

Diversity and Distribution of Riparian Plant Communities in Relation to Stream Size and Eutrophication

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The present study was conducted in 47 different riparian areas distributed throughout Denmark to investigate diversity and distributional patterns of plant communities along a lowland stream size gradient (first to fifth order). The investigated areas were representative for Danish riparian areas not in use for agricultural production. We investigated plant community richness along a stream size gradient and the influence of eutrophication on the abundance of different plant communities. Vegetation analyses were performed in transects placed perpendicular to the stream channel, with a total of 1798 plots analyzed. Overall, we found a positive relationship between stream mean depth as a measure of stream size and the number of plant community types identified in the riparian areas. We also found that the abundance of the identified communities was positively correlated with their nutrient preference and negatively correlated with their moisture preference. The abundance of alkaline fens and *Molinia* meadows (protected community types) in riparian areas decreased with increasing size of the stream, whereas the abundance of humid meadows and wet herb fringes increased with increasing size of the stream. Based on our findings, we recommend that wide buffer zones be established along streams with protected habitat types in the associated riparian areas to reduce the direct impact from agriculture. Furthermore, we recommend that wide buffer zones be established along middle-sized and large streams because several community types may develop.

THE ABILITY OF RIPARIAN AREAS to capture or buffer sediment and nutrient losses from agricultural fields in catchments before they enter water bodies such as streams, lakes, reservoirs, and estuaries has increasingly been used during the last decade to reduce sediment and nutrient losses to surface waters (Sharpley et al., 1994; Venterink et al., 2003; Kronvang et al., 2008, 2009). The processes involved include mechanical trapping of sediment-bound nutrients, denitrification of nitrate, and sorption of inorganic P to iron and aluminum hydroxides (Vought et al., 1995; Hoffmann et al., 2006, 2009; Smith et al., 2008). Recently, emphasis has been laid on the importance of riparian areas for maintaining and enhancing biodiversity in agricultural environments (e.g., Sabo et al., 2005), reflecting that riparian areas are core habitats for a wide range of semiaquatic and terrestrial species and can function as wildlife corridors linking habitat patches in an agricultural landscape (Forman, 1995). It has also been acknowledged that the diversity of the vegetation in the buffer zone (e.g., species richness, vertical structure, and species composition) is important for its function to protect from agrochemical runoff and from erosion of nutrient enriched stream banks (Sharpley et al., 1994; McDowell et al., 2003; Kronvang et al., 2011).

The purpose of the present study was to gain insight into plant diversity patterns in riparian areas in an agricultural landscape that can be used in the establishment of buffer zones to optimize conditions for plant community diversity. Specifically, we investigated community diversity and abundance along a stream size gradient. Generally, biodiversity in natural riparian areas is sustained by high spatial and temporal variability in the environmental conditions, reflecting that strong environmental gradients exist at different spatial scales (e.g., Naiman and Decamps, 1997; Ward et al., 2002). In particular, the complexity in the geomorphology and hydrology increases with increasing stream size (Brinson, 1993; Dahl et al., 2007) and with the size of the aquifer (Grootjans et al., 2002); we therefore expected to find an increasing number of plant community types with increasing stream size, in particular water-dependent types (e.g., surface water habitats and habitats that depend on saturation conditions caused where groundwater is at or near the surface of the ground or where surface water flooding is frequent, such as fens and meadow types).

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Abbreviations: DCA, detrended correspondence analysis; HD, Habitats Directive.

Intensification of land use throughout most of Europe within the last decades has changed the environmental conditions dramatically in lowland stream and river ecosystems. Particularly, stream modifications (e.g., channels have been straightened, dredged, and confined by levees; Brookes [1987]) have changed the hydrology of riparian areas, and the increase in the use of fertilizer during the second half of the 20th century has increased the availability of nutrients. Nutrient loading is one of the most important threats to plant diversity and a major reason for the continuing decline of species that were formerly widespread (Venterink et al., 2001, 2003). High-intensity agricultural production may therefore have reduced community diversity significantly and possibly interferes with the expected increase in the number of plant communities with increasing stream size described above. We used an extensive dataset covering a total of 47 different sites and 1798 plots distributed throughout Denmark to investigate (i) plant community richness along a stream size gradient and (ii) the influence of eutrophication on the abundance of different plant communities. We discuss our results in relation to the establishment of buffer zones along streams in agricultural landscapes to improve conditions for biodiversity.

Materials and Methods

Selection of Stream Sites

A total of 47 sampling sites, all with open vegetation, were selected in 11 large stream systems distributed throughout Denmark (Fig. 1) representing existing variability in geological, hydrological, and climatic conditions. The investigated areas are representative of Danish riparian areas not in use for agricultural production, but they may have been used formerly for grass production. The selected sites were located in both upstream and downstream reaches, with approximately four sites in each system to cover a gradient in stream size. For all sites, the catchment was delineated from elevation contours on a national digital topographic map (1:25,000) (Nielsen et al., 2000), and total stream length upstream to a site was determined using AIS software (Denver, CO) in GIS.

Each sampling site was delineated as a 100-m-long reach along the stream channel. The starting point (at 0 m in the upstream direction) was registered by the use of GPS, and sites were precisely marked on aerial photographs. Six cross-sectional transects, placed perpendicular to the stream channel, were established 0, 20, 40, 60, 80, and 100 m from the starting point (Fig. 2). Each transect reached 10 m into the riparian areas on both sides of the stream.

Vegetation Surveys

Vegetation surveys were performed in 2004 using a semi-stratified approach. Frequency analyses were performed in a total of 1798 randomly selected plots of 100 × 25 cm in the 47 areas (varying between 20 and 48 plots in each of the areas). These plots were located along the cross-sectional transects to cover the most significant environmental gradient of importance for the vegetation (Fig. 2). The presence of all vascular plant spe-

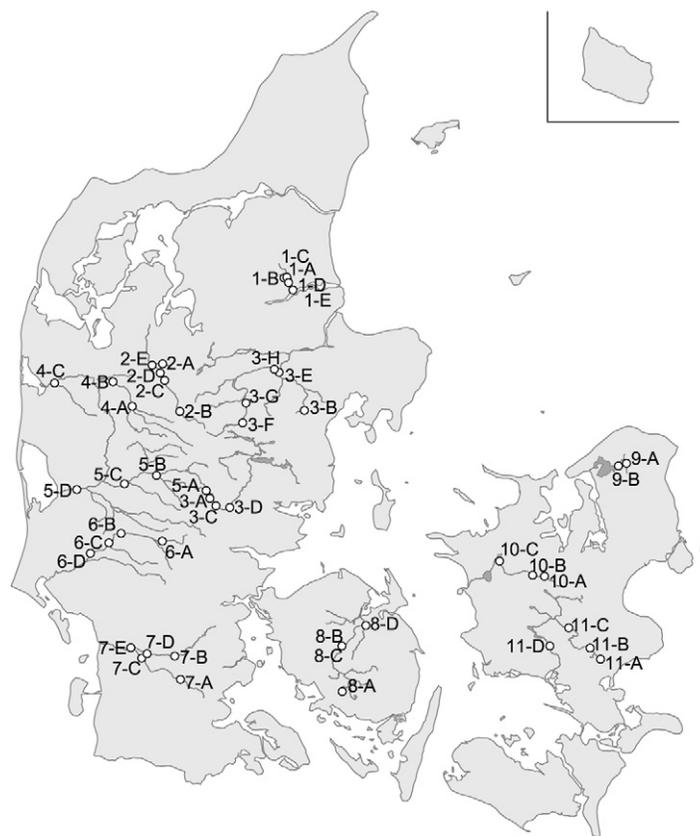


Fig. 1. Map showing the distribution of the 11 investigated stream systems. Sampling sites within stream systems are denoted with different letters.

cies was recorded (Økland, 1990) following the nomenclature of Hansen (1981).

Site Characteristics

Stream depth and width were measured in each sampling site. Stream depth was calculated as a mean from approximately 200 point measures allocated along the cross-sectional transects in the stream channel. Stream width was calculated as a mean of the width of the established transects. Selected environmental variables were measured in the riparian areas. The groundwater table was measured in April and October at 2 and 25 m from the stream channel in piezometers (PEH tubes; Rotek, Denmark), and the level of the groundwater table was calculated in the sample plots assuming linearity between groundwater measurements. The flood potential of the sample plots was calculated using the following approach: (i) aerial photographs with detailed markings of all plots were imported into GIS, (ii) aerial photographs were fitted with a topographic map (Danish National Digital Elevation Model 160 cm; Lidar DK-DEM, Copenhagen, Denmark), (iii) flooding of the riparian areas was simulated by raising the stream water level 50 and 100 cm above normal, and (iv) each plot was assigned to one of the following classes: 1 = no flooding, 2 = flooding at 50 cm water level rise, and 3 = flooding at 100 cm water level rise. Soil texture and type were characterized in the upper 30 cm of the soil in the surveyed plots using a 3-cm-diameter core sampler. Texture was categorized into clay; silt; fine-, medium-, and coarse sand; fine and coarse gravel; and stone. Soil type was categorized into gytja, peat, and mineral components (Schroeder,

1984). Gytja is an organic matter-rich material deposited in standing waters.

Data Analysis

The vegetation data were analyzed using three different approaches. (i) Plant community structure was analyzed applying a detrended correspondence analysis (DCA) on the dataset. Species occurring in fewer than four plots were excluded, leaving 213 species for the analyses. Species scores for the first three DCA axes were used to describe community structure. (ii) Species indices (e.g., richness [S] and shannon diversity [H]) and weighted averages of Ellenberg's indicator values for nutrient availability (Ell-N) and moisture (Ell-F) (Ellenberg et al., 1992) were calculated for each plot, where Ell-N is closely linked to the productivity of the plant community (Ertsen et al., 1998). These values are based on an assignment of indicator values for specific environmental conditions to a large number of species (>3000) in the western part of Central Europe. Weighted averages can therefore be used to interpret environmental gradients from assemblage patterns and are widely used in ecological studies (Ertsen et al., 1998; Van Landuyt et al., 2008; Dupré et al., 2010). (iii) The species list of each plot was categorized into vegetation types using a species-based classification model for seminatural and natural riparian vegetation types (Nygaard et al., 2009). This model was developed to achieve a statistical and standardized interpretation of the plant community types protected by the Habitats Directive (HD) (Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and wild fauna and flora) for application in the monitoring, assessment, and restoration of habitats in Denmark and is in accordance with CORINE Biotopes manual (Devillers et al., 1991). The model builds on a total of 13,000 plots and a total of 700 species covering a gradient in human impact ranging from natural habitats with spontaneous vegetation (e.g., mires and flushes) to meadows and pastures. The CORINE lists biotopes or broad habitats, which are differentiated by the growth form of the vegetation and ecosystem functions. These broad habitats encompass a range of vegetation types differentiated by species composition.

Relations between stream size characteristics (average width, depth, length and catchment size), soil characteristics of the site (average percentage values of mineral soil, peat, and gytja), and groundwater levels of the site (minimum and maximum values in April and October) were determined by regression analyses using number of community types as the response variable. Relations between categorical soil characteristics (i.e., number of soil textures and number of soil types) were analyzed using contingency tables. Logistic regression analyses were performed for each plant community type to analyze the relationship between the frequency of the community type and stream size using mean depth as a size measure. Detrended correspondence analysis axes scores, species richness, and Shannon diversity were calculated using PC-ORD 4.35 (MjM Software, Gleneden Beach, OR). Statistical analyses comparing indices among plant community types and relating community diversity to environ-

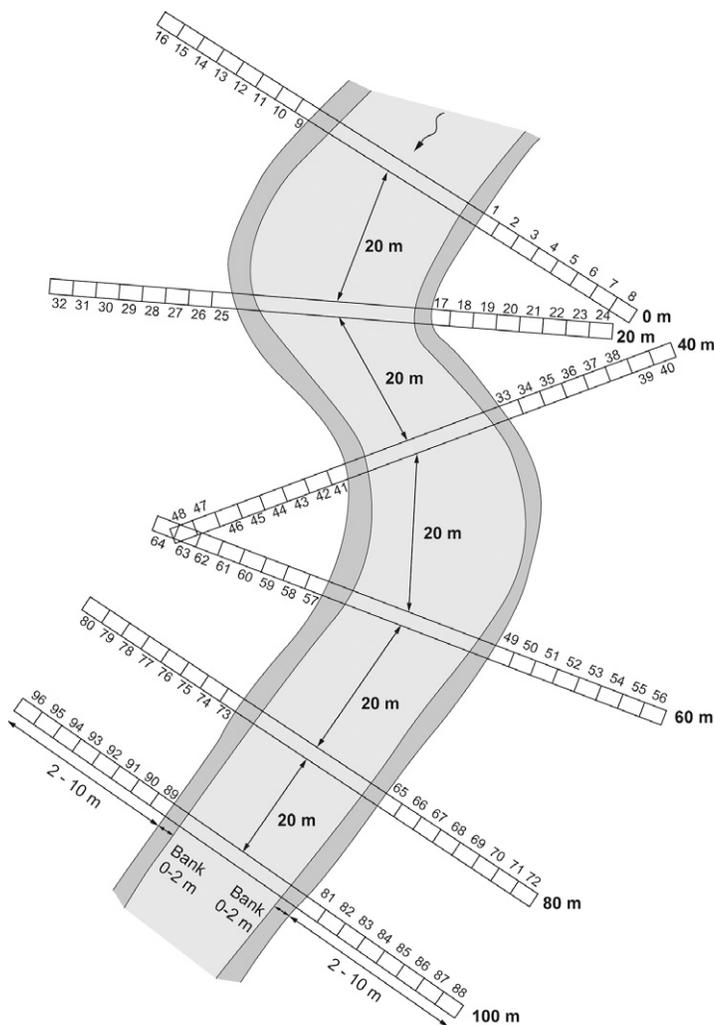


Fig. 2. Each sampling site was delineated as a 100 m long reach. Six cross-sectional transects were placed perpendicular to the stream channel 0, 20, 40, 60, 80, and 100 m from the starting point. Each transect reached 10 m into the riparian areas on both sides of the stream.

mental site characteristics were performed using SAS (Systat Software, Inc., Chicago, IL).

Results

Plant Community Characteristics

We found high floristic variability in the investigated areas (Fig. 3a). The gradient lengths were 6.3 and 6.8 for DCA axes 1 and 2, respectively (Fig. 3a). Based on the species-based classification model for seminatural and natural riparian vegetation types used, 10 different vegetation types were identified: alkaline fens (HD Annex 1; type 7230 [Supplemental Table S1]), dry fallow field, dry herb fringe, humid fallow field, humid meadow, hydrophilous tall herb fringe, improved meadow, *Molinia* meadow (HD Annex 1; type 6410 [Supplemental Table S1]), wet herb fringe, and wet meadow (Fig. 3a). Indicator species of these different communities are given in Appendix A. Alkaline fens were located to the left and hydrophilous tall herb fringes to the right of the first DCA axis and wet herb fringes in the lower part and improved meadows in the upper part of the second DCA axis.

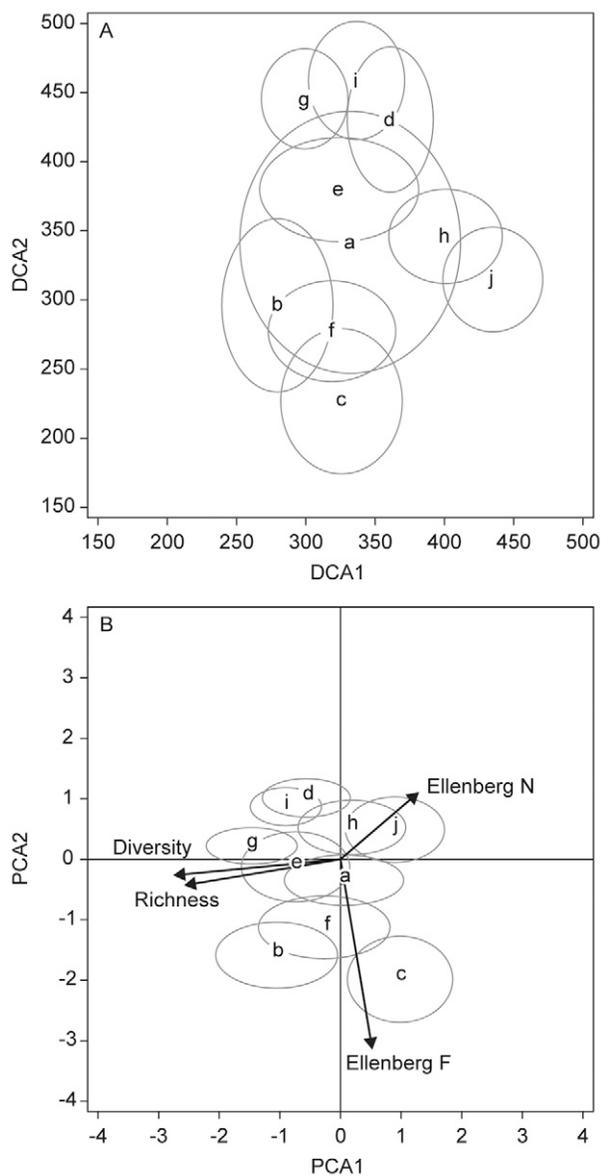


Fig. 3. (A) Detrended correspondence analysis biplot based on presence-absence data of plant species identified in 1798 randomly selected plots in a total of 47 riparian areas. The delineations (a–j) encompass the upper 90% and lower 10% of the detrended correspondence analysis (DCA) plot scores for each of the identified communities (see Appendix A), where a = Molinia meadow (EU code 6410), b = alkaline fen (EU code 7230), c = wet herb fringe, d = dry fallow field, e = humid fallow field, f = wet meadow, g = humid meadow, h = dry herb fringe, i = improved meadow, and j = hydrophilous tall herb fringe. (B) Summary of plant community variation based on richness, Shannon diversity, Ellenberg N, and Ellenberg F in the investigated plots. Principal components analysis axis 1 explained 38% and PCA2 explained 20% of total variance. The lengths of the vectors denote their significance for the analysis.

The identified plant communities were distinct with respect to all calculated metrics (species richness, Shannon diversity, DCA1–3, Ell-F, and Ell-N) (ANOVA; $P < 0.0001$) (Table 1 and Fig. 3b). The high variability in DCA 1–3 axes values is indicative of the significant underlying environmental gradients within and among the investigated areas (Fig. 3a). Low species richness and diversity were associated with the different types of fringe vegetation (Fig. 3b). Sample plots with hydrophilous tall herb fringe vegetation had on average 5.1

species, and plots with wet herb fringe vegetation had on average 5.4 species (Table 1). These communities were eutrophication tolerant, as inferred from high Ell-N values (6.9 and 6.5 for hydrophilous tall herb fringes and wet fringes, respectively) (Table 1). In contrast, high richness and diversity were associated with alkaline fens and humid meadow vegetation (Fig. 3b). Sample plots with alkaline fens had on average 8.1 species, and plots with humid meadow vegetation had on average 7.8 species (Table 1). These communities were also associated with low amounts of nutrients, with average Ell-N values being 4.3 for alkaline fens and 4.9 for humid meadows (Table 1). High moisture values were associated with sample plots, with wet herb fringe vegetation (8.1) (Table 1), alkaline fen vegetation (6.9), and wet meadow vegetation (6.9). In contrast, low moisture values were associated with sample plots with dry fallow field vegetation (5.4) and improved meadow vegetation (5.5).

Community Diversity, Abundance, and Environmental Characteristics

There was a significant increase in the number of plant community types encountered in the riparian areas and the size of the streams in terms of mean depth but not in terms of mean width, length, or catchment area (Table 2). We also found an increase in the number of community types with increasing amounts of gyttja in the areas and with decreasing amounts of mineral soil (Table 2). We did not find significant relations between the number of community types and hydrological descriptors (groundwater and flooding potential) or the number of soil textures or types encountered in the areas (Table 2).

The most abundant plant communities encountered were hydrophilous tall herb fringes (27% of the areas) (Fig. 4) and improved meadow vegetation (12% of the areas). The rarest plant communities were Molinia meadows (2%), alkaline fens (6%), and wet herb fringes (7%). The frequency of the plant communities identified was positively correlated with their nutrient preference in terms of Ell-N ($r = 0.61$; $p < 0.0001$) (Fig. 4a) and negatively correlated with their moisture preference in terms of Ell-F ($r = -0.12$; $p < 0.0001$) (Fig. 4b).

Four out of 10 identified community types were differently distributed along the stream size gradient (Table 3). The abundance of alkaline fens, hydrophilous tall herb fringe, and Molinia meadows decreased with increasing stream depth, whereas the abundance of humid meadows and wet herb fringes increased with increasing stream depth (Table 3).

Discussion

Several community types were identified in the investigated areas, including very species-rich types (e.g., alkaline fens and humid meadows) and species-poor types (e.g., dry and hydrophilous tall herb fringes). In particular, alkaline fens and Molinia meadows deserve attention because they are HD Annex 1 listed habitat types (Council Directive 92/43/EC). Previous studies have revealed that alkaline fens occur in approximately 29% of all riparian areas that are not in use for agricultural production in Denmark and that Molinia meadows occur in 24% of these areas but with a very restricted abundance when present (Baattrup-Pedersen et al., unpublished data).

Table 1. Plant community characteristics of the identified plant community types in the 1798 investigated plots located in 47 different riparian areas in Denmark. For further description of the identified communities, see Appendix A.

Community type	Species richness	Shannon diversity	DCA1†	DCA2	DCA3
Alkaline fen (7230)‡	8.14 ± 3.81a§	1.98 ± 0.49a	285.8 ± 61.4a	295.8 ± 91.4a	380.4 ± 45.2a
Dry fallow field	6.94 ± 3.31ab	1.84 ± 0.46ab	374.9 ± 75.4b	430.9 ± 78.0b	380.8 ± 64.1ab
Dry herb fringe	6.09 ± 2.98bc	1.67 ± 0.57bc	416.4 ± 101.4	344.0 ± 75.5c	375.6 ± 109.0abc
Humid fallow field	7.54 ± 3.45abd	1.90 ± 0.51abd	353.8 ± 136.5bc	378.4 ± 74.8	376.8 ± 87.6abc
Humid meadow	7.84 ± 3.08abde	1.98 ± 0.41abde	306.9 ± 76.5ad	436.9 ± 84.6bd	333.6 ± 38.7e
Hydrophilous tall herb fringe	5.24 ± 2.18f	1.56 ± 0.46cf	445.5 ± 94.8	315.1 ± 67.7ae	397.1 ± 99.1abcdf
Improved meadow	6.77 ± 2.56bcdg	1.83 ± 0.42abdeg	363.8 ± 111.9bce	454.0 ± 83.8bd	351.8 ± 60.1abcdeg
Molinia meadow (6410)	5.75 ± 3.07bcdgfh	1.61 ± 0.57bcdgfh	323.1 ± 5.1abcdef	318.0 ± 123.8acef	389.2 ± 77.5abcdgfh
Wet herb fringe	5.46 ± 2.89cfh	1.57 ± 0.53cfh	326.4 ± 8.8acdfg	232.9 ± 104.8f	348.8 ± 64.2abcdgghi
Wet meadow	7.31 ± 3.39abdegh	1.87 ± 0.50abdegh	325.2 ± 6.5acdfg	284.0 ± 73.9a	377.3 ± 58.4abcdgghi

† Detrended correspondence analysis.

‡ The EU code of HD Annex I habitat types is given in parentheses.

§ Different letters denote significant differences between means (*t* tests with Bonferonni correction to account for multiple tests; *P* < 0.05).

We found a positive relationship between stream mean depth as a measure of stream size and plant community richness in the riparian areas, but we did not find that this observation could be explained by a general increase in the environmental heterogeneity in the riparian area with increasing stream size (Brinson, 1993; Ward et al., 2002; Grootjans et al., 2002). Thus, soil type was the only variable found to play a significant role for the observed pattern, with an increase in the number of community types encountered with increasing percentages of gytja and decreasing percentages of mineral soil in the areas, whereas no significant linkages were found to the hydrological measures used (i.e., groundwater minimum and maximum levels in spring and autumn and flooding potential).

The lack of significance between the hydrological measures used to describe site hydrology and community richness may reflect the fact that the spatial and especially short-term period of measurements restricts our ability to identify linkages. The finding that soil type played a significant role for community richness supports this. Thus, soil type can be regarded as an integrated measure that, over time, besides reflecting the geomorphology of an area, reflects the hydrological conditions; for example, high peat content indicates that the soil is waterlogged during a major part of the year and high gytja content indicates waterlogged conditions, whereas high mineral content indicates that the moisture content is low (Goodall, 1983).

Our setup did not allow for a separation of the different groundwater sources, such as shallow local and deep regional groundwater, that may be very different regarding physio-chemical characteristics (Winter, 1999; Dahl et al., 2007) and hence contribute differently to the environmental heterogeneity in the areas. For example, discharge of deep groundwater into a riparian area is associated with low water temperature, low amounts of nutrients, and a steady supply of water (Almendinger and Leete, 1998; van Loon et al., 2009), whereas shallow groundwater can have high levels of nutrients, in particular in catchments with high agricultural activity (Allan et al., 1997; Davies and Neal, 2007). Because different groundwater sources provide habitats for different community types spanning from high-productive

types (e.g., high tall herb fringes) to very low-productive types (e.g., alkaline fens) (DeMars et al., 1997; Wassen et al., 2003; Grootjans et al., 2006), a high community richness is likely to evolve in areas with discharge of different types of groundwater (Jansson et al., 2007).

High levels of eutrophication in the areas may also explain why environmental variability explained only a limited amount of the observed variation in community richness in the investigated areas. The positive coupling found between community abundance and Ell-N indicates that eutrophication tolerance is an important regulatory mechanism of community distribution in the riparian areas studied, reflecting that the anthropogenic impact is generally high in Denmark and relates primarily to farming activities, atmospheric deposition, and urban developments in the catchments (Kronvang et al., 2008). Thus, erosion and leaching of nutrients from diffuse sources in the direct drainage area to the riparian area, atmospheric deposition of NH₃ and NO_x from local and distant sources, and nutrients deposited during inundation from upstream catchment areas

Table 2. Results of a series of regression analyses using the number of plant community types encountered in a total of 47 different riparian areas as a response variable and a range of size, soil, and hydrological parameters as independent variables.

	F values	<i>P</i> value†	<i>P</i> value (χ ²)
Size			
Stream depth, cm	11.45	<i>0.0017</i>	–
Stream width, m	2.98	0.097	–
Stream length, km	1.19	0.28	–
Catchment area, km ²	0.43	0.65	–
Soil			
Number of soil textures	–	–	0.77
Number of soil types	–	–	0.054
Average mineral percentage	2.17	<i><0.0001</i>	–
Average peat percentage	0.91	0.34	–
Average gytja percentage	49.60	<i><0.0001</i>	–
Hydrology			
Flooding potential	–	–	0.87
Groundwater, Apr. min	0.08	0.77	–
Groundwater, Apr. max	3.02	0.090	–
Groundwater, Oct. min	0.68	0.42	–
Groundwater, Oct. max	0.22	0.64	–

† *P* values < 0.05 are in italics.

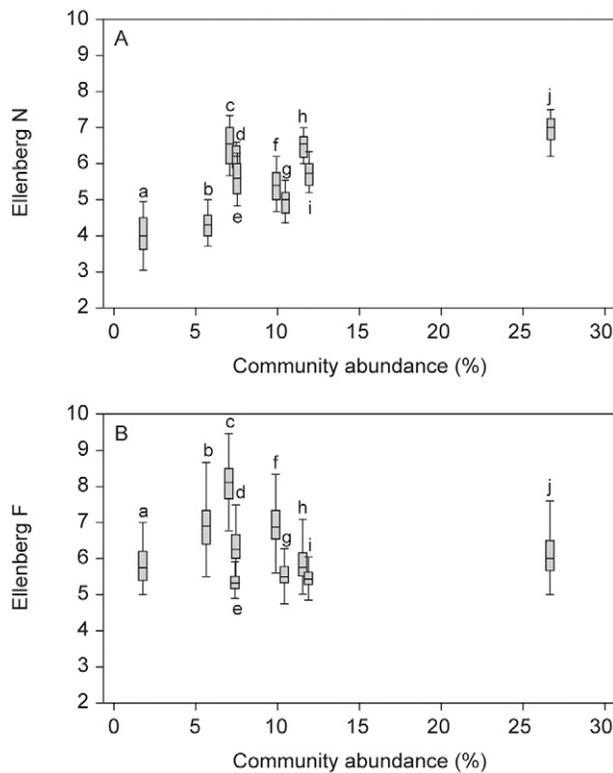


Fig. 4. Relationships between the abundance of the identified communities (Table 1 and Appendix A) and Ellenberg N (A) and Ellenberg F (B). The community abundance increased with increasing Ellenberg N ($r = 0.61$; $p < 0.05$) and decreased with increasing Ellenberg F ($r = -0.12$; $p < 0.05$). Letters denote different plant community types, where a = Molinia meadow (EU code 6410), b = alkaline fen (EU code 7230), c = wet herb fringe, d = dry fallow field, e = humid fallow field, f = wet meadow, g = humid meadow, h = dry herb fringe, i = improved meadow, and j = hydrophilous tall herb fringe.

enhance the nutrient availability in riparian areas (McDowell et al., 2003; Hoffmann et al., 2006; Hoffmann et al., 2009). High nutrient availability promotes species that have fast growth and at the same time strong competitive capabilities for nutrients and light (Grime, 1973). The highly abundant tall herb fringe community that was identified in 27% of the areas consists of species with these functional characteristics (see Appendix) (Grime, 1973, 1979), whereas alkaline fens that require permanent high water tables and a continuous supply of unpolluted groundwater (Boomer and Bedford, 2008) are particularly sensitive to agricultural improvement. The low tol-

erance of alkaline fens and Molinia meadows to high levels of nutrients may also explain their distributional pattern along the investigated streams. Both community types decreased in abundance in the investigated areas with increasing stream size, which may reflect that the risk of having high levels of nitrate in the discharging groundwater increase with increasing recharge area in Denmark because of high levels of agriculture (~66%) (Grant et al., 2009).

The results presented here demonstrate that several plant community types can be encountered along lowland streams in agricultural landscapes and that diversity values should be considered in the planning and management of these areas for water quality improvement (e.g., Hill, 1996; Venterink et al., 2006) and agricultural developments. Based on our findings, we suggest that wide buffer zones should be established along streams with eutrophication-sensitive, protected habitat types in the associated riparian areas to reduce the direct impact from agriculture. Furthermore, we suggest that wide buffer zones should be established along middle-sized and large streams because several community types may develop. Flooding is also more likely to occur along middle-sized and large streams, as compared with small streams, which may aid the maintenance of species-rich, moderately nutrient-rich fen and meadow vegetation provided that the water is not heavily polluted (Wassen et al., 2003).

Conclusions

Our study demonstrates that the vegetation in riparian areas is closely linked to stream size and eutrophication. We found a positive relationship between stream mean depth as a measure of stream size and the number of plant community types identified in the riparian areas and found that the abundance of the identified communities was positively correlated with their nutrient preference and negatively correlated with their moisture preference. The abundance of protected community types (e.g., alkaline fens and Molinia meadows) decreased with increasing stream size, whereas the abundance of wet herb fringes and humid meadows increased with increasing stream size.

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Table 3. Results of logistic regression analyses applied to analyze the distribution of the identified plant community types along a stream size gradient using mean depth as size parameter.

Community type	Parameter estimate	χ^2	<i>P</i> value†
Alkaline fen (7230)	0.0372	56.78	<0.0001
Dry fallow field	0.00436	1.08	0.297
Dry herb fringe	-0.00263	0.51	0.473
Humid fallow field	-0.00614	1.84	0.176
Humid meadow	-0.0114	10.29	0.001
Hydrophilous tall herb fringe	0.00962	14.42	<0.0001
Improved meadow	-0.00403	1.26	0.262
Molinia meadow (6410)	0.0165	4.34	0.037
Wet herb fringe	-0.0217	27.65	<0.0001
Wet meadow	-0.00571	2.63	0.1051

† *P* values <0.05 are in italics.

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