Do wild ungulates contribute to the dispersal of vascular plants in central European forests by epizoochory? A case study in NE Germany

Trägt Schalenwild durch Epizoochorie zur Ausbreitung von Gefäßpflanzen in mitteleuropäischen Wäldern bei? Eine Fallstudie aus Nordostdeutschland

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Zusammenfassung

Die Ausbreitung von Gefäßpflanzen-Diasporen (Samen und Früchte) durch äußerliche Anhaftung („Epizoochorie“) an Rehen und Wildschweinen, den beiden häufigsten Schalenwild-Arten in Mitteleuropa, wurde im 6,5 km^2 großen Forst Brieselang bei Berlin (Bundesland Brandenburg) untersucht, in dem mesophile Laubwälder vorherrschen. Dazu wurden die Felle und Hufe von 25 geschossenen Rehen und neun Wildschweinen ausgekämmt und die Diasporen anschließend bestimmt. Die Ergebnisse wurden mit der Waldvegetation verglichen. Während Wildschweine große Mengen verschiedener Diasporentypen transportierten, war die Bedeutung von Rehen für die Ausbreitung von Pflanzen auf Grund des glatten Fells und der im Vergleich zum Wildschwein unterschiedlichen Verhaltensweisen wesentlich geringer. Insgesamt wurden 55 Phanerogamenarten epizoochor transportiert. Da nur ein kleiner Teil der ausgebreiteten Pflanzen Waldhabitate bevorzugt, war das Offenland eine mindestens ebenso wichtige Quelle anhaftender Diasporen wie die Waldvegetation. Die meisten Waldpflanzenarten wurden nicht ausgebreitet; insbesondere solche Arten, die ausschließlich in Wäldern wachsen, wurden nicht nachgewiesen. Viele Pflanzenarten sind – vermutlich auf Grund ihrer Diasporenmorphologie – weitgehend vom Transport ausgeschlossen, obwohl sie sehr häufig in der Krautschicht des untersuchten Waldes vorkommen. Daher ist Schalenwild in der Agrarlandschaft Mitteleuropas vermutlich vor allem für die Ausbreitung von Ruderal-, Segetal- und Grünlandpflanzen von Bedeutung. Die Ausbreitung einiger Pflanzenarten der Krautschicht in norddeutschen Wäldern z.B. *Agrostis capillaris*, *Brachypodium sylvaticum*, *Deschampsia flexuosa*, *Galium aparine* und *Urtica dioica*, könnte jedoch wesentlich auf Schalenwild zurückgehen. Obwohl Großsäuger insgesamt ein wichtiger Vektor für die Fernausbreitung von Pflanzen sind, zeigt unsere Studie, dass die meisten charakteristischen Waldbodenpflanzen mesophiler Laubwälder kaum ausgebreitet werden, also nur ein geringes epizoochores Ausbreitungspotenzial aufweisen. Die Bedeutung der Ergebnisse für den Waldnaturschutz und den Waldbau wird diskutiert.

Schlüsselwörter: Diasporenmorphologie, Epizoochorie, Brandenburg, Reh, Waldbodenpflanzen, Wildschwein

Summary

The external dispersal (“epizoochory”) of vascular plant diaspores (seeds and fruits) by roe deer and wild boar, i.e. the most common wild large mammals with a large home range in central Europe, was investigated in a 6.5-km^2 forest area in NE Germany dominated by mesic deciduous forests. The study involved brushing out the diaspores from the coats and hooves of 25 shot roe deer and nine wild boar. The results were compared with the forest vegetation of the study area. Whilst wild boar transported large amounts of various diaspores in the coat, the significance of roe deer for epizoochory was low due to their sleek fur and different behaviour compared to wild boar. Altogether, 55 vascular plant species were transported externally. Since only a limited number of seeds came from woodland habitats, the open landscape was at least as important as a source of attached seeds as the forest vegetation. Thus, most plant species occurring in the studied forest area, especially characteristic woodland herbs, showed no adaptations to epizoochorous dispersal, although being very abundant in the herb layer. We conclude that hoofed game play a particular role concerning the dispersal of ruderal and grassland species in the agricultural landscape of central Europe. However, the actual spread of some herb species in forests of northern Germany, e.g. *Agrostis capillaris*, *Brachypodium sylvaticum*, *Deschampsia flexuosa*, *Galium aparine* and *Urtica dioica*, may be mainly facilitated by wild ungulates. Though dispersal by large mammals is an important mechanism for long-distance dispersal of plants in general, our results suggest that most of the characteristic herb species of mesic deciduous forests have only low epizoochorous dispersal potentials. The implications for nature conservation and silviculture are discussed.

Key words: diaspore morphology, epizoochory, forest plant species, NE Germany, roe deer, wild boar

1 Introduction

In recent years field studies on the dispersal of plant diaspores by animals have received much attention (for studies from central Europe see e.g. KOLLMANN 1994, FISCHER et al. 1996, HEINKEN 2000). This interest has occurred as especially long-distance dispersal is essential both for the long-term viability of plant populations by maintaining migration between isolated habitats (e.g. POSCHLOD 1996), and for the colonization of new potential habitats which are nowadays created as a result of the rapid change in land use (e.g. POSCHLOD et al. 1996).

Today, in the lowlands of central Europe, isolated patches of near-natural deciduous forests are embedded in a matrix of intensively managed farmland, roads and settlements, and many afforestations are created on formerly cultivated land (cf. REIF 2001). However, in locations supporting mesic deciduous forests (Fagetalia sylvaticae), afforestations often lack several characteristic species of the understorey for decades or sometimes for even longer than 100 years, especially on isolated stands (e.g. WULF 1997). The lack of an obvious, efficient means of long-distance dispersal of many forest floor species (e.g. MÜLLER-SCHNEIDER 1986) is regarded as being the most important reason for this (e.g. WULF 1997). Moreover, in the last decades existing forested areas have been affected by atmospheric depositions, fertilization, and changing silvicultural practices (e.g. SCHMIDT 1999, RÖDER et al. 1996, FISCHER 1999a) which resulted in significant changes of habitat quality and forest vegetation. For the future, vegetational changes are expected by the projected transformation of conifer monocultures into multi-species near-natural forests (e.g. HEINZEL and PETERS 2001) and as a consequence of climatic changes (e.g. HOFMANN 1995).

To understand and predict the development of plant populations in both existing and newly created forest patches, field research into long-distance dispersal of forest plant species is required. Epizoochory (external dispersal) and endozoochory (internal dispersal) by wild large mammals are supposedly very important mechanisms to facilitate such long-distance dispersal (BONN and POSCHLOD 1998). While both endo- and epizoochorous dispersal by livestock on grassland vegetation has been extensively studied by FISCHER et al. (1995, 1996) and STENDER et al. (1997), data concerning dispersal by wild mammals in central European forests is, to date, largely lacking. Until now, the dispersal potential of forest plant species was nearly exclusively derived from their diaspore morphology (e.g. MÜLLER-SCHNEIDER 1986, WULF 1997), and information on actual pathways of dispersal is limited (BONN and POSCHLOD 1998). Recently, HEINKEN et al. (2001a) investigated endozoochorous dispersal by hares, roe deer, fallow deer and wild boar. Epizoochorous dispersal of vascular plants by wild boar was only studied thoroughly by MROTZEK et al. (1999). HEINKEN et al. (2001b) presented data concerning bryophyte fragments transported by roe deer and wild boar. Both studies emphasized that especially wild boar may have an important role for the dispersal of various plant species.

In the present study, epizoochory of vascular plants by roe deer and wild boar, i.e. the most common wild mammals with a large active range, are investigated in a forest area in Brandenburg (NE Germany). We compared the results of two different dispersal vectors with the forest vegetation of the study area, and aim to assess the role of mammals with a large home range for dispersal in deciduous forests. The following questions are addressed:

1) Which vascular plant species and quantities of diaspores are dispersed externally in species-rich deciduous forests by roe deer and wild boar?
2) Which factors influence the diaspore´s attachment to the animals?
3) Do the investigated mammal species contribute to long-distance dispersal of forest species?
4) What are the consequences for silviculture and nature conservation?

2 Materials and Methods

2.1 Study area

The study was carried out in the “Brieselang” forest (Oberförsterei Finkenkrug), in the state of Brandenburg, 10 km WNW. of the city boundary of Berlin/Germany. Mean annual precipitation is about 500 mm; mean temperature in July is 17.9 °C, mean temperature in January –0.8 °C. The forest area is ancient woodland and encompasses 6.5 km^2. It is surrounded predominantly by agricultural land and settlements; neighboring forest patches are located at a considerable distance, or separated by roads or railways. Geological substrate of the Brieselang forest is valley-bottom sand from the Weichsel glacial. It is mainly characterized by relatively moist, mesotrophic and eutrophic soils, but small patches are slightly dry with acidic and more nutrient-poor soils. Mixed oak-hornbeam forest (Stellario holosteae-Carpinetum) with *Quercus robur*, *Carpinus betulus*, *Tilia cordata*, *Fraxinus excelsior* and *Betula pendula* prevails. The species-rich herb layer is dominated by spring-flowering Querco-Fagetea- and Fagetalia-species like *Anemone nemorosa*, *Stellaria holostea*, *Milium effusum*, *Ranunculus ficaria* and *Lamiastrum galeobdolon*. Acidic mixed oak forest (Betulo-Quercetum roboris) with *Quercus robur* and *Pinus sylvestris* is found in nutrient-poor areas. Here, *Deschampsia flexu-*

osa, Convallaria majalis, Maianthemum bifolium, Vaccinium myrtillus and *Pteridium aquilinum* prevail in the herb layer. Dense pine as well as some poplar plantations are interspersed with near-natural deciduous forests. In total, the growing stock of the Brieselang forest is 34% oak, 13% birch, 10% high-value hard wood species, 8% poplar and 19% pine. Additionally, there are small open places such as waysides, fields and clear-cuts within the forest area.

2.2 Survey of forest vegetation

To reconstruct the source of epizoochorous diaspores and to assess the role of dispersal by roe deer and wild boar in the studied forest, we recorded the vegetation of the Brieselang area in 76 sample plots (20 x 20 m), which were evenly distributed within the forest stands (two each in the 38 forest compartments). In each plot the cover of all the vascular plant species was estimated using the cover-abundance scale according to FREY and LÖSCH (1998, p. 41). Additionally, presence of fruits was checked. For all sample plots, the mean cover of each species in relation to that of all species present was calculated (cf. FREY and LÖSCH 1998, p. 75). The tree and shrub, and herb layers were calculated separately. Only fruiting species were considered. Tree and shrub species were only taken into account in the layers where fruits were present. Nomenclature of plant species follows WISSKIRCHEN and HAEUPLER (1998).

2.3 Assessing epizoochorous dispersal

Since it was not possible to study live wild animals, we investigated roe deer (*Capreolus capreolus* L.) and wild boar (*Sus scrofa* L.) shot in the Brieselang forest from 02 July through 09 November 1998. Killed animals (25 roe deer and nine wild boar) were lifted on a tarpaulin and disembowelled by the hunters within the forest. The coats were then thoroughly brushed out with a louse comb (space between the teeth 0.3 mm) in a cold-storage depot to remove all adhering plant structures. Additionally, the hooves were brushed out with a toothbrush. As the procedure took place after the animals had been disembowelled, plant structures adhering to the belly region may have been recorded incompletely. Four big wild boar (>30 kg) which were dragged across the forest floor before transportation might have lost or gained epizoochorous diaspores after death. Diaspores in the samples were then determined after BERTSCH (1941), BROUWER and STÄHLIN (1975), as well as a diaspore herbarium, and counted. The Mann-Whitney U-test was performed to compare the number of diaspores and plant species transported by roe deer and wild boar.

2.4 Comparison of dispersed diaspores with the forest vegetation

To determine whether morphological diaspore characters thought to facilitate specific dispersal modes were associated with a high diaspore abundance on the dispersal vectors, all diaspores (seeds, fruits, or spores) of vascular plants, both dispersed by the investigated animals and fruiting in the sample plots of the study area, were classified according to their dispersal-relevant properties:

- hooked: diaspores with hooked or barbed appendages (adapted to epizoochory),
- bristly: diaspores with markedly developed, straight appendages (adapted to epizoochory),
- winged: flat diaspores or diaspores with wing-like structures enabling flying,
- with tuft of hair: diaspores with long hairs enabling flying,
- big nut: heavy nuts rich in nutrients adapted to dyszoochory,
- with fruit pulp: fleshy diaspores (adapted to endozoochory),
- with elaiosome: diaspores adapted to myrmecochory (dispersal by ants),
- no features: diaspores without characteristics furthering dispersal. For these diaspores, the weight was also determined according to MÜLLER-SCHNEIDER (1986) and own measurements.

Regional habitat preference in the north-eastern German lowlands (according to JÄGER and WERNER 2002 and own observations) was classified for all plant species dispersed and inhabiting the Brieselang forest:

- forests: species largely restricted to forests,
- forests and open landscape: species that occur both in forests and in the open landscape,
- open landscape: species restricted to the open landscape (trampled areas, ruderal vegetation, arable land, grasslands, clear-cuts).

Furthermore, we determined whether plant species inhabiting the Brieselang forests are associated with ancient forests, i.e. woodland areas existing at least for 150 years, in the northern German lowlands according to WULF (1997). Additions for acid-soil forest species were made with reference to HEINKEN (1998). Finally, for these plant species we determined whether or not they showed a significant increase in abundance in northern German lowland forests and adjoining regions during the last decades (with reference to SCHMIDT 1999, AMARELL 2000 and ZERBE et al. 2000).

The biological significance of the plant species groups defined afore both in the forest vegetation and on the dispersal vectors was assessed by setting up group spectra. For the forest vegetation, this was calculated using the mean group quantity fraction (MGF), which is defined as the sum of mean cover portions of all species belonging to a respective group (cf. FREY and LÖSCH 1998, p. 75), the tree and shrub, and the herb layer being handled separately. For the dispersal vectors, diaspore abundance throughout the year was used. "Dispersal rates" were then calculated to evaluate the preference or exclusion of certain plant species groups of the forest understorey in dispersal. These are defined by the ratio between the diaspore proportion of the respective group on the dispersal vectors (Σ roe deer + Σ wild boar) and the proportion of their MGF in the forest vegetation. Preference or discrimination of forest herb layer species for dispersal according to the afore-mentioned species groups was also χ^2-tested, comparing the number of dispersed species with the total number of species in the 76 sample plots.

3 Results

3.1 Epizoochorous diaspores

We detected seeds or fruits of vascular plants on all investigated roe deer and wild boar individuals. On average, roe deer transported only 16 diaspores externally, while wild boar transported about twenty times the number of diaspores (Tab. 1). Although the diaspore number varied within a wide range (roe deer 2-54, wild boar 26-1626), the difference was highly significant (Mann-Whitney U-test; df = 1, $n_1 = 25$, $n_2 = 9$, U = 6.5, $p<0.001$). Also the mean number of plant species transported by individual wild boar was significantly higher than in deer (Mann-Whitney U-test; df = 1, U = 31, $p<0.001$). Seeds or fruits were carried both on the coats and the hooves: Diaspores were attached to the coats of 24 roe deer (96%) and nine wild boar (100%), and to the hooves of 15 roe deer (60%) and 8 wild boar (89%). However, most seeds and fruits were transported in the coats (roe deer: 66%, wild boar: 93%; Tab. 1). Though the mean number of diaspores attached to the hooves of wild boar was also higher than that of roe deer, the difference is not significant (Mann-Whitney U-test; df = 1, U = 72, $p>0.5$).

Table 1. Epizoochorous dispersal of vascular plant diaspores by roe deer and wild boar in the Brieselang forest, and characterization of the animals acting as dispersal vectors.

Tabelle 1. Epizoochore Ausbreitung von Gefäßpflanzen-Diasporen durch Reh und Wildschwein im Forst Brieselang, und Charakterisierung der Tiere als Ausbreitungsvektoren.

Animal species	Roe deer	Wild boar
Coat structure	sleek, dense hair	long bristles, thick undercoat, with dried mud crust
Home range [ha]	2-24 [1)]	100-700 [2)]
Minimum territory diameter [m]	160-550 [3)]	1100-3000 [3)]
Population density [individuals per km^2] (estimated)	~8-10 [4)]	~3-8 [4)]
Number of individuals investigated for epizoochory	25	9
Number of individuals with attached diaspores (total/coats/hooves)	25/24/15	9/9/8
Mean number of transported diaspores per individual	16.2	308.2 ***
- Coats	10.7	285.4 ***
- Hooves	5.5	22.8 ns
Mean species number of transported diaspores per individual	4.6	9.1 ***

References: [1)] TUFTO et al. (1996), SANJOSE and LOVARI (1998); [2)] HAHN and KECH (1995); [3)] calculated from [1)] and [2)]; [4)] SCHWIDETZKY (pers. comm.). ***: $p<0.001$; ns: $p>0.05$ (Mann-Whitney U-test).

Contrary to the diaspore numbers, the spectra of frequent epizoochorous plants on both animal species were rather similar (Tab. 2), including *Betula pendula/pubescens*, *Poa trivialis/pratensis*, *Poa nemoralis* and *Urtica dioica* (>10% of the total diaspore number). However, *Poa nemoralis* was only detected on one wild boar. Altogether, these four species make up 61% of the total diaspore number. Further abundant adhesive seed or fruit species (>1%) were *Deschampsia flexuosa*, *Conyza canadensis*, *Agrostis capillaris*, *Arctium nemorosum*, *Bromus sterilis*, *Geum urbanum*, *Deschampsia cespitosa*, *Poa annua* and *Polygonum aviculare*, their proportion being 33% of the total diaspore number. Thus, the proportion of the 42 remaining species is only 6%, while many species are only represented by a single diaspore. Altogether, 55 vascular plant species were transported epizoochorically (Tab. 2). Twenty species were dispersed by both animal species, 18 by roe deer only and 17 exclusively by wild boar. Though all roe deer and wild boar were shot within the forest area, 60% of the plant species detected on the animals are species which do not occur in the forest stands but are restricted to arable land, grasslands, trampled areas, ruderal vegetation, or clear-cuts (see Tab. 2). Only nine dispersed species occur ± exclusively in forests. Besides *Betula pendula/pubescens* and *Poa nemoralis*, the most abundant forest species are *Brachypodium sylvaticum*, *Circaea lutetiana* and *Milium effusum*.

Table 2. Vascular plant diaspores recovered from the coats and hooves of 25 roe deer (*Capreolus capreolus*) and 9 wild boar (*Sus scrofa*) from the Brieselang forest, their diaspore morphology and habitat preference.

Tabelle 2. Gefäßpflanzen-Diasporen aus Fell und Hufen von Rehen (*Capreolus capreolus*) und Wildschweinen (*Sus scrofa*) aus dem Forst Brieselang, ihre Diasporenmorphologie und Habitatbindung.

	Diaspore morphology	Habitat preference	Roe deer (n=25)		Wild boar (n=9)		Total (n=34)
			Proportion [%]	Coats/ hooves	Proportion [%]	Coats/ hooves	Proportion [%]
Total number of diaspores			406	268/138	2774	2569/205	3180
Total species number			38	33/15	37	37/8	55
Acer pseudoplatanus	winged	I	0.2	+/–			<0.1
Achillea millefolium	winged	¡			0.1	+/–	0.1
Agrostis cf. *viminalis*	bristly	¡			0.4	+/–	0.3
Agrostis capillaris	≤1 mg	¤	13.1	+/+	4.0	+/+	5.2
Alnus glutinosa	winged	I	0.2	–/+	<0.1	+/–	0.1
Apera spica-venti	bristly	¡	0.2	+/–	0.1	+/–	0.1
Arctium nemorosum	hooked	¤			5.9	+/–	5.2
Arenaria serpyllifolia	≤1 mg	¡	2.0	–/+			0.3
Betula pendula/pubescens	winged	I	18.2	+/+	21.8	+/+	21.3
Brachypodium sylvaticum	bristly	I	1.0	+/–	0.2	+/–	0.3
Bromus sterilis	bristly	¡			5.6	+/–	4.8
Bromus tectorum	bristly	¡			<0.1	+/–	<0.1
Calamagrostis epigejos	hair	¤	0.5	+/–	0.6	+/–	0.6
Capsella bursa-pastoris	≤1 mg	¡	1.7	+/–			0.2
Carex pallescens	>1 mg	¡			<0.1	+/–	<0.1
Carex remota	≤1 mg	I			<0.1	+/–	<0.1
Cerastium holosteoides	≤1 mg	¡	0.2	+/+			0.1
Chenopodium album	>1 mg	¡	0.5	+/–			0.1
Circaea lutetiana	hooked	I	1.7	+/–			0.2
Conyza canadensis	hair	¡	5.7	+/–	5.2	+/+	5.3
Crepis tectorum	hair	¡	0.2	+/–			<0.1
Dactylis glomerata agg.	bristly	¤	2.7	+/+	<0.1	+/–	0.4
Deschampsia cespitosa	bristly	¤	3.2	+/+	1.3	+/+	1.6
Deschampsia flexuosa	bristly	¤	1.5	+/+	6.8	+/–	6.1
Descurainia sophia	≤1 mg	¡	0.2	+/–			<0.1
Erysimum cheiranthoides	≤1 mg	¡	0.2	+/–			<0.1
Festuca ovina agg.	bristly	¤			<0.1	+/–	<0.1
Galium aparine	hooked	¤	2.7	+/–	0.4	+/–	0.7
Geranium pusillum	bristly	¡			<0.1	+/–	<0.1
Geum urbanum	hooked	¤	14.3	+/–	0.1	+/–	1.9

Helictotrichon pubescens	bristly	¡			0.1	+/–	0.1
Holcus lanatus	bristly	¡			0.1	+/–	0.1
Hypericum perforatum	≤1 mg	¡	0.5	+/–			0.1
Juncus effusus	≤1 mg	¤	0.5	–/+			0.1
Leontodon autumnalis	hair	¡	1.0	+/–			0.1
Milium effusum	>1 mg	l			0.1	+/–	0.1
Molinia caerulea	≤ 1 mg	¤	0.2	+/–	0.4	+/–	0.4
Oxalis acetosella	>1 mg	l			<0.1	+/–	<0.1
Persicaria dubia	>1 mg	¡	1.0	+/–	<0.1	+/–	0.2
Persicaria maculosa	>1 mg	¡	0.5	+/–			0.1
Persicaria minor	>1 mg	¡	2.5	+/+	0.1	+/–	0.4
Phleum pratense	bristly	¡			<0.1	+/–	<0.1
Plantago major	≤1 mg	¡	1.0	+/–			0.1
Poa annua	bristly	¡	3.7	+/+	1.7	+/–	1.9
Poa nemoralis	bristly	l			15.9	+/+	13.9
Poa pratensis/trivialis	bristly	¤	3.5	+/–	17.3	+/+	15.5
Polygonum aviculare agg.	>1 mg	¡	3.2	+/+	0.7	+/+	1.0
Rumex thyrsiflorus	winged	¡	0.2	+/–			<0.1
Sagina procumbens	≤1 mg	¡	3.0	–/+			0.4
Setaria cf. *viridis*	≤1 mg	¡	0.2	–/+	<0.1	+/–	0.1
Spergula arvensis	≤ 1 mg	¡			<0.1	+/–	<0.1
Stellaria alsine	≤1 mg	¤	0.5	+/–			0.1
Trifolium arvense	hair	¡	0.2	+/–			<0.1
Tripleurospermum perforatum	≤1 mg	¡			<0.1	+/–	<0.1
Urtica dioica	bristly	¤	7.6	+/+	10.6	+/+	10.2

Diaspore morphology: bristly: with straight appendages; hair: with long hairs enabling flight; hooked: with hooked or barbed appendages; winged: flat or with wing-like structures enabling flight; ≤1 mg: without characteristics furthering dispersal, diaspore weight ≤1 mg; >1 mg: without characteristics furthering dispersal, diaspore weight >1mg.
Regional habitat preference: l Forest species, ¤ Forest and open landscape species, ¡ Open landscape species.

3.2 Comparison of seed dispersal and forest vegetation

Diaspore features of the epizoochorous plant species were compared with the frequency of plants in the study area (Fig. 1). About 40% (roe deer) and 65% (wild boar), respectively, of the epizoochorous diaspores belong to diaspore types which are apparently adapted to attachment. Of these, hooked diaspores (*Arctium nemorosum*, *Geum urbanum*, *Galium aparine* and *Circaea lutetiana*, see Tab. 2) were of minor importance compared to bristly ones (*Poa* spp., *Urtica dioica*, *Deschampsia* spp., *Bromus sterilis* etc.). However, considerable amounts of winged diaspores (especially *Betula* sp.), diaspores with a tuft of hair (especially *Conyza canadensis*) and those without any features facilitating dispersal (e.g. *Agrostis capillaris*, *Polygonum aviculare* agg., *Persicaria* sp.) were also transported. Diaspore features varied between the coats and hooves of the investigated animals: While burrs were completely absent on the hooves, small seeds without appendages like those of *Sagina procumbens* and *Arenaria serpyllifolia* dominated here.

Comparison with the species fruiting in the forest vegetation revealed that, with the exception of the small winged nutlets of *Betula* sp. which lay on the vegetation and soil in large amounts, very few diaspores from the tree and shrub layer were dispersed. In comparison to the herb layer of the forest, hooked and bristly diaspores were favoured by epizoochory, as expected. In contrast, large diaspores (>1 mg) without special features, and diaspores with elaiosome or fruit pulp – nearly all of them also weighing more than 1 mg –, whilst being very abundant in the herb layer, were excluded from adhesive dispersal both to a large extent and totally, respectively. Consideration of the regional habitat preference of the dispersed diaspores (Fig. 2) revealed that plant species which are largely restricted to forests and are dominating the herb layer of the Brieselang forest, were strongly under represented in the dispersal spectra. Instead, a considerable amount of the diaspores transported, i.e. about 30% in roe deer and 15% in wild boar, respectively, originated from the open landscape.

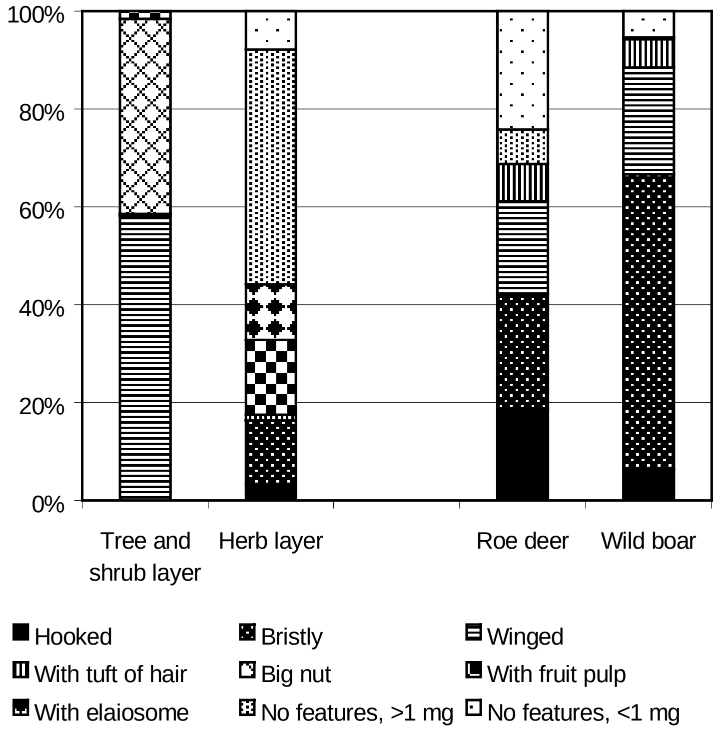

Fig. 1. Comparison of diaspore morphology of the seeds and fruits transported by roe deer and wild boar (right hand) with the plant species fruiting in the Brieselang forest (left hand). Forest vegetation: Mean group quantity fraction (MGF). Epizoochorous species: proportions of dispersed diaspores. Diaspore morphology: see Table 2.

Abb. 1. Vergleich der Diasporenmorphologie der von Rehen und Wildschweinen transportierten Samen und Früchte (rechts) mit denen der im Forst Brieselang fruchtenden Pflanzenarten (links). Waldvegetation: Mittlere Gruppenmenge (MGF). Epizoochore Arten: Anteile der ausgebreiteten Diasporen. Diasporenmorphologie: s. Tab. 2.

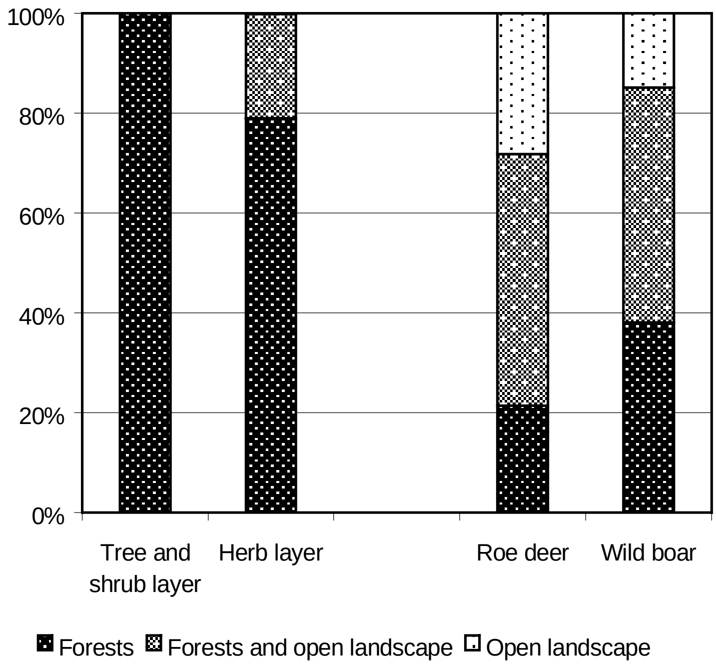

Fig. 2. Comparison of regional habitat preference of the diaspores dispersed by roe deer and wild boar (right hand) with the plant species fruiting in the Brieselang forest (left hand). Forest vegetation: Mean group quantity fraction (MGF). Epizoochorous species: proportions of dispersed diaspores.

Abb. 2. Vergleich der regionalen Habitatbindung der von Rehen und Wildschweinen ausgebreiteten Diasporen (rechts) mit den im Forst Brieselang fruchtenden Pflanzenarten (links). Waldvegetation: Mittlere Gruppenmenge (MGF). Epizoochore Arten: Anteile der ausgebreiteten Diasporen.

Thus, only about one-quarter of the 80 species occurring in the sample plots' herb layer in the forest stands were found to be dispersed epizoochorically by the investigated mammals at least once (Tab. 3), and most of those only in small amounts. With the exception of ***Milium effusum***, none of the dominating forest herbs (***Anemone nemorosa***, ***Convallaria majalis***, ***Stellaria holostea***, ***Lamiastrum galeobdolon***, ***Maianthemum bifolium***, ***Ranunculus ficaria***, ***Vaccinium myrtillus*** and ***Impatiens parviflora***) were transported by roe deer or wild boar (Tab. 4, column epizoochory). Dispersal probability was dependent on diaspore morphology (as defined in Tab. 3) of the plant species (χ^2-test; df = 6, $\chi^2 = 30.070$, $p<0.001$). Dispersal was most frequent in hooked and bristly diaspores which gives a significant advantage for dispersal when compared with the whole species pool (χ^2-test; df = 1, $p<0.01$ and $p<0.001$). Furthermore the amount of dispersed seed and fruit reveals a clear preference for hooked and bristly diaspores (dispersal rates >>1). On the other hand, species with diaspores with elaiosomes or fruit pulps, which are adapted to dispersal by ants or frugivory, respectively, were significantly under represented (χ^2-test; df = 1, $p<0.1$). For all other diaspore types dispersal probability did not deviate significantly. However, dispersal rates elucidate, that heavy diaspores without features and those with a tuft of hair or wings are also largely excluded from adhesive dispersal (dispersal rate <<1).

Table 3. Numbers and proportions of epizoochorically dispersed plant species by roe deer and wild boar in comparison to the species in the herb layer of the Brieselang forest (76 sample plots), according to diaspore morphology, regional habitat preference and tendency of spread.

Tabelle 3. Artenzahl und Anteil der von Rehen und Wildschweinen epizoochor ausgebreiter Pflanzenarten im Vergleich zu den Arten der Krautschicht des Forstes Brieselang (in 76 Probeflächen), ausgewertet nach Diasporentypen, regionaler Habitatbindung und Ausbreitungstendenz.

	Number of species in the herb layer	Number of species dispersed	Proportion of species dispersed [%]	Preference (+) or discrimination (–)		Dispersal rate
				+/ –	P	
Diaspore features						
Hooked	5	4	80.0	+	**	2.86
Bristly	13	9	69.2	+	***	4.78
With tuft of hair or wings	7	1	14.3	–	ns	<0.01
With elaiosome	8	0	0.0	–	(*)	0
With fruit pulp	10	0	0.0	–	(*)	0
No features, > 1mg	18	2	11.1	–	ns	<0.01
No features, ≤ 1 mg	19	4	21.1	–	ns	0.92
Habitat preference						
Forests	41	5	12.2	–	*	0.23
Forests and open landscape	39	15	38.5	+	*	2.91
Association to ancient forests						
Yes	22	3	13.6	–	ns	0.03
No	58	17	29.3	+	ns	1.98
Tendency of spread						
Yes	12	6	50.0	+	*	2.27
No	68	14	20.6	–	*	0.58
All species	80	20	25.0			0.80

***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; (*): $p < 0.1$; ns: $p > 0.1$ (χ^2-test).

Species that are not characteristic for forests, i.e. that also occur in the open landscape, were significantly favoured in dispersal (χ^2-test; df = 1, p<0.01), while shade-requiring species that are largely restricted to forests were disadvantaged (Tab. 3, see also Tab. 4). About half of the characteristic woodland herbs in the Brieselang forest are largely restricted to "ancient forests", i.e. those having existed for at least 150 years, in northern Germany (Tab. 4). Only three of these 22 species (*Brachypodium pinnatum*, *Geum urbanum*, *Oxalis acetosella*) were dispersed externally by roe deer or wild boar. Dispersal rates revealed that very small amounts of diaspores of this species group were transported (Tab. 3). Finally, herb layer species which have increased in abundance in the northern German lowland forests and adjoining regions during the past decades were favoured in epizoochorous dispersal (χ^2-test; df = 1, p<0.01; Tab. 3, see also Tab. 4).

Table 4. Fruiting vascular plant species in the herb layer of the Brieselang forest (frequency >10% in 76 sample plots), their epizoochorous transport by roe deer and wild boar in the current study, diaspore morphology, fruiting period, habitat preference, and tendency of spread.

Tabelle 4. Fruchtende Gefäßpflanzenarten in der Krautschicht des Forstes Brieselang (Stetigkeit >10% in 76 Probeflächen), ihr epizoochorer Transport durch Rehe und Wildschweine in der vorliegenden Untersuchung, ihre Diasporenmorphologie, Fruchtzeit, Habitatbindung und Ausbreitungstendenz.

	Abundance in the Brieselang forest		Epizoochory	Diaspore morphology	Fruiting period	Ancient forest	Tendency of spread
	Frequency [%]	MGF [%]					
Forest species:							
Anemone nemorosa	100	31.40		>1 mg	**V-VI**	✦	
Stellaria holostea	92	3.99		≤1 mg	VI-VII		é
Maianthemum bifolium	86	3.39		pulp	IX-XII	✦	
Milium effusum	81	2.06	⊙	>1 mg	VII-IX		
Convallaria majalis	76	5.11		pulp	VIII-XI	✦	
Moehringia trinervia	76	1.58		elai	VI-IX		é
Viola reichenbachiana	64	1.60		elai	VI-VIII	✦	
Dryopteris carthusiana agg.	63	1.37		≤1 mg	VII-VIII		é
Ranunculus auricomus agg.	60	1.60		>1 mg	V-VII	✦	
Brachypodium sylvaticum	57	1.54	⊙	bristly	VII-Xw	✦	é
Polygonatum multiflorum	56	1.41		pulp	IX-XII	✦	
Ranunculus ficaria	51	3.08		>1 mg	**V-VI**		
Melica nutans	46	1.01		elai	VI-VII		
Lamiastrum galeobdolon	44	3.78		elai	VI-VII	✦	
Hepatica nobilis	43	1.58		elai	**V-VI**	✦	
Luzula pilosa	43	0.67		elai	V-VII	✦	
Paris quadrifolia	42	1.33		pulp	VII-IX	✦	
Impatiens parviflora	38	2.11		>1 mg	VII-X		
Oxalis acetosella	32	1.17	○	>1 mg	VI-IX	✦	
Galium odoratum	25	1.83		hooked	VII-XI	✦	
Pulmonaria obscura	22	0.62		elai	**V-VI**	✦	
Stachys sylvatica	19	0.36		>1 mg	IX-XI	✦	
Vaccinium myrtillus	18	2.57		pulp	VII-IX		
Festuca gigantea	18	0.22		bristly	VII-X	✦	
Pteridium aquilinum	14	2.33		≤1 mg	VII-IX	✦	
Holcus mollis	14	0.64		bristly	IX-X		
Melampyrum pratense	14	0.43		elai	VII-IX	✦	
Poa nemoralis	13	0.16	**I**	bristly	VII-IX		é
Forest and open landscape species							
Deschampsia cespitosa	61	1.93	**O**	bristly	VIII-XI		
Dactylis glomerata agg.	52	1.57	⊙	bristly	VI-X		
Urtica dioica	46	1.06	**I**	bristly	IX-Xw		é

Rubus caesius	39	0.79		pulp	VII-IX		
Geum urbanum	38	1.05	**O**	hooked	VII-XII	✦	
Lysimachia vulgaris	38	0.78		≤1 mg	X-XIw		
Galium aparine	34	0.51	⊙	hooked	VIII-X		é
Geranium robertianum	32	0.77		>1 mg	VI-IX		
Deschampsia flexuosa	28	5.13	**O**	bristly	VIII-X		é
Carex pilulifera	25	0.54		>1 mg	VI-VIII		
Calamagrostis epigeios	17	0.66	⊙	hair	VIII-X		é
Rubus idaeus	17	0.30		pulp	VII-IX		é
Rubus fruticosus agg.	16	0.24		pulp	VII-IX		é
Agrostis capillaris	14	0.50	**O**	≤1 mg	VIII-XI		é
Alliaria petiolata	14	0.23		> mg	VII-X		
Molinia caerulea	13	1.58	⊙	≤ 1 mg	IX-XI		
Poa pratensis/trivialis	13	0.28	❙	bristly	VI-IX		
Galeopsis tetrahit	12	0.14		>1 mg	VIII-X		é

MGF: Mean group quantity fraction.
Epizoochory: ❙ >10% of the total diaspore amount; **O** >1-10%; ⊙ >0,1-1%; ○ ≤0,1%.
Fruiting period: according to MÜLLER-SCHNEIDER (1986), HEINKEN (2000) and own observations in the study area, spore dispersal of pteridophytes after HEGI (1984); w: presentation of fruits for the whole winter period ("Wintersteher"); boldface: species not fruiting during the study period.
Diaspore morphology: big nut: heavy nuts rich in nutrients; elai: with elaiosome; pulp: with fruit pulp; for other abbreviations see Tab. 2.
✦: association to ancient forests.
é: increase of abundance in forests of the northern German lowlands and adjoining regions.

4 Discussion

4.1 Epizoochorous diaspores in the Brieselang forest

Our study shows that a number of seeds and fruits, as well as a broad spectrum of vascular plant species, is dispersed externally by roe deer and wild boar in central European forests. Wild boar is much more important for epizoochory than roe deer as wild boar coats, with their long bristles combined with a thick undercoat of curly hair are ideal for diaspore adherence, whereas roe deer have sleek, dense fur. In addition dispersal by wild boar is promoted by wallowing activities, which coats the animals (with the exception of their dorsal ridge) in a dried, diaspore-containing mud crust. This factor is further enhanced by their difficulties in grooming certain parts of the body (cf. BRIEDERMANN 1990). Furthermore many diaspores may come in contact with the coats of wild boar during rooting activities and the extensive rest periods.

The large number of seeds and fruits of several plant species dispersed externally by wild boar confirms the results of MROTZEK et al. (1999), who studied eight shot wild boar in southern Lower Saxony. However, they detected significantly more diaspores and plant species per individual than in the current study. The total number of transported diaspore species (109) was also much higher than in the Brieselang forest. This can be explained by the differing soil types of the study areas. While loamy soils which optimally adhere to coats prevail in southern Lower Saxony, the Brieselang area is characterized by sandy soils which do not stick to a comparable degree. Moreover, the wild boars investigated by MROTZEK et al. (1999) originated from landscapes with a different geology and thus a different flora. Despite differing study areas, the spectra of plant species which were found to be dispersed abundantly were rather similar in both studies. MROTZEK et al. (1999) detected especially large amounts of *Urtica dioica* and *Deschampsia cespitosa* diaspores, and *Poa* spp. were also transported abundantly. However, *Betula* sp. was not dispersed in southern Lower Saxony. Its dominance in the Brieselang forest is a result of its large growing stock here and may be typical for several regions of the northern German lowlands. As *Betula* sp. is dispersed by wind over the longest distances of all native tree species (cf. MILES and KINNAIRD 1979), secondary epizoochorous dispersal may be of minor importance.

Both animal species do not only disperse diaspores adapted for attachment by hooks or bristles, but also large amounts of other diaspore types, especially small ones (cf. FISCHER et al. 1995, 1996, STENDER et al. 1997, MROTZEK et al. 1999). In their hooves, they mainly transported diaspores without adaptations for adherence, which were enclosed within a mud crust. Thus, we assume that in principle almost all types of diaspores, and thus vascular plant species can be dispersed epizoochorically. However, hooked, bristly or small diaspores are much more likely to be dispersed than large diaspores without clinging structures.

As in the study by MROTZEK et al. (1999), large amounts of seed must have been picked up outside the forest stands. This elucidates that arable land, grasslands, ruderal vegetation and waysides are important habitats for the roe deer and wild boar of the Brieselang forest, because they are an important source of food (cf. HEINKEN et al. 2001a). Despite this, the small amounts of diaspores from forest floor species which do not also occur in the open landscape, is striking. Most of them seem to have hardly any chance of being dispersed by hoofed animals. This is because the diaspores of many forest species lack morphological adaptations for epizoochory: They have no appendages aiding attachment, and are too large to be attached without hooks or bristles. This is true for almost all diaspores with fruit pulps promoting ingestion, with elaiosome promoting ant dispersal and those with no features weighing more than 1 mg. The results correspond with those of an experiment with a dog investigated by HEINKEN (2000) in similar forest vegetation, where most of the common and characteristic species of the herb layer lacked any epizoic transport. Yet it must be considered in this context that some ant-dispersed species abundant in the Brieselang forest (***Anemone nemorosa***, ***Hepatica nobilis***, ***Pulmonaria obscura*** and ***Ranunculus ficaria***) were fruiting in spring and thus before the study period (see Tab. 4). However, a twelve-month experiment with a dog (HEINKEN 2000) also showed no evidence of epizoochorous transport of these species. Moreover, it revealed that spring and early summer may be negligible for epizoochory of phanerogams as most herb layer species ripen in late summer and in early autumn, and spring herbs in forests are usually ant-dispersed. Besides diaspore morphology, the low diaspore production of most forest floor species (e.g. BIERZYCHUDEK 1982) negatively affects their dispersal probability. It must also be taken into account that plant species with few, large diaspores have an advantage in establishment compared with those with small diaspores (EZOE 1998). The dispersal of few diaspores can, therefore, be relatively effective.

4.2 Dispersal distances and deposition places of epizoochorous diaspores

Dispersal distances and patterns of epizoochorous plant species are mainly a function of retention rate of the seed in the coats or on the hooves, and the active range of the dispersal vector (e.g. BONN and POSCHLOD 1998), where the retention rate depends on the structure and characteristics of the fur and the diaspores, and the grooming behaviour of the host animal (SORENSEN 1986, KIVINIEMI 1996).

Experiments with domesticated fallow deer (***Cervus dama*** L., KIVINIEMI 1996), cattle (KIVINIEMI and ERIKSSON 1999) and sheep (FISCHER et al. 1995, 1996) revealed that the number of attached diaspores decreases continuously and often rapidly over time, but retention times of several hours and up to several days are usual especially among animal species which have curly or matted, sometimes sticky hair like sheep and galloway cattle. Diaspores with well-developed morphological characters such as hooks or bristles have significantly larger retention rates than diaspores without such features (KIVINIEMI 1996, KIVINIEMI and ERIKSSON 1999). Thus, long retention times may occur, above all, for burrs attached to wild boar, while diaspores without appendages may adhere to roe deer only for a few minutes. Given the relatively large home ranges of the animals (Tab. 1) a considerable amount of diaspores can theoretically undergo long-distance dispersal of up to several hundred metres by roe deer, and a few kilometres by wild boar. Longer distances may very rarely occur especially by wild boar, as young individuals sometimes make exceptional migrations of up to 200 km (BRIEDERMANN 1990, HAHN and KECH 1995). In contrast, most roe deer spend their whole life within 1.5 km from their birthplace (MÜRI 1999).

For the subsequent establishment of dispersed diaspores it is important that they are deposited in suitable habitats. Of course, this will only happen for a fraction of the dispersed seeds and fruits. As shown by an investigation of the soil seed bank by MROTZEK et al. (1999), wild boar's epizoochorous diaspores are often deposited near rubbing trees and thus within forest stands. Extensive disturbances in forest stands caused by wild boar rooting during their search for food (e.g. BRIEDERMANN 1990) may promote germination and establishment of dispersed forest herb seeds as germination of many species is increased by litter removal (cf. ERIKSSON 1995).

Taking the dispersed seeds and fruits, and the dispersal distances, as well as the landscape configuration of the study area into consideration, the epizoochorous dispersal processes caused by roe deer and wild boar in the Brieselang area can be characterized at the landscape level as follows: Seeds from grasslands, arable land and ruderal stands are dispersed (a) within the open landscape, (b) between the open landscape and the open areas within the forest (waysides, fields, clear-cuts), and (c) between open areas within the forest. Also large amounts of seeds from open places may be transported into the forest stands, where they are unable to emerge, but possibly enter the seed bank (see FISCHER 1987). However, many of them will germinate and establish during clear-cuts or other large-scale disturbances and thus may have an effect on the biodiversity of forest ecosystems. As mammals venture outside the forest, some forest species seeds will be deposited in open places, where seedlings will also not emerge. Only relatively few seeds from forest plant species which are (a) transported within the forest area, or (b) – presumably very rarely – between isolated, remote forest stands will be dispersed effectively.

4.3 The role of wild ungulates in dispersal processes in mesic deciduous forests

Our results may be generalized to assess the role of epizoochorous dispersal by hoofed game in species-rich, deciduous forests in central European lowlands: On the one hand the study area represents both the widespread forest vegetation of mesic habitats and a typical landscape section. On the other hand other large mammal species, which were not studied here, will probably not create different dispersal spectra as shown by the similarity of results between roe deer and wild boar.

To assess the role of deer and wild boar for dispersal in general, internal dispersal must also be considered. Investigations of faeces of animal species in NE Germany by HEINKEN et al. (2001a) revealed that the seed content in the faeces was high for roe and fallow deer, but very low for wild boar. However, deer dispersed nearly exclusively weeds, ruderal plants and species occurring in both oligotrophic grasslands and acid-soil forests, all of them with very small seeds, whereas wild boar transported a broad spectrum of plant species, among them typical forest herbs such as ***Moehringia trinervia*** and ***Ranunculus ficaria***. Though the dispersal spectra obviously differed from the epizoochorous ones, the importance of these animal species for the dispersal of mesophilous forest plant species is not significantly enlarged by endozoochory.

Thus, in an agricultural landscape with species-rich deciduous forests, wild ungulates inhabiting these forests generally play a role rather in the dispersal of ruderal, clear-cut and grassland species than of deciduous forest vegetation. The most important forest species are largely dependent on other dispersal vectors: While most tree and shrub species are effectively dispersed by wind, or frugivorous or nut-storing birds (e.g. MÜLLER-SCHNEIDER 1986, KOLLMANN 1994, STIMM and BÖSWALD 1994), many herb layer species are dispersed by ants (e.g. ***Anemone nemorosa, Hepatica nobilis, Lamiastrum galeobdolon*** and ***Viola*** spp., cf. MÜLLER-SCHNEIDER 1986). This is a completely different situation to that of pasture landscapes, where sheep and cattle with their large populations transport a great amount of diaspores of characteristic plant species (FISCHER et al. 1995, 1996, STENDER et al. 1997). Considering the decline of dispersal processes, above all in woodland pasture by domestic livestock (formerly a widespread historical land use), and the increasing fragmentation of habitats (cf. BONN and POSCHLOD 1998), hoofed game may nevertheless have an important function for landscape ecology in the cultivated landscape of central Europe.

In the lowland areas of central Europe and other regions with a fragmented woodland distribution, many typical forest floor species are restricted to ancient woodlands, especially in locations supporting mesic deciduous forests (survey in HERMY et al. 1999). Newly created or disturbed sites are only colonized if they are located adjacent to existing populations (e.g. BRUNET and OHEIMB 1998, BOSSUYT et al. 1999). Isolated afforestations on formerly cultivated land lack many typical forest floor species for decades and more, probably because of the lack of efficient long-distance dispersal (e.g. PETERKEN and GAME 1984, WULF 1997, GRAAE 2000). This is confirmed by the current study as most of the typical forest herbs were not observed as being transported by the mammals investigated. However, the transport of some large diaspores without any features facilitating long-distance dispersal, i.e. ***Milium effusum*** and ***Oxalis acetosella***, especially by wild boar elucidates that almost all diaspore types can be dispersed by large mammals (cf. FISCHER et al. 1996, MROTZEK et al. 1999). Such „accidental dispersal“ of forest herbs (CAIN et al. 1998) may be the reason for their occasionally successful colonization of isolated woodlands today (BRUNET and OHEIMB 1998, BONN and POSCHLOD 1998). Nowadays, forestry vehicles and machinery may be more important dispersal vectors enabling forest plants to colonize changing forest habitats and isolated afforestations (cf. BONN and POSCHLOD 1998).

In the last decades central European forests have been widely effected by altered silvicultural practices, atmospheric depositions, and liming. Changes of habitat quality, i.e. eutrophication, acidification and locally alkalisation, resulted in significant changes of forest floor vegetation, in the course of which several herb layer species increased in abundance and appeared in previously unoccupied habitats (e.g. SCHMIDT 1999, AMARELL 2000, LAMEIRE et al. 2000, WENDT and SCHMIDT 2000, ZERBE et al. 2000). As these species were favoured in dispersal in our study, we presume that epizoochory by wild ungulates is an important means to facilitate their spread into new habitats. This may be true especially for ***Brachypodium sylvaticum***, ***Galium aparine*** and ***Poa nemoralis*** (cf. Tab. 4), and for ***Agrostis capillaris***, ***Deschampsia flexuosa*** and ***Urtica dioica*** which are also endozoochorously dispersed (HEINKEN et al. 2001a).

4.4 Implications for silviculture and forest nature conservation

To date, population densities of hoofed game have been discussed in silviculture and nature conservation nearly exclusively with regard to damage to forest vegetation, especially to saplings (e.g. KÖNIG and BAUMANN 1990, PRIEN 1997, KRIEBITZSCH et al. 2000). Our study suggests that ungulates, especially wild boar, also have positive effects on forest vegetation (see also FISCHER 1999b) by enabling several plant species to maintain migration between isolated habitats which is essential to the long-term viability of many plant populations. Moreover, they enable plant species to colonize new potential habitats which are created especially by afforestations on former arable land and by transformation of conifer monocultures to multi-species forests. As biodiversity maintenance and enhancement are supposed to be important factors for the stability of forest ecosystems, and important objectives for both nature conservation and sustainable silviculture (e.g. BMVEL 2001), population densities of hoofed game should be revalued. Their considerable role in dispersal suggests that the increase of barriers, such as motorways, which hinder the migration of wild mammals, may lead to a further decrease of long-distance dispersal processes in the central European landscape.

However, despite the considerable amounts of seed dispersed, our study confirms the observations of several former investigations (e.g. WULF 1997, BRUNET and OHEIMB 1998, BOSSUYT et al. 1999), that for habitats supporting mesic deciduous forests, a rapid regeneration of the understorey layer can not be expected either after afforestation of arable land remote from existing forest patches, or in the transformation of large-scale conifer forests. Thus, from the point of view of nature conservation, afforestations should be laid out preferentially adjacent to ancient forest stands (WULF 1995, FINCK and SCHRÖDER 1997, GRUTTKE 1997, HERMY et al. 1999). For isolated stands of secondary forest, artificial introduction of seed or plants may be a useful means to support the restoration of the understorey layer (cf. BOSSUYT and HERMY 2000). This should also be considered during the transformation of large-scale conifer forests into semi-natural, mixed or deciduous forests. Moreover, the results emphasize that conservation of existing ancient woodland should be of first priority (e.g. STEGINK-HINDRIKS 1994, WULF 1993), and large-scale clear-cuts and soil scarification, which both have negative effects on shade-tolerant forest floor species, should be avoided (see BRUNET and OHEIMB 1998), as is already practised in German state forests (e.g. PLACHTER et al. 2000).

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