantitative structure as well as in the frequency of particular species in the seed bank of various vegetation types show that the dispersal of seeds and fruits is not effective.
2. In the analysed plant communities, the most effective methods of seed dispersal seem to be endozoochory and myrmecochory, in other words the methods of transporting seeds with the help of animals. The seeds and fruits with this type of dispersal had the highest frequency in the seed bank of the woodland, where tree-crowns host many birds.
3. I observed very effective dispersal for diaspores of *Hypericum perforatum* (anemo-

chore), *Sambucus ebulus* (endozoochore) and *Betula pendula* (anemochorous pioneer species which is a typical 'coloniser' in the sense of Ehrlén and van Groenendael (1998). These diaspores were transported from outside the study area and the process can be called long-distance seed dispersal.

## Acknowledgements

I thank prof. Bożenna Czarnecka for verification of the thesis of this work and mgr Anna Majewska and mgr Krystyna Kowalska for their help in field and laboratory work. I also thank two anonymous referees for valuable comments on the manuscript.

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