

Long-term dynamics of macrophyte dominance and growth-form types in two north-west German lowland streams

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SUMMARY

1. Continuous multiyear data sets can help to detect long-term trends and allow predictions with respect to environmental and biological variables. While the use of taxon-based approaches for bio-monitoring of watercourses is well established, little information exists concerning long-term variability of dominance and growth form composition of aquatic macrophyte communities. We analysed patterns in dominance and growth forms of macrophytes over a period of 21 years in relation to changes in water chemistry, disturbance regime and extreme weather conditions in two reference streams in the north-west German lowlands.

2. Rank–abundance curves of annual observations indicated five core species. The pattern of abundance resembled a broken-stick rather than a log-normal distribution. The core species, which reached both the highest absolute and average cover values, were *Sparganium emersum*, *Elodea canadensis*, *Callitriche hamulata*, *Potamogeton natans* and *Ranunculus peltatus*.

3. An analysis of change in dominance showed that in 67.5% of all observed cases, the same species became dominant in the subsequent year. *Sparganium emersum* (80.6%) and *E. canadensis* (68.8%) were the most successful species in retaining their relative dominance. Calculation of transition probabilities showed a strong attractor function of states dominated by *Sparganium* and *Elodea*. However, dominance patterns broke down over time and after 20 years, only one of the sites still showed the same dominance type. On average, dominance was preserved for around 4 years.

4. Reaches were mostly dominated by six growth forms, namely vallisnerids, potamids, peplids, nymphaeids, myriophyllids and graminids. In each reach, two, three or five growth forms shared the highest cover percentages. An analysis of traits of successfully established and dominant species identified three strategies: a facultative wintergreen growth habit in combination with effective means of vegetative reproduction; strong maintenance traits (in particular rhizomes); short-life span in combination with seed and turion production.

5. Strong oscillations of growth form types were observed. Six growth form clusters were defined, up to four of which may occur in one reach. Most frequent clusters were one characterised by strong vallisnerid dominance and another characterised by dominant potamids with peplids and myriophyllids. Both clusters showed the highest frequencies, durations and transition probabilities from other clusters. On average, growth form clusters persisted for 4.5 years.

6. An analysis of the influence of environmental factors on growth form dynamics showed that chemical and physical parameters distinguish the sample sites but cannot explain the observed changes.

7. We conclude that dynamics of species dominance as well as the occurrence of growth form assemblages are not controlled by physicochemical environmental factors such as nutrient composition at the scale of observation in this type of river. Instead, stochastic interactions between species characteristics and single disturbance events or weather extremes must be assumed. Implications for nature conservation, biomonitoring and reconstruction of reference sites are

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discussed. Continuous multiyear sampling is essential to understand the temporal behaviour of the system.

Keywords: aquatic plants, discriminant analysis, rank–abundance curve, transition matrix, vital attributes

Introduction

Since the 1970s, taxon-based systems involving aquatic macrophytes have been widely used as indicators of water quality of streams and rivers (Kohler, Wonneberger & Zeltner, 1973; Wiegleb, 1979; Haslam, 1982). Macrophyte composition indices of nutrient enrichment based on species occurrence have repeatedly been criticised for a variety of reasons (summary in Demars *et al.*, 2012). High intercorrelation of variables, spatial autocorrelation and a high number of influential factors, as compared to the number of species, often make it impossible to disentangle the effects of single variables (Demars & Harper, 2005; Paal, Trei & Viik, 2007; Demars & Edwards, 2009). In managed streams, these factors are augmented by on-site construction and maintenance measures such as cutting, dredging and bank construction (Baattrup-Pedersen *et al.*, 2006; Weyer, 2007).

In macrophyte ecology, representative sites are often sampled only once or, at best, twice in one or two consecutive years (Szozkiewicz *et al.*, 2010; Steffen *et al.*, 2014). A high number of samples cannot always compensate uncertainties resulting from short-term fluctuations of environmental parameters, spontaneous vegetation dynamics and long-term effects of natural and anthropogenic disturbance. If spatial and temporal variation in the system is unknown, this may lead to considerable bias, which is partly inevitable because of restrictions in money and available time. Long before the Water Framework Directive of the European Union (WFD, 2000) was implemented, a complementary approach was proposed, namely exhaustive mapping of larger physiographic regions in combination with long-term observations of macrophyte vegetation change. In Germany, for example, river vegetation was mapped in Schleswig–Holstein (Herr & Wiegleb, 1984), Lower Saxony (Wiegleb, 1983b; Herr, Wiegleb & Todeskino, 1989b) and the former West Germany (Zander, Wohlfahrt & Wiegleb, 1992). In Britain, pioneered by Haslam (1978) and Holmes (1983), the mapping approach preceded the German studies. Nowadays, comparable overviews are available for Estonia (Paal *et al.*, 2007), Latvia (Grinberga, 2011), Denmark (Baattrup-Pedersen, Larsen & Riis, 2003) and the lowland part of Poland (Staniszewski *et al.*, 2006; Szozkiewicz *et al.*, 2010). Even though there

are still considerable gaps, the main patterns of the influence of geographical and landscape parameters are known. While the mapping approach is widely accepted, published long-term observations are still rare.

Because the historical reconstruction of river vegetation based on published and unpublished vegetation data was regarded as partly unsatisfactory (see Wiegleb, 1979; Herr, Todeskino & Wiegleb, 1989a; Wiegleb, Brux & Herr, 1991), long-term observation projects were started by Brux *et al.* (1988) and Wiegleb, Herr & Todeskino (1989), covering time series of 9–11 continuous years. Among the long-term observations, the account of Schweinitz *et al.* (2012) is unrivaled, describing repeated sampling of a pre-alpine river over 40 years. Only a few papers have combined the study of vegetation change with the study of change in growth form and vital attributes (Demars & Harper, 2005; Lorenz *et al.*, 2012; Steffen *et al.*, 2013). Willby, Abernethy & Demars (2000) paved the ground for a more detailed account of single attributes beyond the growth form approach (Wiegleb, 1991).

Long-term continuous monitoring can provide a new perspective, if it is based on methodological accuracy and biological knowledge of species and their roles in the river ecosystem. Here, we report substantial changes in river vegetation from six river reaches in the north German lowland over 21 consecutive years. Preliminary analyses of vegetation change were provided by Wiegleb (1983a) and Wiegleb *et al.* (1989). The present study goes beyond this work, first by asking whether there are trends or regularities in the temporal behaviour of community properties such as species dominance and growth form composition. Second, we try to explain the observed annual patterns of dominance and growth form relations in terms of measured and observed environmental variables. Third, we summarise our knowledge about vegetation dynamics as a basis for future predictive modelling of growth form dynamics in lowland rivers.

Methods

Study area and study sites

The study was carried out in two lowland streams in north-west Germany. The study area and study locations

are shown in Fig. 1 (see also Wiegleb, 1984). The River Lethe is a 4th-order stream 37 km in length while the River Delme is 3rd-order and 46 km long. Both streams belong to the main catchment of the River Weser running in north-south directions between parallel ridges of the ground moraines of the Ems-Hunte moraine country, a natural unit which was formed by the penultimate ('Saale') glaciation (Herr *et al.*, 1989a). Both streams are classified as sandy lowland brooks according to Birk & Willby (2010). The upper and middle courses of both streams were still connected to ground water during the observation period. The main land use in both catchments was intensive agriculture, leading to diffuse inputs of nutrients. Six reaches were selected for permanent sampling, three in the River Lethe (L3, L6 and L9) and three in the River Delme (D5, D7 and D10). The reaches along the two rivers represent upper, middle and lower course conditions, respectively, with different species composition and dominance in 1978 (Wiegleb *et al.*, 1989). Stream morphology was considerably altered in all reaches, but contained natural elements such as pools and riffles in L3, D5 and D7. During the observation period, cutting of the streambed and bank vegetation was carried out at irregular intervals. An

overview of hydrological and chemical data is provided in Table S1.

Field survey

The field survey was carried out between 1978 and 1998 using the sampling method described in Wiegleb (1983a, b, 1984) and Wiegleb *et al.* (1989). All sites were resampled in July 2013. Reaches of 50–70 m length were sampled by hand or with a telescopic rake while walking along the reach on both sides and, wherever necessary, by wading in the stream. Sampling was always carried out by two observers. All macrophytes growing in the water or rooting below the water surface were sampled. Cover of species was estimated as percentages (continuous numbers), except for filamentous green algae, which were estimated as 1 – present, 2 – subdominant (<10%), 3 – dominant (>10%). Cover of <1% was estimated as 0.1. In cases of approximately equal dominance, special care was taken to identify the most abundant species. Specimens of *Potamogeton*, *Ranunculus* and *Callitriche* are deposited in the herbarium of Landesmuseum Natur und Mensch, Oldenburg (LMO).

The reaches were marked in the field. The marks were partly destroyed, but sketches of the exact field positions allowed sampling of the same reach every year. All reaches were located either 10–50 m above (L6, L10, D10) or below bridges (D5, D7). Site Lethe 9 was situated between two bridges. Photographs of the reaches were taken several times to record distinctive features of the sites. Morphology was classified in a five-category assessment scheme of naturalness (see Steffen *et al.*, 2014). Shading was recorded as percentage of tree growth along the banks.

Sampling intensity varied over the years due to financial and personal restrictions. For 1979–1981, continuous sampling is available for 25 consecutive months (Wiegleb, 1983a). For 1979–1992, at least one winter observation (January–March) is available. Otherwise, sampling was restricted to the vegetation period from June to September. At least one sample was taken during this main vegetation period. Statistical analyses showed that sampling only once might lead to underestimation of total cover and species richness, as compared to 2–4 samples. This did not affect the rank order of species and growth forms.

Data preparation and analyses

Vegetation. For the present analysis 43 species (of 94 found in total) were considered, including hydrophytes and amphiphytes (according to Willby *et al.*, 2000),

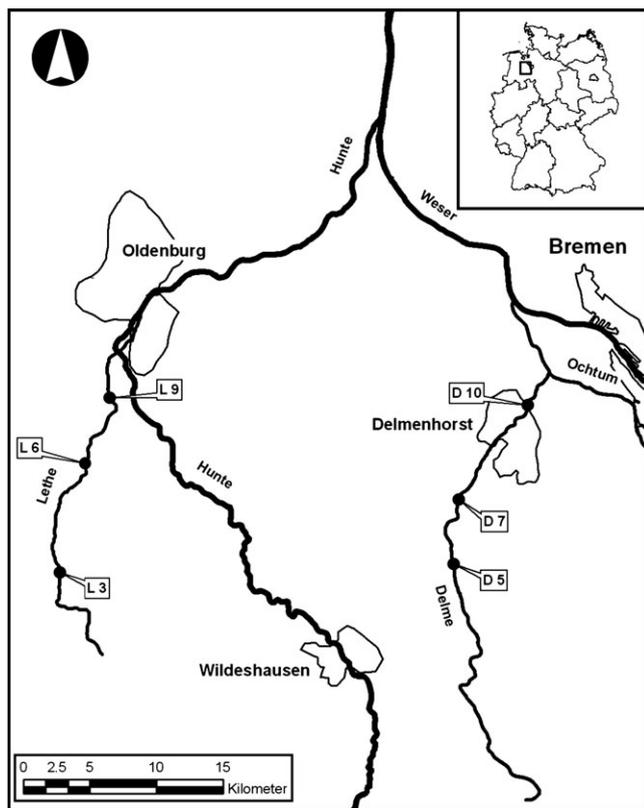


Fig. 1 Study area and study sites.

helophytes that behave like amphiphytes in the study area and hydrophytic 'cryptogams'. Accidental helophytes and land plants growing on eroded banks were excluded. Nomenclature of Tracheophyta–Euphyllophytina (vascular plants in part) follows Jäger (2011). For the dominance analyses, the highest cover value of each species during the respective vegetation period was used. If two species had exactly the same maximum cover, the second highest cover was considered as well. Frequency, average cover and maximum cover were calculated for all species. Shannon diversity H' was calculated both for empirical data and under the assumption of a broken-stick and lognormal distribution, respectively, according to the formulas in May (1975).

Attributes and growth forms. Vascular plant species were assigned to 19 attribute groups of Willby *et al.* (2000). Mosses and algae were added as a separate group. Seventeen growth forms were classified according to Wiegleb (1991). As both attribute types and growth forms contained too many types in relation to the number of species, nine growth forms were finally distinguished, based on morphological criteria and use of space (cryptogams, graminoids, herbids, myriophyllids, nymphaeids, peplids, pleustophytes, potamids and vallisnerids). The potamid group comprises parvopotamids and elodeids, as magnopotamids were not present. Hibernation types were distinguished according to our own observations during the sample period. They were coded as 2 – wintergreen at all sites, 1 – partly winter or summer-green, 0 – summer-green at all sites. Attributes related to vegetative growth and maintenance (rhizomes and stolons), vegetative dispersal (fragments, turions, tubers and buds) and sexual dispersal (seeds) were coded separately according to Willby *et al.* (2000: 2 – important, 1 – less important, 0 – not observed). Estimates were adjusted to the local circumstances. Both for the maintenance traits and the vegetative reproduction traits, a summary variable was calculated, ranging from 1 to 4. A species list including traits is given in Table S2.

Water chemistry. The data used in Wiegleb *et al.* (1989, partly provided by water authorities, partly from our own control measurements) were supplemented by data extracted from Water Quality Reports published by Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz (NLWKN, 2012) for the years 1985–2005. For 1985 and 1986, there is an overlap of both data sets. All values for $\text{PO}_4\text{-P}$, $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ were converted into NLWKN quality classes for annual averages. As the nutrient concentrations did not show any

significant influence on dominance or growth form pattern, they were not used for final analyses.

Weather. Data were reconstructed from Deutscher Wetterdienst (2013) for the nearest site with continuous measurement for 1978–1998 (Bremen Airport). Three variables were selected and coded as Cold winter [1 – mild winter without frost days, 2 – normal winter (coldest day between 1 and 20 °C), 3 – winter with temperatures below –20 °C (leading to ice scour in rivers)]; Warm summer [1 – heat period of 8–9 days (daily maximum above 25 °C)]; 2 – heat period of 10–12 days, 3 – prolonged heat period; and Wet summer [1 – precipitation during vegetation period more than 130% of average; 2 – in addition single precipitation events (>30 mm day⁻¹)]. Additionally, we used number of days with mean daily temperature below –10 °C during the winter, and number of days higher than 20 °C in the summer.

Disturbance. Disturbance events were recorded during field work or reported on request by water authorities. The following types of disturbance were recognised: cutting, dredging, construction work in the stream bed, bridge construction above reach, construction work at margins, turbidity because of construction work upstream, malfunction in sewage plant above stream, intensification of adjacent agricultural areas, planting of trees along margins, fallen trees causing logjam, unusually low water (50% of normal water level), and high water 1 m above normal. Each single disturbance event was coded as 1, and subsequently summed. Up to three events have been observed per year. Additionally, we used number of days with discharge $Q > Q_{10}$ prior (February–May), during (June–September) and after (October–January) the growing season.

Exploratory data analyses. All variables were tested for normal distributions. No vegetation variables were normally distributed according to Lilliefors and Shapiro–Wilk tests, and data were $\log(x + 1)$ - or z -transformed for all exploratory analyses. The data were centred and standardised prior to analysis. Influence of sampling intensity on cover was analysed using correlation analysis (IBM SPSS Statistics 21; IBM Deutschland GmbH, Ehningen, Germany).

Analysis of vegetation data. Vegetation was classified according to single species dominance and growth form composition. The number of dominant occurrences was counted for each species per site and in total. The

number of occurrences with cover over 50% was also counted. A transition matrix was constructed, showing how often a dominant species was observed to still be dominant the following year. Transition matrices can describe vegetation dynamics as a sequence of discrete states (Baltzer, 2000). Given that both the transition probability and the conditions under which a transition can take place are known, a transition matrix can be used to predict future changes. Number of changes in dominance state, average and maximum duration of dominance states were all calculated.

The percentage of growth forms was calculated for all yearly observations. To define independent states of growth form composition, hierarchical (Ward's method, using Euclidean distances and z-transformed data) and non-hierarchical cluster analyses [KMEANS, using $\log(x + 1)$ -transformed data] were carried out in combination with discriminant analysis. Analyses were carried out with IBM SPSS Statistics 21 (IBM Deutschland GmbH). Finally, six growth form states were defined. The number of transitions between growth form states was calculated, as well as average and maximum duration of growth form states. Ordination (DCA) based both on the presence/absence data and $\log(x + 1)$ -transformed cover of growth forms was run for all sites, for both individual rivers and the whole data set separately, using CANOCO 4.51 (Ter Braak & Šmilauer, 2002).

Analysis of relations between environmental variables, dominant species and growth forms. The aim was to test whether changes in growth form composition can be ascribed to more specific drivers. We used the full data set in these analyses but removed the effect of sites (spatial differences) before running cyclic permutation tests (Ter Braak & Šmilauer, 2002) to keep the temporal structure of the data (due to temporal autocorrelation). Growth form and traits data were related to time and

environmental data using partial redundancy analysis (pRDA) with $\log(x + 1)$ -transformed abundance data. We selected the best and significant explanatory variables in different permutations and tested the extent to which the variables could substitute for each other. A Bonferroni correction was applied to all results. These analyses were run with Canoco 4.51 (Ter Braak & Šmilauer, 2002).

Results

Relative abundance and dominance

The rank-order plot of the relative abundance of 43 species using $\log(x + 1)$ -transformed cover data shows an abrupt decrease after the first species and then after the 34th species (Fig. 2). In between, the decrease was almost linear with minor breaks after the 5th and 23rd species. The curve neither fits the log-normal nor the broken-stick distribution. Combined H' was calculated as 2.583, being closer to the theoretical expectation of a broken-stick model ($H' = 3.1$) than a log-normal model ($H' = 1.41$). The River Delme was more species diverse and contained more species of medium abundance ($H' = 2.429$). The River Lethe was less diverse on average ($H' = 2.183$) and contained more rare and accidental species.

Table 1 shows the frequency of species that reached the highest relative dominance. In total, 11 species became dominant in at least one site. *Sparganium emersum* was the most frequent dominant (63 times), followed by *Elodea canadensis* (18), *Ranunculus peltatus* (9), *Callitriche hamulata* (7) and *Potamogeton natans* (6). *Callitriche platycarpa*, *Callitriche obtusangula* and *Potamogeton trichoides* dominated only once. No dominants were found in 13 observation years. *Sparganium emersum* was by far the most dominant species in the River Lethe (41

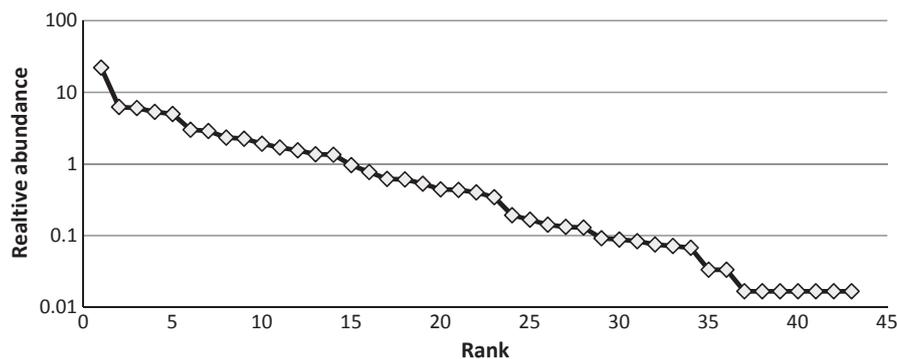


Fig. 2 Relative abundance of 43 species (rank-order plot), based on $\log(x + 1)$ -transformed cover data of all available observations.

Table 1 Number of dominant occurrences of species per site, river (L – Lethe, D – Delme) and in total

No. of yearly observations	L3	L6	L9	L _{tot}	D5	D7	D10	D _{tot}	Tot
	21	21	21	63	21	21	21	63	126
<i>Sparganium emersum</i>	10	12	19	41	0	7	15	22	63
<i>Elodea canadensis</i>	0	0	0	0	16	2	0	18	18
<i>Ranunculus peltatus</i>	5	1	0	6	0	3	0	3	9
<i>Callitriche hamulata</i>	0	0	0	0	4	3	0	7	7
<i>Potamogeton natans</i>	0	6	0	6	0	0	0	0	6
<i>Nuphar lutea</i>	0	0	0	0	0	3	0	3	3
<i>Elodea nuttallii</i>	0	0	0	0	2	1	0	3	3
<i>Myriophyllum alterniflorum</i>	0	2	0	2	0	0	0	0	2
<i>Callitriche platycarpa</i>	1	0	0	1	0	0	0	0	1
<i>Callitriche obtusangula</i>	1	0	0	1	0	0	0	0	1
<i>Potamogeton trichoides</i>	0	0	1	1	0	0	0	0	1
No dominant species	4	0	1	5	0	2	6	8	13

of 63 observations), while in the River Delme *S. emersum* (22 of 63) and *E. canadensis* (18 of 63) were most frequently dominant. Only site D5 was never dominated by *Sparganium*.

Table 2 shows the maximum cover values reached by dominant species. The highest cover was reached by *S. emersum* (80%), followed by *R. peltatus* and *P. natans* (70%). *Sparganium emersum* (19 times), *P. natans* (4), *E. canadensis* (3) and *R. peltatus* (2) reached cover values of 50% or more. *R. peltatus*, *E. canadensis* and *C. hamulata* reached an average cover of more 10% in one site only, *S. emersum* in four of six sites and in total. Three species reached cover values of more than 10% without becoming dominant; *Potamogeton bertholdii* (20%) and the helophytes *Phalaris arundinacea* and *Glyceria fluitans* (10%).

Table 3 shows a transition matrix of dominance states from year to year. One hundred and twenty-six annual observations imply 120 observed transitions. Twelve dominance states were observed. *Sparganium emersum* remained dominant in 50 of 62 cases after 1 year (80.6%), followed by *E. canadensis* (11 of 16; 68.8%). The same dominance state was observed 81 times (=67.5% of all cases) in the following year. Almost all transitions between dominance states are possible, at least indirectly. The transition from the state 'no dominant species' back to high cover vegetation was only observed three times of 11. *Callitriche platycarpa*, *C. obtusangula* and *Myriophyllum alterniflorum* dominated only once or twice and were unable to maintain dominance in the following year.

Table 2 Maximum cover reached by dominant species in all sites (in percentage; the exponent shows the number of observations with cover >50%; Average covers above 10% are printed in bold)

No. of years (observations)	L3	L6	L9	L _{tot}	D5	D7	D10	D _{tot}	Tot
	21	21	21	63	21	21	21	63	126
<i>Sparganium emersum</i>	30	60⁴	80⁸	80¹²	20	50¹	60⁶	60⁷	80¹⁹
<i>Potamogeton natans</i>	10	70⁴	5	70⁴	0.1	1	8	8	70⁴
<i>Ranunculus peltatus</i>	70²	25	25	70²	8	20	3	20	70²
<i>Elodea canadensis</i>	0	0	0	0	60³	20	0.1	60³	60³
<i>Elodea nuttallii</i>	0	0	0	0	40	15	0	40	40
<i>Callitriche platycarpa</i>	35	10	5	35	10	5	1	10	35
<i>Callitriche hamulata</i>	0	0.1	0	0.1	33	15	1	33	33
<i>Myriophyllum alterniflorum</i>	0	30	3	30	0.1	4	0.1	4	30
<i>Callitriche obtusangula</i>	25	3	0	25	0	0	0	0	25
<i>Nuphar lutea</i>	0	0	0	0	0.1	12	0	12	12
<i>Potamogeton trichoides</i>	0	0	30	30	0	0	0	0	30

Table 4 summarises important parameters characterising the dynamics of the dominance states. Between 3 and 7 (in D7), different dominance states were observed. In D7, also the greatest number of transitions between states was found (12). Most stable dominance relations were found in D10 and L9, which lasted 15 or 18 years, respectively. The average persistence of a dominance state ranged from 1.61 years to 10.5 with an overall average of 4.13 years. Six times dominance states lasted 5 years or longer, four times of *S. emersum* and once of *E. canadensis* and *P. natans*, respectively.

Dominant core species never showed an outlying position in any ordination diagram. Changes in dominance were distributed evenly over the observation period. Dominance changes were negatively correlated with disturbance frequency (Spearman's $\rho = -0.218$; $n = 39$; $P = 0.355$). The conditions under which changes in state occur were not obvious. The change of dominance of the most frequent species *S. emersum* was evenly distributed over the observation period as well. For most species, the number of observed changes was too small for statistical analysis.

Table 5 shows the dominant species and their vital attributes. Three groups of species can be distinguished. The first group was made up by peplids, potamids and

Table 3 Transition matrix of dominance states from year to year (state is defined by the species with maximum cover above 10%, see Wiegand *et al.*, 1989). Species are in alphabetic order, and transitions to the same state printed in bold

State	Before	After	1	2	3	4	5	6	7	8	9	10	11	12	Total
1	<i>Callitriche hamulata</i>		3	0	0	2	0	0	0	0	0	0	2	0	7
2	<i>Callitriche obtusangula</i>		0	0	1	0	0	0	0	0	0	0	0	0	1
3	<i>Callitriche platycarpa</i>		0	0	0	0	0	0	0	0	0	0	1	0	1
4	<i>Elodea canadensis</i>		2	0	0	11	2	0	0	0	0	1	0	0	16
5	<i>Elodea nuttallii</i>		0	0	0	1	1	0	1	0	0	0	0	0	3
6	<i>Myriophyllum alterniflorum</i>		0	0	0	0	0	0	0	0	0	0	2	0	2
7	<i>Nuphar lutea</i>		0	0	0	0	0	0	1	0	0	0	0	1	2
8	<i>Potamogeton natans</i>		0	0	0	0	0	0	0	4	0	1	1	0	6
9	<i>Potamogeton trichoides</i>		0	0	0	0	0	0	0	0	0	0	0	0	0
10	<i>Ranunculus peltatus</i>		0	0	0	1	0	0	0	0	0	3	4	1	9
11	<i>Sparganium emersum</i>		1	1	0	1	0	1	0	2	1	2	50	3	62
12	No dominant species		0	0	0	0	0	0	1	0	0	1	1	8	11
	Total		6	1	1	16	3	1	3	6	1	8	61	13	120
	Diagonal														81

Table 4 Parameters characterising the dynamics of dominance states in sampled reaches

Site name	No. of dominance states	Number of changes in dominance state	Average duration of state (years)	Maximum duration (years)
Lethe 3	5	9	2.1	6
Lethe 6	4	8	2.33	8
Lethe 9	3	3	5.25	18
Delme 5	3	6	3.0	10
Delme 7	7	12	1.61	4
Delme 10	3	1	10.5	15
Average	4.16	6.5	4.13	–

myriophyllids, which are slender and mostly submerged plants. Most were at least facultative wintergreens, additionally characterised by effective means of vegetative reproduction. Myriophyllids differed from the other groups by also having well developed mechanisms for maintenance. A second group was made up by *S. emersum*, *Nuphar lutea* and *P. natans*, characterised by strong mechanisms of maintenance such as thick rhizomes. In addition, these differed both in terms of morphology and hibernation type. In between was *P. trichoides*, an ephemeral summer-green potamid that has both effective vegetative (turions) and means of sexual reproduction (seeds).

Growth form and vital attributes

Figure 3 shows a discriminant analysis run after repeated hierarchical and non-hierarchical clustering of growth form composition, which resulted in a six-cluster

solution. Cluster 1 (15 yearly observations) mostly contains low cover vegetation, found in sites L3, L9 and D5-10. Cluster 2 (12 yearly observations) is characterised by codominant occurrence of vallisnerids, myriophyllids and peplids, mostly found in L6 and rarely in L9. Cluster 3 (23 yearly observations) is diverse in growth forms and often dominated by vallisnerids and myriophyllids. It was found in L3, L6 and D7. Cluster 4 is the most frequent one (38 yearly observations) and also occurred in L3-9 and D10. It is dominated by vallisnerids (i.e. *Sparganium*) and generally shows lower growth form diversity. Cluster 5 (6 yearly observations) was only found in L3 and is made up by codominant vallisnerids and myriophyllids. Cluster 6 (32 yearly observations) is the second most frequent cluster and is mostly dominated by potamids. It frequently occurred in D6 and D7 and rarely in L6 and L9. Discriminant analysis shows a good match with the final six-cluster solution of KMEANS. Only two yearly observations from L9 (1987, 1989) were misclassified and were found in cluster 4 instead of cluster 6. Eighty-four per cent of the assignments to a cluster were significant at the 0.05 level. Clusters 1 and 4 were not significantly separated on the first two discriminant functions.

Table 6 shows the transitions between growth form types and again 120 transitions were observed. In 89 cases (=74.2%) the same growth form type was observed the next year. The percentages ranged from 67% for cluster 2–80% for cluster 5. However, only clusters 4 and 6 can be regarded as attractor types, as their column sums exceed their row sums by 1.3 and 1.12, respectively.

Table 7 shows parameters characterising the dynamics of growth form clusters. All River Lethe sites showed

Table 5 Growth form and traits of successful dominants. Hibernation type: 0 – summer-green, 1 – wintergreen in some sites, 2 – wintergreen in all sites. Maintenance: from 0 – rhizomes and stolons regularly absent, to 4 – strong rhizomes always present. Vegetative reproduction (from 0 = not observed, to 4 = various effective means such as turions, tubers, and fragments present). Seed formation (from 0 – no seed formation observed to 2 – regular seed formation). Essential properties are printed in bold

	Growth form	Hibernation type	Maintenance	Vegetative reproduction	Seed formation
<i>Callitriche hamulata</i>	Peplid	2	0	2	2
<i>Callitriche obtusangula</i>	Peplid	1	0	2	2
<i>Callitriche platycarpa</i>	Peplid	2	0	2	1
<i>Elodea canadensis</i>	Potamid	2	0	4	0
<i>Elodea nuttallii</i>	Potamid	1	0	3	0
<i>Myriophyllum alterniflorum</i>	Myriophyllid	2	2	2	2
<i>Ranunculus peltatus</i>	Myriophyllid	2	1	2	2
<i>Potamogeton trichoides</i>	Potamid	0	0	2	2
<i>Sparganium emersum</i>	Vallisnerid	1	4	0	2
<i>Nuphar lutea</i>	Nymphaeid	1	4	0	2
<i>Potamogeton natans</i>	Nymphaeid	2	4	2	2

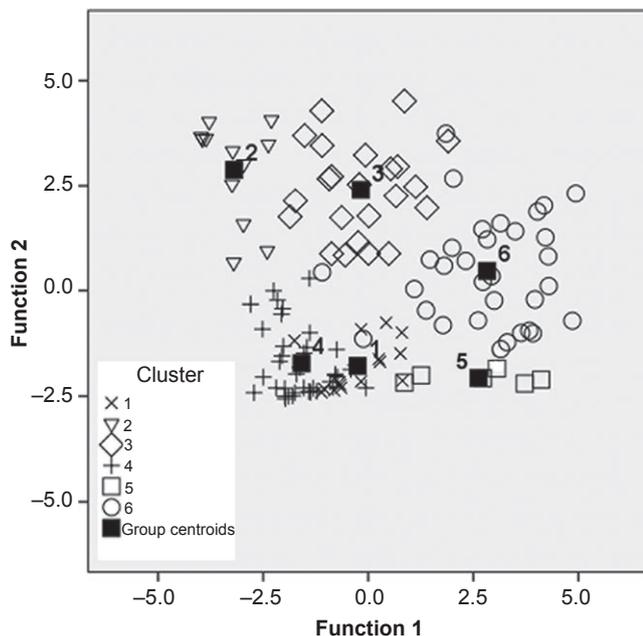


Fig. 3 Discriminant analysis of yearly observations of sites (open symbols), based on $\log(x + 1)$ -transformed cover data. Group centroids of six clusters are shown as solid symbols. Canonical discriminant functions 1 and 2 explain 40.1 and 32.9% of variance.

four clusters per sites, while River Delme sites only showed 2–3. The number of changes between clusters varied between 1 (D10) and 8 (L6). Maximum duration was 15 years in D10 and 16 years in D5. Average duration of persistence of a growth form state was 4.53 years.

Changes in growth form clusters were evenly distributed over the observation period (see Table S3). Neither a correlation with disturbance events (Spearman's

$\rho = 0.134$; $n = 31$; $P = 0.543$) nor with weather extremes was found. Further analyses were carried out to test the effect of magnitude, frequency and timing of temperature and discharge variability. Both for growth forms and traits time explained 22 and 25%, respectively, of the variability in growth forms and traits after taking out the effect of site. No other explanatory variable was significant, after time was selected. However, c. 50% of the effect of time could be due to shade (increased at two sites) and number of winter/summer days with low (-10 °C)/high (20 °C) temperature, respectively, which together explained c. 15% of the variability in both growth form and traits (10 and 12%, respectively, confounded with the effect of time). Results of pRDA were all statistically significant after Bonferroni correction.

Discussion

Relative abundance and dominance

Species abundance distributions indicate differential abilities to acquire resources (Magurran & Henderson, 2012). They have rarely been used for analysing macrophyte communities (Demars, 2002; Baattrup-Pedersen *et al.*, 2006), even though relative plant mass data (e.g. Kohler *et al.*, 2003) can be interpreted in a similar way. The shape of the rank–abundance curve resembles a broken-stick distribution (Wilson, 1991). We assume that only *S. emersum* can find optimal growth conditions in these sites. It is accompanied by 2–3 satellite species, namely *R. peltatus*, *M. alterniflorum* and *P. natans* in the River Lethe, and *E. canadensis* and *C. hamulata* in the River Delme. The sharp decline in the rank–abundance curve after the 34th species may signify the carrying

Table 6 Transition dynamics of growth form types. For description of clusters, see text

	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6	Total
Cluster 1	8	0	0	0	1	2	11
Cluster 2	0	8	1	2	0	1	12
Cluster 3	0	2	17	2	0	2	23
Cluster 4	3	2	0	29	1	2	37
Cluster 5	0	0	0	1	4	0	5
Cluster 6	4	0	3	2	0	23	32
Total	15	12	21	36	6	30	120
Diagonal							89

Table 7 Parameters characterising the dynamics of growth form clusters in sampled reaches

Site name	Number of growth form clusters	No. of changes between growth form clusters	Average duration of state (years)	Maximum duration (years)
Lethe 3	4	5	3.50	9
Lethe 6	4	8	2.33	9
Lethe 9	4	7	2.62	8
Delme 5	2	3	5.25	16
Delme 7	3	6	3.00	6
Delme 10	2	1	10.50	15
Average	3.16	5.0	4.53	–

capacity of the streams. Species do not exclude each other but simply use the available space and resources differently. Further species occur only accidentally after lateral or longitudinal immigration.

Maximum cover is limited to 80%, a figure reached only once by *S. emersum*. Three other species, *R. peltatus* and *P. natans* in the River Lethe and *E. canadensis* in the River Delme, reached over 50%. This coincides with the observations of Sand-Jensen, Andersen & Andersen (1999) who found 70% to be an upper limit of cover in *Callitriche cophocarpa* caused by interactions between cover and flow regime. Cover values above 10% are rather the exception than the norm. The highest cover reached by a helophyte in our study was 10%. Helophyte cover is particularly limited by cutting and bank construction measures of water authorities.

Neither repeated dominance nor constant occurrence can prevent a species from going at least temporarily extinct. In site L3, *R. peltatus* was dominant with 30% cover in 1985. It disappeared in 1990, but returned in 1996. Similar changes were observed in *C. platycarpa*, which dominated in 1993 (35%), was lost in 1995, but returned immediately in 1996. *Callitriche obtusangula* was dominant with 25% in 1992 (a warm summer), but was not found in 1993, an extremely wet summer. In the

River Delme, *C. hamulata* dominated site D5 in 1989 with 30%, but was not seen from 1990 to 1998. *R. peltatus* dominated site D7 in 1986 with 20%, but was lost in 1992, while *S. emersum* still dominated D10 in 1992 with 20% (30–65% in the previous years), but was finally lost in 1998. Both species were present again in 2013. Only two hydrophytic species that were constantly present in the first 10 years (*P. natans* in L3 and *M. alterniflorum* in L9) were lost completely.

Species dominance is an important parameter in vegetation classification of watercourses. In the present case, 67.5% of the sites belonged to the same dominance type as in the previous year. For the first 10 years, an average value of 65% had been observed (Wiegleb *et al.*, 1989). Dominance relations were slightly more stable in the second half of the observation period, but the increase was partly due to the fact that vegetation became so scarce in some sites that dominance could not be assigned to any species. Interestingly, both *M. alterniflorum* and *N. lutea* reached dominance at relatively low cover values, but only *N. lutea* was able to defend its position the following year. After 10 years (1988), three of six sites still belonged to the original dominance type (see Wiegleb *et al.*, 1989). Four of six sites were dominated by *S. emersum*.

If we had finished the study in 1997, no site would have belonged to the original dominance type and in 1998 only one site (D5) belonged to the same dominance type (*E. canadensis*) as in 1978. *Sparganium emersum* only dominated one site in 1998 (L6) while in 2013, no site was dominated by *S. emersum* (see Table S4). Theoretically, the high probability in dominance persistence and the high attractor function of *S. emersum* (diagonal and column sum) suggests that all sites should become *Sparganium*-dominated after a few transitions. However, even for this frequent species, the number of observations is still too low for a final judgment.

A previous study in northern Germany (Herr *et al.*, 1989b) showed that only 28 of 118 sites in total (=23%)

colonised by a *S. emersum* community in 1946 had a similar species composition after 40 years. Thirty-five sites (or 29%) were still recognisable as *S. emersum* communities (with *Sparganium* being dominant) while 10 sites (or 8%) switched to a Callitricho–Myriophylletum community, which is found in different forms in our sites L2, L5, D5 and D7. Thirteen of 58 (or 22%) of the sites colonised by a ‘Callitricho–Myriophylletum’ remained similar after 40 years, while 15 (or 25%) showed a dominance shift of the characteristic species *M. alterniflorum*, *C. hamulata* and *R. peltatus*. Ten sites (or 17%) developed into a *S. emersum* community.

Dominance of species may change between seasons (Körs *et al.*, 2012). In our case, in five of 84 available observations were different species dominant after the vegetation period. In those cases, either wintergreen species such as *E. canadensis* and *C. hamulata* became dominant after the decay of mostly summer-green *S. emersum*, or *E. canadensis* and *C. hamulata* changed their rank order in abundance. These changes had no overall influence on the results.

Growth forms and attributes

We reduced the growth forms of Wiegleb (1991) and attribute groups of Willby *et al.* (2000) to a simplified typology with nine growth forms. A similar classification was used by van de Weyer (2001), Daniel, Bernez & Haury (2006), Szoszkiewicz *et al.* (2010) and Steffen *et al.* (2013). Relevant attributes were reduced to four (seasonality, maintenance, vegetative reproduction and seed production). Other simplified species groupings have been used by Mesters (1995), Riis, Sand-Jensen & Vestergaard (2000), Kohler *et al.* (2003), Demars & Harper (2005; alternative to the attribute-based approach), and Daniel *et al.* (2006; in combination with growth forms).

Barrat-Segretain, Bornette & Hering-Vilas-Boas (1998) classified all the river plant species they investigated as *r*-strategists. In our data set, this holds for *Elodea*, *Callitriche*, *Myriophyllum* and *Ranunculus* species. *Luronium natans*, which was identified as a disturbance tolerant species by Barrat-Segretain *et al.* (1998), never colonised site L3 even though it grew abundantly 500 m upstream. On the other hand, *S. emersum* clearly behaved like a *K*-strategist, or rather competitive dominant. In fact, rhizomatic species increased despite increased disturbance. Some species with effective vegetation dispersal means prevailed (*P. alpinus*) or entered the scene (*P. trichoides*, *Elodea nuttallii*).

Biological properties of successful species differed considerably (see also Wiegleb *et al.*, 1991). In more

rhithral reaches (L3, L6; D5, D7), three different growth forms with similar traits could occur as dominants (peplids, potamids and myriophyllids). These are able to form dense patches and fill the whole water column. No single decisive trait allowed persistence and abundant growth; rather the species of this group belong to four attribute types in the sense of Willby *et al.* (2000). Differences were more pronounced among the three potamal species *S. emersum*, *N. lutea* and *P. natans*. They have no traits in common except rhizomes and frequent formation of floating leaves. Willby *et al.* (2000) classified them into three different attribute types.

We are confronted with a seeming paradox. There seems to have been an ongoing ‘potamatisation’, as ‘rhithral species’ such as *M. alterniflorum*, *C. hamulata* and *R. peltatus* were replaced as dominants by ‘potamal species’ such as *S. emersum* and *N. lutea* without any obvious change in hydrological conditions. None of the successful species can be regarded as a true rheophyte (*sensu* Van Steenis, 1981) or rheophilic species (Trempe, 2007). All species except *S. emersum* are found more often in stagnant waters.

Nevertheless, oscillations in the proportions of growth forms were observed in all our sites (see Figure S1) with two to five growth forms being combined into two to four growth form clusters. None of the sites was colonised by all six growth form types. There was an apparent dominance hierarchy. Vallisnerids seem capable of dominating in all sites. If they do not reach dominance, peplids and potamids take over. If unfavourable conditions, such as repeated disturbances, prevent the development of these growth forms, myriophyllids and nymphaeids can occupy the empty space. Mesters (1995) has also observed an antagonistic relationship between elodeid and vallisnerid/nymphaeid groups. The observed oscillations are not necessarily caused by competition but rather by rapid occupation of empty sites, mostly after anthropogenic disturbance such as weed cutting. Both clusters 4 and 6 show a high degree of stability. In addition, both clusters have the highest attractor values (see column sums in Table 7). Theoretically, these clusters should gain dominance in all reaches of the streams studied. In 2013, however, low probability clusters (such as clusters 1–3) were also found in the studied reaches.

Growth form dynamics (both expressed as absolute cover and clusters according to relative abundance of the nine growth forms) showed a more regular picture than dynamics of species composition and dominance relations. Members of some growth form (peplids: *C. hamulata*, *C. platycarpa*, *C. obtusangula*; myriophyllids:

M. alterniflorum, *R. peltatus*; potamids: *E. canadensis* and *E. nuttallii*) can be regarded as niche equivalents. They can replace each other without any functional change in the ecosystem. Dominance states are more sensitive to sampling error resulting from disruption of seasonal development by anthropogenic (cutting) and natural disturbance. Nevertheless, the order of magnitude in short-term stability was remarkably similar (4.5 years for growth form clusters, 4.1 years for dominance states), which is also supported by similar periodicity in species turnover and temporal autocorrelation of community composition.

Influence of environmental variables

In accord with the findings of Wiegleb *et al.* (1989), we were mostly unable to relate changes in dominance and growth form performance to environmental variables. This means that either the variables are inadequately represented in the data set or that random extinction-colonisation is the major driving force of vegetation change in this type of watercourse. As we analysed all major environmental variables usually considered important in macrophyte ecology (water chemistry, sediment, hydromorphology, geography, disturbance and climate), we can rule out the first alternative, even though intensity or duration of disturbance events were not always completely recorded.

Wiegleb *et al.* (1989) showed that a single ice winter (1986) had a considerable influence on species abundance the following year in site L6, damaging all wintergreen species. Similar sensitivity of wintergreens was reported by Greulich & Bornette (2003). 'Ice winters' only occur every 30–40 years (but more frequently in recent years: 2009, 2010 and 2012). In total, 42% of our species are always wintergreen, 44% facultative wintergreen, and only 14% summer-green. Thus, being at least a facultative wintergreen species seems to be important. Overall, the influence of harsh winters may be negligible, given enough time for recovery and an intact species pool, which is suggested by the findings from 2013. Also the effect of the extremely warm and long-lasting summer 1992 was short-lived. *Callitriche obtusangula* reached a growth maximum in that year, but retreated in the study sites from the next year on. Elsewhere in northern Germany, it has become well established in the meantime (H. Brux, G. Wiegleb, pers. obs.). Strong external signals such as major disturbance events and extreme weather conditions may have a short-term influence but no long-lasting effect (see also Kohler, Blumenthal & Zeltner, 1994).

The geographical ranges of our core species differ considerably (Jäger, 2011). *C. hamulata*, *C. obtusangula*, *C. platycarpa* and *R. peltatus* are European endemics, two of which are found in boreal areas (*C. hamulata*, *R. peltatus*) and one at lower latitudes (*C. obtusangula*). Two of these species are able to colonise brackish habitats in parts of their range (*C. obtusangula* and *R. peltatus*). The other native species *M. alterniflorum*, *S. emersum*, *P. natans* and *P. trichoides* have wide geographical ranges and extend to more continental areas. *Sparganium emersum*-dominated communities are found from Finland (Sirjola, 1969) over Estonia (Paal *et al.* (2007) to Bashkiria (Central Russia; Klotz & Köck, 1984), Mongolia (Hilbig & Schamsran, 1977) and Japan (Wiegleb & Kadono, 1988). Two of the species (*P. trichoides* and *S. emersum*) can likewise be found in tropical areas.

We have shown that beyond the previous study of the first 10 years (Wiegleb *et al.*, 1989), substantial changes have occurred with state changes not observed before, including changes in species dominance (new dominant species, more sites lacking dominant species) or complete turnover of dominant growth forms. Reaches cannot be easily classified by their growth form composition as proposed by Herr *et al.* (1989a), van de Weyer (2001) and Szoszkiewicz *et al.* (2010). Instead they can rather be characterised by a set of two to five growth forms, oscillating in relative abundance, thus producing up to six growth form types. Despite some anecdotal evidence, we cannot directly relate observed changes to weed cutting (Baattrup-Pedersen *et al.*, 2003). Neither increase nor decrease in abundance of *S. emersum* can be attributed to management intensity. In particular, the breakdown of the *Sparganium*-dominated vegetation in site D10 remains unexplained.

Our findings have important implications for biomonitoring and conservation. Spatial surveys conducted over 1–3 years will generally not show significant changes in species dominance or relative abundance of growth forms. However, our data also suggest that species cover and community richness may change over a shorter time scale. Long-term annual sampling seems mandatory, as long as long the dynamics of the system is not yet understood. The results of discontinuous sampling (see e.g. Mesters, 1995; Steffen *et al.*, 2013) may simply reflect different states of growth form composition, which may change within certain limits without any relevant change in hydrochemical or physical conditions. On the other hand, even with drastic changes in physicochemical conditions, the basic flora of a river may remain largely unchanged over 50 or even 100 years (Schütz, Veit & Kohler, 2008).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Hydrological and morphological characteristics of sampled reaches (based on Wiegleb *et al.*, 1989, and recent observations; additional data on discharge, morphology and water quality were provided by NLWKN).

Table S2. Overview of species, ordered according to growth forms (growth forms, simplified after Wiegleb, 1991), showing additional vital attributes.

Table S3. Affiliation of yearly observations to site clusters based on growth form composition [KMEANS, six clusters, $\log(x + 1)$ transformation; bold = smallest distance to cluster centre].

Table S4. Frequency of dominance states at the beginning (1978) and after 10, 20 and 35 years. Maximum denotes total number of sites (of 6) that were observed in this state.

Figure S1. Change of proportions (stacked percentages of total cover) of growth forms over time; (a) Lethe 6, (b) Delme 7, (c) Lethe 9.

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