European Bison Conservation Newsletter Vol 1 (2008) pp: 14–29

Diversity of plant species eaten and dispersed by the European bison *Bison bonasus* in Białowieża Forest

Bogdan Jaroszewicz[1], Ewa Pirożnikow[2]

[1] Białowieża Geobotanical Station, Institute of Botany at the Faculty of Biology, University of Warsaw, Sportowa 19, 17–230 Białowieża; e-mail: b.jaroszewicz@uw.edu.pl
[2] Institute of Biology, University of Białystok

Abstract The European bison influences vegetation by e.g. endozoochoric seed dispersal. The diet of the European bison includes 454 vascular plant species, i.e. close to 40% of the flora of Białowieża Forest. Seeds contained in 75 samples of bison faeces developed into 12,392 seedlings, classified as 173 different plant species, of which 80% were perennials. Species whose seeds are disseminated via the gastrointestinal tract of the bison constitute 16% of the vascular plants recorded in Białowieża Forest. The total number of plant species dispersed by bison is close to double the number recorded for domestic cattle, horses or *Cervidae*. The biodiversity of plant species dispersed by free-roaming bison is lower (102 species) than that of bison living in captivity (140 species). In the faeces of both free-roaming and captive bison the number of anthropogenic and meadow plant species was higher in winter than in summer. The European bison plays a significant role in the dispersal of plants, especially of non-forest species, which ensures their existence in the forest community. Plant seeds present in bison faeces which do not naturally occur in Białowieża Forest (probably introduced with hay used for supplementary feeding) contributes to the stability of flora biodiversity, but could also introduce the risk of invasion by alien species.

Introduction

Large herbivorous mammals exert an influence on vegetation as they eat plants and are responsible for endo and epizoochoric transport of plant propagules within and between plant communities (e.g. Faliński 1986; Olff and Ritchie 1998). The significance of this process for the diversity of flora and plant communities has been the subject of many studies (e.g. Welch 1985; Pakeman et al. 2002; Bakker and Olff 2003; Jaroszewicz et al. 2008). Their authors demonstrated that large herbivorous mammals: domestic cattle (*Bos taurus s. str.*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and bison (*Bison bonasus*) transfer thousands of seeds of close to hundred species each. For this reason endo and epizoochoric transport of plant propagules has become a tool in nature conservation used for the maintenance of flora diversity, as well as for restoration ecosystem management (Fischer et al. 1996; Zobel et al. 1998;

Cosyns 2004). The zoochoric transport of plant propagules can also introduce a risk to nature by facilitating and accelerating the invasion of alien plant species (e.g. Campbell and Gibson 2001; Mouissie 2004; Constible et al. 2005).

In pre-agricultural times, when forest vegetation predominated on the European continent, the habitats of the majority of herbaceous plants which are found today on fallow land, pastures, meadows and roadsides were probably of a highly non-continuous character. These were gaps in forests resulting from disturbances such as windfalls, fires, massive insect infestations, landslides, etc. Such small island ecosystems were excellent, though ephemeral sites for the development of heliophilous and thermophilous plants, which most likely underwent fast regenerative succession. In the primeval forest heliophilous plants could only survive if they were able to adapt to existence in the soil seed banks for decades, or colonize newly created open spaces through the migration of propagules from older, overgrowing gaps. Many of these plants have seeds which are morphologically adapted for transport by wind, water, in fur or in the gastrointestinal tracts of animals. Small dimensions and an almost round shape are the traits of seeds creating permanent soil seed banks (Thompson et al. 1997), as well as a feature reflecting their adaptation to endozoochoric transport (Janzen 1984).

Historically, the bison lived in the larger part of Europe and was a regularly found ungulate on the European continent (Pucek et al. 2004; Krasińska and Krasiński 2004). This animal uses forest ecosystems and non-forest ones with the same frequency whenever it has access to them (Krasińska and Krasiński 2004). Hypothetically, the bison has played a significant role in the process of biodiversity maintenance in forest ecosystems by eating plants together with their propagules, and their dispersal (Jaroszewicz 2008). For over a century Białowieża Forest has been the subject of studies focused on the composition of plant species eaten by bison (e.g. Wróblewski 1927; Borowski and Kossak 1972; Gębczyńska and Krasińska 1972; Gębczyńska et al. 1991). Korochkina (1972) summarized all the findings on the diet of this ruminant by listing 375 plant species, including 44 trees.

The objective of this study is to: (a) extend the knowledge of the plant species eaten by the European bison; (b) compare previous findings on the bison's diet with data on the plants dispersed by the European bison; (c) demonstrate the role of the European bison as a vector of plant propagules in forest ecosystems.

Materials and methods

The study was carried out in the forest ecosystems of the Polish part of Białowieża Forest and in the Bison Breeding Centres of the Białowieża National Park. Białowieża Forest is one of the best preserved forest complexes on the European Lowland. Its fauna and flora are very rich and of relict character, with numerous species of organisms able to live exclusively in forest ecosystems preserved in a condition close to primeval (Gutowski and Jaroszewicz 2001; Faliński 2003; Tomiałojć and Wesołowski 2005). The vascular flora is represented by close to 1 100 plant species (Sokołowski 1995).

Białowieża Forest is inhabited by a free-roaming population of 439 European bison (as of 31 December 2007, European Bison Pedigree Book, unpubl. data). Bison in the wild are provided with supplementary fodder in winter, especially when the snow cover is abundant and reduces access to natural food sources. There are 47 bison in the Bison Breeding Centres of the Białowieża National Park (31 December 2007, European Bison Pedigree Book, unpubl. data), which are provided with supplementary fodder all year (hay, cereals, potatoes, beets, apples, acorns), although they also graze on plants growing within their pens.

Two and a half litre samples of bison faeces used for the purpose of the study on the transport of plant propagules were taken between September 2005 and September 2006, once a week on average, alternately from pens in Bison Breeding Centres and from the area of Białowieża Forest where bison live in the wild. To avoid impurities from seeds of anemochoric origin, only the most recent faeces were sampled, from the layer on the ground, which ensured no admixtures of seeds from the soil seed bank. One sample contained faeces produced by various individuals. Faeces were mixed in a proportion of 1:2 with sand which had previously been sterilized over 48 hours at 110°C, and after that poured into 30 x 40 x 10 cm trays, forming about a 6 cm layer. Trays with samples were stored in a greenhouse over one year and left over winter to stimulate the germination of plant seeds which require vernalisation. Samples were watered during the vegetation season when necessary. Material in the trays was mixed each time after the removal of all seedlings.

Seedlings were counted and immediately removed from trays whenever their determination as species was possible. The seedlings of plants which were impossible to determine as species were replanted in flower-pots and, in the case of sedges, also on a plot in the experimental garden of the Białowieża Geobotanical Station of the University of Warsaw. Only *Viola riviniana* Rchb./*Viola reichenbachiana* Jord. ex Boreau and *Carex spicata* Huds./*Carex muricata* L. were impossible to determine as species, and for analytical purpose were treated as 'collective species'. For the purpose of simplification in this paper we use the term 'species' also when referring to those plants whose seedlings could only be determined to genus (e.g. *Carex* spp., *Agrostis* spp., *Alchemilla* spp., *Betula* spp., *Epilobium* spp., *Juncus* spp.). Close to 3.7% of seedlings died prior to their determination (Table 1). They are listed in this paper as 'non-determined bicotyledones' and as 'Poaceae'.

Table 1. Alphabetic list of plant species dispersed endozoochorically by the European bison in Białowieża Forest. The number (#) of seedlings, mean # of seedlings per sample, frequency of occurrence in samples (number of trays where individual species were recorded; maximum 72), # of seedlings from samples collected in captivity, # of seedlings from samples collected in the wild, lifeforms by Raunkiaer, groups of ecosystems where species are found, morphological adaptation of seeds for dispersal and species presence in summer and winter samples, as well as literature data referring to bison diet (by Korochkina, 1972) are provided.

No.	Species	# seedlings	Mean # seedlings/sample	Frequency	Captivity	Wild	Life form	Group of ecosystem	Dispersal adaptations	Winter	Summer	Korochkina 1972
1	2	3	4	5	6	7	8	9	10	11	12	13
1	*Achillea milefolium* L.	2	0.03	1	2	0	H	M	N	–	+	+
2	*Agrostis canina* L	14	0.19	3	14	0	H	F	E	–	+	+
3	*Agrostis capillaris* L.	23	0.31	10	9	14	H	M	E	+	+	+
4	*Agrostis gigantea* Roth	1	0.01	1	1	0	H	M	E	–	+	+
5	*Agrostis* sp.	1	0.01	1	1	0	NC	NC	NC	–	+	+
6	*Agrostis stolonifera* L.	47	0.63	12	32	15	H	M	E	+	+	–
7	*Alchemilla monticola* Opiz	3	0.04	2	3	0	H	M	N	–	+	–
8	*Alchemilla* sp.	3	0.04	2	3	0	NC	NC	NC	–	+	+
9	*Alopecurus pratensis* L.	1	0.01	1	1	0	H	M	E	+	–	+
10	*Anthemis arvensis* L.	36	0.48	11	36	0	T	O	N	+	+	–
11	*Anthemis cotula* L.	6	0.08	6	6	0	T	O	N	+	+	–
12	*Anthoxanthum odoratum* L.	5	0.07	4	3	2	H	M	E	+	+	+
13	*Arabidopsis thaliana* (L.) Heynh.	1	0.01	1	1	0	T	O	N	–	+	–
14	*Artemisia campestris* L.	1	0.01	1	1	0	A	M	N	+	–	+
15	*Artemisia vulgaris* L.	3	0.03	2	1	2	H	O	N	–	+	+
16	*Avena sativa* L.	21	0.28	4	21	0	T	O	E	+	+	–
17	*Betula pendula* Roth	18	0.24	5	14	4	P	F	A	–	+	+
18	*Betula* sp.	6	0.08	3	0	6	NC	NC	A	+	+	+
19	*Briza media* L.	1	0.01	1	1	0	H	M	N	–	+	+
20	*Bromus inermis* Leyss.	1	0.01	1	1	0	H	M	E	–	+	–
21	*Callitriche verna* L. em. Loennr.	21	0.28	1	21	0	C	F	N	–	+	–

1	2	3	4	5	6	7	8	9	10	11	12	13
22	*Capsella bursa-pastoris* (L.) Medik.	9	0.12	3	9	0	H,T	O	N	+	+	+
23	*Cardaminopsis arenosa* (L.) Hayek	3	0.04	1	3	0	H	O	N	–	+	–
24	*Carex canescens* auct. non L.	13	0.17	6	10	3	H	F	N	+	+	+
25	*Carex dioica* L.	1	0.01	1	1	0	C	F	N	–	+	+
26	*Carex elongata* L.	11	0.15	4	10	1	H	F	N	–	+	–
27	*Carex hirta* L.	19	0.25	9	17	2	C	M	N	+	+	+
28	*Carex nigra* (L.) Reichard	8	0.11	2	0	8	C	F	N	+	–	+
29	*Carex ovalis* Gooden.	11	0.15	3	11	0	H	F	N	–	+	+
30	*Carex panicea* L.	5	0.07	1	0	5	H,C	M	N	+	+	–
31	*Carex pilosa* Scop.	2	0.03	1	0	2	H,C	F	N	+	–	+
32	*Carex pseudocyperus* L.	2	0.03	2	0	2	H,C	F	N	+	+	–
33	*Carex remota* L.	49	0.65	10	23	26	H	F	N	+	+	+
34	*Carex* sp.	212	2.83	43	141	71	NC	NC	NC	+	+	+
35	*Carex spicata* Huds. /*Carex muricata* L.	30	0,39	4	25	5	H	F	N	–	+	–
36	*Carex sylvatica* Huds.	6	0.08	2	3	3	H	F	N	+	+	–
37	*Cerastium holosteoides* Fr. em. Hyl.	33	0.44	12	27	6	A,H	M	N	+	+	–
38	*Chamomilla recutita* (L.) Rauschert	2	0.03	2	2	0	H,T	O	N	+	+	–
39	*Chamomilla suaveolens* (Pursh) Rydb.	1	0.01	1	1	0	T	O	N	–	+	–
40	*Chenopodium album* L.	38	0.51	12	38	0	T	O	N	+	+	+
41	*Circaea intermedia* Ehrh.	2	0.03	1	0	2	C	F	E	–	+	–
42	*Circaea lutetiana* L.	1	0.01	1	0	62	C	F	E	–	+	–
43	*Cruciata gabra* (L.) Ehrend.	1	0.01	1	0	1	H	M	E	–	+	–
44	*Dactylis aschersoniana* Graebn.	3	0.04	2	3	0	H	F	E	+	+	–
45	*Dactylis glomerata* L.	10	0.13	9	8	2	H	M	E	+	+	+
46	*Deschampsia cespitosa* (L.) P.Beauv.	17	0.23	8	7	10	H	F	E	+	+	+
47	*Deschampsia flexuosa* (L.) Trin.	1	0.01	1	1	0	H	F	E	–	+	–
48	*Digitaria sanguinalis* (L.) Scop.	2	0.03	1	2	0	T	O	E	+	–	–
49	*Echinochloa crus-galli* (L.) P.Beauv.	8	0.11	7	6	2	T	O	E	+	+	–

1	2	3	4	5	6	7	8	9	10	11	12	13
50	*Elymus repens* (L.) Gould.	1	0.01	1	1	0	H	O	E	+	–	+
51	*Epilobium adnatum* Griseb.	7	0.09	1	7	0	A,H	M	A	–	+	–
52	*Epilobium ciliatum* Raf.	1	0.01	1	0	1	H	O	A	–	+	–
53	*Epilobium montanum* L.	3	0.04	2	0	3	H	F	A	–	+	+
54	*Epilobium palustre* L.	1	0.01	1	0	1	H	M	A	–	+	+
55	*Epilobium roseum* Schleb.	2	0.03	2	1	1	H	F	A	–	+	–
56	*Epilobium* sp.	1	0.01	1	0	1	NC	NC	A	+	–	–
57	*Erysimum cheiranthoides* L.	2	0.03	2	2	0	T	O	N	–	+	–
58	*Fallopia convolvulus* A.andA.Löve	10	0.13	7	10	0	T,H	O	N	+	+	+
59	*Festuca gigantea* (L.) Vill.	6	0.08	5	3	3	H	F	E	+	+	+
60	*Festuca pratensis* Huds.	1	0.01	1	0	1	H	M	E	–	+	+
61	*Festuca rubra* L.	71	0.95	17	53	18	H	M	E	+	+	+
62	*Gagea lutea* (L.) Ker Gawl.	5	0.07	2	0	5	C	F	N	–	+	+
63	*Galeobdolon luteum* Huds.	1	0.01	1	0	1	A	F	M	–	+	+
64	*Galinsoga parviflora* Cav.	1	0.01	1	1	0	T	O	A	–	+	–
65	*Geranium robertianum* L.	7	0.09	5	3	4	H,T	F	S	+	+	+
66	*Geum urbanum* L.	1	0.01	1	0	1	H	F	E	–	+	+
67	*Holcus lanatus* L.	6	0.08	2	4	2	H	M	E	+	+	+
68	*Holcus mollis* L.	2	0.03	2	0	2	C,H	F	E	+	+	–
69	*Hordeum vulgare* L.	3	0.04	2	3	0	T	O	E	–	+	–
70	*Hypericum perforatum* L.	4	0.05	3	1	3	H	M	N	+	+	+
71	*Juncus articulatus* L.	21	0.28	6	21	0	H	F	N	+	+	–
72	*Juncus bufonius* L.	128	1.71	14	97	31	T	F	N	+	+	–
73	*Juncus bulbosus* L.	6	0.08	3	6	0	H	F	N	–	+	–
74	*Juncus effusus* L.	452	6.03	21	71	379	H	M	N	–	+	+
75	*Juncus* sp.	21	0.28	4	21	0	NC	NC	N	–	+	+
76	*Juncus tenuis* Willd.	18	0.24	9	15	3	H	O	N	+	+	–
77	*Lamium maculatum* L.	2	0.03	2	0	2	H	M	N	–	+	–
78	*Lapsana communis* L.	3	0.04	2	0	3	H,T	F	N	–	+	+
79	*Lathyrus pratensis* L.	1	0.01	1	0	1	H	M	N	+	–	+
80	*Leontodon autumnalis* L.	1	0.01	1	1	0	H	M	A	–	+	–
81	*Lolium multiflorum* Lam.	1	0.01	1	1	0	H,T	M	E	–	+	–

1	2	3	4	5	6	7	8	9	10	11	12	13
82	*Lolium perenne* L.	2	0.03	1	2	0	H	O	E	–	+	+
83	*Lotus corniculatus* L.	4	0.05	2	4	0	H	M	N	–	+	+
84	*Luzula campestris* (L.) DC.	20	0.27	8	11	9	H	M	M	+	+	+
85	*Luzula multiflora* (Retz.) Lej.	4	0.05	3	3	1	H	M	M	+	+	+
86	*Lychnis flos-cuculi* L.	1	0.01	1	1	0	H	M	N	–	+	+
87	*Lycopus europaeus* L.	3	0.04	2	1	2	H,C	F	N	+	+	+
88	*Lythrum salicaria* L.	2	0.03	1	0	2	H	M	N	–	+	–
89	*Malus domestica* Borkh.	4	0.05	1	3	0	P	O	F	–	+	–
90	*Matricaria perforata* Mérat	17	0.23	8	17	0	H,T	O	N	+	+	–
91	*Medicago lupulina* L.	12	0.16	3	0	12	H,T	M	N	+	–	–
92	*Melandrium album* (Mill.) Garcke	7	0.09	3	4	3	T,H	O	N	–	+	+
93	*Melica nutans* L.	1	0.01	1	0	1	C,H	F	N	–	+	+
94	*Mentha arvensis* L.	1	0.01	1	1	0	C	O	M	–	+	+
95	*Milium effusum* L.	22	0.29	8	0	22	H	F	N	+	+	+
96	*Moehringia trinervia* (L.) Clairv.	9	0.12	1	8	1	H,T	F	N	+	–	+
97	*Oxalis acetosella* L.	2	0.03	1	1	1	C,H	F	S	+	–	+
98	*Oxalis dilleni* Jacq.	3	0.04	2	2	1	T,H	O	S	+	+	–
99	*Phleum pratense* L.	4	0.05	2	2	2	H	M	E	–	+	+
100	*Plantago lanceolata* L.	37	0.49	15	147	46	H	M	N	+	+	+
101	*Plantago major* L.	1138	15.17	22	859	279	H	O	N	+	+	+
102	*Poa angustifolia* L.	82	1.09	16	65	17	H	O	E	+	+	+
103	*Poa annua* L.	50	0.67	9	41	9	H,T	O	E	+	+	+
104	*Poa chaixii* Vill.	26	0.35	11	21	5	H	O	E	+	+	–
105	*Poa compressa* L.	2	0.03	2	2	0	H	O	E	+	+	+
106	*Poa nemoralis* L.	8	0.11	4	2	6	H	F	E	–	+	–
107	*Poa palustris* L.	13	0.17	7	12	2	H	F	E	+	+	+
108	*Poa pratensis* L.	131	1.75	19	48	83	H	M	E	+	+	+
109	*Poa subcaerulea* Sm.	72	0.96	12	20	52	H	O	E	+	+	–
110	*Poa trivialis* L.	20	0.27	10	11	9	H	M	E	+	+	–
111	*Polygonum aviculare* L.	15	0.2	6	15	0	T	O	N	–	+	–
112	*Polygonum hydropiper* L.	19	0.25	4	14	5	T	F	N	+	+	–
113	*Polygonum lapathifolium* L.	8	0.11	4	7	1	T	O	N	+	+	–

1	2	3	4	5	6	7	8	9	10	11	12	13
114	*Polygonum minus* Huds.	25	0.33	6	13	12	T	F	N	–	+	–
115	*Polygonum mite* Schrank	27	0.36	2	12	15	T	F	N	–	+	–
116	*Polygonum nodosum* Pers.	7	0.09	4	3	4	T	O	N	+	+	+
117	*Polygonum persicaria* L.	21	0.28	11	17	4	T	O	N	+	+	–
118	*Polygonum tomentosum* Schrank	5	0.07	4	5	0	T	O	N	+	+	–
119	*Potentilla erecta* (L.) Raeusch.	10	0.13	5	10	0	H	M	N	–	+	+
120	*Potentilla norvegica* L.	1	0.01	1	0	1	H,T	M	N	+	+	+
121	*Potentilla reptans* L.	370	4.93	9	335	35	H	O	N	+	+	–
122	*Prunella vulgaris* L.	14	0.09	3	14	0	H	M	N	–	+	+
123	*Ranunculus acris* L.	8	0.11	1	1	7	H	M	E	+	+	+
124	*Ranunculus lanuginosus* L.	8	0.11	7	1	7	H	F	E	+	+	+
125	*Ranunculus repens* L.	48	0.64	7	3	45	H	F	E	+	+	+
126	*Rorippa palustris* (L.) Besser	1	0.01	1	1	0	T,H	O	N	–	+	–
127	*Rubus idaeus* L.	286	3.81	13	149	137	P	F	F	–	+	+
128	*Rubus saxatilis* L.	1	0.01	1	0	1	H	F	F	–	+	+
129	*Rumex acetosa* L.	13	0.17	7	9	4	H	M	N	+	+	+
130	*Rumex acetosella* L.	85	1.03	19	75	10	C,H	O	N	+	+	+
131	*Rumex confertus* Willd.	2	0.03	2	2	0	H	M	N	+	+	+
132	*Rumex conglomeratus* Murray	2	0.03	2	2	0	H	M	N	+	+	–
133	*Rumex crispus* L.	2	0.03	2	2	0	H	M	N	+	–	–
134	*Rumex hydrolapathum* Huds.	2	0.03	2	2	0	H,C	M	N	+	–	+
135	*Rumex obtusifolius* L.	29	0.39	15	25	4	H	O	N	+	+	–
136	*Rumex sanguineus* L.	5	0.07	1	5	0	H	F	N	+	+	–
137	*Sagina procumbens* L.	138	1.84	7	138	0	A,T	O	N	+	+	–
138	*Scirpus sylvaticus* L.	1	0.01	1	0	1	C	M	E	–	+	+
139	*Scrophularia nodosa* L.	9	0.12	5	0	9	H	F	N	–	+	+
140	*Setaria pumila* (Poir.) Schult.	2	0.03	2	2	0	T	O	N	+	+	–
141	*Setaria viridis* (L.) P.Beauv.	6	0.08	5	6	0	T	O	N	+	+	–
142	*Sonchus arvensis* L.	1	0.01	1	1	0	C,H	O	A	+	–	+
143	*Spergula arvensis* L.	10	0.13	5	10	0	T	O	N	+	+	–
144	*Stachys sylvatica* L.	35	0.47	8	0	35	H	F	N	–	+	–
145	*Stellaria crassifolia* Ehrh.	1	0.01	1	0	1	H	F	N	–	+	–

1	2	3	4	5	6	7	8	9	10	11	12	13
146	*Stellaria graminea* L.	4	0.05	4	1	3	H	M	M	+	+	+
147	*Stellaria media* (L.) Vill.	44	0.59	14	31	13	T,H	O	N	+	+	+
148	*Stellaria nemorum* L.	2	0.03	1	2	0	H	F	N	–	+	+
149	*Stellaria uliginosa* Murray	1	0.01	1	0	1	H	F	N	–	+	–
150	*Succisa pratensis Moench*	5	0.07	1	5	0	H	M	E	–	+	–
151	*Taraxacum* sp.	3	0.04	3	3	0	NC	M	A	+	+	+
152	*Trifolium dubium* Sibth.	15	0.20	8	11	4	T	M	E	+	+	–
153	*Trifolium hybridum* L.	25	0.33	3	0	25	H	M	E	+	–	+
154	*Trifolium montanum* L.	3	0.04	3	1	2	H	M	E	+	+	+
155	*Trifolium pratense* L.	49	0.65	15	7	42	H	M	E	+	+	+
156	*Trifolium repens* L.	283	3.77	18	238	45	C,H	M	E	+	+	+
157	*Triticum aestivum* L.	3	0.04	2	3	0	T	O	E	+	+	–
158	*Urtica dioica* L.	6973	93.00	37	2478	4495	H	F	N	+	+	+
159	*Urtica urens* L.	1	0.01	1	1	0	T	O	N	–	+	–
160	*Veronica beccabunga* L.	3	0.04	2	3	0	C,A	M	N	–	+	–
161	*Veronica chamaedrys* L.	118	1.57	18	49	69	A	F	N	+	+	+
162	*Veronica hederifolia* L.	1	0.01	1	1	0	T	O	N	–	+	–
163	*Veronica longifolia* L.	19	0.25	3	3	16	H	M	N	+	+	–
164	*Veronica officinalis* L.	97	1.29	13	37	60	A	F	N	+	+	+
165	*Veronica persica* Poir.	4	0.05	1	4	0	T	O	N	–	+	–
166	*Veronica serpyllifolia* L.	66	0.88	10	47	19	H	O	N	+	+	–
167	*Vicia angustifolia* L.	1	0.01	1	1	0	T	O	N	+	–	–
168	*Vicia cracca* L.	3	0.04	2	3	0	H	M	N	+	–	+
169	*Vicia sepium* L.	1	0.01	1	0	1	H	M	N	+	–	+
170	*Vicia tetrasperma* (L.) Schreb.	2	0.03	2	2	0	T	O	N	–	+	+
171	*Viola odorata* L.	1	0.01	1	1	0	H	F	M	–	+	–
172	*Viola reichenbachiana* Jord. ex Boreau	14	0.19	4	10	6	H	F	M	+	+	+
173	*Viola tricolor* L.	2	0.03	1	2	0	T	O	M	+	–	+
	Nierozpoznane INNE	142	1.89									
	Nierozpoznane POACE	88	1.17									
	TOTAL	12392										

Raunkiær life forms (after Zarzycki K, Trzycińska-Tacik H, Różański W, Szeląg Z, Wołek J, Korzeniak U (2002) Ecological indicator values of vascular plants of Poland. W. Szafer Institute of Botany Polish Academy of Scieces, Kraków):
P – Phanerophytes
T – Therophytes
C – Cryptophytes
H – Hemicryptophytes
A – Chamaephytes
NC – not classified

Habitat groups (after Matuszkiewicz W (2001) Przewodnik do oznaczania zbiorowisk roślinnych Polski [Guidebook to determination of Polish plant associations]. Wydawnictwo Naukowe PWN, Warszawa):
F – forests (including forest open spaces and forest roads)
M – meadows, pastures, grasslands
O – others (segetal, ruderal, cultivated, other anthropogenic habitats, not native for the region of studies)
NC – not classified

Morfologic dispersal adaptations (based on observations in nature and on Cappers RTJ, Bekker RM, Jans JEA (2006) Digital seed atlas of the Netherlands. Groningen Archaeological Studies 4, Barkhuis Publishing, Eelde)
M – myrmecochory
E – epizoochory
A – anemochory
F – endozoochory (fleshy fruits)
N – not adapted morphologically
S – autochory
NC – not classified

Results

Seeds contained in 75 samples of bison faeces developed into 12 392 seedlings, classified as 173 plant species (Table 1). In several samples macromycetes and bryophytes were developed which were not identified as species. The total number of plants growing on the samples of bison faeces included 138 perennials, 25 annuals and 3 trees (Table 1). According to the Raunkiær classification 63.4% of plant species dispersed endozoochorically by bison were hemicryptophytes; 23.8% therophytes; 6.2% chamaephytes; 7.9% cryptophytes; 1.8% phanerophytes (Table 1). Seeds of over a half of the species endozoochorically dispersed by bison (56.1%) had no morphological adaptation for long-distance transport, and the seedlings of these species constituted 78.9% of all germinated seeds, 29% of the species germinating from samples had seeds with adaptation to epizoochoric dispersal, while species adapted to other types of dispersal represented a considerably lower proportion (Table 1). Only a few species of plants endozoochorically dispersed by bison were featured by relatively large seeds (over 3 mm long): *Avena sativa*, *Hordeum vulgare*, *Malus domestica*, *Millium effusum* and *Triticum aestivum*. Many species of plants dispersed by bison were anthropophytes introduced into Białowieża Forest and connected with agricultural cultivation and other transformed ecosystems. Species not natural for the flora of Białowieża Forest also germinated from the samples (e.g. *Oxalis dillenii*, *Poa chaixii*).

The diversity of plant species dispersed by free-roaming bison was lower

(102 species) in comparison to the diversity of plant species dispersed by bison living in captivity (140 species). The list of species recorded in samples taken from free-roaming bison was to a large extent covered by the list of species obtained from the samples taken from captive bison. Species characteristic for forest ecosystems predominated among plants developed from the samples of faeces taken from free-roaming bison, while in the samples taken from closed breeding centres species characteristic for anthropogenic ecosystems, natural and semi-natural meadows, pastures, grasslands etc. predominated (Table 2).

The vast majority of plant species (89.0%) maintaining the germination potential of their seeds after having passed through the bison's gastrointestinal tract were present in the bison's diet throughout the year. Samples taken during winter contained 61.3% of all plant species. A large number of plant species (19) were recorded in samples only in winter, of which 4 were forest species. The number of plant species characteristic for anthropogenic and meadow communities and dispersed endozoochorically by bison was higher in winter than in summer, while the number of forest species in samples taken in winter considerably decreased (Wilcoxon $z = 4.905$, $p << 0.001$). Such differences were found both in the samples taken from bison living in captivity and in the wild (Table 2).

Table 2. Proportion (in %) of plant species typical for forest, meadow (meadows, pastures, grasslands) and anthropogenic (ruderal, segetal, roadsides and trampled habitats) communities whose seedlings germinated from the samples of bison faeces collected in Białowieża Forest.

Groups of ecosystems	Total	Captivity			Wild		
		Winter	Summer	Total	Winter	Summer	Total
Forests	33,5	22,7	27,3	27,1	32,9	43,0	43,1
Grasslands	34,8	36,4	32,8	32,9	40,0	34,4	35,3
Anthropogenic	31,7	40,9	39,9	40,0	27,1	22,6	21,6
No. of species	173	88	128	140	70	93	102

Discussion

The European bison transports in its gastrointestinal tract seeds of 173 plant species with germinating potential, which constitutes 16% of all vascular plants recorded in Białowieża Forest. From this number 79 species (including one tree species) were not listed by Korochkina (1972) as a diet component of this herbivorous animal. After including the new findings the list of plants eaten by bison covers 454 species, of which 409 are herbaceous plants and 45 woody species (Table 1). Previous studies by other authors (Borowski and Kossak 1972; Gębczyńska and Krasińska 1972; Korochkina 1972; Gębczyńska et al. 1991) were based on direct observations of bison grazing on plants, or the analysis of plant remains contained in its stomach, and it was not always possible to determine grasses from the *Poaceae* family or sedges *Carex* sp.

The total number of plant species dispersed endozoochorically by bison is almost double the number provided in the literature for domestic cattle, horses or European wild ungulates (e.g. Bonn and Poschlod 1998; Cosyns et al. 2005; Cosyns and Hoffmann 2005; Eycott et al. 2007). Such differences may result from the diet-related preferences of these animals, or the survival of seeds in their gastrointestinal tract resulting from the physiology of the digestion process. The higher diversity of plant species dispersed endozoochorically by bison in comparison to other ruminants may also result from the high diversity of vascular plant species in Białowieża Forest. Comparative studies carried out in comparable environmental conditions are required to explain the importance of individual animal species making up the gilts of ungulates in Białowieża Forest for the dispersal of plant propagules, as well as the role of the entire population in this process.

The role of animals as a vector in the dispersal of plant propagules increases with increased animal mobility and the size of territory used by them. The European bison is an animal which plays a significant role in plant dispersal. The size of the average home range used by one animal in the snow-free period is between 69 km^2 (cows) and 70 km^2 (bulls) and 220 km^2 (herd of over twenty animals). Bison use their territory in a rotation system, foraging in a continuous slow movement and returning every few days to the same site. Occasionally, they can migrate very far in distance, from over twenty to several hundred kilometres (Krasińska and Krasiński 2004). Additionally, the bison also has a physiological predisposition typical for vectors of plant propagules: the time of food retention in the gastrointestinal tract exceeds 14 days (Gill 1967), rumen volume can exceed 100 litres (Pytel 1969), and one litre of rumen gorge can contain from over twenty to several thousand seeds (Jaroszewicz unpubl.)

The proportion of non-forest plant species (72.9% of plant species dispersed endozoochorically by bison in captivity and 56.9% in the wild) is unexpectedly high in comparison with data provided in literature mainly referring to the use of forest ecosystems on the Polish side of Białowieża Forest by the European bison. During the snow-free season this is probably the result of a deliberate search by bison for even small gaps in the forest and grazing on plants growing there. Similar results were demonstrated in studies by Gill and Beardall (2001), Heinken et al. (2002), Myers et al. (2004) and von Oheimb et al. (2005) for other ungulates naturally found in forest ecosystems: red deer *Cervus elaphus* L. in Europe, and white-tailed deer *Odocoileus virginianus* Zimm. in North America. During the snowy season and in the case of captive bison the seeds of many non-forest plants are derived from hay used for the supplementary feeding of animals.

The large number of non-forest species dispersed endozoochorically by the European bison also contradicts published data referring to its diet (Borowski and Kossak 1972; Krasiński and Krasińska 2004). From among four tree and shrub species preferred by bison and listed by Borowski and Kossak (1972) only raspberry seeds (*Rubus idaeus)* are dispersed endozoochorically by this ruminant. The largest number of seeds contained in bison faeces developed into seedlings of birch *Betula* sp., whose seeds may be accidentally grazed together with other plants growing on the forest floor or with hay. Besides that, from among seven herbaceous plant species preferred by bison and indicated by Borowski and Kossak (1972) the seedlings of only four species were recorded in this study: an insignificant number of wood-sedge *Carex sylvatica*, hairy sedge *C. hirta* and woolly buttercap *Ranunculus lanuginosus*, and an abundant number of stinging nettle *Urtica dioica*. In this case the divergence may result not only from the supplementary feeding of bison with hay obtained from non-forest ecosystems, but also from different adaptations demonstrated by individual plant species to endozoochoric dispersal (attractiveness of fruit and its location above plant parts attractive for grazing, survival of seeds in the gastrointestinal tract and many other traits). The preference of animals for plants at younger phenological stages, prior to seed development, may also be an important factor.

Bison endozoochorically disseminate propagules of many plant species which do not naturally occur in the forest ecosystems of Białowieża Forest. Many weeds (e.g. *Oxalis dillenii*, *Setaria* sp., *Echinochloa crus-gali*), or grass species typical for cultivation (*Poa subcaerulea, Poa angustifolia*) are most likely derived from hay, a hypothesis which is supported by the fact that a large number of these species were recorded exclusively in the samples taken in winter (Table 1). *Poa chaixii*, a grass formerly found only in Palace Park in Białowieża Forest, is a particular example (Sokołowski, 1995). The presence of the seeds of this grass in bison faeces is most likely connected with the supplementary feeding of bison with hay prepared in Palace Park.

The presence of seeds in bison faeces does not necessarily result in the successful colonization of new ecosystems. Under natural conditions many seeds disseminated endozoochorically are foraged by granivores. The majority of seeds do not germinate instantly, but become a part of the soil seed bank (Willems and Huijsmans 1994; Pakeman et al. 1998; Dai 2000). However, a large number of seeds are able to germinate, develop into plants and produce seeds, even in habitats offering significantly different conditions from the ecological optimum for particular species (Jaroszewicz et al. 2008).

Conclusions

1. The European bison plays a significant role in the dispersal of plants, especially of non-forest species. This fact confirms the role of the main factor responsible for the maintenance of the biodiversity of small-size open spaces

distributed in island systems in large forest complexes, which has been assigned to herbivores by many authors (e.g. Janzen 1984; Bonn and Poschlod 1998; Eycott et al. 2007).

2. The bison's particularly diversified diet, including over 40% of the vascular plant species recorded in Białowieża Forest, makes this animal potentially highly significant for the preservation of heliophilous species populations in this forest complex. The endozoochoric dissemination of plant propagules by bison can facilitate plant 'escape' from overgrowing gaps to newly created open spaces.

3. The supplementary feeding of bison in winter increases the diversity of plant species disseminated by these animals, although it can also introduce the risk of invasion by many species alien to Białowieża Forest and intensify the synanthropisation of its flora.

4. Owing to the above fact the origin and quality of hay used for supplementary animal feeding has become a fundamental problem: it should be derived from semi-natural meadows located in Białowieża Forest or in its direct vicinity.

5. Hay used for bison feed should also be obtained from the earliest possible harvest, when it contains a relatively low number of seeds, to optimally reduce the risk of invasion by alien species.

Acknowledgements:

We would like to thank the Management of the Białowieża National Park for permission to collect samples from the Bison Breeding Centres in Białowieża. We would also like to thank Ms Alicja Wiktoruk for her technical help in the experimental part of the study. The scientific work was financed from the budget of the Ministry of Science and Higher Education – grant No. 2 P04F 035 30.

References

Bakker E. S., Olff H. 2003. The impact of different-sized herbivores on recruitment opportunities for subordinate herbs in grasslands. J. Veg. Sci. 14: 465–474.

Bonn S., Poschlod P. 1998. Ausbreitungsbiologie der Pflanzen Mitteleuropas. Quelle and Meyer Verlag, Wiesbaden.

Borowski S., Kossak S. 1972. The natural food preferences of the European bison in seasons free of snow cover. Acta theriol. 17: 151–169.

Campbell J. E., Gibson D. J. 2001. The effect of seeds of exotic species transported via horse dung on vegetation along trail corridors. Plant Ecol. 157: 23–35.

Cappers R. T. J., Bekker R. M., Jans J. E. A. 2006. Digital seed atlas of the Netherlands. Groningen Archaeological Studies 4, Barkhuis Publishing, Eelde.

Constible J. M., Sweitzer R. A., Van Vuren D. H., Schuyler P. T., Knapp, D. A. 2005. Dispersal of non-native plants by introduced bison in an island ecosystem. Biol. Invasions 7: 699–709.

Cosyns E. 2004. Ungulate seed dispersal. Aspects of endozoochory in a seminatural landscape. Institute of Nature Conservation, Brussels.

Cosyns E., Delporte A., Lens L., Hoffmann M. 2005. Germination success of temperate grassland species after passage through ungulate and rabbit guts. J. Ecol. 93: 353–361.

Cosyns E., Hoffmann M. 2005. Horse dung germinable seed content in relation to plant species abundance, diet composition and seed characteristics. Basic Appl. Ecol. 6: 11–24.
Dai X. 2000. Impact of cattle dung deposition on the distribution pattern of plant species in an alvar limestone grassland. J. Veg. Sci. 11: 715–724.
Eycott A. E., Watkinson A. R., Hamami M. R., Dolman P. M. 2007. The dispersal of vascular plants in a forest mosaic by a guild of mammalian herbivores. Oecologia 154: 107–118.
Faliński J. B. 1986. Vegetation dynamics in Temperate Forests (Ecological Studies in Białowieża Forest). W. Junk Publishers, Dordrecht.
Faliński J. B. 2003. The Białowieża forest, a relict ecosystem in Poland and Belarus. Biodiversity – Journal of Life on Earth 4(1): 18–27.
Fischer S. F., Poschlod P., Beinlich B. 1996. Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. J. Appl. Ecol. 33: 1206–1222.
Gębczyńska Z., Gębczyński M., Martynowicz E. 1991. Food eaten by free-living European bison in Białowieża Forest. Acta theriol. 36: 307–313.
Gębczyńska Z., Krasińska M. 1972. Food preferences and requirements of the European bison. Acta theriol. 17: 105–117.
Gill J. 1967. The physiological properties of the European Bison. Acta theriol. 12: 349–360.
Gill R. M. A., Beardall V. 2001. The impact of deer on woodlands: The effects of browsing and seed dispersal on vegetation structure and composition. Forestry 74: 209–218.
Gutowski J. M., Jaroszewicz B. (Eds) 2001. Catalogue of the fauna of Białowieża Primeval Forest. Instytut Badawczy Leśnictwa, Warszawa.
Heinken T., Hanspach H., Raudnitschka D., Schaumann F. 2002. Dispersal of vascular plants by four species of wild mammals in a deciduous forest in NE Germany. Phytocoenologia 32: 627–643.
Janzen D. H. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. Am. Nat. 123: 338–353.
Jaroszewicz B. 2008. Po co żubr roślinom Puszczy Knyszyńskiej? [in:] A. Górniak, B. Poskrobko (edit.) Park Krajobrazowy Puszczy Knyszyńskiej w systemie ochrony przyrody i edukacji środowiskowej. Conference materials, 86–93.
Jaroszewicz B., Pirożnikow E., Sagehorn R. 2008. The European bison as seed dispersers: the effect on the species composition of a disturbed pine forest community. Botany 86: 475–484.
Korochkina L. N. 1972. Travyanistaya rastitelnost' v pitaniu zubrov Belovezhskoj Pushchi. Belovezhskaya Pushcha, Issledovanija 3: 204–221.
Krasińska M., Krasiński Z. A. 2004. Żubr. Monografia przyrodnicza. Agencja Fotograficzno--Wydawnicza Hajstra, Warszawa.
Matuszkiewicz W. 2001. Przewodnik do oznaczania zbiorowisk roślinnych Polski. Wydawnictwo Naukowe PWN, Warszawa.
Mouissie A. M. 2004. Seed dispersal by large herbivores. Implications for the restoration of plant biodiversity. Van Denderen, Groningen.
Myers J. A., Vellend. M., Gardescu S., Marks P. L. 2004. Seed dispersal by white-tailed deer: Implications for long-distance dispersal, invasion, and migration of plants in eastern North America. Oecologia 139: 35–44.
von Oheimb G., Schmidt M., Kriebitzsch W. U., Ellenberg H. 2005. Dispersal of vascular plants by game in northern Germany. Part II: Red deer (*Cervus elaphus*). Eur. J. Forest Res. 124: 55–65.
Olff H., Ritchie M. 1998. Effects of herbivores on grassland plant diversity. Trends Ecol. Evol. 13: 261–265.
Pakeman R. J., Attwood J. P., Engelen J. 1998. Sources of plants colonizing experimentally disturbed patches in an acidic grassland in eastern England. J. Ecol. 86(6): 1032–1041.
Pakeman R. J., Digneffe G., Small J. L. 2002. Ecological correlates of endozoochory by herbivores. Funct. Ecol. 16: 296–304.
Pucek Z., Belousova I. P., Krasińska M., Krasiński Z. A., Olech W. 2004. European bison. Status Survey and Conservation Action Plan. IUCN/SSC Bison Specialist Group, Gland and Cambridge.

Pytel S. M. 1969. Morphology of digestive tract of the European bison. Acta theriol. 14: 349–402.
Sokołowski A. 1995. Atlas flory roślin naczyniowych Puszczy Białowieskiej. Białowieski Park Narodowy, Białowieża.
Thompson K., Bakker J. P., Bekker R. M. 1997. Soil Seed Banks of NW Europe: Methodology, Density and Longevity. Cambridge University Press, Cambridge.
Tomiałojć L., Wesołowski T. 2005. The avifauna of the Białowieża Forest: a window into the past. British Birds 98: 174–193.
Welch D. 1985. Studies on the grazing of heather moorland in north-east Scotland. IV. Seed dispersal and plant establishment in dung. J. Appl. Ecol. 22: 416–472.
Willems J. H., Huijsmans K. G. A. 1994. Vertical seed dispersal by earthworms: a quantitative approach. Ecography 17: 124–130.
Wróblewski K. 1927. Żubr Puszczy Białowieskiej. Wydawnictwo Polskie. Poznań.
Zarzycki K., Trzcińska-Tacik H., Różański W., Szeląg Z., Wołek J., Korzeniak U. 2002. Ecological indicator values of vascular plants of Poland. W. Szafer Institute of Botany Polish Academy of Sciences, Kraków.
Zobel M., van der Maarel E., Dupré C. 1998. Species pool: the concept, its determination and significance for community restoration. Appl. Veg. Sci. 1: 55–66.