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REVIEW

Changing dispersal processes in the central European landscape since the last ice age: an explanation for the actual decrease of plant species richness in different habitats?

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INTRODUCTION

Species richness in plant communities until now has been regarded as a function of abiotic factors characteristic of a habitat or ecosystem such as hydrological conditions, nutrients and light or other factors such as mycorrhiza which are important for the coexistence of species (Ellenberg 1996, Ozinga *et al.* 1997). Further hypotheses were recently summarized by Zobel (1992). However, most of these hypotheses assume that all species have the same mobility or even that each species can reach all suitable habitats. Although it is obvious that this is unlikely it was supposed by most vegetation ecologists until recently[1], even in textbooks on dispersal ecology (Ridley 1930; Müller-Schneider 1977; Van der Pijl 1982). Recently species pool theory considers species richness as a function of historical processes (Pärtel *et al.* 1996; Zobel 1997). However, this is only another hypothesis and there has been no review on processes (except Bonn & Poschlod 1998) which could be responsible for the dispersability of plant species

[1] The classification of plant communities (plant sociology) is based on the occurrence of distinct species in their habitats (character species) although there are no ideas which dispersal processes and vectors are responsible for its distribution (Dierschke 1994). However, Gleason (1926) had already mentioned that species composition of vegetation is the result of migration ability and environmental sorting (see also Salisbury 1964).

until now, taking into account that nearly all plant communities in central Europe are man-made or at least modified by man. In any case, it is clear that land use practices combined with vectors such as livestock are more important for the dispersal of plant species in comparison to their own dispersability, as pronounced in the above-mentioned textbooks.

In this context processes existing in natural (in central Europe after the last ice age), traditional and actual man-made landscapes which are important for the dispersal of plant species, are analysed here. The comparison of the changing number and type of processes during the evolution of the central European man-made landscape since the last glaciation and especially the neolithic age should allow a first critical assessment of these processes for the species richness of plant communities, especially after restoration management.

PLANT DISPERSAL IN THE POSTGLACIAL VEGETATION

During the postglacial period, before human settlement, there was also a change in the composition of vegetation. However, although the change of vegetation is well known throughout palynological research (Lang 1994), there are only a few ideas on the dispersal and spread of plant species during that time. Consequently, Kollmann (1992) calls the middle European 'Grundfolge' (postglacial vegetation development after Firbas 1949), the most speculative application of the knowledge on dispersal ecology of plants.

Important dispersal vectors in the 'natural landscape' were wind, water and animals. Whereas in an open tundra landscape wind could have been an important factor of plant dispersal this was not the case in a wooded landscape, where wind probably only caused patterns of plant distribution on a small scale. Water was probably a more important dispersal vector during that time. At least trees and shrubs are regarded as hydrochoric (Ridley 1930; Delcourt & Delcourt 1991; Lang 1994). However, Fuchs (in Poschlod *et al.* 1997) found germinable diaspores from at least 63 species in drifted material and in the sediment of the Upper Loire River (France), most of them species from open habitats such as disturbed places and grasslands (Table 1). The amount of drifted diaspores in rivers can be high. In a study of the seasonal variation of drifted diaspores in small rivers more than 80 000 diaspores per day were caught in a 15×24 cm^2 area represented by the size of a drift net (Table 2; Trottmann, R. & Poschlod P. unpublished data). In both studies, most of the species were not known to be dispersed by water. Only four of 63 species in the first study and 12 of 43 species, respectively, in the second study were regarded as nautochoric (Müller-Schneider 1986).

Animals are assumed to be the most important dispersal vectors in postglacial time, especially with respect to long distances. Most trees and shrubs may have been spread by birds, according to Müller-Schneider (1949), Sauer (1986), Johnson & Adkisson (1988) and Johnson & Webb (1989). Darley-Hill & Johnson (1981) and Mattes (1982) reported that 54% and up to 60%, respectively, of the whole diaspore production of oaks and *Pinus cembra* can be dispersed by different species of jay. However, large herbivores are regarded as more effective with respect to the number of species (Janzen 1981, Malo & Suarez 1995), especially non-woody plants. Herrera (1989) believes that carnivorous species also probably acted as important dispersal vectors during postglacial time. Willson (1993) found thousands of germinable diaspores in only one dung deposit. Most of these studies included only endozoochoric dispersal. Fischer *et al.* (1995, 1996) and Stender *et al.* (1997) showed, although only for livestock, that ectozoochoric

Table 1. Number of species with germinable diaspores in drifted material and in the sediment (sand, gravel) in a region of the upper Loire in the south of Le Puy (France, after Poschlod *et al.* 1997)

Vegetation types	Only in the drifted material	In the drifted material and the sediment	Only in the sediment	Total
Freshwater and peatland vegetation	1	1	2	4
Vegetation of disturbed places	4	13	3	20
Artemisietea	2	6	1	9
Alpine vegetation	—	—	2	2
Grassland	3	8	3	14
Sedo–Scleranthetea	—	5	2	7
Molinio–Arrhenatheretea	3	2	—	5
Fringe and shrubland	—	1	2	3
Woodland	1	3	—	4
Species from other vegetation types	2	5	9	16
Total number of determinable species	11	31	21	63

Table 2. Number of diaspores drifted by open water per day and $15 \times 24\,cm^2$ area (size of the water body which was caught by a drift net) in little rivers of the plainlands around Munique and Augsburg (study period from June 1995 to February 1996; from Trottmann & Poschlod, unpublished)

Site/time of sampling	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Feb.
Viertelsgraben (upper reaches)	1464	504	864	144	312	144	240	24
Viertelsgraben (central reaches)	2784	10 368	1272	1152	1080	960	648	4896
Pullinger Graben	1968	3648	432	1008	1152	672	288	384
Vorflutgraben, Nord	—	6624	744	96	144	48	576	—
Friedberger Ach (central reaches)	24 624	82 512	50 832	21 744	22 032	23 472	19 008	20 160
Moosach (central reaches)	26 064	55 008	18 000	11 664	12 672	16 272	15 120	27 792

dispersal on fleece or fur and also by hoofs can be much more important with respect to the number of species. Seeds can be transported over a long period. During that time animals can cover long distances depending on migration behaviour (Fischer *et al.* 1996, Kiviniemi 1996). Since we know that, in particular, the number of species of large herbivores and also carnivores decreased continuously during postglacial time until the 17th century due mainly to the impact of man (Beutler 1996) we have probably lost many important dispersal vectors for plants. In this context it is important to state that at the same time, most of these species created the habitats and also the germination niches for most plant species by disturbing the turf through trampling.

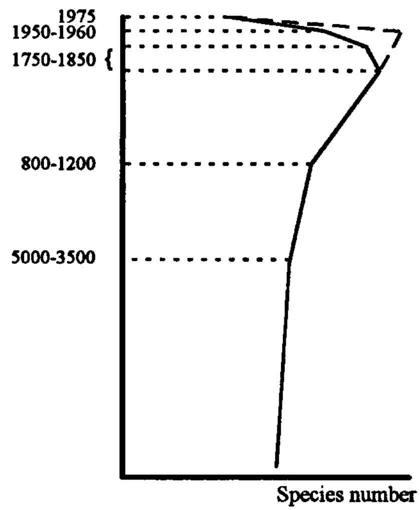

Fig. 1. The change of the number of plant species since the last glaciation (from Sukopp & Trepl 1987, after Fukarek 1980).

ASPECTS OF PLANT DISPERSAL IN THE MAN-MADE LANDSCAPE

With the beginning of the neolithic age and the settlement of man a continuous period of rapid changes of landscape and vegetation began. Along with the settlement of man natural processes decreased, separation of functions and processes as well as fragmentation of habitats and active land use management increased. Di Castri (1989) recently summarized the most important processes which were the driving forces for the spread of plants and animals since the neolithic revolution to the 15th century, from the 15th century until recently, and since the last century with the introduction of intensive agricultural practices, trade, traffic and others. However, one of his most important conclusions was that since the beginning of human settlement the globalization and acceleration of dispersal processes increased. Compared to vegetation changes during early postglacial time the speed of floristic change caused by anthropogenous dynamics is tremendously higher (Fig. 1).

Dispersal by agricultural practices

Different agricultural practices resulted in different plant communities, e.g. for arable fields in different weed communities (Table 3). However, although until now abiotic factors have been assumed as the most selective processes for the composition of plant communities, it is obvious that agricultural practices also included important processes for the dispersal of plants to reach suitable sites (Schneider *et al.* 1994). Therefore, many plants in agricultural habitats became extinct or endangered due to the change of practices which no longer include the dispersal of those plants.

Dispersal by sowing seed. Many weeds which were formerly extremely common were spread by uncleaned seed. In former times crop seed could contain a high amount of weed diaspores (Witmack 1888; Schneider *et al.* 1994). Most of these species lack other

Table 3. Development of agriculture and agricultural weed vegetation in central Europe (modified after Hüppe 1987, 1990, Burrichter *et al.* 1993)

Phase	Dominant form	Characteristics	Agricultural weed flora
Prehistoric time from neolithicum up to the Roman time	Alternating arable field-pasture farming	Fallow >arable field cultivation	Perennial species, species-poor weed communities, habitat typical vegetation similar to grasslands, from Roman times on immigration of submediterranean species
Early middle ages up to the end of 17th century	Three-field rotation; never-ending rye; arable field-forest-/ fire-field-cultivation	Fallow <cultivation; no fallow, sod cutting; arable field cultivation < forest exploitation	Open weed vegetation, annual and perennial species, beginning separation of arable field and grassland vegetation
Since 18th century	Improved three-field rotation	Replacement of the fallow by root crop cultivation, since about 1830 use of mineral fertilizer	Differentiation of communities of annuals, final separation of arable field and grassland vegetation
Present	Mechanized large-area farming	Standardized, mechanized methods of cultivation, narrow crop species spectrum	Increasing uniformity, impoverishment; development of species poor one-year or several year-old fallows

regeneration possibilities such as a long-term persistent diaspore bank (Table 4). In the last century Stebler (1878) wrote about *Bromus secalinus*: 'It is in cereal fields an extremely harmful weed and occurs together with the bearded darnel in such huge numbers in wet years that the legend originated of cereal being converted to brome'. However, clover and grass seed were also highly contaminated by many species, some of which are endangered or extinct today, such as *Cuscuta epithymum* ssp. *trifolii*. Salisbury (1953) estimated the number of sown seeds by uncleaned clover and grass seeds in the first decade of the 20th century in Great Britain to be between two and six billion per year! Since the 1950s and 1960s cleaning of seeds has been improved by new methods. According to the rules of seed prescription cereal seed must have a purity of at least 98% or 99% at certificated and base seed (Fuchs *et al.* 1979, Kuhnhardt 1986). Therefore, many weeds sown by uncleaned seed today are regarded as extinct or endangered (Table 4). Schneider *et al.* (1994) listed a minimum of 43 endangered species which were formerly spread by cereal seed.

In former times additional sowing in grasslands was done by hayseeds which were collected in the barn, fallen out from hay and second-hay (Stebler 1878). Before the sale of grassland seed this was the only way to establish new grasslands. Although in the middle of the last century hay seed was no longer recommended (Häfener 1847),

Table 4. Endangered or extinct arable weeds of Germany, which were often or obligately spread with cereal seed (after Wehsarg 1918; Kornas 1972, 1988; Schneider *et al.* 1994). dbtype (diaspore bank type): ts = transient, sps = short-term persistent, lps = long-term persistent (after Schneider *et al.* 1994; Thompson *et al.* 1997), fat = if more than two data are given the most frequent result is given as fat; * = extinct according to the German Red Data Book (Korneck *et al.* 1996)

Species	dbtype	dbtype	
Adonis aestivalis	?	Only in the summer cereal seed	
Adonis flammea	?	*Lolium temulentum*	?
*Agrostemma githago**	ts	*Vaccaria hispanica* ssp *hispanica*	?
Bromus secalinus	ts		
Fagopyrum tataricum	ts?	Only in flax seed	
Galium tricornutum	ts	*Camelina alyssum**	sps?
Lathyrus aphaca	ts?	*Cuscuta epilinum**	?
Rhinanthus alectorolophus ssp. *bucalis*	ts	*Galium spurium* ssp. *spurium**	?
Rhinanthus serotinus ssp. *apterus*	ts	*Lolium remotum**	?
		*Silene linicola**	?
		*Silene cretica**	?
		Spergula arvensis ssp. *linicola**	ts-lps

new grasslands were still being established in this way until the beginning of this century, e.g. species-rich mountain meadows (Hard 1964) and calcareous grasslands on abandoned vineyards (Schumacher *et al.* 1995). However, species-rich litter meadows, today an endangered habitat with many rare species (Korneck & Sukopp 1988), were also artificially established not only by sowing but also by planting (Stebler 1898). This was done especially in those regions where there were no arable fields to gain straw as litter, such as in the foothills of the Alps. *Molinia caerulea*, the dominant species of the litter meadows in the foothills of the Alps, the seeds of which were collected and sown, became almost a cultivated plant (Stebler 1898, Konold & Hackel 1990).

Dispersal by fertilizing with manure. Agricultural practices also guaranteed the dispersal of species between different habitats in the historical man-made landscape (Fig. 2). Sods from heathlands, field or way margins, litter from the forest, hay from litter meadows, ditch and pond mud excavation were used as manure, as well as rubbish from cleaning stables hay stocks, roads and farms which were put on to fields. Manure, which was the most widespread fertilizer in historical times, contained many diaspores depending on which materials were put on the manure heep (Korsmo 1930). Some dung of livestock contained almost 20 000 000 diaspores which were spread onto 1 ha of an arable field (Korsmo 1930, Table 5). Today most fertilizers applied to arable fields are mineral fertilizers or animal slurry containing no or only few diaspores (Fig. 2). The most obvious causes for the low content of diaspores are that, today, hay as fodder is mown earlier and more often so most plant species cannot reproduce or have not yet reproduced generatively. However, longevity of diaspores in animal slurry is mainly lower than in manure, due to the toxicity of ammonia and methane and eventually oxygen deficiency (Rieder 1966a, 1966b; Chytil 1986; Kellerer & Albrecht 1996); additionally, by applying animal slurry, species are selected with hard seed coats which are not so sensitive to ammonia (Rieder 1966a). This means that we do not only

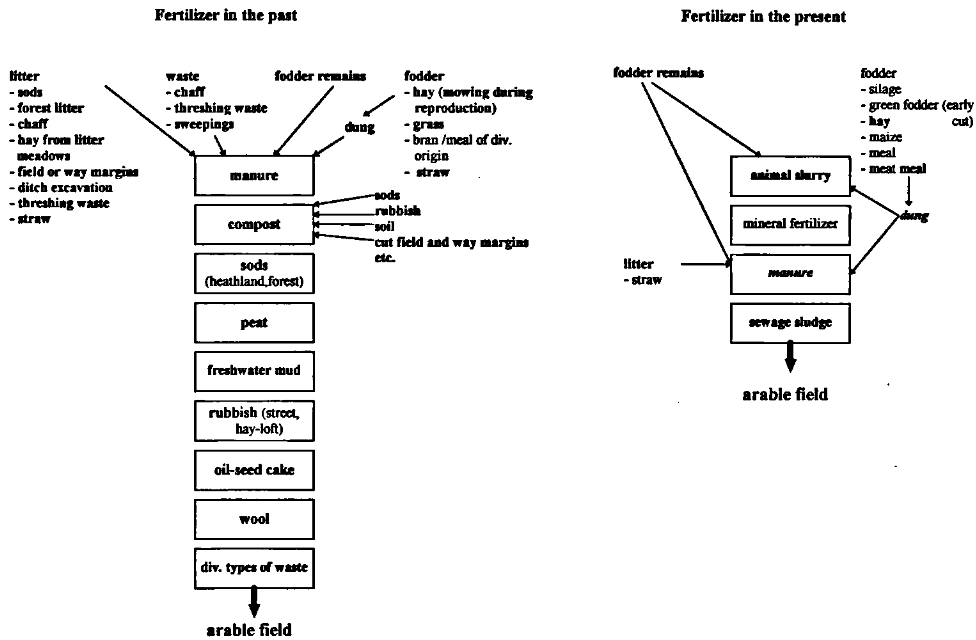

Fig 2. Fertilizers applied to arable fields in the past and present. Bold: seed containing material; bold and italic: strongly reduced seed content compared to the same material in the past.

Table 5. Diaspore contents of different materials of fodder, litter or manure used as fertilizer for arable fields (after data from Korsmo 1930; Chytil 1986; Poschlod *et al.* 1996b). * = amount which was used to fertilize 1 ha

Materials used as fodder, litter or manure	Diaspore content	Number of species
Threshing waste	16.500–1.734.500/kg	14–27
Chaff	4.500–170.000/kg	?
Hay-loft sweepings	182.500/kg	13
Straw fodder/litter	No given number	10–17
Bran/meal	80–6.800/kg	?
Scouring waste from mills	287.800/kg	22
Horse dung (fermented, storage <0·5 years)	326.440–958.960/60t*	?
Cow dung (fermented, storage <0·5 years)	488.230–58.960/60t*	?
Pig dung (fermented, storage <0·5 years)	326.440–511.490/60t*	?
Sheep dung (fermented, storage <0·5 years)	825.000/60t*	?
Hen dung (fermented, period of storage unknown)	1.042.039/60t*	?
Compost (dung and soil from field margins, roadsides, etc.)	19.000.000/40t*	?
Pond mud	>6000/1	up to 42

have a lower input of diaspores by spreading slurry or mineral fertilizer instead of manure, but also an input of viable seeds different in composition and dominance.

Dispersal by harvest methods. Methods of crop harvesting also caused the dispersal and wide distribution of plant species, especially weeds. In the neolithic age cereal crop was

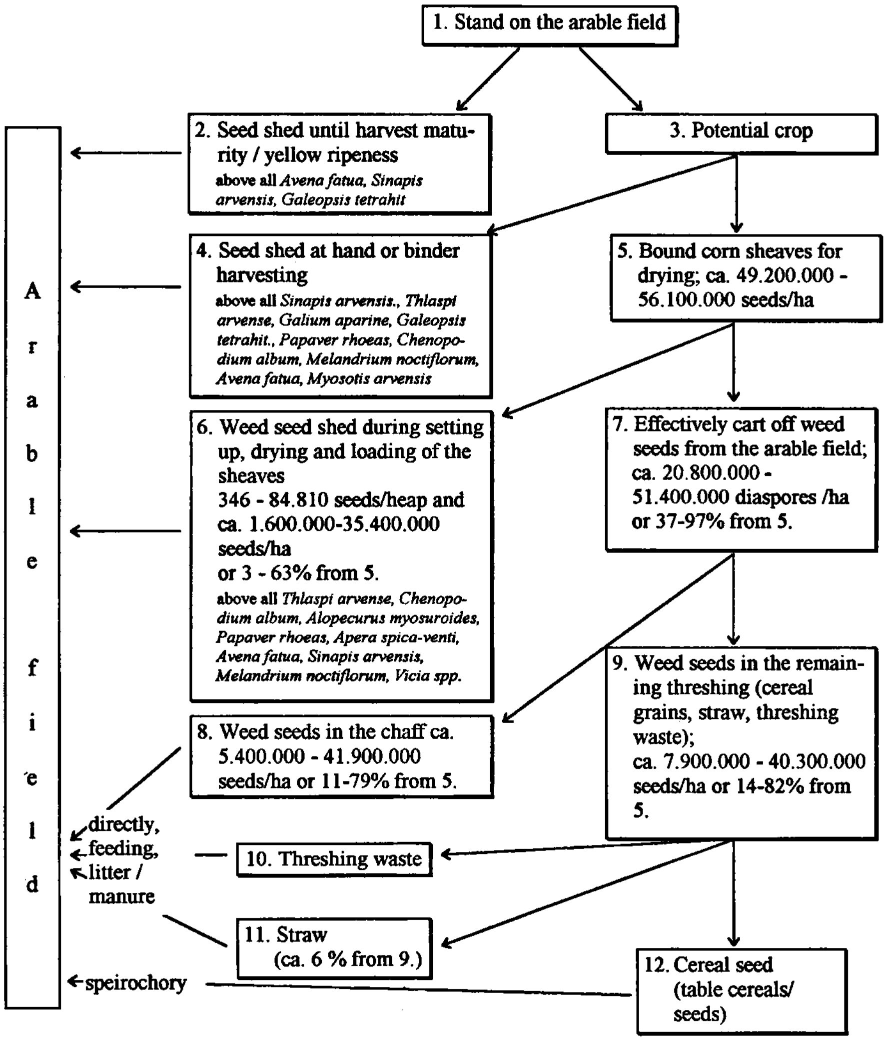

Fig. 3. Dispersal destiny of weed diaspores at hand or binder harvesting with sheaf recovery (data from Petzoldt 1957, 1959).

picked or cut by a harvest knife. This caused a selection of weeds with the same height as the crop, which were spread again by uncleaned seed on the fields (Willerding 1986). This led to a rapid areal expansion of tall weeds such as *Agrostemma githago* (Knörzer 1971a).

Only in the iron age was the crop harvested near the soil surface by a sickle. Then, low-growing or prostrate weeds had the opportunity to be spread over long-distances by uncleaned seed (Willerding 1986). The method of harvesting did not change for a long time. Cereal crop was harvested by mowing during yellow ripeness, corn sheaves were bound and dried on the field and then carted off, threshing, separation from straw, cereal seed and chaff at the farm (Fig. 3). About half the weed diaspores remained on the field (Korsmo 1930; Petzoldt 1957, 1959). However, by binding and setting up weed

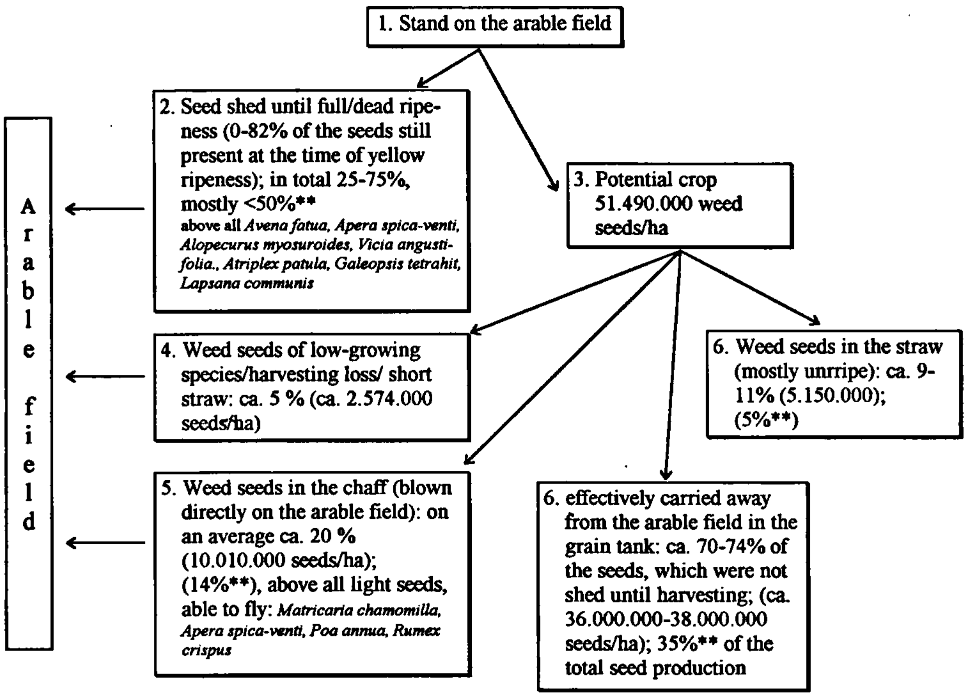

Fig. 4. Dispersal destiny of weed diaspores at combine harvesting (data from Petzoldt 1957, 1959; Fogelfors 1982 (with ** marked numerical values are according to Fogelfors 1982). Discrepancies in the percentage values are founded on single studies that the sum of single values can also be more than 100%.

diaspores were spread over the field. The weed diaspores in the corn sheaves were transported to the farm and threshed together with the crop. The weed diaspores remained partially in the threshing and could be spread again on the field by sowing the seed which was uncleaned (Table 4) or was mixed with the chaff or other threshing waste used as fodder, litter or put onto the manure heap. The chaff could contain up to almost 90 000 diaspores per kg , the other threshing waste more than 300 000, which were spread again sooner or later on the field (see Fig. 3). This practice was the cause of the rapid spread of *Bromus tectorum* in North America (Mack 1981). Finally, the supply of flails supported the scarification which accelerated germination of species with hard-coated diaspores such as *Adonis* spp., *Legousia speculum-veneris* and *Neslia paniculata* (Sieben & Otte 1992).

Since the end of the 1960s most of the fields have been harvested by combine. This harvesting practice did not allow the drying of the corn-sheaves on the field. Therefore, cereal was harvested during full ripeness, which was two to three weeks later. Chaff and straw were also already separated on the field. The consequence was that most of the weed diaspores remained on the same field and that those weeds became dominant, shedding their diaspores until the later date of harvesting such as *Avenua fatua*, *Apera spica-venti* and *Alopecurus myosuroides*, which became only problematic weeds from that time (Dollinger 1988; Albrecht 1989). Other weeds which became increasingly dominant for the same reason were *Atriplex patula*, *Galeopsis tetrahit*, *Lapsana communis* and *Vicia angustifolia* (Petzoldt 1957, 1959; see Fig. 4). Another effect was due to the

Table 6. Number of species from grasslands and other habitats (total) dispersed by galloways and sheep in north-west German lowland dry and wet grasslands and south-west German dry calcareous grasslands, respectively (from Stender *et al.* 1997; Fischer *et al.* 1995, 1996)

	Number of species dispersed by			
	Galloways		Sheep	
Dispersal medium	from glasslands	Total*	from grasslands	Total*
Fleece/fur	29	29	44	86
Hoofs	41	41	36	47
Dung	57	57	20	28
Total	69	69	57	109
% of the local/regional grasslands species pool which produced seeds	50		52	

* The total amount of transported seeds of sheep is higher because they also grazed on fields, roadsides, etc. whereas the Galloways only moved in between grasslands

internal seed purification in the combine, resulting in the blowing-out of the lightest seeds with the removed chaff (e.g. *Apera spica-venti*, *Poa annua*, *Matricaria chamomilla*, *Papaver rhoeas*, *Rumex crispus*, *Sonchus arvensis*) whereas heavy and relatively large diaspores (*Galium aparine*) were carried away in the grain tank of the combine (Petzoldt 1957; Fogelfors 1982; Dollinger 1988). About 40–70% of all weed diaspores pass through the combine; one-third remains in the grain tank, two-thirds are sown again on the field together with the chaff, waste or straw (Fogelfors 1982; Fig. 4).

This example shows that the change of land use practices also resulted in the selection of plant species due to their size and weight of diaspores; those with large and heavy diaspores over those with small, light and flying diaspores (Aamisepp *et al.* 1967; Dollinger 1988). Finally, harvesting by combine led from a clumped to a more homogeneous distribution of weeds due to the dispersal of diaspores over long distances, as demonstrated for *Datura ferox* (Ballaré *et al.* 1987), *Bromus interruptus* and *B. sterilis* (Howard *et al.* 1991; Ghersa *et al.* 1993). Another example of dispersal by machines was given by Strykstra *et al.* (1996), who showed that hay-making machinery is an important dispersal vector whereas mowing by scythe had no seed dispersal effect.

Dispersal by livestock

From a local species pool of 118 species in calcareous grasslands on the Swabian mountains in south-west Germany diaspores of 57 species (52% of the local species pool producing seeds; Table 6) were dispersed by sheep (Fischer *et al.* 1995, 1996). However, this study was done on only one tamed sheep of a flock of 400 sheep and most species were dispersed in only small numbers. Therefore, it is clear that a far higher number of species is dispersed, probably more or less all grassland species, at least in exceptional cases. Fischer *et al.* (1995) calculated that more than 8 000 000 diaspores were dispersed by a flock of 400 sheep during the vegetation period. Diaspores can be transported by the fleece for about 100 days (Fischer *et al.* 1995). The distances which can be walked during that period could come to hundreds of kilometres. Transhumance was formerly widespread in many European countries and herding trails to the domestic livestock markets occurred throughout the whole of central Europe (Hornberger 1959). It is clear that dispersal of species at least from grazed areas was not a limiting factor of the survival of plant populations during that time. This assumption is also supported by studies on the vegetation development of abandoned arable fields after reintroduction of sheep, which caused the invasion of many species which were present neither in the actual vegetation nor in the seed bank (Gibson *et al.* 1987). However, until now there has been no study which could prove the extinction of local populations or even species due to the lack of dispersal by livestock. There are only assumptions such as those from Krauss (1977), who holds the ending of the former migrating sheep and goats responsible for the decrease of *Chenopodium bonus-henricus* populations. Similar causes are supposed by Matthies (1984) with respect to the actual rarity of *Melampyrum cristatum* in calcareous grasslands.

Management of livestock by transhumant or local herding, however, vanished almost totally throughout central Europe and was replaced by stable or paddock management (Erdmann 1983). Only in some places does local herding still occur. Additionally, the number of livestock, especially sheep, decreased tremendously at the beginning of the century (Germany, 1870: 25 million sheep, 1907: 5 million sheep; Lahrkamp 1928) due to cheap imports of wool, fleece and meat, even from overseas.

Dispersal by artificial flooding

The artificial flooding of meadows in flood plains and even in mountain areas for fertilizing after snow melting or heavy rainfall events as well as for irrigation in dry periods was common in Central Europe (Klapp 1971). Some work has been done on the effect these flooding events have had on the species richness of these meadows by dispersing seeds. More than 30 species could be found dispersed by water during an experiment after artificially flooding meadows in the Eder River valley near Marburg (Germany) in June using the old irrigation ditch system (unpublished results). Kelley & Bruns (1975) identified 84–136 species in one year in ditches irrigating arable fields in North America. The quantities extended from 268 to 875 seeds/100 m^3. Schwabe-Braun (1980) and Schüle & Schwineköper (1988) assumed that *Genista tinctoria*, *Hypericum perforatum* and *Tussilago farfara* established in mountain meadows after dispersal by irrigation water.

This traditional land use form became almost totally lost after World War II. However, in 1941/1942 in some regions, e.g. in the Black Forest and Southern Westphalia, more than 20% of the agricultural land was still flooded artificially (Klapp 1971).

DISPERSAL PROCESSES BETWEEN HABITATS

In the traditional man-made landscape, most habitats were connected by dispersal processes (Fig. 5). The type of arable field management in historical times, such as the alternating arable field–fallow or arable field–pasture management (Table 3), connected arable fields to other habitats. In many regions arable fields were used for some years and then abandoned or grazed by livestock (Abel 1962; Pott 1988). Depending on the fertility of the soil, type of management and distance to the village, the fallow or grazing period could be up to 40 years. Abandoned fields were also used in different ways such as pastures. Since the end of the 18th century this alternating arable field–fallow or pasture management was replaced by rotational field management where

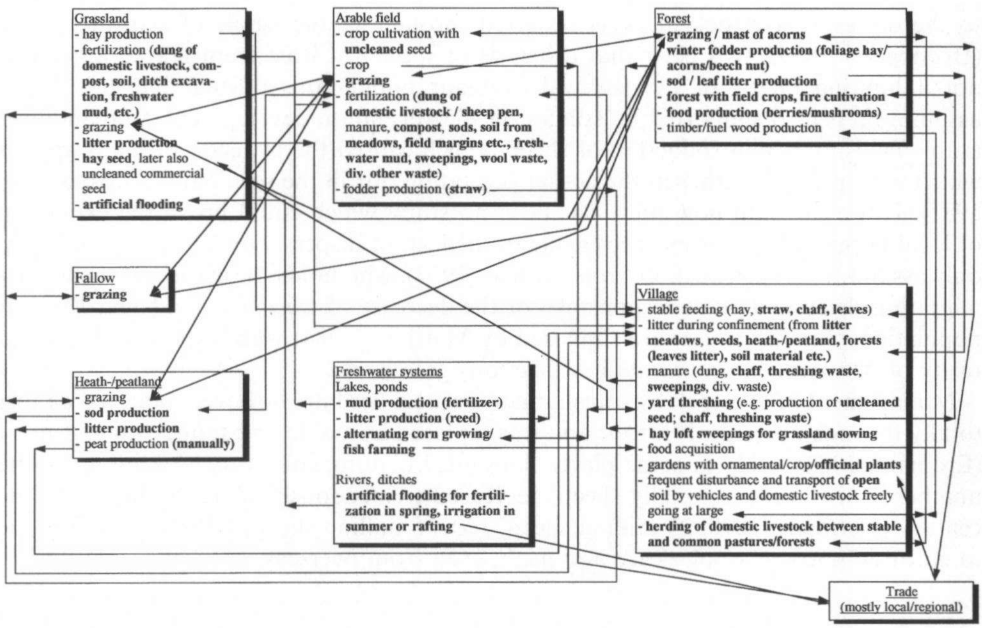

Fig. 5. Processes in the historical man-made landscape more or less relevant for dispersal and reproduction. Bold: forms of farming which have been lost today; arrows: direction of dispersal.

the year or period of abandonment was replaced by the cultivation of root and oil-seed crops, flax, hemp and dye plants (Burrichter *et al.* 1993). Since that time the dispersal of diaspores between arable fields and other habitats occurs only at a very low level or not at all.

Alternating management also occurred in forest habitats such as coppiced woods in southern Westphalia. After coppicing sites were burned and used as arable fields to grow cereal and common buckwheat for 1 or 2 years. During the fallow period *Sarothamnus scoparius* was spread and used as a fodder for sheep and litter for the stables. When the tree canopy again began to dominate the coppice forest was grazed for some years before it was cut again (Pott 1985). Each of these land use forms was connected with the dispersal of seeds mentioned above (Bonn & Poschlod 1998). Taking into account that livestock was more widespread in the traditional man-made landscape and that it was probably the most important local and regional dispersal vector, it connected not only arable fields and grasslands, but also heathlands, peatlands and forests. Of 86 plants indicating forest grazing in the Bavarian Alps (according to Storch 1983; Liss 1988; Rösch 1990) at least 34 are dispersed ectochorously and 55 endochorously by livestock (Bonn & Poschlod 1998). Artificial flooding connected not only meadows to each other (Kleinschmidt & Rosenthal 1995) but more or less all habitats which were adjacent to these ditches. Often ditches coming from villages or towns were used for flooding because they were rich in nutrients (Konold 1987). Sometimes artificial ponds were established in the vicinity of farms in which the slurry and liquid manure were poured into to irrigate or fertilize the meadows (Endriss 1952).

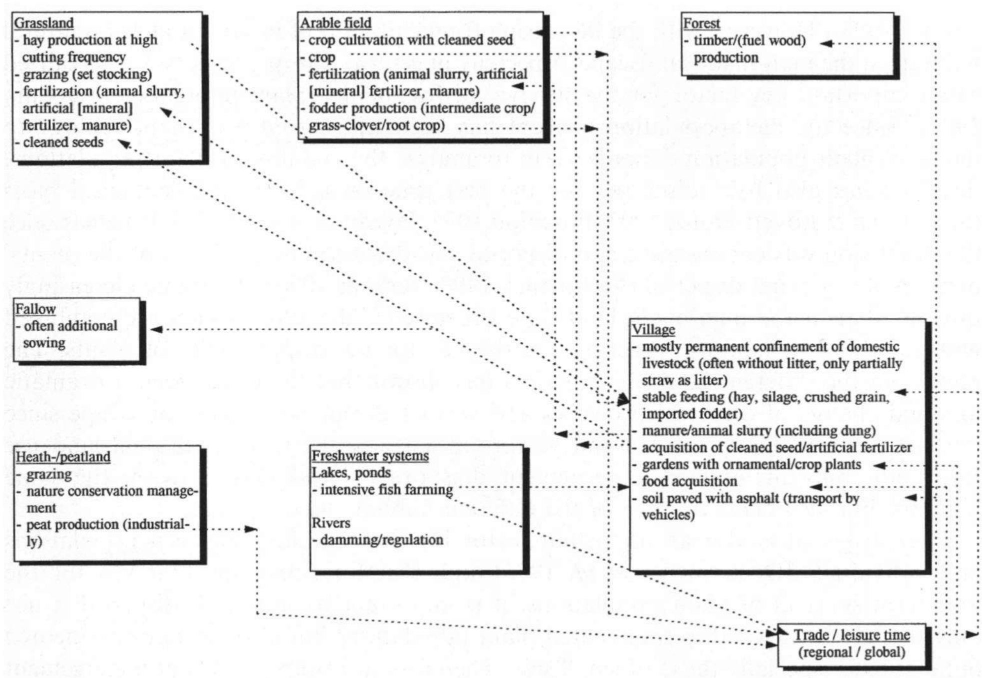

Fig. 6. Processes in the present man-made landscape relevant for dispersal. Arrows: direction of dispersal; dotted line: reduced dispersal relevance compared to the historical man-made landscape.

Today, all these connections have been more or less interrupted (Fig. 6). If there are any processes left, at least the quantities of diaspores dispersed between habitats have been reduced. However, one can stress that trade and traffic increased hugely during the last decades, acting as important dispersal vectors (see above, Di Castri 1989). Trade in particular caused the dispersal of adventive and weedy species (Thellung 1915, Salisbury 1964, Bonn & Poschlod 1998) which established on heavily or often disturbed sites. Of over 12 000 plant species which were introduced into the central European flora by trade only 385 established, 228 from these (mostly cultivated plants) in the semi-natural vegetation, such as *Onobrychis viciifolia* in calcareous grasslands (Kowarik & Sukopp 1986; Lohmeyer & Sukopp 1992). However, agricultural practices were responsible for the dispersal of the species within the landscape. Today, motor vehicles and railways are also known as to be very important dispersal vectors. Wace (1977) found 18 566 seeds from 259 plant species in the mud of a motorcar-washpark in Canberra, Australia. However, it could be shown by Schmidt (1989) that most of species dispersed by cars are growing alongside the roads. That means that dispersal by traffic occurs only alongside the roads. This was also shown along railway lines (Suominen 1979). Therefore, this dispersal vector cannot substitute vectors and processes from the traditional man-made landscape.

IMPLICATIONS FOR RESTORATION ASPECTS

Until recently, dispersal has not been discussed as a limiting factor for the viability of plant populations (Müller-Schneider 1977, 1986; Van der Pijl 1982; Murray 1986;

Fenner 1993). However, with the increasing fragmentation of natural and semi-natural habitats in the man-made landscape, especially in central Europe, dispersal was realized as an important key factor for the survival of fragmented plant populations (Opdam 1990). Since the metapopulation concept has been transferred into plant ecology to interpret plant population dynamics and to analyse the viability of plant populations, dispersal has also been discussed for the first time on a landscape ecological basis (Silvertown & Lovett-Doust 1993; Poschlod 1996, Poschlod *et al.* 1996a). Whereas once the discussion was conservative and dispersal was discussed on the basis of the plants' own traits, e.g. wind dispersal (McCartney 1990; Verkaar 1990), it became increasingly obvious that in the man-made landscape processes and vectors which are combined with the different land-use practices are the key for the dispersability of plants. The review on the different land use practices has shown that there has been a dramatic loss and change of dispersal processes and vectors in our man-made landscape since the last century. The processes and vectors in a landscape with traditional land use forms not only maintained a permanent diaspore or seed flow between the same habitats, but also between most of the different habitats used by man.

Since dispersal is also an important factor for the gene flow between populations and individuals (Oostermeijer *et al.* 1996) and, therefore, an important key for the long-term survival of plant populations, it is important to state that dispersal is not only the key to survival in fragmented plant populations but also for non-fragmented populations, especially those of small size. Therefore, it is important that management and restoration practices in nature conservation include this knowledge in future practices. If dispersal processes cannot be restored it is clear that any efforts in restoration management will be at odds with the goal to provide new habitats for locally or even regionally extinct species, except if they could survive in the diaspore bank. If this is not the case, dispersal processes have to be simulated or replaced by others which can include the artificial reintroduction of species (Tränkle & Poschlod 1995; Biewer & Poschlod 1996).

SUMMARY

During the evolution of the Central European landscape and especially since the settlement of man there has been a permanent change of processes affecting dispersability of plants. In a traditional man-made landscape there was the highest diversity of dispersal processes combined with a high diversity of land use practices. In the actual man-made landscape most of these processes became lost or changed. Due to the rules of seed prescription many weeds became extinct, which were spread in former times with uncleaned seed. Traditional manure contained huge amounts of diaspores whereas today animal slurry with low contents of diaspores or mineral fertilizer are used. Changing harvest methods have selected the dominance of weeds which ripen later and have light diaspores. Herded and transhumant domestic livestock decreased or became locally extinct, which was probably the most important dispersal vector in the Central European man-made landscape. Artificial flooding practices favoured the migration of species in meadows of mountain and floodplain regions.

Whereas in the traditional man-made landscape all habitats were more or less connected due to alternating management or grazing, today most habitats are isolated. With respect to restoration efforts in habitats dispersal processes or vectors should be

included before planning. If there is no possibility of restoring traditional or similar dispersal processes, artificial reintroduction of species is the only option.

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