



River corridor plants (Stromtalpflanzen) in Central European lowland: a review of a poorly understood plant distribution pattern

MICHAEL BURKART *Institute of Biochemistry and Biology, Plant Ecology and Nature Conservation, University of Potsdam, PB 601 553, D-14415 Potsdam, Germany. E-mail: mburkart@rz.uni-potsdam.de*

ABSTRACT

Aim and location In Central European lowlands certain plant species grow mainly or exclusively in the corridors of large rivers. In German-speaking plant geography, they are known as 'Stromtalpflanzen'. The aim of this paper is to review the literature about definitions, explanations and species characteristics and to suggest future directions in research concerning this species group.

Results A preliminary list contains 129 ecologically heterogeneous plant species. The mechanisms generating the peculiar distribution pattern may include hydrochory along river corridors, high levels of disturbance by water, variable water availability including inundation and summer drought, warm summers and high nutrient supply on alluvial soils. There is evidence from observational studies for all above mechanisms. However, none of them has been tested experimentally. Demographic

data of river corridor plants are limited to very few species, including mainly invasive annuals (*Artemisia annua*, *Bidens frondosa*, *Cuscuta campestris*, *Xanthium albinum*) and annual (hemi)parasites (*Cuscuta campestris*, *Melampyrum cristatum*). Meta-population studies do not exist to date for European species. Apart from their habitat requirements, river corridor plants were grouped according to their similarities in overall distribution pattern or their distribution within particular river corridors.

Main conclusions River corridor plants include a high proportion of threatened plant species. In order to preserve them, and in order to understand the mechanisms generating the peculiar distribution pattern, much more has to be known about their population biology and metapopulation dynamics.

Key words Central Europe, flooding, floodplain, linear distribution pattern, plant geography, river corridors, spatial scale.

INTRODUCTION

Rivers form the most important natural corridors through the landscape (Forman, 1983; Forman & Godron, 1986; Borchert, 1992; Gurnell *et al.*, 1994; Puth & Wilson, 2001). In temperate zones, river corridors contain many plant and animal species. In particular, the riparian zones are considered hotspots of species diversity (Gepp *et al.*, 1985; Naiman *et al.*, 1993; Décamps & Tabacchi, 1994; Brandes, 1996; Naiman & Décamps, 1997). In many regions of the world the occurrence of certain vascular plant species is restricted to river

corridors. Therefore, understanding the mechanisms which generate the plant species diversity in these parts of the landscape is a challenge. One element is an understanding of the factors which limit the distribution range of plant species that are restricted to river corridors.

One important factor is the water. This is obvious in arid and semi-arid environments, where restrictions in water supply may bind trees, lianas and herbs to watercourses (Bruner, 1931; Hughes, 1988; MacMahon, 1988; Hovestadt *et al.*, 1999; Van den Berg & Oliveira-Filho, 1999). In humid areas, however, the causal connection is less obvious.

This paper deals with the lowlands of humid Central Europe. Central Europe consists of the Alps in the south, of the highlands of south and central Germany, the Czech Republic and Poland and of the northern lowland with its German and Polish parts. The phenomenon that plant species may occur in a river corridor distribution pattern in the lowland has long been recognized (Ascherson, 1859, 1864; Steinvorth, 1864). The term 'Stromtalpflanzen' was coined for species showing such a pattern in German plant geography by Loew (1879), who described the detailed distribution of 45 species in the river systems of the Vistula (Wisla, Weichsel), the Oder (Odra) and the Elbe (Labe). As several others have done since (Potonié, 1887; Preuss, 1909; Steffen, 1924; Hegi & Beger, 1925; Waldenburg, 1934), he regarded present-day river corridor distributions of plants as remnants of prehistoric migration routes. In contrast, according to Schalow (1912), the river corridor distribution pattern was a remnant of a different climate rather than a remnant of migration routes. He maintained that a postglacial period of warmer climate allowed the river corridor plants to spread throughout the landscape and later colder periods pushed them back to the warmest parts of the river corridors.

The scientific controversy between migration-related and climatic explanations was fought for several decades (e.g. Scholz, 1905; Schulz, 1907; Schalow, 1912, 1921; Ulbrich, 1925; Libbert, 1931, 1938), but with little evidence beyond the observed distribution patterns themselves. The controversy was based partly on misunderstandings and inconsistencies in the species pool concerned. For example, Loew had related his migration theory also to steppe xerophytes, which supposedly used different migration routes than river corridor plants.

Later, Meusel (1943) emphasized the role of environmental factors in controlling plant distribution patterns. He pointed to the general difficulty in explaining corridor-like patterns along linear structures such as rivers, although identifying the pattern as such was easy. In the subsequent boom of plant geography in East Germany, species distribution maps of river corridor plants were presented by the Arbeitsgemeinschaft mitteldeutscher Floristen (1955, 1960), by Fischer (1959), Jage (1962), Müller-Stoll *et al.* (1962) and Vent & Benkert (1984). These and later works focused on ecological explanations for the river

corridor distribution patterns they found. In this work, I review the various ecological explanations and discuss their plausibility.

Although long established in German plant geography, the term 'Stromtalpflanze' has no equivalent in international literature. It is neither included in German-English dictionaries of botany, biogeography, landscape ecology and related fields (with the exception of Eichhorn, 1999), nor is it used in reviews (Gaston, 1990; Dawson, 1994; Barrat-Segretain, 1996; Brown *et al.*, 1996), or textbooks (Forman & Godron, 1986; Myers & Giller, 1988; Sauer, 1988; Mitsch & Gosselink, 1993). Even authors who were familiar with German and French textbooks from the late 19th and early 20th century did not use this term (Wulff, 1950; Dansereau, 1957; Polunin, 1960; Good, 1974). Two appropriate English translations may include 'river valley plants' and 'river corridor plant species'. I suggest the term 'river corridor plants' for international use. 'River valley plants' may imply plants growing in deeply incised valleys, while the slopes of river corridors in Central European lowland are usually neither steep nor high and sometimes even merge with the surrounding landscape.

The aim of this review is to present an overview of the knowledge about river corridor plants, which is scattered through various mainly German-written papers and books. Emphasis is laid on hypotheses that try to explain the phenomenon 'river corridor plants' in the Central European lowland. A preliminary, unassessed list encompassing 129 river corridor plant species of that region is given in the appendix, including authorities of species names and an explanation of the compilation criteria.

DEFINITION AND FUNDAMENTALS

Since river corridor plants are not an ecologically uniform group, the definition should refer only to the distribution pattern (Brandes, 1996; Korsch, 1999). A river corridor plant may be defined as a plant species that occurs exclusively or predominantly in the corridors of large rivers in a given area and time (Müller-Stoll *et al.*, 1962; Vent & Benkert, 1984; Zacharias & Garve, 1996).

Rivers may be classified as large according to their length, drainage area or discharge (Arbeitsgemeinschaften der Landesanstalten ... , 1994; Dynesius & Nilsson, 1994; Herschy, 1998). Accordingly, in

Table 1 Large river systems of northern Central Europe. Discharge data according to Herschy (1998). VMAD ('virgin mean annual discharge') is 'the discharge before any significant human manipulations' (Dynesius & Nilsson, 1994)

Name	Length (km)	Catchment area (1000 km ²)	Discharge (m ³ /s)	VMAD (m ³ /s)
Vistula/Wisla/Weichsel + Bug	1200	194	1040	1080
Elbe/Labe	1160	144	703	750
Odra/Oder	950	119	560	580
Weser + Werra	730	46	334	360

northern Central Europe, the systems of the Weser, Elbe (Labe), Oder (Odra) and Vistula (Wisla, Weichsel) rivers may be classified as large (Table 1). The advantage of using the discharge classification is that it allows the use of a set threshold from where downstream a river can be called large, excluding its upper smaller courses. According to Dynesius & Nilsson (1994), an appropriate discharge threshold is 350 m³ s⁻¹.

A river corridor consists of the water body, the river banks, the floodplain, i.e. those parts of the landscape that experience periodical flooding (recent floodplain) or did so in former times (historical floodplain) and surrounding, episodically flooded or non-flooded areas that can be assigned to the river corridor by geomorphological traits, including older terraces and valley slopes (Forman, 1983; Forman & Godron, 1986; 'stream corridor'). A special case of river corridors are the glacial valleys in the Central European lowland, which are only partly corridors of recent rivers. Other parts are covered with mires, mainly drained today, with relatively small streams running through. Some species of river corridor plants are restricted to corridors of recent rivers, while others are also found in the glacial valleys (Zacharias & Garve, 1996).

The river corridor distribution type is a special case of disjunction (Walter & Straka, 1970; Brandes, 1996). It is found typically only towards the border of a plant species' range (Fig. 1). Therefore, it is necessary to specify the region where the attribute 'river corridor plant' applies (Vent & Benkert, 1984; Zacharias & Garve, 1996).

Invasive species often start to spread along watercourses, and 'inland' areas are possibly invaded later (Sauer, 1988; DeFerrari & Naiman, 1994; Pyšek & Prach, 1994; Müller & Okuda, 1998; Pyšek *et al.*, 1998). At certain times they might

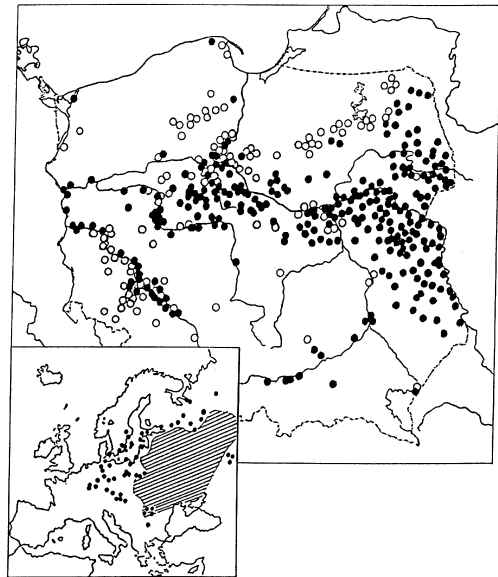


Fig. 1 Distribution of *Cnidium dubium* in Europe from Hultén & Fries (1986; small map) and in Poland (large map), both modified from Zaluski (1995). Solid dots in the large map: occurrences confirmed by Zaluski, open dots: occurrence not confirmed. *Cnidium* is a river corridor plant in Central Europe, but not in Eastern Europe. The map of Poland displays part of the transition zone. The map of Europe is approximately 4500 × 4500 km², the map of Poland 730 × 770 km² in size.

therefore appear as river corridor plants. In such cases the time span for when the assignment is valid must be specified to avoid misunderstanding (Zacharias & Garve, 1996).

In order to recognize a river corridor distribution pattern, i.e. the distribution pattern of a river corridor plant in a given area and time, the spatial scale of observation must be appropriate.

The grid in Haeupler & Schönfelder (1989; about 11×11 km) is approximating the upper limit, as can be seen directly on the maps (see Figs 2 and 3 for examples). A lower boundary does not exist, although it will often be set by limits of available manpower for distribution mapping in the field. However, the total area examined must be large enough. Zacharias & Garve (1996) operated near this lower limit. Their study area of about 250 km² still yielded satisfactory results (see below).

Ward *et al.* (1999) provided a hierarchical framework for research in floodplains, proceeding from physiographic region (the highest level) over catchment and floodplain to biotope (originally called 'water body' because only aquatic and semi-aquatic biotopes were considered) and habitat patch. In this framework, floodplain clearly is the appropriate level to recognize river corridor distribution patterns, whereas the lower levels are suitable for the examination of habitat requirements of the species studied.

EXPLANATORY HYPOTHESES

The distribution range of any given species is the result of the characteristics of the species that interact with the ecological conditions over time. For any given river corridor plant species there must be a combination of certain abiotic and biotic variables, whose historical and recent interplay determines the river corridor distribution pattern of that species.

The large group of Central European river corridor plants is very heterogeneous. It includes species growing on different substrates such as dry sand, floodplain clay or in the water. Life-forms consist of herbaceous annuals, biennials, perennials, hemiparasites, parasites and woody plants. It is therefore unlikely that a single encompassing hypothesis may explain the river corridor distribution patterns of such a variety of species (Vent & Benkert, 1984). The mechanisms that generate the distribution pattern most probably vary among groups of taxa with different site requirements, life forms or strategy types.

Migration and invasion

The range expansion of plants, sometimes called 'spread' (Bennett, 1986), is here termed 'migration' (Sauer, 1988; Dingle, 1996). I distinguish

between 'natural migration' and 'invasion', the latter being initiated or facilitated by human activities (Pyšek, 1995). Originally, there was a strong connection between the term 'Stromtalpflanze' and the idea of river corridors as migration routes for plants (Loew, 1879). Water was suggested to be the main migration vector (Ascherson, 1864; Loew, 1879). Later, ornithochory received particular attention (see below). Zoochore migration may also take place via mammals, which are believed to use river corridors for their migrations. However, there is very little evidence for the use of river corridors as migration routes by any group of vertebrates except fish (Forman, 1983; Décamps *et al.*, 1987; Dawson, 1994; Machtans *et al.*, 1996; Naiman & Décamps, 1997). Anecdotal evidence suggests dispersal of seeds by domestic sheep in the highlands of southern Germany, which grazed especially in basins and river valleys during winter (Hornberger, 1959; after Bonn & Poschlod, 1998).

Obviously, river corridor plants cannot reach the catchments of different rivers by *trans*-corridor migration, unless there is a connecting corridor between them. It is true that the glacial valleys connect all large river systems in the Central European lowland. Such connections do not exist, however, between the watersheds of the Rhine, the Danube and the lowland rivers, although some river corridor plant species occur in the floodplains of all of them. This fact shows the general restriction of all migration-related explanations. As a specific example, genetic analyses of *Corrigiola litoralis* populations did not support the idea of the colonization of whole catchments by migration along the river corridors by this species (Durka, 1999).

Hydrochory

Hydrochory is the most straightforward explanation for river corridor distribution patterns. Therefore, it played a prominent role from the beginning of scientific interest in river corridor plants (Ascherson, 1859; Loew, 1879; Zobel, 1930; Walas, 1938; Jage, 1964). While the emergence of seedlings from flood debris has often been observed (Behning, 1928; Dierschke, 1984; Xiong & Nilsson, 1997; Gerken *et al.*, 1998), the emerging species are not predominantly river corridor plants, but commonly distributed ruderals (Hölzel & Otte, 2001).

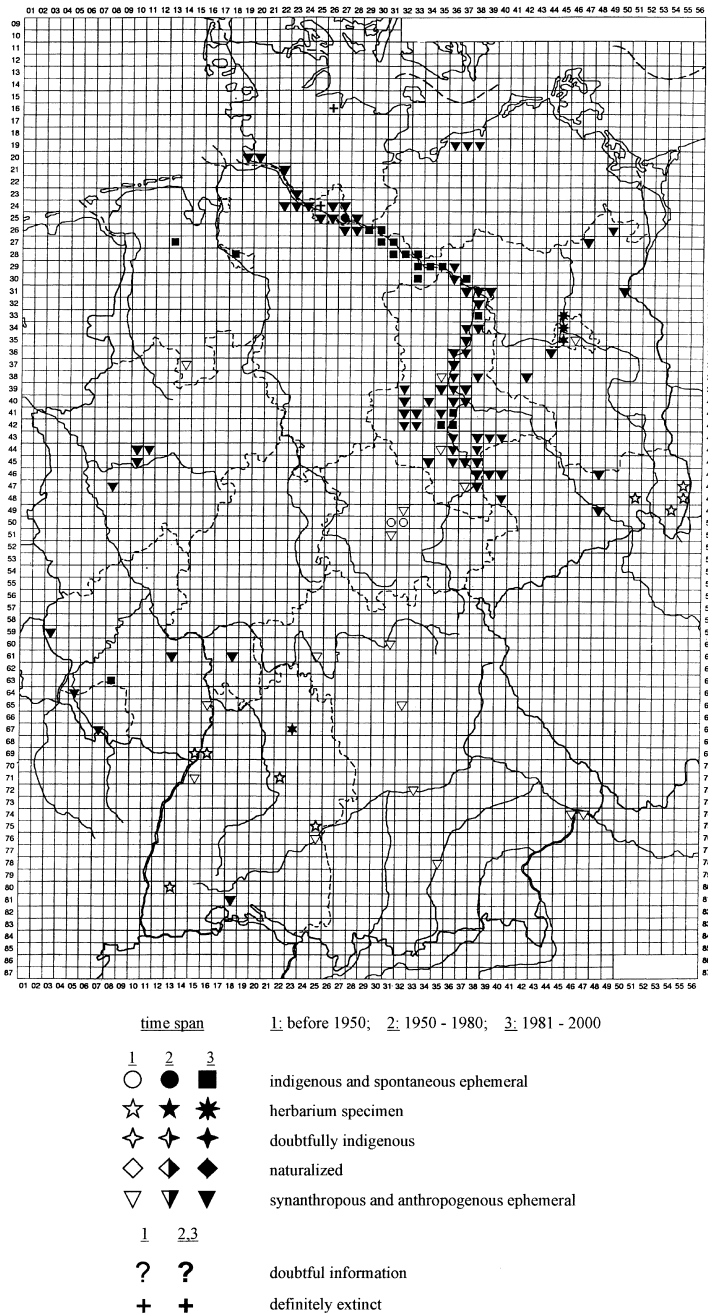


Fig. 2 Distribution map of the invasive river corridor plant *Artemisia annua* in Germany. Findings from the northern part of East Germany are all after 1960 (Brandes & Sander, 1995). The mouth of the Saale, tributary to the Elbe, is in grid cell 4037; both rivers are flowing from the south. Unpublished data from the German Federal Agency for Nature Conservation (1999). Data are not corrected for the status in the Elbe corridor, where the species is fully naturalized. The grid is equivalent to 10' longitude and 6' latitude, which corresponds to approximately 11 × 11 km².

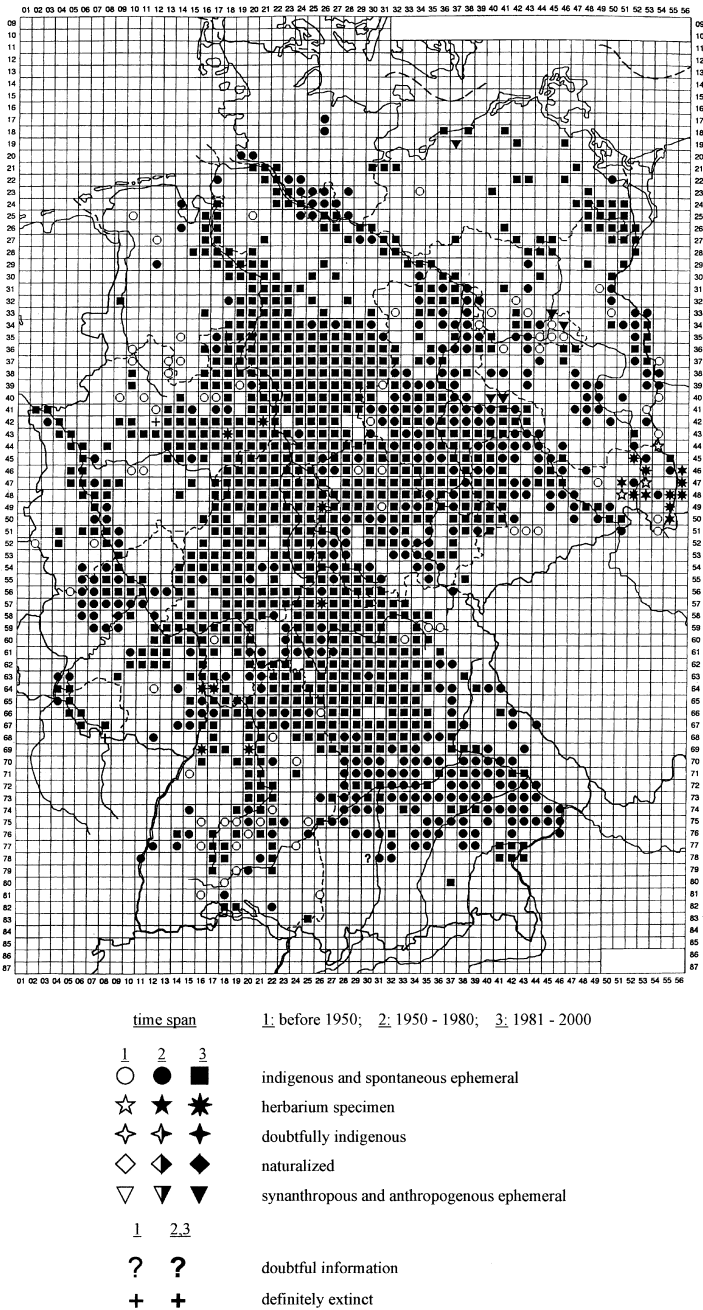


Fig. 3 Distribution of *Chaerophyllum bulbosum* in Germany. *C. bulbosum* is a river corridor plant in the north-western lowland, but not in the Central and southern highlands. Unpublished data from the German Federal Agency for Nature Conservation (1999). The grid is equivalent to 10' longitude and 6' latitude, which corresponds to approximately 11 × 11 km².

Hydrochory is only possible downstream. Both buoyant and non-buoyant seeds can be transported by flowing water over a long time, as is the case for floating seedlings (Barrat-Segretain, 1996). Thebaud & Debussche (1991) showed evidence for a downstream migration of *Fraxinus ornus* L. on the river Hérault in southern France, at a speed of as much as 1 km a⁻¹, which could only be explained if seeds were transported by water. Johansson & Nilsson (1993) found that the native helophyte *Ranunculus lingua* L. was exclusively propagated by water in a northern Swedish river system. In the same area, Johansson *et al.* (1996) showed a positive correlation between frequency of occurrence and diaspore floating capacity of plant species on river banks in contrast to boreal forests and grasslands. Brandes & Sander (1995) argued for a downstream migration of the invasive river corridor plant *Artemisia annua*, a native of Central Asia, and of some other species along the river Elbe from the mouth of its tributary Saale (Fig. 2). Bonn & Poschlod (1998) reviewed a number of studies which indicate downstream diaspore transport by water in several parts of Europe, mostly in mountainous areas. They argue for a more adequate appraisal of the role of hydrochory for plant dispersal, which they consider to be underestimated, especially in relation to anemochory (see Cook, 1987).

All the above examples refer to invasive species or to regions outside the Central European lowland. There is little evidence that hydrochory is the main cause for the river corridor distribution pattern of indigenous species in the Central European lowland and highlands.

Ornithochory

Recently, ornithochory of European river hydrophytes was reviewed by Barrat-Segretain (1996). He concluded that 'external transport of propagules ... is probably effective at relatively short distances', but admitted that the effectiveness of both external and internal transport is difficult to evaluate. External (epizoochore) diaspore transport by birds was rarely observed (Cook, 1987; Bonn & Poschlod, 1998). Kerner von Marilaun (1898) and Bernhardt (1989) found diaspores of several plant species of wet environments in mud crusts on the feet and beaks of birds or directly attached to the plumage. These diaspores included the river corridor plants *Juncus compressus* and *Lindernia*

procumbens. Internal (endochore) and dyschore ornithochory (seeds lost before being swallowed) are probably less relevant for Central European river corridor plants, since only a few species have fruits attractive to birds (e.g. *Cucubalus baccifer*).

Many wetland plants occur in both the northern and southern hemispheres, but they are often restricted to the New or the Old World. Such an extrazonal distribution pattern is rarely found in plants from other habitats. The reason for this phenomenon may be in external propagule transport by migratory birds (Jäger, 1992). Observations of colonizing plants in newly created and/or isolated habitats are scattered through the literature, and are often explained by ornithochory.

Gams (1927) postulated a relationship between the Central European river corridor range of *Scutellaria hastifolia* and bird migration routes (as did Wein, 1930), for *Salvinia natans* in south-west Europe). For Central Europe, this hypothesis is easy to refute. In Central Europe, corridor-like routes of migration have been recognized to be rare and restricted to a few large bird species (Berthold, 1990; W. Fiedler, pers. comm.), such as crane (*Grus grus* L.) and stork (*Ciconia ciconia* L.). Whereas they migrate roughly in a south-western–north-eastern direction (W. Fiedler, pers. comm.), the large rivers in the Central European lowland flow in northern or north-western directions.

To summarize, diaspore transport by birds may be important for the general dispersal of some river corridor plants, but it is not responsible for their river corridor distribution pattern in the Central European lowland.

Disturbance

Disturbance, particularly by water, is an important ecological factor in river corridors (Hejny, 1960; Van der Valk, 1981; Day *et al.*, 1988; Baker, 1990; Naiman *et al.*, 1993; Plachter & Reich, 1998; Pollock *et al.*, 1998; Ward, 1998). The importance of disturbance in the occurrence of river corridor plants was emphasized by Tüxen (1950), Walter & Straka (1970), Vent & Benkert (1984) and Jentsch & Seitz (1997).

Disturbance by water in floodplains has two aspects. First, flooding results in a strong reduction of gas exchange below- and above-ground. Plants must be adapted to such conditions to survive in these habitats (Crawford, 1987; Blom

et al., 1990; Janiesch, 1991; Blom, 1999). Secondly, extended periods of flooding may significantly reduce survival or establishment of perennial terrestrial plants, while on the other hand, the terrestrial phase, although perhaps short, inhibits establishment of the hydrophytes (Hejny, 1960). The resulting sites with reduced plant cover are open for colonization. Moreover, strong floods can erode and deposit substrate and thus create colonizable sites.

Flooding

Several studies have investigated the effects of flooding on river corridor plants and other plant species. For example, *Bolboschoenus maritimus* (river corridor plant) survived for a longer time under anoxia than most other reed plants (Braendle & Crawford, 1987; Crawford *et al.*, 1989). *Thalictrum flavum* (river corridor plant) was more tolerant to flooding than *Lychnis flos-cuculi* L., *Cardamine pratensis* L., *Senecio aquaticus* Hill and *Bromus racemosus* L. which occurred in the same meadow complex near Bremen in north-west Germany (Bernhardt *et al.*, 1999). *Chenopodium rubrum* (river corridor plant), however, proved to be more susceptible to flooding than *Rumex palustris* and *R. maritimus*, which grew on the same sites but are not river corridor plants (Van der Sman *et al.*, 1993). The river corridor plant *Rumex thyrsiflorus* did not show better adaptation to flooding than the closely related *R. acetosa* L. growing on similar sites (Blom *et al.*, 1990). *Bolboschoenus* and *Thalictrum* grow in rather wet places, while *Chenopodium* is a strictly terrestrial annual of long-flooded sites, and both *Rumex thyrsiflorus* and *R. acetosa* are not found in long-flooded places (Wisskirchen, 1995; Burkart, 1998). To summarize, flood tolerance may be an important adaptation for perennial river corridor plants that grow in wet places, but it does not explain the distribution patterns of many others.

Providing open sites

Open sites may be colonized by short-lived terrestrial plants that form characteristic phytocoenoses (classes Isoëto-Nanojuncetea and Bidentetea in the Braun-Blanquet system). The species of this group normally build up a perennial seed bank that enables them to survive several unfavourable years (Poschlod, 1996; Abernethy & Willby, 1999; Poschlod *et al.*, 1999). Such species usually play a prominent role in open riparian habitats with

moderate sediment dynamics. They are not found exclusively in river corridors, but also in similar habitats such as lake shores and drained fishponds. However, some of the species are river corridor plants, such as *Lindernia* spp. and *Cyperus michelianus*.

Riparian habitats are exceptionally rich in invasive plants, and many invasive plant species show a river corridor distribution at least in the early periods of their invading history (Pyšek & Prach, 1994). Availability of open colonizable soil is the most likely reason for this pattern (Crawley, 1987; Ramakrishnan & Vitousek, 1989; Jäger, 1992; Pyšek & Prach, 1994; Löscher *et al.*, 1995; Müller, 1996; Müller & Okuda, 1998; Pyšek *et al.*, 1998). Similar to invaders, some native herbaceous perennials which have a river corridor distribution in Central Europe are known as pioneer colonizers. These include *Gratiola officinalis* (Rijpert, 1977; Peintinger, 1994; Burkart & Prasse, 1996), *Juncus atratus* (Burkart, 1995), *Petasites spurius* (Walther, 1977) and *Scutellaria hastifolia* (Andres & Westhus, 2000; C. Andres, pers. comm.).

Despite the fact that disturbances are widely accepted as important ecological factors in river corridors, their importance for the river corridor distribution pattern of plant species is clearly recognizable only for invaders and a few native species.

Water supply

In floodplains, hydrological conditions are the major force controlling plant distribution (Ellenberg, 1996). In temperate regions, water-levels of rivers with prevailing highland catchments have maximum discharge in spring and minimum discharge in late summer and autumn. In large rivers, annual water-level variations may be several meters, causing alternating inundation of vast areas of the floodplain relief. During times of low water-levels, even parts of the formerly inundated areas may suffer severe drought, which may be amplified by low precipitation (Passarge, 1993). For example, summer drought may explain the distribution of the river corridor plant *Juncus atratus* in north-east Germany (Burkart, 1995; Fig. 4). Similar conditions have been found in southern East Europe, where snow accumulates in depressions away from floodplains during the permanent winter frost and flooding occurs when

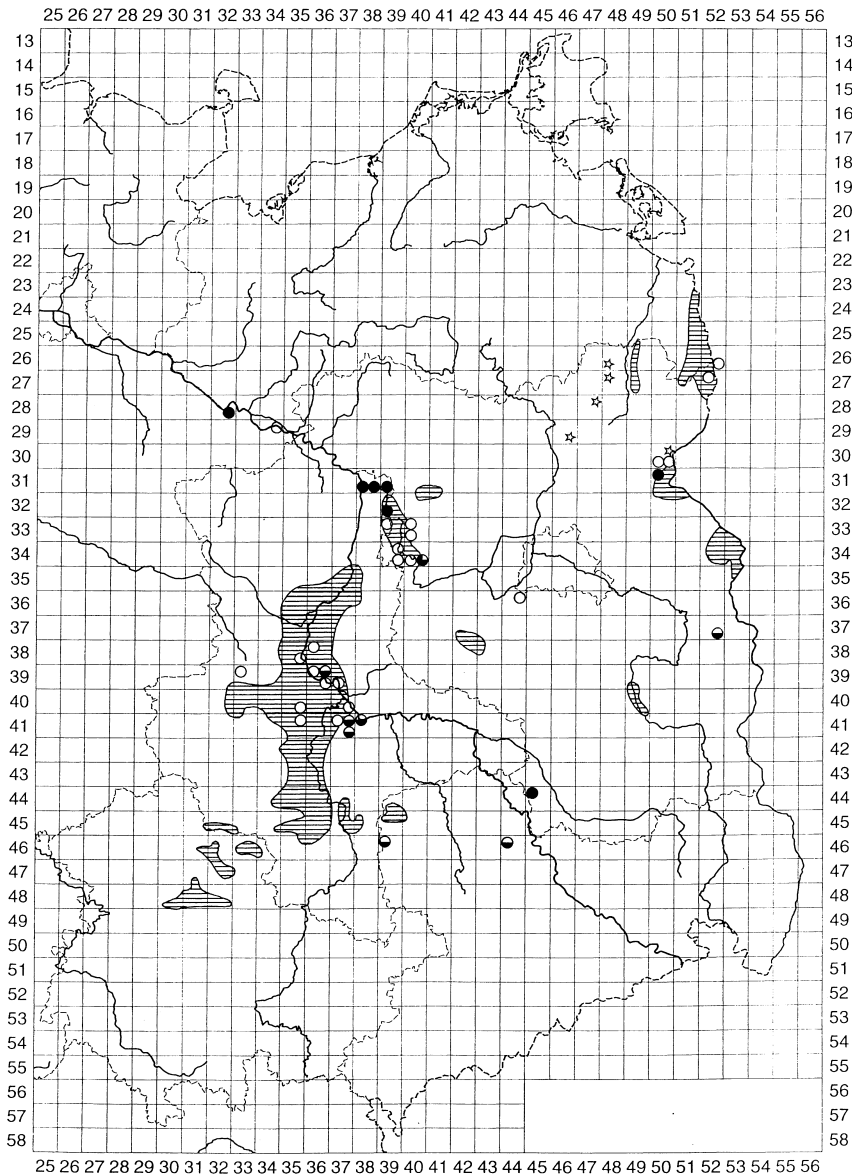


Fig. 4 Former and recent distribution of *Juncus atratus* in North-East Germany (dots) and areas with precipitation April–September < 300 mm (hatched). From Burkart (1995). The grid is equivalent to 10' longitude and 6' latitude which corresponds to approximately $11 \times 11 \text{ km}^2$, while the species is mapped with double resolution (5' longitude and 3' latitude). ● recent observations (after 1970); ● before 1945; ○ before 1900; ☆ uncertain.

the snow melts in spring, while in summer, marked dry conditions occur (Grimm, 1968; Walter & Straka, 1970; Walter, 1974; Golub & Saveljeva, 1991). Here, river corridor plant species of Central Europe can be found, for example, *Achillea*

salicifolia, *Juncus atratus*, *Euphorbia palustris* and *Gratiola officinalis* (Golub & Saveljeva, 1991; Golub & Tchorbadze, 1995).

These observations suggest that summer drought is a relevant climatic factor for the river corridor

distribution pattern of some species. However, no suggestions have been published concerning the underlying mechanisms. These may include effects on flowering or seed ripening.

Summer warmth

Valleys show higher thermic continentality than their surroundings (Jäger, 1968; Van Eimern & Häckel, 1984). However, the influence of temperature on floodplain plants is less well investigated than that of water conditions (Naiman & Décamps, 1997). Jäger (1968) suggested that high summer temperature may be the main factor determining the north-western distribution boundary of certain continental plant species. Also, warm summer conditions in river corridors was stated to be an important factor for river corridor plants in Brandenburg in north-eastern Germany (Müller-Stoll *et al.*, 1962; Vent & Benkert, 1984). However, Vent & Benkert (1984) point to the lack of climatic data to confirm the above hypothesis.

Some evidence for the climatic hypothesis was found by Goebel (1995), who compared climatic data from the Rhine–Main river floodplain (80–90 m a.s.l.) and the adjacent cooler and wetter Messel highlands (140–230 m a.s.l.; Hesse, south-west German highlands, about 30 km distance). He found a gradient in mean summer warmth of 2 K (and in mean growing-season precipitation of 185 mm), which corresponded to the occurrence of river corridor plants such as *Cnidium dubium*, *Allium angulosum*, *Senecio paludosus* and *Euphorbia palustris* in the warmer and drier river valley. These species were not found in the Messel highlands adjoining to the east (Goebel, 1995), as well as in the Palatinate highlands in the west (Orschiedt, 1996).

In the Central European lowland, however, evidence for the summer warmth hypothesis is weak. Here, the river corridors are generally much less marked valleys than in the southern highlands, with correspondingly less pronounced climatic deviations.

Nutrients

In the Central European lowland, the corridors of large rivers are mainly covered by Holocene sediments rich in clay, while sandy material is prevalent in their surrounding areas. In addition, the

regular flooding of the areas in the bottom of the valley implies an increased input of nutrients. This leads to a marked difference in nutrient supply, with the floodplains representing relatively nutrient-rich corridors in a nutrient-poor landscape (Jage, 1962; Vent & Benkert, 1984; Fischer, 1996).

There are many river corridor plant species that require high nutrition levels. They are often herbaceous perennials and biennials growing in floodplain forests or on their margins and in herbaceous riparian vegetation (*Convolvuleta* communities; Freitag, 1962; Vent & Benkert, 1984; Fischer, 1996). Among them are also many river corridor neophytes (i.e. non-native species introduced after 1500 AD), e.g. *Aster* spp., *Amaranthus* spp. and *Bidens* spp. If nutrient supply due to soil differences is the main factor for the river corridor distribution of plant species, they should show no such pattern in regions without a marked difference of soil conditions. This is easy to detect by comparison of their distribution area with soil maps. For example, *Chaerophyllum bulbosum* is a river corridor plant in the north-western lowland, but not in the adjacent highlands, where the surroundings of the river corridors are not generally poor in nutrients (Fig. 3). Detecting the connection is not as easy for invasive species which do not yet occupy their whole potential range.

Although it is easy to delimit the group of river corridor plants for which the nutrient hypothesis may be relevant by comparison of maps, such an evaluation only exists for Lower Saxony (West Germany; Zacharias & Garve, 1996; see below).

Other factors

The variety of possible ecological factors mentioned above suggests that combinations between them should be taken into consideration. Temperature and water supply in combination were suggested to determine the river corridor distribution pattern of *Euphorbia palustris* (Meusel, 1943). For Lower Saxony, Zacharias & Garve (1996) suggested that both high cation supply and summer warmth may be responsible for the lowland river corridor distribution pattern of some species (mainly grassland perennials) that have a wide distribution range in the highlands.

Also, there may be corridor-specific indirect effects mediated through other ecosystem features. For example, herbivore insects or slugs may be negatively affected by floods or drought.

A certain group of perennial herbs occurs both in corridors of recent rivers as well as in glacial valleys with only small streams. These species are relatively long-lived and have been regarded as relics from the early Holocene or late Glacial, when these valleys were formed by large glacial rivers with much higher discharge and a correspondingly high disturbance potential (Zacharias & Garve, 1996).

To summarize, there are numerous relevant factors and the relative importance of them differs greatly between species and between regions.

POPULATION ECOLOGY

There are few studies on the population ecology of river corridor plants. Köck (1988) compared the invasive *Bidens frondosa* with the native *B. tripartita* L., and he explained the invasion success of the former by lower germination temperature, faster growth and higher diaspore production. Matthies (1991) undertook detailed demographic studies on the hemiparasites *Melampyrum cristatum* and other *Melampyrum* species, but the results are not from river corridors. Demographic data are also available on the river corridor plants *Xanthium albinum* and its parasite *Cuscuta campestris* (Belde, 1996) and on *Artemisia annua* (Müller, 1996; Müller & Brandes, 1997). The latter authors suggest that *A. annua* is only a temporary river corridor plant whose spread into the surrounding landscape has been delayed.

Several studies were conducted about diaspore longevity and diaspore banks of different species including river corridor plants (Bernhardt & Kundel, 1993; Poschlod, 1993; Kleinschmidt & Rosenthal, 1995; Kallen, 1996; Vogel, 1997; Abernethy & Willby, 1999; Albrecht, 1999; Poschlod *et al.*, 1999). However, there is no synopsis of this field with sufficient representation of river corridor plants, except for the comprehensive database by Thompson *et al.* (1997), which contains information about 31 of the 129 species in the appendix. No metapopulation study is available for any European river corridor plant species to date, although a study about the lower Elbe endemic *Oenanthe conioides* is in preparation (P. Poschlod, pers. comm.).

SPECIES CHARACTERISTICS

Distribution types

Grisebach (1847) combined plant species with common or very similar ranges into chorological groups and thus founded a long tradition of comparative phytochorology in Germany (e.g. Meusel, 1943; Meusel *et al.*, 1965, 1978; Jäger, 1968, 1970; 1970; 1990; 1992; Meusel & Jäger, 1992). Six groups ('chorotypes') of river corridor plants can be distinguished in Central European lowland according to the core of their distribution range: (sub)continentals, (sub)Mediterraneans, (sub)oceanics, montane-alpines, neophytes and river corridor endemics.

Some river corridor plants are limited strictly to river corridors in a given area. Others spread along smaller watercourses as well, they may occur sporadically throughout the landscape, or are found both in recent floodplains and glacial valleys. Similar chorotypes were distinguished by Vent & Benkert (1984) and Zacharias & Garve (1996) based on country-wide maps. The latter developed an additional, but corresponding grouping based on small-scale spatial distribution patterns in one section of the Elbe floodplain (250 km²).

Only very few river corridor plants of Central European lowland are restricted to river corridors throughout their whole range. For example, *Cyperus michelianus* (see map in Von Lampe, 1996) and *Euphorbia lucida* (see map in Slavik, 1973) occur almost exclusively in river corridors. *Deschampsia wibeliana* and *Oenanthe conioides* are endemic to the tidal zone of the Elbe river (see Garve, 1994; for a detailed map).

Each of the large rivers in the Central European lowland contains a unique set of river corridor plant species and only few species occur in the corridors of all of them. Long ago, Ascherson (1859) distinguished between river corridor plant species of the Elbe, the Oder and species common to both rivers. Similarly, Korsch (1999) distinguished between four groups of river corridor plants based on grid maps of their distribution in East Germany. A clustering based on the grid map data of the flora of the Palatinate (south-west German highlands) resulted in 74 chorotypes (Orschiedt, 1995, 1996), including three species groups that consist mainly of river corridor plants. However, the term 'Stromtalpflanzen' was not used for these plant species groups.

Functional groups

There are not yet many answers to the question of which features of river corridor plants may be important for classifying them into functional groups. Brandes (1995, 1996) found a high percentage of plants with a C_4 metabolic pathway among floodplain vegetation of Central Europe. Hills *et al.* (1994) analysed West European riverine ecosystems using Grime's CSR model (but omitting the R strategy type). They computed competitive ability and stress-tolerance as survival strategies per population by discriminant analysis of measured population traits, such as plant height, dry weight of leaves and seeds. The examined species included the Central European river corridor plants *Eryngium campestre* and *Mentha pulegium*. The latter was found to be a weak competitor with intermediate stress-tolerance, *Eryngium* was classified as highly competitive.

It has been found that many river corridor plants are invaders. The question of whether traits of plants can be identified that make them successful invaders has often been addressed (Pyšek *et al.*, 1995; Rejmánek, 1995; Pyšek, 1997, and references therein). There is some agreement that no common answer can be given, but Pyšek *et al.* (1995) found that invasion success in seminatural habitats (including wetlands and water-courses) was favoured by plant height, hemicryptophyte life form and C-strategy. Also, on the average, successful (i.e. abundant) invaders were colonizing wetter sites more frequently than unsuccessful species.

Functional investigations of North American wetland species were conducted by Van der Valk (1981), Day *et al.* (1988) and Boutin & Keddy (1993). Life-history traits and growth manner were especially included in their analyses, resulting in 12, five and seven functional groups, respectively. Naiman & Décamps (1997) distinguished three broadly defined categories of plant adaptations to flood disturbance in floodplains, i.e. invaders (characterized by many anemochore or hydrochore seeds), endurers (resprouting after the flood) and flood resisters, supplemented by avoiders (all other species) that lack adaptations to flooding and are therefore only rarely found in floodplains.

Distribution characteristics were often used to combine river corridor plants of Central Europe

into groups. A grouping based on other features of the species, especially functional traits, does not yet exist for Central Europe.

CONCLUSIONS

Recently, there has been an increasing number of studies dealing with numerical analyses of distribution data of plant species (e.g. Orschiedt, 1995, 1996; Márquez *et al.*, 1997; Kunin, 1998; Nimis *et al.*, 1998; Kadmon & Danin, 1999). However, quantitative approaches to distribution patterns are still relatively uncommon in plant biogeography. Until now, no attempt has been made to develop 'hard' criteria for determining whether a given species is a river corridor plant or not. For example, one may attempt to establish quantitatively, whether there is a genuine correlation between the occurrence of large rivers and certain plant species in grid map cells of a selected area.

While much has been written about the river corridor plant distribution pattern itself, almost nothing is known about the mechanisms causing the observed pattern. Evidence is often anecdotal and based on correlative rather than experimental studies. However, in order to establish a causal understanding of the relationship between pattern and process, an experimental testing of hypotheses is required. For example, the old and still unresolved controversy between migration-related and site-related explanations could be investigated for selected species by transplantation experiments. If a species is able to survive and reproduce outside the river corridor, dispersal limitation is the most likely factor for the restricted range. If it is not able to survive outside the river corridor, certain corridor-specific site conditions are likely to favour the species directly or indirectly. Special attention should be paid to the early establishment of floodplain species, since the floodplain-specific levels, frequencies and kinds of disturbance are likely to facilitate establishment of particular plant species.

European floodplains are particularly rich in species. Habitat diversity and richness in ecotones (transition zones between the habitats) may be two main reasons for this observation (Nilsson *et al.*, 1991; Foeckler & Bohle, 1993; Naiman *et al.*, 1993; Décamps & Tabacchi, 1994; Ward *et al.*, 1999). Disturbances, occurring both periodically (regularly changing water tables) and stochastically

(high flood events, ice scour, erosion and sedimentation), may increase species diversity on a medium to landscape scale by creating a high spatial and temporal habitat diversity (Naiman & Décamps, 1997). From this viewpoint, river corridor plants may be relatively weak competitors, but adapted to the peculiar disturbance regime of floodplains. This idea seems promising for experimental testing.

The floodplains of Central Europe have been subject to human impact since the Neolithic age. For example, riparian forests have been cleared almost completely. Furthermore, runoff and flooding dynamics have been altered by dams, dikes and locks (Dynesius & Nilsson, 1994; Müller, 1995; Ward *et al.*, 1999). Therefore, floodplains have been classified as highly endangered ecosystems in Central Europe (Gerken, 1988; Foeckler & Bohle, 1993). Many endangered species can be found in river corridors. Only one river corridor species (*Lycopus exaltatus*) is already extinct here, but one of the two river corridor endemics in this endemism-poor region, *Oenanthe conioides*, is also considered to be threatened by extinction. Maintaining the plant species diversity of Central Europe must take into account the river corridors and the conservation of endangered river corridor plants.

Knowledge of population biology and meta-population dynamics of endangered species are indispensable elements of a conservation strategy. Nearly all species of river corridor plants are *terrae incognitae* in this respect despite the fact that they are such a promising subject for meta-population studies, as is shown by Menges (1990). Furthermore, such studies might help reveal the mechanisms that lead to the peculiar distribution patterns which are so difficult to understand at present.

ACKNOWLEDGMENTS

I wish to thank H. Bruelheide and E. Jäger, who contributed considerable knowledge toward my understanding of river corridor plants. For permission of using unpublished data from plant species mapping of Germany, thanks are due to R. May and P. Schönfelder. Comments from J. Heimann, M. Ristow, C. Ernsting, K. Tielbörger and two anonymous referees greatly improved the manuscript.

REFERENCES

- Abernethy, V.J. & Willby, N.J. (1999) Changes along a disturbance gradient in the density and composition of propagule banks in floodplain aquatic habitats. *Plant Ecology*, **140**, 177–190.
- Albrecht, H. (1999) Vergesellschaftung, Standortgemeinschaften und Populationsökologie von Arten der Klasse Isoeto-Nanojuncetea auf Ackerflächen. *Mitteilungen des Badischen Landesvereins für Naturkunde und Naturschutz N.F.*, **17**, 403–417.
- Andres, C. & Westhus, W. (2000) Artenhilfsmaßnahmen für hochgradig gefährdete Stromtalpflanzen. *Landschaftspflege und Naturschutz in Thüringen*, **37**, 33–38.
- Arbeitsgemeinschaft mitteldeutscher Floristen (1955) Verbreitungskarten mitteldeutscher Leitpflanzen, 8. Reihe. *Wissenschaftliche Zeitschrift der Universität Halle, Math.-Nat. R.* **5**, 297–334.
- Arbeitsgemeinschaft mitteldeutscher Floristen (1960) Verbreitungskarten mitteldeutscher Leitpflanzen, 9. Reihe. *Wissenschaftliche Zeitschrift der Universität Halle, Math.-Nat. R.* **9**, 165–224.
- Arbeitsgemeinschaften der Landesanstalten und-ämter für Naturschutz, Bundesamt für Naturschutz (1994) Die Elbe und ihr Schutz — eine internationale Verpflichtung. *Natur und Landschaft*, **69**, 239–250.
- Ascherson, P. (1859) Pflanzengeographische Studien über die Flora der Mark Brandenburg. II. Über die dem Alluvium, Diluvium (und den älteren Bildungen) eigentümlichen Gefäßpflanzen (mit Pflanzenverzeichnis). *Verhandlungen des Botanischen Vereins der Provinz Brandenburg*, **1**, 27–41.
- Ascherson, P. (1864) Vegetation der Elb- und Oder-niederung. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg*, **6**, XII–XVII.
- Baker, W.L. (1990) Species richness of Colorado riparian vegetation. *Journal of Vegetation Science*, **1**, 119–124.
- Barrat-Segretain, M.H. (1996) Strategies of reproduction, dispersion, and competition in river plants: a review. *Vegetatio*, **123**, 13–37.
- Behning, A. (1928) *Das Leben der Wolga, zugleich eine Einführung in die Fluß-Biologie*. Schweizerbart, Stuttgart.
- Belde, M. (1996) Untersuchungen zur Populationsdynamik von *Xanthium albinum* an der Mittelelbe. *Braunschweiger Geobotanische Arbeiten*, **4**, 59–69.
- Bennett, K.D. (1986) The rate of spread and population increase of forest trees during the post-glacial. *Philosophical Transactions of the Royal Society*, **B 314**, 523–531.
- Bernhardt, K.-G. (1989) Pflanzliche Strategien der Pionierbesiedlung terrestrischer und limnischer Sandstandorte in Nordwestdeutschland. *Drosera*, **89**, 113–123.
- Bernhardt, K.-G. & Kundel, W. (1993) Untersuchungen zum Diasporenvorrat im Boden von Grünlandgräben.

- Biologie semiaquatischer Lebensräume. Aspekte der Populationsbiologie* (ed. by K.-G. Bernhardt, H. Hurka and P. Poschlod), pp. 43–50. Solingen.
- Bernhardt, K.-G., Spitzer, M., Gall, M. & Runde, A. (1999) Auswirkungen künstlicher Überstauungen auf das Wachstum von ausgewählten Grünlandarten. *Botanisches Jahrbuch für Systematik*, **121**, 233–268.
- Berthold, P. (1990) *Vogelzug. Eine kurze, aktuelle Gesamtübersicht*. Wissenschaftliche Buchgesellschaft, Darmstadt.
- Blom, C.W.P.M. (1999) Adaptations to flooding stress: from plant community to molecule. *Plant Biology*, **1**, 261–273.
- Blom, C.W.P.M., Bögemann, G.M., Laan, P., van der Sman, A.J.M., van de Steeg, H.M. & Voeseek, L.A.C.J. (1990) Adaptations to flooding in plants from river areas. *Aquatic Botany*, **38**, 29–47.
- Bonn, S. & Poschlod, P. (1998) *Ausbreitungsbiologie der Pflanzen Mitteleuropas. Grundlagen und kulturhistorische Aspekte*. UTB Quelle & Meyer, Wiesbaden.
- Borchert, J. (1992) Flußkorridore als überregionale Verbundstrukturen. Auen-, Niederungs- und Talbereiche der Bundeswasserstraßen (ohne Kanäle) und Zuflüsse 1. Ordnung nach der naturräumlichen Gliederung. *Natur und Landschaft*, **67**, 413–418.
- Boutin, C. & Keddy, P.A. (1993) A functional classification of wetland plants. *Journal of Vegetation Science*, **4**, 591–600.
- Braendle, R. & Crawford, R.M.M. (1987) Rhizome anoxia tolerance and habitat specialization in wetland plants. *Plant life in aquatic and amphibious habitats* (ed. by R.M.M. Crawford), pp. 397–410. Blackwell, Oxford.
- Brandes, D. (1995) Breiten sich die C4-Pflanzen in Mitteleuropa aus? *Schriftenreihe für Vegetationskunde*, **27**, 365–372.
- Brandes, D. (1996) Flußufer als Untersuchungsobjekte der Geobotanik und der Biogeographie — Versuch eines Fragenkatalogs. *Braunschweiger Geobotanische Arbeiten*, **4**, 7–23.
- Brandes, D. & Sander, C. (1995) Neophytenflora der Elbufer. *Tuexenia*, **15**, 447–472.
- Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597–623.
- Bruner, W.E. (1931) The vegetation of Oklahoma. *Ecological Monographs*, **1**, 99–188.
- Burkart, M. (1995) *Juncus atratus* in Nordostdeutschland. *Verhandlungen des Botanischen Vereins von Berlin und Brandenburg*, **128**, 83–107.
- Burkart, M. (1998) Die Grünlandvegetation der unteren Havelaue in synökologischer und syntaxonomischer Sicht. *Archiv Naturwissenschaftlicher Dissertationen*, **7**, 1–259.
- Burkart, M. & Prasse, R. (1996) Zur pflanzlichen Besiedlung wechsellasser Pionierstandorte im Elbhavelwinkel. *Untere Havel Naturkundliche Berichte*, **5**, 38–50.
- Cook, C.D.K. (1987) Dispersion in aquatic and amphibious vascular plants. *Plant life in aquatic and amphibious habitats* (ed. by R.M.M. Crawford), pp. 179–190. Blackwell Science, Oxford.
- Crawford, R.M.M. (1987) Introduction and tribute to the late Professor D.H.N. Spence. *Plant life in aquatic and amphibious habitats* (ed. by R.M.M. Crawford), pp. xi–xii. Blackwell Science, Oxford.
- Crawford, R.M.M., Studer, C. & Studer, K. (1989) Deprivation indifference as a survival strategy in competition: advantages and disadvantages of anoxia tolerance in wetland vegetation. *Flora*, **182**, 189–201.
- Crawley, M.J. (1987) What makes a community invisable? *Colonization, Succession and Stability* (ed. by A.J. Gray, M.J. Crawley and P.J. Edwards), pp. 429–453. Blackwell Science, Oxford.
- Dansereau, P. (1957) *Biogeography. An ecological perspective*. Ronald, New York.
- Dawson, D. (1994) Are habitat corridors conduits for animals and plants in a fragmented landscape? A review of the scientific evidence. *English Nature Research Report*, **94**, 1–89.
- Day, R.T., Keddy, P.A., McNeill, J. & Carleton, T. (1988) Fertility and disturbance gradients: a summary model for riverine marsh vegetation. *Ecology*, **69**, 1044–1054.
- Décamps, H., Joachim, J. & Langa, J. (1987) The importance for birds of the riparian woodlands within the alluvial corridor of the River Garonne, S.W. France. *Regulated Rivers*, **1**, 301–316.
- Décamps, H. & Tabacchi, E. (1994) Species richness in vegetation along river margins. *Aquatic ecology: scale, pattern and process* (ed. by P.S. Giller, A.G. Hildrew and D.G. Raffaelli), pp. 1–20. Blackwell Science, Oxford.
- DeFerrari, C.M. & Naiman, R.J. (1994) A multi-scale assessment of the occurrence of exotic plants on the Olympic peninsula, Washington. *Journal of Vegetation Science*, **5**, 247–258.
- Dierschke, H. (1984) Auswirkungen des Frühjahrshochwassers 1981 auf die Ufervegetation im südwestlichen Harzvorland mit besonderer Berücksichtigung kurzlebiger Pioniergesellschaften. *Braunschweiger Naturkundliche Schriften*, **2**, 19–39.
- Dingle, H. (1996) *Migration: the biology of life on the move*. Oxford University Press, Oxford.
- Durka, W. (1999) Genetic diversity in peripheral and subcentral populations of *Corrigiola litoralis* L. (Illecebraceae). *Heredity*, **83**, 476–484.
- Dynesius, M. & Nilsson, C. (1994) Fragmentation and flow regulation of river systems in the northern third of the world. *Science*, **266**, 753–762.
- Eichhorn, M., ed. (1999) *Langenscheidts Fachwörterbuch Biologie. 2. Deutsch-Englisch*. Langenscheidt, Berlin.
- Ellenberg, H. (1996) *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht*, 5th edn. Ulmer, Stuttgart.
- Fischer, W. (1959) Pflanzenverbreitung und Florenbild in der Prignitz. Ein Beitrag zur Landschaftsökologie

- Brandenburgs. *Wissenschaftliche Zeitschrift der Pädagogischen Hochschule Potsdam, Math.-Naturwiss. Reihe*, **5**, 49–84.
- Fischer, W. (1996) Die Stromtalpflanzen Brandenburgs. *Untere Havel Naturkundliche Berichte*, **5**, 4–13.
- Foekler, F. & Bohle, H.W. (1993) Fließgewässer und ihre Auen – prädestinierte Standorte ökologischer und naturschutzfachlicher Grundlagenforschung. *Berichte aus der ökologischen Forschung*, **4**, 236–266.
- Forman, R.T.T. (1983) Corridors in a landscape: their ecological structure and function. *Ekologia*, **2**, 375–387.
- Forman, R.T.T. & Godron, M. (1986) *Landscape ecology*. Wiley, New York.
- Freitag, H. (1962) *Biogeographie von Mitteleuropa unter besonderer Berücksichtigung von Deutschland*. Fischer, Stuttgart.
- Gams, H. (1927) Labiatae. *Illustrierte Flora von Mittel-Europa VI/4* (ed. by G. Hegi), pp. 2255–2548. Lehmanns, München.
- Garve, E. (1994) Atlas der gefährdeten Farn- und Blütenpflanzen in Niedersachsen und Bremen. *Naturschutz und Landschaftspflege in Niedersachsen*, **30**, 1–897.
- Gaston, K.J. (1990) Patterns in the geographical ranges of species. *Biological Reviews*, **65**, 105–129.
- Gepp, J., Baumann, N., Kauch, E.P. & Lazowski, W. (1985) Auengewässer als Ökozellen. Fluß-Altarme, Altwässer und sonstige Auen-Stillgewässer Österreichs — Bestand, Ökologie und Schutz. *Grüne Reihe des Bundesministers für Gesundheit und Umweltschutz*, **4**, 1–322.
- Gerken, B. (1988) *Auen — Verborgene Lebensadern der Natur*. Rombach, Freiburg.
- Gerken, B., Böttcher, H., Böwingloh, F., Dörfer, K., Leushacke-Schneider, C., Robinson, A. & Wienhöfer, M. (1998) Treibgut und Genist — Landschaftsmüll oder Quelle und Antrieb dynamischer Lebensvorgänge in Auen? *Auen-Regeneration. Hinweise für die Praxis aus dem Erprobungs- und Entwicklungsvorhaben. Oberweserniederung*. pp. 1–24. Gesamthochschule Paderborn, Höxter.
- Goebel, W. (1995) Die Vegetation der Wiesen, Magerrasen und Rieder im Rhein-Main-Gebiet. *Dissertationes Botanicae*, **237**, 456.
- Golub, V.B. & Saveljeva, L.F. (1991) Vegetation of the Lower Volga Limans (basins without outflow). *Folia Geobotanica et Phytotaxonomica*, **26**, 403–421.
- Golub, V.B. & Tchorbadze, N.B. (1995) Vegetation communities of western substeppe ilmens of the Volga delta. *Phytocoenologia*, **25**, 449–466.
- Good, R. (1974) *The geography of the flowering plants*, 4th edn. Longmans, London.
- Grimm, F. (1968) Das Abflußverhalten in Europa – Typen und regionale Gliederung. *Wissenschaftliche Veröffentlichungen des Deutschen Instituts für Länderkunde N.F.*, **25/26**, 18–180.
- Grisebach, A. (1847) Ueber die Vegetationslinien des nordwestlichen Deutschlands. Ein Beitrag zur Geographie der Pflanzen. *Göttinger Studien*, 1847, *Abt.* **1**, 461–562.
- Gurnell, A.M., Angold, P. & Gregory, K.J. (1994) Classification of river corridors: issues to be addressed in developing an operational methodology. *Aquatic Conservation*, **4**, 219–231.
- Haeupler, H. & Schönfelder, P. (1989) *Atlas der Farn- und Blütenpflanzen der Bundesrepublik Deutschland*, 2nd edn. Ulmer, Stuttgart.
- Hegi, G. & Beger, H. (1925) Euphorbiaceae. Unter Mitwirkung von W. Zimmermann. *Illustrierte Flora Von Mittel-Europa VII* (ed. by G. Hegi), pp. 113–190. Lehmanns, München.
- Hejny, S. (1960) *Ökologische Charakteristik der Wasser- und Sumpfpflanzen in den slowakischen Tiefebene (Donau- und Theißgebiet)*. Verlag der slowakischen Akademie der Wissenschaften, Bratislava.
- Hersch, R.W. (1998) Rivers. *Encyclopedia of Hydrology and Water Resources* (ed. by R.W. Herschy and R.W. Fairbridge), pp. 571–583. Kluwer, Dordrecht.
- Hills, J.M., Murphy, K.J., Pulford, I.D. & Flowers, T.H. (1994) A method for classifying European riverine wetland ecosystems using functional vegetation groups. *Functional Ecology*, **8**, 242–252.
- Hölzel, N. & Otte, A. (2001) The impact of flood-regime on the soil seed bank of flood-meadows. *Journal of Vegetation Science*, **12**, 209–218.
- Hornberger, T. (1959) Die kulturgeographische Bedeutung der Wanderschäferei in Süddeutschland. *Forschungen zur deutschen Landeskunde*, **109**, I, 1–173.
- Hovestadt, T., Yao, P. & Linsenmair, K.E. (1999) Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoé National Park, Ivory Coast). *Plant Ecology*, **144**, 1–25.
- Hughes, F.M.R. (1988) The ecology of African floodplain forests in semi-arid and arid zones: a review. *Journal of Biogeography*, **15**, 127–140.
- Hultén, E. & Fries, M. (1986) *Atlas of North European vascular plants*. Koeltz, Königstein.
- Jage, H. (1962) Beitrag zur Kenntnis der Flora der Dübener Heide und der angrenzenden Auengebiete. *Wissenschaftliche Zeitschrift der Universität Halle, Math.-Naturwiss. Reihe*, **11**, 179–192.
- Jage, H. (1964) *Lindernia dubia* auch in Deutschland. Zur Flora und Vegetation des mittleren Elbtales und der Dübener Heide 3. *Wissenschaftliche Zeitschrift der Martin-Luther-Universität Halle-Wittenberg, Math.-Naturwiss. Reihe*, **13**, 673–680.
- Jäger, E. (1968) Die pflanzengeographische Ozeanitätsgliederung der Holarktis und die Ozeanitätsbindung der Pflanzenareale. *Feddes Repertorium*, **79**, 157–335.
- Jäger, E. (1970) Charakteristische Typen mediterrann-mitteleuropäischer Pflanzenareale. *Feddes Repertorium*, **81**, 67–92.
- Jäger, E. (1990) Pflanzenarealgrenzen als Leistungsgrenzen. *Biologische Rundschau*, **28**, 295–306.

- Jäger, E. (1992) *Kausale Phytochorologie und Areal-dynamik*. Martin-Luther-Universität of Halle-Wittenberg, Halle.
- Janiesch, P. (1991) Ecophysiological adaptations of higher plants in natural communities to water-logging. *Ecological responses to environmental stresses* (ed. by J. Rozema and J.A.C. Verkleij), pp. 50–60. Kluwer, Dordrecht.
- Jentsch, H. & Seitz, B. (1997) Stromtalpflanzen im Spreewald. *Verhandlungen des Botanischen Vereins von Berlin und Brandenburg*, **129**, 25–36.
- Johansson, M.E. & Nilsson, C. (1993) Hydrochory, population dynamics and distribution of the clonal aquatic plant *Ranunculus lingua*. *Journal of Ecology*, **81**, 81–91.
- Johansson, M.E., Nilsson, C. & Nilsson, E. (1996) Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science*, **7**, 593–598.
- Kadmon, R. & Danin, A. (1999) Distribution of plant species in Israel in relation to spatial variation in rainfall. *Journal of Vegetation Science*, **10**, 421–432.
- Kallen, H.W. (1996) Beobachtungen zum Diasporenreservoir von Auenböden des Elbtals und der Jeetzelniederung. *Braunschweiger Geobotanische Arbeiten*, **4**, 225–237.
- Kerner von Marilaun, A. (1898) *Pflanzenleben 2: Geschichte der Pflanzen*, 2nd edn. Bibliographisches Institut, Leipzig, Wien.
- Kleinschmidt, C. & Rosenthal, G. (1995) Samenbankpotential und Diasporenverdriftung in überschwemmten Feuchtwiesen. *Kieler Notizen zur Pflanzenkunde in Schleswig-Holstein*, **23**, 40–44.
- Köck, U.-V. (1988) Ökologische Aspekte der Ausbreitung von *Bidens frondosa* L. in Mitteleuropa. Verdrängt er *Bidens tripartita* L.? *Flora*, **180**, 177–190.
- Korsch, H. (1999) Chorologisch-ökologische Auswertung der Daten der Floristischen Kartierung Deutschlands. *Schriftenreihe für Vegetationskunde*, **30**, 1–200.
- Kunin, W.E. (1998) Extrapolating species abundance across spatial scales. *Science*, **281**, 1513–1515.
- Libbert, W. (1931) Die Pflanzengesellschaften im Überschwemmungsgebiet der unteren Warthe in ihrer Abhängigkeit vom Wasserstande. *Jahrbuch des Naturwissenschaftlichen Vereins der Neumark*, **3**, 25–40.
- Libbert, W. (1938) Flora und Vegetation des neu-märkischen Plönetales. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg*, **78**, 72–137.
- Loew, E. (1879) Über Perioden und Wege ehemaliger Pflanzenwanderungen im norddeutschen Tieflande. *Linnaea*, **42**, 511–660.
- Löscher, R., Schmitz, U. & Cours, F. (1995) Cuscuta am Niederrhein: Verbreitungsfähigkeit und Wasserpotentialgradienten zwischen Wirt und Parasit. *Verhandlungen der Gesellschaft für Ökologie*, **24**, 567–470.
- Machtans, C.S., Villard, M.C. & Hannon, S.J. (1996) Use of riparian buffer strips as movement corridors by forest birds. *Conservation Biology*, **10**, 1366–1379.
- MacMahon, J.A. (1988) Warm deserts. *North American terrestrial vegetation* (ed. by M.G. Barbour and W.D. Billings), pp. 231–264. Cambridge University Press, Cambridge.
- Márquez, A.L., Real, R., Vargas, J.M. & Salvo, A.E. (1997) On identifying common distribution patterns and their causal factors: a probabilistic method applied to pteridophytes in the Iberian Peninsula. *Journal of Biogeography*, **24**, 613–631.
- Matthies, D. (1991) *Die Populationsbiologie der annualen Hemiparasiten Melampyrum arvense, Melampyrum cristatum und Melampyrum nemorosum (Scrophulariaceae)*. University of Bochum, Germany.
- Menges, E.S. (1990) Population viability analysis for an endangered plant. *Conservation Biology*, **4**, 52–62.
- Meusel, H. (1943) *Vergleichende Arealkunde*. Borntraeger, Berlin.
- Meusel, H. & Jäger, E. (1992) *Vergleichende Chorologie der Zentraleuropäischen Flora 3*. Fischer, Jena.
- Meusel, H., Jäger, E. & Weinert, E. (1965) *Vergleichende Chorologie der Zentraleuropäischen Flora 1*. Fischer, Jena.
- Meusel, H., Jäger, E. & Weinert, E. (1978) *Vergleichende Chorologie der Zentraleuropäischen Flora 2*. Fischer, Jena.
- Mitsch, W.J. & Gosselink, J.G. (1993) *Wetlands*, 2nd edn. Van Nostrand Reinhold, New York.
- Müller, M. (1996) Populationsbiologie von *Artemisia annua* L. *Braunschweiger Geobotanische Arbeiten*, **4**, 71–83.
- Müller, M. & Brandes, D. (1997) Growth and development of *Artemisia annua* L. on different soil types. *Verhandlungen der Gesellschaft für Ökologie*, **27**, 453–460.
- Müller, N. (1995) River dynamics and floodplain vegetation and their alterations due to human impact. *Archive of Hydrobiology*, **9**, Suppl. 101 (Large rivers), 477–512.
- Müller, N. & Okuda, S. (1998) Invasion of alien plants in floodplains — a comparison of Europe and Japan. *Plant invasions. ecological mechanisms and human responses* (ed. by U. Starfinger, K. Edwards, I. Kowarik and M. Williamson), pp. 321–332. Backhuys, Leiden.
- Müller-Stoll, W.R., Fischer, W. & Krausch, H.-D. (1962) Verbreitungskarten brandenburgischer Leitpflanzen. Vierte Reihe. *Wissenschaftliche Zeitschrift der Pädagogischen Hochschule Potsdam, Math.-Naturwiss. Reihe*, **7**, 95–150.
- Myers, A.A. & Giller, P.S., eds (1988) *Analytical biogeography*. Chapman & Hall, London.
- Naiman, R.J. & Décamps, H. (1997) The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics*, **28**, 621–658.

- Naiman, R.J., Décamps, H. & Pollock, M. (1993) The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications*, **3**, 209–212.
- Nilsson, C., Grelsson, G., Dynesius, M., Johansson, M.E. & Sperens, U. (1991) Small rivers behave like large rivers: effects of postglacial history on plant species richness along river banks. *Journal of Biogeography*, **18**, 533–541.
- Nimis, P.L., Malyshev, L.I., Bolognini, G. & Friesen, N. (1998) A multivariate phytogeographic analysis of plant diversity in the Putorana Plateau (N. Siberia). *Opera Botanica*, **136**, 1–72.
- Orschiedt, O. (1995) Arealtypen pfälzischer Gefäßpflanzen. *Mitteilungen der Pollichia*, **82**, 247–295.
- Orschiedt, O. (1996) Arealtypen pfälzischer Gefäßpflanzen II. *Mitteilungen der Pollichia*, **83**, 77–110.
- Passarge, H. (1993) Lianenschleier-, fluviatile und ruderaler Staudengesellschaften in den planaren Elb- und Oderauen. *Tuexenia*, **13**, 343–371.
- Peintinger, M. (1994) Verbreitung, Rückgang und Soziologie von *Gratiola officinalis* L. am Bodensee. *Carolinea*, **52**, 25–34.
- Plachter, H. & Reich, M. (1998) The significance of disturbance for populations and ecosystems in natural floodplains. *Proceedings of the International Symposium on River Restoration* (ed. by N. Müller, S. Okuda and N. Tamai), pp. 29–38. Tokyo.
- Pollock, M.M., Naiman, R.J. & Hanley, T.A. (1998) Plant species richness in riparian wetlands — a test of biodiversity theory. *Ecology*, **79**, 94–105.
- Polunin, N. (1960) *Introduction to plant geography*. Longmans, London.
- Poschlod, P. (1993) 'Underground floristics' — keimfähige Diasporen im Boden. Zum floristischen Inventar einer Landschaft am Beispiel der Teichbodenflora. *Natur und Landschaft*, **68**, 155–159.
- Poschlod, P. (1996) Population biology and dynamics of a rare short-lived pond mud plant, *Carex bohemica* Schreber. *Verhandlungen der Gesellschaft für Ökologie*, **25**, 321–337.
- Poschlod, P., Böhringer, J., Fennel, S., Prume, C. & Tiekötter, A. (1999) Aspekte der Biologie und Ökologie von Arten der Zwergbinsenfluren. *Mitteilungen Des Badischen Landesvereins für Naturkunde und Naturschutz N.F.*, **17**, 219–260.
- Potonié, H. (1887) *Illustrierte Flora Von Nord- und Mittel-Deutschland mit einer Einführung in die Botanik*, 3rd edn. Boas, Berlin.
- Preuss, H. (1909) Die boreal-alpinen und 'pontischen' Associationen der Flora von Ost- und Westpreußen. II. 'Pontische' Associationen. *Berichte der Deutschen Botanischen Gesellschaft*, **27**, 334–341.
- Puth, L.M. & Wilson, K.A. (2001) Boundaries and corridors as a continuum of ecological flow control: lessons from rivers and streams. *Conservation Biology*, **15**, 21–30.
- Pyšek, P. (1995) On the terminology used in plant invasion studies. *Plant invasions: general aspects and special problems* (ed. by P. Pyšek, K. Prach, M. Rejmánek and M. Wade), pp. 71–81. SPB Academic Publishers, Amsterdam.
- Pyšek, P. (1997) Clonality and plant invasions: can a trait make a difference? *The ecology and evolution of clonal plants* (ed. by H. de Kroon and J. van Groenendael), pp. 405–427. Backhuys, Leiden.
- Pyšek, P. & Prach, K. (1994) How important are rivers for supporting plant invasions? *Ecology and management of invasive riverside plants* (ed. by L.C. de Waal *et al.*), pp. 19–26. Wiley, Chichester.
- Pyšek, P., Prach, K. & Mandak, B. (1998) Invasions of alien plants into habitats of central European landscape: an historical pattern. *Plant invasions. Ecological mechanisms and human responses* (ed. by U. Starfinger, K. Edwards, I. Kowarik and M. Williamson), pp. 23–32. Backhuys, Leiden.
- Pyšek, P., Prach, K. & Smilauer, P. (1995) Invasion success related to plant traits: an analysis of Czech alien flora. *Plant invasions: general aspects and special problems* (ed. by P. Pyšek, K. Prach, M. Rejmánek and M. Wade), pp. 39–60. SPB Academic Publishers, Amsterdam.
- Ramakrishnan, P.S. & Vitousek, P.M. (1989) Ecosystem-level processes and the consequences of biological invasions. *Biological invasions: a global perspective* (ed. by J.A. Drake, *et al.*), pp. 281–300. Wiley, Chichester.
- Rejmánek, M. (1995) What makes a species invasive? *Plant invasions: general aspects and special problems* (ed. by P. Pyšek, K. Prach, M. Rejmánek and M. Wade), pp. 3–13. SPB Academic Publishers, Amsterdam.
- Rijpert, J.M.S. (1977) Ecological demands of *Gratiola officinalis* (Scrophulariaceae) in the Netherlands. *Proceedings of the Koninklijke Nederlandse Akademie de Wetenschappen Series C*, **80**, 190–200.
- Sauer, J.D. (1988) *Plant migration. The dynamics of geographic patterning in seed plant species*. University of California Press, Berkeley.
- Schalow, E. (1912) Über die Stromtalflora des Brieger Kreises. Ein Beitrag zur Geschichte der Pflanzendecke im schlesischen Odertal. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg*, **53**, 1–5.
- Schalow, E. (1921) Die Verbreitung der schlesischen Stromtalpflanzen. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg*, **63**, 20–30.
- Scholz, J.B. (1905) Die Pflanzengesellschaften Westpreußens. *Schriften der Naturforschenden Gesellschaft zu Danzig N.F.*, **11**, 1–302.
- Schulz, A. (1907) Über die Entwicklungsgeschichte der gegenwärtigen phanerogamen Flora und Pflanzendecke des norddeutschen Tieflandes II. *Berichte der Deutschen Botanischen Gesellschaft*, **25**, 536–553.
- Slavik, B. (1973) Phytochorologische Charakteristik der Art *Euphorbia lucida* Waldst. et Kit. in bezug auf ihre Verbreitung in der Tschechoslowakei. *Preslia*, **45**, 119–131.

- Steffen, H. (1924) Die Bedeutung der Allensteiner Senke für die Besiedlung Ostpreußens mit pontischen Arten. *Feddes Repertorium Beiheft*, **26**, 1–406.
- Steinworth, H. (1864) *Zur Wissenschaftlichen Bodenkunde Des Fürstenthums Lüneburg* (printed from the Johanneum program). Lüneburg.
- Thebaud, C. & Debussche, M. (1991) Rapid invasion of *Fraxinus ornus* L. along the Hérault River system in southern France: the importance of seed dispersal by water. *Journal of Biogeography*, **18**, 7–12.
- Thompson, K., Bakker, J. & Bekker, R. (1997) *The soil seed banks of North West Europe: methodology, density and longevity*. Cambridge University Press, Cambridge.
- Tüxen, R. (1950) Wanderwege der Flora in Stromtälern. *Mitteilungen der Floristisch-Soziologischen Arbeitsgemeinschaft N.F.*, **2**, 52–53.
- Ulbrich, E. (1925) Über die Vegetationsverhältnisse der Umgebung von Tangermünde. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg*, **67**, 114–137.
- Van den Berg, E. & Oliveira-Filho, A.T. (1999) Spatial partitioning among tree species within an area of tropical montane gallery forest in south-eastern Brazil. *Flora*, **194**, 249–266.
- Van der Sman, A.J.M., Joosten, N.N. & Blom, C.W.P.M. (1993) Flooding regimes and life-history characteristics of short-lived species in river forelands. *Journal of Ecology*, **81**, 121–130.
- Van der Valk, A.G. (1981) Succession in wetlands: a Gleasonian approach. *Ecology*, **62**, 688–696.
- Van Eimern, J. & Häckel, H. (1984) *Wetter- und Klimakunde. Ein Lehrbuch der Agrarmeteorologie*, 4th edn. Ulmer, Stuttgart.
- Vent, W. & Benkert, D. (1984) Verbreitungskarten brandenburgischer Pflanzenarten. 2. Reihe. Stromtalpflanzen (1). *Gleditschia*, **12**, 213–238.
- Vogel, A. (1997) Die Verbreitung, Vergesellschaftung und Populationsökologie von *Corrigiola litoralis*, *Illecebrum verticillatum* und *Herniaria glabra*. *Dissertationes Botanicae*, **289**, 1–282.
- Von Lampe, M. (1996) Wuchsform, Wuchsrhythmus und Verbreitung der Arten der Zwergbinsengesellschaften. *Dissertationes Botanicae*, **266**, 1–355.
- Walas, J. (1938) Wanderungen der Gebirgspflanzen längs der Tatra-Flüsse. *Bulletin Academia Poloniae, Classis Scientiarum Math.-Nat., Sér. B* **1938**, 59–80.
- Waldenburg, I. (1934) Die floristische Stellung der Mark Brandenburg. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg*, **75**, 1–80.
- Walter, H. (1974) *Die Vegetation Osteuropas, Nord- und Zentralasiens*. Fischer, Stuttgart.
- Walter, H. & Straka, H. (1970) *Arealkunde. Floristisch-Historische Geobotanik*. Ulmer, Stuttgart.
- Walther, K. (1977) Die Flußniederung von Elbe und Seege bei Gartow (Kr. Lüchow-Dannenberg). *Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins zu Hamburg N.F.*, **20** (Suppl.), 1–123.
- Ward, J.V. (1998) Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation*, **83**, 269–278.
- Ward, J.V., Tockner, K. & Schiemer, F. (1999) Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers: Research and Management*, **15**, 125–139.
- Wein, K. (1930) Die Verbreitung der *Salvinia natans* im südwestlichen Europa in ihren Beziehungen zum Vogelzug. *Feddes Repertorium Beiheft*, **61**.
- Wisskirchen, R. (1995) Verbreitung und Ökologie von Flußufer-Pioniergesellschaften (*Chenopodium rubri*) im mittleren und westlichen Europa. *Dissertationes Botanicae*, **236**, 376.
- Wulff, E.V. (1950) *An Introduction to Historical Plant Geography*. Authorized translation by E. Brissenden. Chronica Botanica, Waltham/MA.
- Xiong, S. & Nilsson, C. (1997) Dynamic of litter accumulation and its effect on riparian vegetation: a review. *Botanical Reviews*, **63**, 240–264.
- Zacharias, D. & Garve, E. (1996) Verbreitung und Häufigkeit von Stromtalpflanzen im ehemaligen Amt Neuhaus (Mittellelbe, Lkr. Lüneburg). *Braunschweiger Geobotanische Arbeiten*, **4**, 35–58.
- Zaluski, T. (1995) Laki selernicowe (Zwiazek Cnidion dubii Bal.-Tul. 1966) w Polsce. *Monographiae Botanicae*, **77**, 1–142.
- Zobel, A. (1930) Zur Flora des mittleren Elbtals. *Berichte des Naturwissenschaftlichen Vereins und des Museums für Naturkunde und Vorgeschichte in Dessau*, **2**, 30–39.

BIOSKETCH

Dr Michael Burkart has worked in the lower Havel floodplain since 1993. Phytocoenological investigations led to questions for causal connections of the floodplain flora and vegetation with history and environment of the river corridor. Other interests include succession of vegetation and plant population ecology on former military training areas in East Germany.

APPENDIX

River corridor plants of the Central European lowland. The list includes all species from Müller-Stoll *et al.* (1962), Vent & Benkert (1984), Zacharias & Garve (1996) and Korsch (1999), and all species that are mentioned in at least two of the following references: Loew (1879), Schalow (1921), Fischer (1996), Jentsch & Seitz (1997). *Deschampsia wibeliana* and *Oenanthe coniooides*, two endemics of the lower Elbe, are added separately.

- Acer campestre* L.
Achillea salicifolia Besser
Alisma gramineum Lej.
Alisma lanceolatum With.
Allium angulosum L.
Allium schoenoprasum L.
Allium scorodoprasum L. s.str.
Amaranthus bouchonii Thell.
Amaranthus emarginatus Moq. ex Uline & W.R. Bray
Androsace elongata L.
Angelica archangelica L.
Anthemis austriaca Jacq.
Arabis nemorensis (Hoffm.) Koch
Artemisia annua L.
Artemisia biennis Willd.
Aster × *salignus* Willd.
Aster parviflorus Nees
Barbarea stricta Andr.
Bidens connata H.L. Mühl.ex Willd.
Bidens frondosa L.
Bidens radiata Thuill
Biscutella laevigata L.
Bolboschoenus maritimus (L.) Palla s.l.
Brassica nigra (L.) W.D.J. Koch
Butomus umbellatus L.
Cardamine parviflora L.
Carex buekii Wimm.
Carex ligerica J. Gay
Carex melanostachya M. Bieb. ex Willd.
Carex praecox Schreb.
Carex pseudobrivooides Clavaud
Carex vulpina L. s.str.
Cerastium dubium (Bastard) Guépin
Chaerophyllum bulbosum L.
Chenopodium ficifolium Sm.
Chenopodium glaucum L.
Chenopodium rubrum L.
Clematis recta L.
Clematis vitalba L.
Cnidium dubium (Schkuhr) Thell.
Corrigiola litoralis L.
Crassula aquatica (L.) Schönland
Cruciata laevipes Opiz
Cucubalus baccifer L.
Cuscuta campestris Yunck.
Cuscuta europaea L.
Cuscuta lupuliformis Krock.
Cyperus michelianus (L.) Link
Deschampsia wibeliana (Sond.) Parl.
Dipsacus fullonum L.
Dipsacus laciniatus L.
Dipsacus pilosus L.
Echinochloa muricata (P. Beauv.) Fernald
Rorippa austriaca (Crantz) Besser
Eragrostis albensis H. Scholz
Eryngium campestre L.
Eryngium planum L.
Erysimum hieracifolium L.
Euphorbia lucida Waldst. & Kit.
Euphorbia palustris L.
Galium boreale L.
Geranium pratense L.
Gratiola officinalis L.
Hierochloa odourata agg. (incl. *H. hirta* [Schrank] Borbás and *H. odourata* [L.] P. Beauv.)
Hypericum hirsutum L.
Inula britannica L.
Juncus atratus Krock
Juncus compressus Jacq.
Jurinea cyanooides (L.) Rchb.
Koeleria macrantha (Ledeb.) Schult.
Lathyrus nissolia L.
Lathyrus palustris L.
Lemna turionifera Landolt
Leonurus marrubiastrum L.
Lepidium latifolium L.
Lindernia dubia (L.) Pennell
Lindernia procumbens (Krock.) Borbás
Lycopus exaltatus Ehrh.
Lythrum hyssopifolia L.
Melampyrum cristatum L.
Mentha pulegium L.
Myosotis sparsiflora J.C. Mikan ex Pohl
Nymphoides peltata (S.G. Gmel.) Kuntze
Oenanthe coniooides Lange
Oenanthe fistulosa L.
Omphalodes scorpioides (Haenke) Schrank
Viola persicifolia Schreb
Petasites spurius (Retz.) Rchb.
Peucedanum officinale L.
Polygonum danubiale Kern.
Populus nigra L.
Portulaca oleracea L.
Potentilla supina L.
Pulicaria vulgaris Gaertn.
Rorippa anceps (Wahlenb.) Rchb.
Rorippa × *armoracioides* (Tausch) Fuss
Rorippa pyrenaica (L.) Rchb.

APPENDIX *continued.*

- Rumex stenophyllus* Ledeb.
Rumex thyrsiflorus Fingerh.
Salvinia natans (L.) All.
Sanguisorba officinalis L.
Scilla bifolia L.
Scilla vindobonensis Speta
Scirpus radicans Schkuhr
Scutellaria hastifolia L.
Senecio erraticus Bertol.
Senecio paludosus L.
Senecio sarracenicus L.
Silaum silaus (L.) Schinz & Thell.
Silene tatarica (L.) Pers.
Sonchus palustris L.
Spergularia echinosperma (Celak.) Asch. & Graebn.
Stratiotes aloides L.
- Symphytum tuberosum* L.
Taraxacum subalpinum Hudziok
Teucrium scordium L.
Thalictrum flavum L.
Thalictrum lucidum L.
Thlaspi caerulescens J. Presl & C. Presl s.str.
Trapa natans L.
Trifolium striatum L.
Trisetum flavescens (L.) P. Beauv.
Urtica galeopsifolia Wierzb. ex Opiz
Urtica kioviensis Rogow.
Verbascum blattaria L.
Veronica longifolia L.
Viola elatior Fr.
Viola pumila Chaix
Xanthium albinum (Widder) H. Scholz
-