Biodiv. Res. Conserv. 34: 53-64, 2014

BRC
www.brc.amu.edu.pl

DOI 10.2478/biorc-2014-0007

Submitted 19.02.2014, Accepted 31.07.2014

Small-scale spatial analysis of river corridor plants distribution in the San River valley (SE Poland)

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Abstract: Spatial distribution and habitat preferences of 55 river corridor plant species were analyzed on a local scale in the valley of a medium-size regulated river. The analysis was based on the results of a detailed mapping on a 50 km-long section of the Lower San River valley (366 cartogram cells of 1 square km). Selected species were divided into two groups: (1) strictly and (2) loosely confined to river corridors. River corridor plants were found throughout the valley (river channel, active and historical floodplain, older terraces, slopes); however, their frequency was diverse in particular areas. The highest concentrations were observed on the floodplain. Their number decreased towards the border areas of the valley. Species which were less confined to rivers were found more frequently in the valley (one species occupied, on average, 12.9% of grid cells), than plants strictly confined to the river system (one species occupied, on average, 5.9% of grid cells); however, the ranges of species of the second group were more restricted to the Holocene part of the valley, especially to the floodplain. River corridor plants were, ecologically, a highly diversified group. In the San river valley, they were found in riparian forests, pioneer ephemeral communities on the banks of water bodies, dry grasslands, meadows and old river beds; a lot of them grew in ruderal habitats.

Key words: river corridor plants, distribution pattern, San River, SE Poland

1. Introduction

Phytochorological studies conducted over the years have enabled researchers to distinguish a peculiar distribution group, composed of species connected with large river systems. The phenomenon was documented as early as the 19th century by German geobotanists. Based on the previous term "Stromtalpflanzen", Burkart (2001) introduced the term "river corridor plants" into international use; this distributional group was defined as "a plant species that occurs exclusively or predominantly in the corridors of large rivers in a given area and time". In his review, Burkart compiled a list of 129 species revealing this distribution pattern in Central Europe, and discussed potential factors which may cause it. In Poland, the issue of river corridor plants was discussed by Kucharczyk (2003) in relation to the Middle Vistula River.

River corridor plants are not an ecologically uniform group and they are found in all parts of river valleys. The group comprises both native and alien species. Confinement of a species to a river corridor may be very strict if the plant is not found outside the valley, or it can be less noticeable if it is dispersed outside a river valley which, nevertheless, remains the centre of its range. In addition, river corridor plants hardly ever maintain this pattern of distribution over their whole range. As a result, making the distinction between a river corridor plant and a plant which does not show this pattern may often be problematic. A list of species restricted to river corridors ought to be established individually for a given study area and a spatial scale adopted (Burkart 2001).

Despite extensive knowledge concerning the functioning of riverine ecosystems (Junk *et al.* 1989; Naiman & Decamps 1997; Ward *et al.* 2002) and the ecological role of rivers in the landscape (Naiman *et al.* 1993; Johansson *et al.* 1996; Bornette *et al.* 1998; Ward *et al.* 1999; Kucharczyk 2003), the river corridor distribution pattern is still a poorly understood phenomenon. The aim of this paper was to perform a distribution analysis of river corridor plants on a local scale in a medium-size regulated river of south-eastern Poland. The characteristics of plant distribution and their concentration are presented in relation to the main river valley landforms zonally distributed along rivers. The general habitat preferences of the studied species were also described. The results were discussed against the background of current explanatory hypotheses of the river corridor plants phenomenon.

2. Material and methods

2.1. Study area

The San River is a Carpathian tributary of the Vistula River, originating at the altitude of 843 m above sea level. The length of its course is 444 km, the drainage basin occupies the area of 16779 km^2. The mean annual discharge near the river mouth is 123 m^3/s.

The main river-control works and embankment construction were carried out at the turn of the 19th century. This resulted in activation of deep erosion, lowering of the water table (especially in the immediate vicinity of the river), a reduction in the area of active floodplain and formation of a lower step of floodplain (Szumański 1977; Wyżga 2008). Despite river-control works, the San River still shows traits of a braided river; during the low-discharge period sand bars are formed in the river channel.

In its lowland section, the river flows through a belt of sub-mountain basins (Sandomierz Basin) separating the Carpathian Mountains from the uplands. In this region, the valley width is approximately 10 km and has a complex system of river terraces (Wojtanowicz 1978; Szumański 1982, 1986). The lowest part of the valley bottom occupies what is traditionally called a riparian terrace, which can be regarded as a floodplain. It was formed between the 18th and the 20th century when the San was a braided river (Szumański 1977). This terrace is mostly composed of sandy and sandy-silty deposits but the share of fine-grained fractions of top mud layer varies greatly (Szumański 1982). Two steps can be distinguished in the topography of the floodplain. The lower step (F1) is a narrow strip formed as a result of channel narrowing and it currently functions as an active floodplain. Most of its area is covered by riparian willow shrubs. The remaining part of the floodplain (F2, historical floodplain) is episodically flooded and is used extensively for agricultural purposes. Above the floodplain, a wide Holocene terrace (T1) is situated. Its sheet is composed of a thick layer of fine-grained muds deposited by the meandering river. In this part of the valley, arable areas are predominant. The highest places within the present river valley are

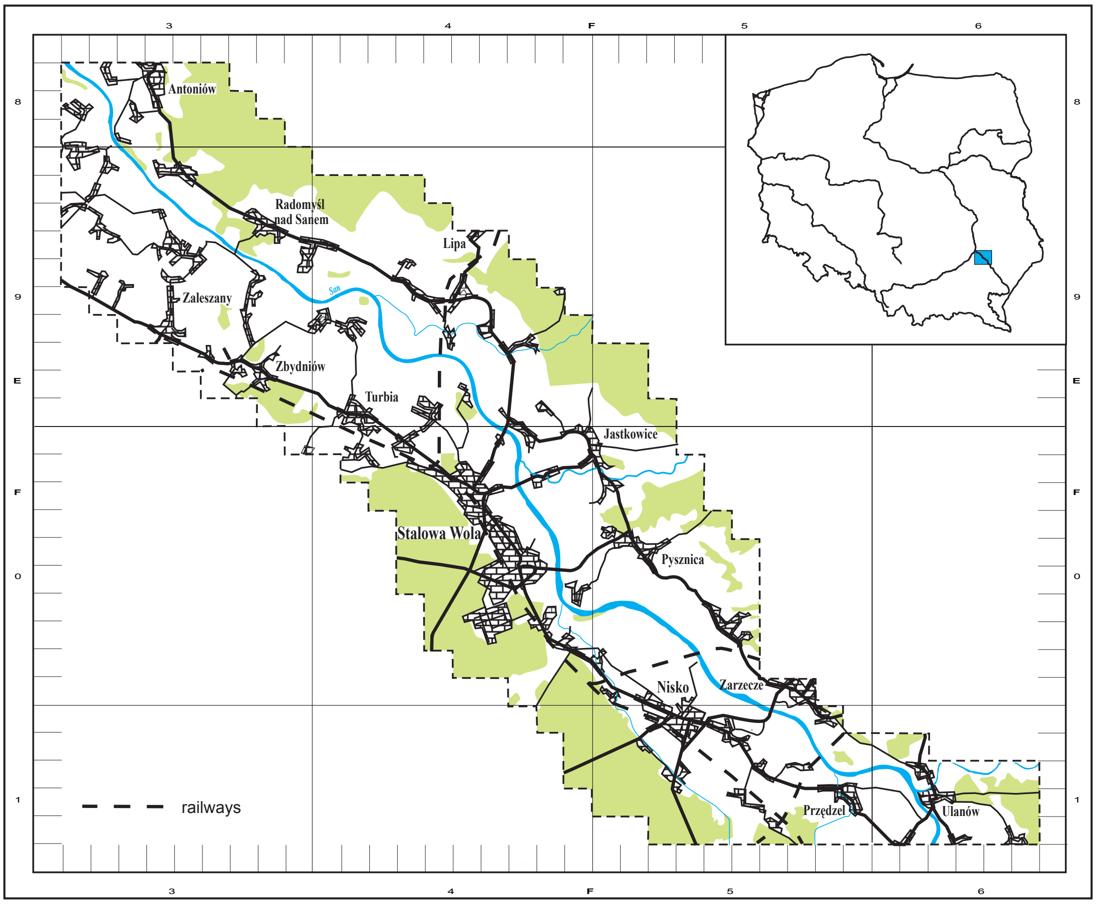

Fig. 1. Location of the study area in ATPOL square grid

occupied by a late Pleistocene terrace (T2). It occurs as isolated patches surrounded by large paleomeanders and is generally composed of sands. The two latter terraces are traditionally described as one single valley landform, named a *rendsina* (*rendzin*, meadow) terrace. Outside the present river valley, we can observe a disproportionately broad sandy glacial (Pleistocene) terrace (G) formed by the braiding river during the Ice Age. Within this plain, a few smaller steps can be distinguished (Wojtanowicz 1978). A large part of the surface of the glacial plain was modified under the influence of aeolian processes. This terrace is largely covered in forests. The inner part of the terrace concentrates the settlement and the main transportation routes along the San River. A medium-sized industrial town is located on the left bank of the river (square FF04) within the study area. Distinct steep slopes occur only in the short section and they are covered with loamy landslides. The plateau is built of Miocene clays underlying a surface of diverse deposits of glacial, fluvioglacial and aeolian origin (Wojtanowicz 1978).

2.2. Floristic data

Distribution analysis was based on the results of a detailed mapping of vascular flora on the 50 km-long valley section of the lower course of the San River (Fig. 1) and was carried out from 2002-2008. The research covered the whole erosion basin, including the present river valley, glacial terraces and slopes with a strip of plateau. Using the ATPOL grid (Zając 1978), the investigated area was divided into 366 basic plots of 1 square km. During the field works, additional information about the plant location was noted when there were several landform types in one grid cell. Vascular flora of the studied area included 1033 taxa; floristic richness in individual grid cells varied from 102 to 391 (Krawczyk 2011).

2.3. List of river corridor plants

When a list of river corridor plants is determined, it must be remembered that the examined area should neither be too large (to avoid geographical variation of species distribution driving by climatic gradient), nor too small (to avoid local distributional phenomena). Therefore, in the study, the river catchment approach was applied; the list of river corridor plants for analyses was compiled for the whole drainage basin of the Vistula River within Polish borders (169100 km^2). The selection of species was conducted only on the basis of visual assessment of cartograms (10x10 km) found in the "Distribution atlas of vascular plants in Poland" (Zając & Zając 2001). Species whose distribution correlated with the location of the Vistula River and its tributaries (visible in the Atlas) were chosen. In the case of dubious species, the Burkart's (2001) list was decisive. Both sporadic and critical taxa were excluded from analyses. This procedure enabled the selection of 73 taxa. Next, the chosen species were divided into two groups: (1) strictly confined to river corridors (group A), and (2) loosely confined to river corridors, more widespread taxa with a center of the range in river valleys (group B). Group A comprised species for which at least 70% of the total occupied grid cells were the cells with river corridors. Approximate width of river valleys was adopted according to Kondracki (2002).

The geographical-historical status of the species was determined following Tokarska-Guzik *et al.* (2012).

2.4. Species characteristics and analyses

The description of river corridor plants distribution in the San River valley was made with species cartograms super-imposed on the landform map and field notes. The frequency of species occurrence in particular parts of the valley was determined with a 3-rank ordinal

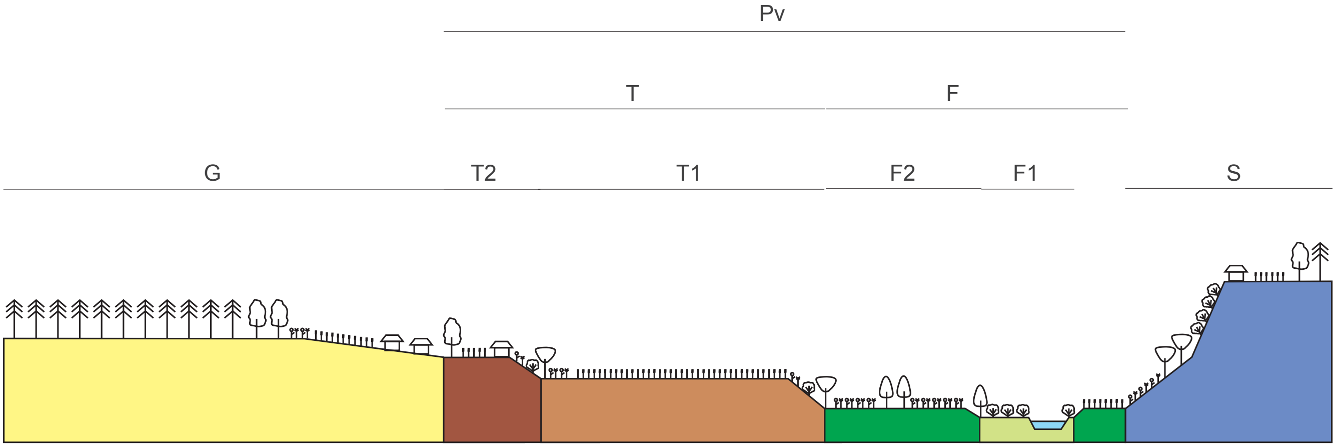

Fig. 2. Cross-section of the Lower San River valley – the scheme
Explanations: F – floodplain, F1 – active floodplain, F2 – historical floodplain, T – meadow terrace, T1 – Holocene meadow terrace, T2 – late Pleistocene meadow terrace, Pv – present (recent) river valley, G – glacial terrace, S – slopes and plateau

scale: 1 – rare, 2 – dispersed, 3 – frequent. The following elements of the valley relief were adopted: R – river channel, F1 – active floodplain and river banks above the mean water level (regularly flooded), F2 – historical floodplain (episodically flooded), T – meadow/*rendsina* terrace (non-flooded, T1 – Holocene terrace, T2 – late Pleistocene terrace), G – glacial terraces, S – slopes and plateau (Fig. 2).

The pattern of river corridor plant density across the San River valley was described by generating a concentration map of species and comparing it to a landforms map. To determine the elements of relief, detailed geological maps (1:50 000) and geomorphological literature (Wojtanowicz 1978; Szumański 1986) were employed.

In order to determine general habitat preferences, all the habitats were divided into eight types: eph – pioneer ephemeral vegetation on the banks of water bodies (*Bidentetea tripartiti*, *Isoëto-Nanojuncetea*), rip – riparian forests and shrubs (*Salicion albae*, *Alno-Ulmion*) and riparian forest edge communities (*Convolvuletalia sepium*, *Glechometalia hederaceae*), wtr – water bodies (*Potametea*, *Phragmitetea*, *Lemnetea minoris*), mdw – seminatural hay meadows (*Molinio-Arrhenatheretea*), grs – dry grasslands and thermophilous fringe communities (*Koelerio-Corynephoretea*, *Festuco-Brometea*, *Trifolio-Geranietea*), seg – segetal habitats (*Centauretalia cyani*, *Polygono-Chenopodietalia*), wst – abandoned agricultural areas (*Artemisietea vulgaris*, *Epilobietea angustifolii*, *Agropyretea intermedio-repentis*), rud – ruderal habitats (*Artemisietalia vulgaris*, *Onopordetalia acanthii*, *Sisymbrietalia*, *Agropyretea intermedio-repentis*). Based on the author's observations, the occurrence of species in a given habitat was assessed using the following scale: + – rare and not numerous, ++ – moderately frequent and usually not abundant, +++ – frequent and usually abundant, habitat optimum. The nomenclature of syntaxa follows Matuszkiewicz (2001).

3. Results

3.1. General characteristics of species distribution and habitats

In the investigated section of the San River valley, 55 of the 73 river corridor plant species of the Vistula catchment were noted (Table 1). Native species (including several taxa of uncertain status in Polish flora) were predominant in this group (82%). Majority of non-native species were neophytes. More than half of the species were rare (<5% grid cells) in the analyzed area, and only 7 taxa could be regarded as common (>25% grid cells).

River species were found throughout the valley; however, their frequency varied in particular areas

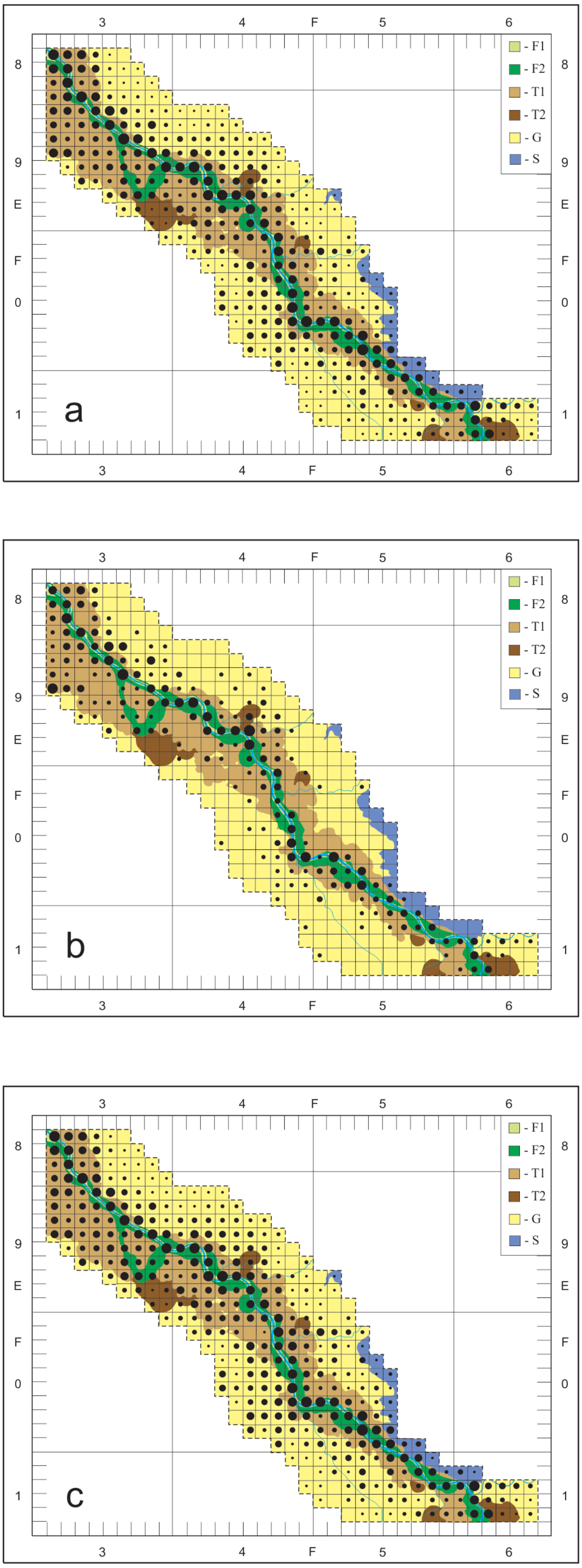

Fig. 3. Concentration of river corridor plants at the background of valley landforms

Explanations: a – total number of species, the largest circle indicates 21 species; b – species strictly confined to river corridors (group A), the largest circle indicates 7 species; c – species loosely confined to river corridors (group B), the largest circle indicates 16 species. Other abbreviations – see Table 1

Table 1. Distribution and habitat preferences of river corridor plants in the San River valley

	gr	n	R	F1	F2	T1	T2	G	S	eph	rip	mdw	grs	wtr	seg	wst	rud
*Chenopodium ficifolium**	B	0.01	░							+							
Limosella aquatica	B	0.04	▓			░				++							
Cyperus fuscus	B	0.19	█		░	▓	░	░	░	++							+
Senecio fluviatilis	A	0.11		█							++						
Bulboschoenus maritimus	A	0.03		▓	░	░								++			
Petasites spurius	A	0.03		░	░								+				
Cuscuta lupuliformis	A	0.02		░		░					++						
Sisymbrium strictissimum	A	0.20		█	░	░		░			+++						+
Chaerophyllum bulbosum	B	0.34		█	▓	░	░	░			+++					+	+
Cucubalus baccifer	B	0.26		█	▓	░	░	░	░		+++						+
*Rumex confertus**	B	0.27		█	▓	▓	░	▓	░		++	++				+	++
Populus nigra	B	0.19	░	█	█	░	░	░		+	+++	+				+	
Allium scorodoprasum	B	0.14		░	█	░		░			+	++	++			+	+
Carex praecox	B	0.38		░	█	▓	░	░				++	+++			+	++
Populus alba	B	0.48	░	█	█	▓	▓	▓	░	+	+++	+	+			++	++
*Bidens frondosa**	B	0.76	█	█	█	█	▓	▓	▓	+++	++					+	+++
Equisetum ramosissimum	A	0.16		▓	█			░			+	+	+++			++	+
Rumex palustris	B	0.01			░					+							
Barbarea stricta	B	0.03		░	░	░					+						
Myosotis sparsiflora	B	0.02		░	░				░		+						
*Valerianella locusta**	B	0.07			▓	░						++			+	+	+
Asparagus officinalis	B	0.16			▓			░	░				++				++
Eryngium planum	B	0.52		░	█	█	▓	░	░			++	++			+	++
Butomus umbellatus	B	0.10			▓	▓								++			
Allium angulosum	A	0.16		░	▓	▓		░				++				+	
Eleocharis acicularis	B	0.07	░	░	░	▓	░	░		++							
Epilobium adnatum	B	0.07	░	░	░	▓	░	░	░	+				+		++	++
Potentilla supina	B	0.07	░			▓		░		+++							+
Salvinia natans	A	0.10		░	░	▓	░	░						+++			
Cnidium dubium	B	0.05				▓	░	░				+++					
Scutellaria hastifolia	A	0.02			░	░	░					+		+			
Thalictrum flavum	B	0.01			░	░	░					+					
Lathyrus palustris	B	0.01				░						+					
Aristolochia clematitis	A	0.02				░					+						+
Mentha pulegium	A	0.01				░				+							
Wolffia arrhiza	B	0.01				░								+			
Nymphoides peltata	A	0.01				░	░							+			
Trapa natans	A	0.03				░		░						+			
Rorippa austriaca	B	0.01		░				░			+						+
Ononis spinosa	B	0.02			░	░	░	░					+				+
*Portulaca oleracea**	B	0.03			░	░	░	░	░						+		++
Kochia laniflora	A	0.01			░			░					+				
*Eragrostis albensis**	A	0.11	▓			░		▓		++							++
*Xanthium albinum**	B	0.19	▓	░		░		▓	░	++	+						++
Chenopodium rubrum	B	0.03	░			░		░		+							+
*Oenothera hoelscheri**	B	0.12		░	░	░	░	▓			+	+	+			++	++
Alisma lanceolatum	B	0.01					░	░						+			
*Oenothera depressa**	B	0.05			░	░		▓								+	++
Lithospermum officinale	B	0.03			░			░	░				+				
Gratiola officinalis	A	0.02				░		░				+		+			
Salsola kali subsp. *ruthenica**	B	0.03						▓									++
Artemisia scoparia	A	0.01						░									+
Erysimum hieracifolium	A	0.01						░									+
Salix daphnoides	B	0.01						░									+
Chondrilla juncea	B	0.02						░	░				+				+

Explanations: n – proportion of cartogram units with species presence; s – distribution subset, A – group A (strictly confined to river corridors), B – group B (loosely confined to river corridors), * – non-native species; R – river channel, F1 – active floodplain, F2 – historical floodplain, T1 – Holocene meadow terrace, T2 – late Pleistocene meadow terrace, G – glacial terrace, S – slopes and plateau; eph – pioneer ephemeral vegetation on the banks of water bodies, rip – riparian forest and shrubs and riparian forest edge communities, wtr – water bodies, mdw – seminatural hay meadows, grs – dry grasslands and thermophilous fringe communities, seg – segetal habitats, wst – abandoned agricultural areas, rud – ruderal habitats; light grey cell – rare, dark grey cell – dispersed, black cell – frequent; + – rare and not numerous, ++ – moderately frequent and usually not abundant, +++ – frequent and usually abundant, habitat optimum

(Table 1, Fig. 3a, 4). Ephemeral habitats forming in the river channel (R) were seldom used by only a few (12) river species; *Cyperus fuscus*, *Eragrostis albensis* and *Xanthium albinum* were quite often found here. The active floodplain (F1) was used more frequently (24 species), and several species were very common. The dominant habitat for the terrace was made up of riparian forests and shrubs (*Salicion albae*) as well as tall herb communities, in which the examined species were usually found. Typical species for this part of the valley comprised: *Cucubalus baccifer*, *Chaerophyllum bulbosum*, *Senecio fluviatilis*, *Sisymbrium strictissimum* and *Cuscuta lupuliformis*. On the higher level of the floodplain (F2), 32 of the investigated species were found, some of them in abundance. The list of species found in this zone was highly diversified in terms of habitat requirements; they occupied wet to dry grasslands (meadows, pastures, wastelands), forest edges, riparian forests and old river beds. The species of the highest density on this terrace included: *Equisetum ramosissimum*, *Allium scorodoprasum*, *Eryngium planum*, *Valerianella locusta*, *Populus alba* and *Carex praecox*. The older non-flooded terraces (T) of the present valley comprised the highest number of river corridor plants (40); however, typical species (reaching a clear optimum) were not observed in this part of the valley. The largest ecological groups on the *rendsina* terrace were meadow species, which occurred numerously at the margins of the present valley, also plants connected with water bodies (e.g. *Salvinia natans*), and ruderals. Thirty seven river corridor plants were observed on the glacial terrace (G); they occurred less frequently and were usually found in ruderal habitats. In the areas outside the valley (slope and plateau – S), 13 rarely occurring species were noted. They grew in seminatural, thermophilous communities and on ruderal sites.

In general, river corridor plants which are less confined to rivers (group B) could be found more frequently in the valley than plants strictly confined to river corridors (group A). Species of the first group were found, on average, in 12.9% of the basic plots, whilst species from the second group were found in 5.9%.

River corridor plants in the San River valley were found in habitats that varied very widely (Table 1, Fig. 5). About half of the species used more than one of the distinguished types of habitats. A lot of the species studied were found in ruderal habitats; some of them exclusively on these sites. The fewest number of species were observed in segetal communities. In the remaining types of habitats, the number of the observed species was similar. Species representing group A were more strictly confined to riverine habitats (riparian forests and shrubs, flooded meadows, old river beds). Species less confined to valleys (group B) were often found in grasslands and much more frequently in ruderal habitats; they could also be observed on arable fields.

Some of the taxa, which may be regarded as restricted to valleys of the Vistula basin, were found to adopt an atypical pattern of distribution in the investigated area. They occurred very seldom outside the Holocene valley, and only in ruderal communities (in the Vistula valley, they are dispersed throughout the valley and occur also in natural and seminatural habitats). Exemplary species are *Artemisia scoparia*, *Salsola kali* subsp. *ruthenica* and *Erysimum hieracifolium*.

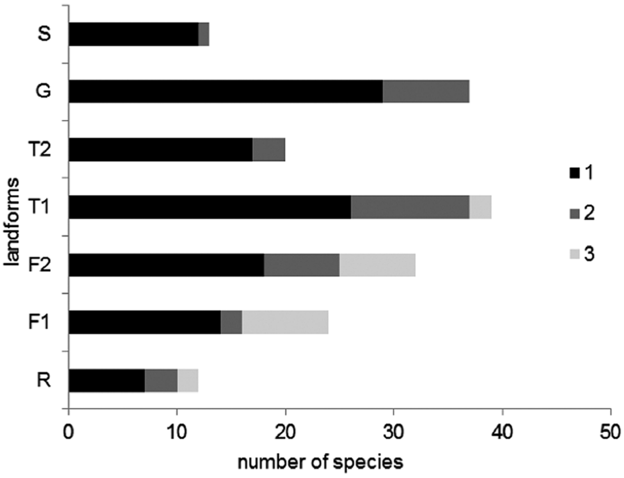

Fig. 4. Distribution of river corridor plants across the San River valley

Explanations: 1 – rare, 2 – dispersed, 3 – frequent. Other abbreviations – see Table 1

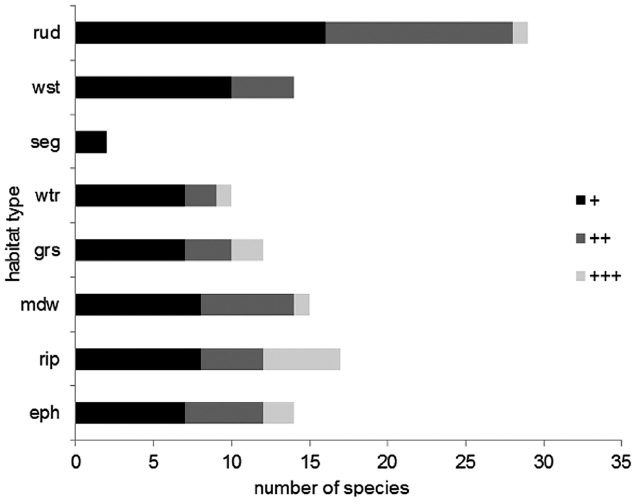

Fig. 5. Habitat preference of river corridor plants in the San River valley

Explanations: + – rare and not numerous, ++ – moderately frequent and usually not abundant, +++ – frequent and usually abundant, habitat optimum. Other abbreviations – see Table 1

3.2. Concentration of river corridor plants

The highest concentration of river corridor plants was observed on the floodplain. Their number decreased towards the border areas of the valley (Fig. 3a). Both species of the active floodplain and species growing in adjacent older terraces could be observed on the higher step of the floodplain (F2). The intensity of the phenomenon on the meadow terrace (T) changed; nevertheless, the number of species was clearly smaller than on the floodplain, and slightly larger than on the glacial terrace. A high concentration of the investigated taxa on this terrace could be observed near the river mouth. The glacial valley was characterized by the lowest frequency of river species. In its inner areas, which usually function as human settlement zones, the stations of the examined species were much more frequent than in the outer, forested parts; the species concentration was the lowest there. A large accumulation of river species could be observed in more urbanized areas. Neophytes clearly illustrate this dependency. The small surface area of the slope and plateau included in the studies made it impossible to form unequivocal conclusions concerning the density of river species in this area; nevertheless, it appeared to be similar to that of the glacial terrace. After dividing the investigated group of plants into groups strictly (group A) and loosely (group B) confined to valleys, it became apparent that this distribution pattern was clearer for the first group (Fig. 3b-c). The ranges of the species from group A were more restricted to the Holocene part of the valley, especially to the floodplain. Outside the Holocene valley, they occurred rarely. In general, group B comprised species of higher frequency in the whole valley, and the species from group A reached a higher density on the floodplain.

The presented distribution pattern depended, to a large extent, on dozens of species occurring frequently on the floodplain, or occurring frequently on the floodplain and less frequently on the meadow terrace. Among species strictly confined to river corridors, there were several species occurring frequently on the floodplain and about 2/3 were rare species scattered in recent valley and internal parts of glacial terraces. The distribution pattern was slightly indistinct due to the adopted cartogram method; in one cartogram unit two or more distinguished landforms could be found.

4. Discussion

The results confirm the thesis that river corridor plants are a highly diversified group. Plant species whose occurrence is confined to rivers differ in terms of habitat preferences and historical-geographical status (native and alien). Within a single river corridor, they may occupy one or more elements of valley relief (river channel, floodplain, older non-flooded terraces, slope). It is noteworthy that some of the species are strongly confined to floodplains, while others are located in the higher parts of the valley. Such variation indicates that the phenomenon is complex and, as Burkart (2001) inferred, cannot be explained with a single hypothesis.

There are currently two groups of hypotheses regarding the river corridor distribution pattern. The first connects the presence of species with conditions and processes occurring on a floodplain, such as floods, erosion, sedimentation or nutrient supply. However, a considerable number of river corridor plants are located in different parts of a valley (older terraces, slopes), away from areas influenced by the river; and only some of them can be classified as habitat relics. The second group of hypotheses points to previous and present migration of plants as the reason for the distribution of plants along rivers (Faliński 2000; Burkart 2001; Kucharczyk 2003).

It must be emphasized that phytogeographical studies based on distributional maps, even in detail scale, reveal only the pattern but cannot provide satisfactory explanation of the mechanisms. Therefore, the discussion has a largely theoretical character and some of the proposed hypotheses are lacking in strong evidence.

4.1. Ecological conditions of floodplains

A floodplain in the landscape is a dynamic and complex ecological system. The flow of water triggers fluvial processes (erosion, transport and deposition of carried material), whereas shifting discharge is the reason for variable water conditions in the adjacent areas. For living organisms, the activity of the river involves disturbance, stress, nutrient and water supply, and transport of propagules. Despite rich literature concerning the ecology of floodplains (Junk *et al.* 1989; Naiman & Decamps 1997; Bornette *et al.* 1998; Ward *et al.* 1999), there is little evidence confirming the process of formation of a river corridor distribution pattern under the influence of river-specific environmental factors.

Some papers show that riverine species evolve various adaptation mechanisms to flooding, including morphological and physiological traits as well as life strategy (Bloom 1999; Hölzel & Otte 2004; Lytle & Poff 2004; Mommer *et al.* 2006; Geissler & Gzik 2008, 2010). However, it is not clear why some of them show limited occurrence restricted to floodplains, while others are widely distributed. A recent experimental study conducted by Fischer *et al.* (2010) proved that some river corridor plants that are tolerant to inundation stress are unable to successfully compete outside an active floodplain because they cannot use resources efficiently in more benign conditions. Competitive advantages of non-river corridor species under water-stable conditions may be connected with greater benefits resulting from interactions with soil microorganisms (Engelaar *et al.* 1991). The results of the study by Fischer *et al.* (2010) do not, however, explain the distribution of a large group of different species occurring on higher terraces. Neither do they discuss why some of these species cannot be found or are found very seldom along small watercourses which are also subjected to floods.

It is noteworthy that the shifting flow rate leads to both inundation and drought during low water-level periods. Thus, a better explanation than flood-adapted species may be the hypothesis that river corridor plants are specialists well-adapted to the conditions of high water table fluctuations leading to double stress (Crawford 1996). Annual water level fluctuations in large rivers reach several meters and they can strongly affect plant communities (Johansson & Nilsson 2002; Leyer 2005; Van Geest *et al.* 2005). Such a large variability of hydrological conditions is not usually observed along small watercourses, where river corridor plants are absent or occur only sporadically. This hypothesis seems to be corroborated by the fact that some river corridor plants can be found outside river floodplains if the habitat is characterized by high annual fluctuation of the water table. For example, *Achillea salicifolia* or *Gratiola officinalis* can be found in depressions away from rivers (Burkart 2001 and references therein). In the valleys of SE Poland, species such as *Allium angulosum* and *Cnidium dubium* grow both on floodplains and in other parts of the valley or outside the valley (Kucharczyk 2001; Nobis 2008). In the study area, they were found on the flanks of the present valley in *Molinion* meadows.

The degree of river regulation and subsequent alteration of hydrological regime will certainly affect the number and abundance of specialized river corridor plants on the floodplain. For the lower San River, a successive decrease of river influence over the valley has been observed since the XIXth century, as a result of embankment construction and river-control works (Szumański 1977; Wojtanowicz 1978; Wyżga 2008). Species such as *Allium angulosum* and *Cuscuta lupuliformis* are more common on the floodplain of the slightly altered valley of the middle Vistula river valley (Kucharczyk 2001) than in the lower San valley with its regulated river channel. However, it should be noted that the river-control works and restriction of flooding entails a change in land management: an increase in arable areas at the expense of riparian forests, grasslands, wetlands and natural pioneer habitats. River regulation, therefore, has both a direct and an indirect influence upon other factors, which may determine the occurrence of some river corridor plants. It may be assumed that in the San River valley, some of the plants separated from the river are floodplain relics.

Adaptation to stress caused by water level fluctuation may be a good explanation for river corridor plants occurring exclusively on active floodplains, but it is rather a small group. In the study area, only a few species (*Senecio fluviatilis*, *Sisymbrium strictissimum*) were strictly confined to recent floodplain.

There is no evidence that edaphic factors can be considered essential for forming the river corridor pattern. The higher density of some species of eutrophic habitats may occur only in valleys located in regions dominated by nutrient-poor soils (Burkart 2001). It is rather a local phenomenon, and can be observed only in some sections of large river valleys. For instance, a lot of species concentrated in the lower San River valley in comparison with the adjacent plateau dominated by sandy soils (Nobis 2008). Fisher *et al.* (2010) experimental study assumed that soils in river valleys are fine-grained and sandy outside valleys. However, these assumptions do not apply to the conditions of SE Poland. In floodplain soils, sand fraction is often predominant, and fine-grained muds are found on river terraces above the recent floodplain (Szumański 1982).

4.2. Climatic dissimilarity of river valleys

A river corridor distribution pattern is usually formed only in a part of the whole species range. A lot of species reaching in Poland their range limit concentrate or extend their range along river corridors (Kucharczyk 2003). Transformation of distribution structure along a climatic gradient may indicate that climatic variables, modified by land relief, contribute to the generation of limited species distribution.

It is known that river valleys show higher thermal continentality than adjacent areas. However, the role of this driver in shaping the species distribution pattern in the lowlands of Central Europe was rather marginalized (Burkart 2001; Fischer *et al.* 2010). No relationships between thermal germination characteristics and river corridor confinement that were found by Hölzel & Otte (2004) constitute an argument for such an opinion.

Studies conducted in the Vistula river valley showed that when compared with their surroundings, they were characterized by higher mean temperatures, a higher water saturation deficit and smaller wind velocities (Gołaszewski 2004; Gołaszewski & Kleniewska 2009). These modifications were certainly dependent on the size and shape of the valley. Furthermore, temperature and air humidity may differ in the cross-section of a large valley, while conditions near a riverbed and on insolated slopes of the valley can be significantly different. It is quite possible that the climate in valleys can be a relevant determinant for many river corridor plants with greater thermal requirements. This is clearly noticeable when they occur mainly outside active floodplains. This group in SE Poland may supposedly be represented by species such as: *Aristolochia clematitis*, *Artemisia scoparia*, *Asparagus officinalis*, *Carex praecox*, *Eryngium planum*, *Kochia laniflora*, *Lithospermum officinale* and *Valerianella locusta*, which most often grow in grasslands, on forest edges and in dry ruderal habitats. Their distribution and density are also connected to soil conditions (light muds) as well as to the lowering of the water table caused by river incision (Bravard *et al.* 1997; Krawczyk 2012). Species of this group could be found in different parts of the valley and frequently showed a rather loose confinement to the river valley. The probable impact of the valley climate on the formation of the corridor range is well illustrated by the map of the potential range of *Pilularia globulifera* in Poland, constructed on the basis of the thermal requirements of the species. In central and south-eastern Poland, the range includes mainly the system of river valleys (Szczęśniak *et al.* 2012).

4.3. Anthropopressure and range dynamics

A river corridor distribution pattern can be the effect of the shift of species ranges occurring over time. A range restricted to valleys can be formed in two ways. In the first case, an expansive plant uses valleys as spreading routes; in the second case, valleys are refuges for receding species (Kucharczyk 2003). Starting from the Neolithic Period, the main force influencing the change in distribution of living organisms had been human activity, which increased considerably in the industrial age.

The thesis which states that rivers play a major role in the spread of alien plants is commonly accepted and well documented (Trzcińska 1961, 1963; DeFerrari & Naiman 1994; Pyšek & Prach 1994; Hood & Naiman 2000; Dajdok & Kącki 2003; Kucharczyk & Krawczyk 2004; Tokarska-Guzik 2005; Marciniuk & Wierzba 2006; Zając *et al.* 2011). Characteristics of a valley which facilitates expansion are: the presence of pioneer and disturbed habitats, a linear and continuous layout of riverine ecosystems and easy transport of propagules downstream. Moreover, it is important that a considerable proportion of human settlements, especially large cities which are usually starting points for expansive neophytes (Jackowiak 2003; Tokarska-Guzik 2005), are located by rivers. The linear structure of valleys and the cities located along them make up an ideal system for alien dispersal. The most probable and frequent scenario of the spread of an exotic species starts in one or several places in areas heavily transformed by man and subjected to high propagule pressure. A plant occupies small ruderal sites for some time until it reaches the critical size of population and it, then, becomes expansive (Jackowiak 2003). Next, it finds its way into an area of river influence. Taking advantage of the above-mentioned characteristics of the river valley, the species pushes the border of its range to further areas, including towns located in the valley. The last stage of expansion is a spreading throughout the areas adjacent to floodplain and penetration of terrains outside the valleys (Faliński 2000). Thus, the river distribution pattern will vanish with time and the confinement to river corridors will depend on the degree of species establishment. The existence of this mechanism is supported by distribution maps of neophytes in SE Poland. In the San River valley, the highest concentration of the total established neophytes occurred in urban areas and, to a smaller extent, on the floodplain (Krawczyk 2011). We observed the same distribution type in the study area among non-native river corridor plants – they concentrated in riverine habitats of floodplain and in ruderal sites across the valley, mainly in the vicinity of towns. *Eragrostis albensis* – a new expansive neophyte – is a good example here. According to national distribution maps (Zając & Zając 2001), it can be regarded as a typical river corridor plant strictly confined to large valleys, which prefers pioneer habitats in river channels (Sudnik-Wójcikowska & Guzik 1996; Kucharczyk 2001), but other studies indicate that it grows mostly in ruderal habitats (Michalewska & Nobis 2005) and can also spread along railways (Wrzesień 2006).

The comparison of river neophyte occurrence in the Vistula and San valleys showed that alien species were more common in the first, as a result of a less altered river system and a large area of natural pioneer habitats (Kucharczyk & Krawczyk 2004).

A similar pattern of territorial expansion can be used by native species altering their ranges as a result of gaining new adaptations or climatic change. It must be considered that if the rate of migration is slow and extended in time, the plant range in initial stages of expansion can be restricted to the valley for a long time. So, the distinction between expansive and site-related species still remains a primary phytogeographical problem in the studies on river corridor plants.

In Poland, the migration of mountain species along river valleys to lower areas was observed in the Carpathian Mountains (Walas 1938; Pacyna *et al.* 1966). The phenomenon, however, was of local character; only *Calamagrostis pseudophragmites* was more widely spread in lowlands along the Vistula River but it was not found in the study area.

Another hypothetical mechanism (in contrast to expansion) of the formation of river corridor pattern is the shrinking of species range in such a way that populations outside river valleys gradually become extinct, usually as a result of human activity. The pressure caused by man contributes to the disappearance of both natural and seminatural habitats, as well as some synanthropic communities connected with primitive settlements and agriculture. Intensive management eliminates many species growing on grasslands, arable fields and ruderal sites. Moreover, humans strive to "order the landscape", set a certain form of usage and then maintain it for a long period of time. As a result, we observe a decrease in frequency and magnitude as well as a change in the spatial distribution of events occurring cyclically and episodically, which disturb the functioning of ecosystems and force their natural dynamics. Thus, plants which use different kinds of disturbances and discontinuities of vegetation lose their habitats (landslides, backwaters, mid-field depressions managed in dry years, burned areas, drawdowns of water bodies, fallen trees, gaps in plant cover caused by livestock or wildlife, ruts of dirt roads, small excavations, etc.). Such changes contribute to the population decrease of species, which realize the R strategy, especially in wet habitats (e.g. *Alisma lanceolatum*, *Limosella aquatica*, *Mentha pulegium*, *Potentilla supina*, *Cyperus fuscus*, *Eleocharis acicularis*). It concerns, to a small extent, pioneer species which prefer dry grasslands (*Artemisia scoparia*, *Kochia laniflora*, *Eryngium planum*, *Equisetum ramosissimum*). Concentration of these species increases in a dynamic landscape where there is enough space for disturbance events involving vegetation cover, soil basement and hydrological conditions. Achieving a new, constrained ecological balance within conditions of human pressure is more difficult to realize in river valleys where a significant reduction of disturbing events is not possible in the long term. At the same time, the unfavorable conditions of the valley (floods, steep slopes) limit its intensive exploitation. Species which acquired the river corridor distribution pattern as a result of this mechanism may be strictly or loosely restricted to valleys and the degree of river confinement will depend on the intensity of anthropopressure in a given region. Such a hypothesis is rather a new concept and could be verified by comparing regions which differ in economical development. In poorly developed regions, the number of river corridor plants should be smaller.

Similarly, the manner and intensity of landscape management may affect the distribution of certain expansive alien species, as was noted by Pyšek & Prach (1994) who compared the frequency of occurrence of *Reynoutria japonica* and *Heracleum mantegazzianum* in the Czech Republic and Great Britain. They observed that in the case of the intensively exploited landscape of GB, the species were more strictly confined to riverine sites when compared to areas in the CzR where the landscape structure was less transformed by man.

4.4. Final remarks

Summing up, it can certainly be observed that a river corridor distribution pattern is formed in various ways. It may be assumed that river corridor plants consist of several hypothetical homogenous groups which should be studied separately during further research. The most probable explanatory hypothesis, discussed above, divide river corridor plants into four ecologically uniform subsets:

(1) Floodplain specialists – a small group of species well-adapted to variable water conditions of floodplains, outcompeted in hydrologically stable sites. Experimental studies on autecology and interspecific interactions in conditions of fluctuating water table should be continued only for species which are strictly confined to active floodplains.

(2) Range expanders – plants which currently increase their ranges, using river valleys as structures most favorable in gaining new areas. There are strong arguments that neophytes should be excluded from further studies.

(3) River corridor climate related plants – species with greater thermal requirements which use favorable modifications of climate occurring in large river valleys. In order to test this hypothesis, relationships between climatic variables and the occurrence of river corridor plants should be analysed in various parts of European lowlands.

(4) Refugees of human-transformed landscape – species withdrawing to river valleys as a result of anthropogenic changes in the landscape. In this case, there is a need for comparative phytogeographical studies in areas that differ in the intensity of management.

It is a very simplified scheme assuming that there is one force limiting the occurrence of plants. However, in some cases, a combination of two or more factors can give a better explanation. For example, it is quite possible that river corridor distribution of species of flooded meadows in Central Europe is a cumulative effect of climate of the valleys (Botta-Dukát *et al.* 2005) and water conditions. At present, there are more questions than answers and comprehensive explanation of the river corridor distribution phenomenon is a real challenge for botanists.

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