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Human impact on the ecological performance of *Potamogeton* species in northwestern Germany

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Abstract

The changes in habitat quality of lowland rivers in Lower Saxony (Germany) during the past 40 years are outlined. Almost all chemical, physical, and morphological parameters have changed, resulting in most cases in an enhanced potential productivity, accompanied by a complex disturbance regime. Historical reconstruction of the change in river vegetation is presented to compare the frequency of macrophyte species 40 years ago with the situation of today. For a total of 289 sampling sites, the floristic change was exactly reconstructed. Nearly all species show a decline in frequency. This trend is also recognizable in *Potamogeton*, with the exception of two narrow-leaved species.

An attempt is made to explain both decline and maintenance in terms of life history characters (vital attributes) allowing the species to react to the changing habitat conditions. The successful species are characterized by certain life history characteristics which enable them to survive under the current disturbance regime. Most important aspects of life history are the ability to reproduce by means of turions and other fragments, a long-lived, deep-rooting rhizome system, phenotypic plasticity of above-ground parts, synchronous shoot polymorphism, and the potential to regenerate quickly from remaining buds after disturbance. The decline of formerly frequent species can be attributed mainly to the lack of certain key characters; however, physiological characters also may be important. The extirpation of some rare species could also be caused by random fluctuations in small populations. The general importance of population ecological research, particularly demography, life history theory, and the modelling of clonal populations in conservation ecology is stressed.

Introduction

In recent years, drastic changes in composition of macrophyte communities of lakes and rivers in Germany have been repeatedly observed (Sukopp 1972; Kohler 1980; Brux *et al.* 1988; Herr *et al.* 1989a, b; Wiegleb *et al.* 1989). The present study focusses on the situation of aquatic plants in north German rivers, notwithstanding that the situation in lakes, ponds and reservoirs may be even more dramatic. More than 50 per cent of the species colonizing aquatic and wetland habitats appear on the regional Red Data book (Haeupler *et al.* 1985), and among them are 15 taxa of *Potamogeton.*

The genus *Potamogeton* comprises between 80 and 100 species, most of which are found in the northern hemisphere (Hagstroem 1916; Wiegleb 1988b). The highest species densities (20–30) are found in eastern North America, Western Europe, Siberia and Japan (Wiegleb 1988b). The members of the genus can be found in almost any type of water, with each species having a more or less distinct preference for a certain combination of chemical and physical parameters (see for example, Pietsch 1972; Seddon 1972; Wiegleb 1978; Felzines 1979; Pip 1979; Hellquist 1980; Kadono 1982). *Potamogeton* stands play an important role in the riverine aquatic ecosystem because of their contribution to primary production, nutrient cycling, exchange of gaseous substances, sediment fixation, and habitat diversification for animals and periphyton (Wilmanns 1973; Dahl & Wiegleb 1984). Therefore, their decline has been a main component of our studies.

In the following we shall deal with two aspects. First, in a descriptive approach, we illustrate the present ecological situation of lowlands rivers with special reference to the changes that have occurred during the past 40 years and the direct consequences for macrophyte growth. In addition, we present data on observed frequency changes of hydrophytes in rivers including *Potamogeton* species during the past 40 years. Subsequently, we summarize our present knowledge on the life history characteristics of broad-leaved *Potamogeton.* We present some evidence that the distribution of life history characters among *Potamogeton* species can explain the differential behavior of the species.

Methods

The present review is based on data collected in the framework of various research projects:

1. A comprehensive survey of the recent macrophyte composition in Lower Saxonian rivers and streams. It was carried out between 1978 and 1983, and was based on 1143 sampling sites, where all species below the actual water level were recorded. A sampling site was a river section of ca. 50 m length (Wiegleb 1984a,c; Herr *et al.* 1989b).
2. Long-term studies of succession in different sets of permanent plots (Brux *et al.* 1988; Wiegleb *et al.* 1989). For 6 plots an uninterrupted time-series of 14 years exists, based on bimonthly sampling.
3. A reconstruction of river floras from 40 years ago, based on historical data of 293 sampling sites (Herr *et al.* 1989a). The floristic data of 1946 were collected by R. Alpers (unpublished data; 1946). Sites were resampled in 1986. The habitat conditions of 1946 and their changes in the interim were inferred from various sources, including data of R. Alpers, old topographical maps, photographs, newspaper articles, and data on water quality, construction activities etc. provided by the regional water authorities.
4. The study of life cycles and population dynamics of broad-leaved *Potamogeton* species (Wiegleb & Todeskino 1983, 1985; Wiegleb 1984b; Brux *et al.* 1987, 1989; Wiegleb & Brux 1991). The study concentrated on the performance of individual shoot complexes, 4000 of which were analyzed in detail (G. Wiegleb and H. Brux, 1981–1989; unpubl. results).

The exact methods used are described in the respective publications.

Results

Changes in the environment

The most important changes in habitat quality of water courses during the last 40 years are listed in Table 1 (see also Haslam 1987; Dahl & Hullen 1989).

Three main types of running waters are distinguished:

- Large rivers of more than 25 m width, which partly spring from the highland area in the central part of Germany. Under natural conditions submerged macrophyte vegetation was re-

Table 1. Trends of human impact on habitat quality in Lower Saxonian running waters between 1946 and 1986 (xxx = very strong increase, xx = strong increase, x = small increase, – = no significant change)

Water type	Large rivers	Small streams	Ditch-like waters
1. Change of chemical factors			
Eutrophication	xxx	xx	xxx
Acidification	–	xx	–
Predicipitation of iron ochre	–	xx	x
Pollution with			
– Heavy metals	xx	–	x
– Pesticides	xx	xx	xx
– Manure	–	xx	xx
– Chloride	xx	x	–
2. Change of river morphology			
Channelization			
– Shortening of water course	x	xxx	–
– Channel and bank erosion	x	xx	–
– Uniformization of banks	xx	xxx	xxx
– Deforestation of banks	–	xx	–
Construction of weirs etc.			
– Unnatural stagnant sections	xx	xx	–
Construction of passage/ducts			
– Migration hindrances	x	xxx	xxx
3. Change of hydrological/hydraulic factors			
Destabilization of sediment	x	xx	–
Lowering of groundwater table	x	xx	xx
Occurrence of unusual drought	–	x	xx
Decrease of retention capacity	xx	x	–
Upper course/tributary effects	xx	x	–
Occurrence of unusual spates	xxx	xx	–
4. Direct mechanical impact			
Dredging	x	xx	xxx
Cutting	–	xxx	xxx
Grazing by cattle	–	xx	xxx
Shipping/boating	x	–	–
Cooling water/power plants	xx	–	–

stricted to marginal parts of the channel in these rivers.

- Small streams and rivulets, which make up the majority of water courses particularly in the diluvial plains. They can be regarded as the genuine 'macrophyte region' in the sense of Roll (1938a), being colonized by submersed plants in their whole width and thus being the main habitat of *Potamogeton.*
- Ditch-like waters of various sizes which can be found both in alluvial and diluvial areas. Both submersed and emergent vegetation is of equal importance in these mostly artificial water bodies.

Even though type and intensity of anthropogenic impact strongly varies among the water types, some general conclusions can be drawn.

Severe eutrophication is evident in most water courses. According to the data available, the eutrophication process is not only characterized by an increased loading with plant nutrients (phosphate, ammonium, nitrate), but by a complete change in hydrochemistry including increased levels of bicarbonate, chloride, calcium and other ions. The eutrophication is caused both by direct input by municipal sewage plants and diffuse input from intensively utilized agricultural areas. The main increase in nutrient loading took place in late 1960's and early 1970's. Since then, the plant-available phosphorus and nitrogen concentrations remained in the same order of magnitude. In the case of phosphate even a slight decrease can be observed during the past five years, because of the introduction of phosphate free detergents. Most other chemical changes (precipitation of iron ochre, pollution with pesticides and manure) are associated with the intensification of agriculture during the past ten years. In some areas with low densities of human settlements and low intensity of agriculture the opposite process of acidification can be observed in some small rivulets.

River morphology underwent considerable changes during the past four decades. Channelization is still going on in most areas, and already channelized sections are furthermore corrected. We estimate that less than one per cent of the length of water courses in the lowlands remained untouched. Channelization led to shortening of water courses, resulting in channel and bank erosion because of the increased current velocity. Banks were mostly constructed in a uniform trapeze profile and deforested. Planting of gallery forest is still a rare exception. Additional construction of various kinds of artificial buildings (weirs, passages etc.) had both short-term consequences such as increased turbidity and long-term consequences, such as the creation of unnatural, stagnant sections and migration hindrances particularly for fish and invertebrates.

The combined impact on the river channel and its drainage area as a whole led to several changes in the hydraulic and hydrological characteristics of the water courses. There is the destabilization of the sediments which lead to a changed pattern of erosion and sedimentation in the whole river course. The general lowering of the ground water table enhanced both channel erosion and unusual drought in summer depending on the local circumstances. The loss of retention capacity in the floodplain area and the increased chanelization of upper courses and small tributaries had various unpleasant side effects in the main rivers such as occurrence of unusual spates in summer. In part the changed hydrological situation is the immediate cause for the necessity of continuing mechanical corrections to hold the river within its present bed. However, dredging and cutting of 'weed' is mainly motivated by the pretended need to keep the water table low in order to drain agricultural areas. Further mechanical influences is caused by cattle grazing, boating, and cooling water of power plants.

Immediate consequences of these anthropogenic activities on habitat quality for aquatic macrophytes can be described as follows: On the one hand a large number of sites formerly suitable for macrophyte growth have been destroyed. Both complete destruction of the sites (because of filling up or desiccation) and inaccessability for macrophytes because of high concentrations of toxic substances or regular summer spates have been observed. For example, Herr *et al.* (1989a) showed that appr. 10 per cent of the sites investigated by Alpers in 1946 were no longer existing. In a further 20 per cent no single macrophyte was found. Dahl & Wiegleb (1984) showed that 61 per cent of the course of the river Leine belonging to the potential macrophyte region were devoid of macrophytes. Grube (1975) reported dense macrophyte communities from that river. Herr *et al.* (1989b) no longer found the species-rich macrophyte communities in the river Oker, which had been described by Weber-Oldecop (1969). Artificial creation of new sites suitable for macrophyte growth also occurs, but is a negligible process compared to the destructions listed above.

In the remaining sites the change in productivity parameters is seemingly favorable for macrophyte growth, as there is an increased availability of nutrients and light in most cases. But as a secondary effect, also increased competition with benthic filamentous algae and phytoplankton must be taken into account. The negative influence of filamentous algae on macrophyte growth has been repeatedly described, for example for Lower Saxonian lowland rivers by Wiegleb (1984a). Additionally, we observed the installation of a very complex disturbance regime, characterized by a high intensity, a high frequency, and a low degree of regularity of disturbance. As to intensity, Wiegleb *et al.* (1989) showed that almost all sections studied lost their complete above-ground vegetation once in a ten year's period because of a catastrophic event (dredging, lethal concentration of herbicides, unusual high summer spate, unusual ice scour). The frequency of minor disturbances (weed cutting, sublethal concentrations of toxic substances) is much higher. Every site will suffer from such an event once or twice a year. The cutting regime in lowland rivers is highly unpredictable, as cutting is not dependent on the actual development of biomass, but on the availability of man power for carrying out the work. Thus, cutting is carried out in different months every year, or it may be skipped, or even carried out twice. The cutting and other minor disturbances have some secondary effects, which may not be negative for plant growth on a larger scale, as they serve for the creation of open sites colonizable by otherwise suppressed species.

Documentation of macrophyte decline in rivers

Data on the long-term vegetation change in European rivers are rare. The data of Holmes & Whitton (1977; based on Butcher 1933), and Weber-Oldecop (1982; based on Roll 1938b) cannot be used for the present purpose, as they refer to single rivers only.

Table 2 shows the change in frequency of those hydrophytes that occurred in more than 10 percent of the sites sampled both in 1946 or 1986 (modified from Herr *et al.* 1989a). This subset of data is not completely representative for the whole lowland area (Herr *et al.* 1989b). For example, *Callitriche platycarpa* is in principle the second most frequent species in that area. For the other species the rank order of frequency is in good accordance with the complete data set (Herr *et al.* 1989b). The most frequent hydrophytic species in 1946 and 1986 was *Sparganium emersum*. High frequency of *Sparganium* spp. is common to most lowland areas of the northern hemisphere (Wiegleb & Kadono 1989a).

However, almost all other hydrophytes suffered from severe losses. This holds for the neophyte *Elodea canadensis*, the nymphaeid species *Potamogeton natans*, *Nuphar lutea* and *Sagittaria sagittifolia*, the batrachids *Callitriche hamulata* and *Ranunculus aquatilis* agg. (mainly *R. peltatus* and *R. penicillatus* subsp. *penicillatus*), and the broad-leaved pondweeds *Potamogeton perfoliatus* and *P. lucens*. The only species that increased in frequency are *Callitriche platycarpa* and *Potamogeton berchtoldii*. The occurrence of the pleustophyte *Hydrocharis morsus-ranae* is highly unstable and thus the increase is not significant. 40 years ago *Butomus umbellatus*, which in most cases is only present in its submersed vallisnerid growth form, may have been either overlooked, as its occurrence was not expected, or confused with submersed forms of *Sparganium*, *Sagittaria* or *Glyceria*.

Table 2. Changes in frequency of the 13 most frequent hydrophytes in Lower Saxonian rivers between 1946 and 1986, based on 293 sampling sites (modified from Herr *et al.* 1989a).

Species	Frequency		Change in %
	1946	1986	
Sparganium emersum	130	131	+ 1
Elodea canadensis	125	99	− 21
Potamogeton natans	118	62	− 47
Sagittaria segittifolia	109	92	− 16
Nuphar lutea	105	68	− 35
Callitriche hamulata	48	22	− 54
Ranunculus aqualitis agg.	46	35	− 24
Potamogeton perfoliatus	46	17	− 63
Potamogeton lucens	42	21	− 50
Callitriche platycarpa	31	51	+ 65
Hydrocharis morsus-ranae	27	32	+ 19
Potamogeton berchtoldii	16	34	+ 113
Butomus umbellatus	4	36	+

In Table 3 a complete overview of the development of all *Potamogeton* species encountered is shown. The data subset contains 14 species and 1 hybrid from the total of 17 species, and 8 hybrids occurring in Lower Saxonian rivers (Wiegleb & Herr 1984; Herr & Wiegleb 1985). One

Table 3. Changes in frequency of *Potamogeton* species in Lower Saxonian rivers between 1946 and 1986, based on 293 sampling sites (modified from Herr *et al.* 1989a). Descriptors of growth form: Leaf width (n – narrow – usually smaller than 5 mm; i – intermediate – usually between 5 and 10 mm; b – broad – usually broader than 10 mm); presence of floating leaves (s – submersed leaves only; f – floating leaves usually present).

Species	Growth form	Frequency		Change in %
		1946	1986	
A. Increased frequency;				
Potamogeton berchtoldii	n-s	16	34	+ 113
Potamogeton trichoides	n-s	1	24	+ +
B. Stationary:				
Potamogeton cripus	i-s	27	27	0
Potamogeton pectinatus	n-s	22	20	− 9
Potamogeton alpinus	b-f	13	12	− 8
C. Strong decline:				
Potamogeton natans	b-f	118	62	− 47
Potamogeton perfoliatus	b-s	46	17	− 63
Potamogeton lucens	b-s	42	21	− 50
Potamogeton compressus	n-s	21	1	− 95
Potamogeton polygonifolius	b-f	14	1	− 93
Potamogeton friesii	n-s	10	4	− 60
Potamogeton acutifolius	n-s	9	2	−
D. Extinction:				
Potamogeton gramineus	i-f	6	0	−
Potamogeton obtusifolius	n-s	3	0	−
Potamogeton x zizii	b-(f)	2	0	−

must bear in mind that the data reported are net differences, and that virtually nothing is known about the processes of immigration and extinction during the 40 years between. Four species groups can be distinguished:

Species with increased frequency

This group comprises only narrow-leaved species such as *P. trichoides* and *P. berchtoldii*. Invasion of narrow-leaved species after increased disturbance was repeatedly observed (for example, Wiegleb 1981; Wiegleb *et al.* 1989).

Species with a stationary frequency

Here we find species of different growth form such as *P. crispus*, *P. pectinatus* and *P. alpinus*. The affiliation of *P. pectinatus* in this group is surprising as it has been reported as spreading after various kind of disturbance in other areas (Wiegleb 1981). For *P. alpinus* Brux *et al.* (1988) showed the high short-term recolonization potential, resulting in a relatively stable frequency in the sites under study.

Species strongly declining in frequency

This is the largest group, containing all formerly frequent species, such as *P. natans*, *P. perfoliatus*, and *P. lucens*, and furthermore *P. compressus*, *P. polygonifolius*, *P. friesii*, and *P. acutifolius*.

Species that have been extirpated in the river sections studied

This group comprises *P. gramineus*, *P. obtusifolius* and *P. x zizii*. Extinction is restricted to the very rare taxa, and may be caused by stochastic population fluctuations.

Besides the question, how it was possible for any macrophyte to survive the drastic habitat changes, the following questions are pertinent: Is it possible to explain why *Potamogeton alpinus* was the only broad-leaved species to maintain its rank? Is it possible to explain why *P. natans* drastically declined, but held its position as the most frequent species? Is it possible to explain why *P. lucens* and *P. perfoliatus* declined in a more dramatic way and are probably bound to get extinct in the near future?

Patterns of life history characters in Potamogeton *species*

Fitness of a modular organism such as *Potamogeton* is based on four mechanisms (cf. Loehle 1987; Wiegleb & Brux 1991):

1. Sexual reproduction which can start the life cycle of a new genet after germination of the seed.
2. Vegetative reproduction, which leads to the formation of new structural individuals. It can be achieved by various means such as turions, tubers, unspecialized winterbuds, rooting shoot fragments etc. (Wiegleb & Brux 1991).
3. Horizontal growth, and
4. Vertical growth. In the first instance, both processes lead to the enlargement of the structural individual. They are likewise prerequisites for potential vegetative reproduction by means of fragmentation.

For a clonal plant, such as *Potamogeton*, in which reproduction by seeds is a very rare event, fitness is mainly determined by optimally allocating resources to fragmentation, vertical and horizontal growth. Table 4 summarizes life history characters related to this conceptual scheme of five *Potamogeton* species, whose characters are well known from a large number of sites. The life history characters summarized here are relatively coarse-grained. Each character may be divided into various subtraits, which may vary among members of the same species.

Sexual reproduction is possible in all species. Even though a high number of seeds is usually produced (see Wiegleb & Todeskino 1985), germination fails in most cases. Therefore, sexual reproduction is a rare event under normal conditions and does not contribute much to the maintenance of riverine populations (Brux *et al.* 1987). It is, however, of some importance for the colonization of new sites. Vegetative reproduction is predominant in all species studied (Wiegleb & Brux 1991). Mobile turions are very important in *P. alpinus*, but also occur in *P. gramineus* and *P. lucens*. All species except *P. alpinus* have unspecialized winter buds, which are most abundant in *P. natans*. Both the formation of turions

Table 4. Important life history characteristics of the most frequent broad-leaved *Potamogeton* species in rivers (xxx = key factors, xx = important factors, x = less important factors, – = structure or process not present).

Potamogeton	Nat	Alp	Gra	Luc	Pol
Agents of colonization					
Sexual reproduction:					
– seeds	x	x	x	xx	x
Vegetative reproduction:					
– mobile turions	–	xxx	x	x	–
– unspecialized winter buds	xx	–	–	–	x
– re-rooting fragments	xxx	xxx	x	x	x
Agents of maintenance					
Horizontal growth:					
– perennating rhizome	xxx	–	xx	xx	–
– perennating stolons	–	(x)	x	x	xx
– fast growing stolons	x	xx	x	x	x
– emergency turions	–	x	–	–	–
Vertical growth:					
– infinite growth	–	–	–	–	xx
– phenotypic plasticity	x	xxx	xxx	xx	x
– synchronous shoot polymorphism	xxx	xx	xx	x	x
– regrowth from reserve buds	xx	xxx	xxx	x	x

and unspecialized winterbuds are seasonal events and mostly restricted to autumn (with the well-known exception of *P. crispus*). Re-rooting from fragments of various shoot types is most successful in *P. natans* and *P. alpinus*, but less important in the other species. The advantage of shoot fragments is that they are produced almost automatically by minor disturbance events at any time of the year.

Horizontal growth by means of a perennating rhizome is found in *Potamogeton natans*, *P. lucens* and *P. gramineus*. We regarded a horizontal shoot as rhizomatous only if it was considerably thickened (twice as large as the vertical shoot) and had obvious storage functions. In *P. lucens* and *P. gramineus*, the life span of the rhizomatous parts of the lower horizontal shoot is restricted (2 years). This indicates that the distinction between 'rhizomes' and 'stolons' is only gradual in *Potamogeton*. Perennating stolons are regularly found in *P. polygonifolius*, *P. gramineus* and *P. lucens*. In *P. alpinus*, they are a rare exception in warm winters. Fast growing stolons play an important role in colonizing vegetation gaps in *P. alpinus*, but also in the other species. Horizontal growth may end in the formation of 'emergency turions' under unfavorable conditions in *P. alpinus*. The aseasonal formation of turions as a reaction to desiccation was first described by Brux *et al.* (1987) for *P. alpinus*, and later also by Wiegleb & Kadono (1989b) for the Japanese species *P. distinctus*.

Vertical growth is finite in most species, ending in the production of spikes. Renewal buds are formed only at the shoot base in case of its survival. In *P. polygonifolius*, where the renewal buds are apical, a quasi-infinite growth of the vertical shoot can be observed. Almost all parts of the vertical shoot show a remarkable degree of phenotypic plasticity. This is highest in *P. alpinus* and *P. gramineus*, and has led to some taxonomic confusion in these species. Another important feature, partly relating to plastic growth of individuals, but also to asynchronous development of shoots due to small-scale habitat heterogeneity, is the synchronous shoot polymorphism. This character is best developed in *P. natans*, a species with a long growing season and a low degree of seasonality. Different kinds of vertical shoots can be found almost all over the year, ranging from small unbranched to large branched ones. After destruction of the canopy, the small ones can quickly regenerate the stand. Regrowth from reserve buds after destruction of above-ground plant parts is most effective in *P. alpinus* and *P. gramineus*, which have the highest growth rate.

The following characters can be regarded as key factors (vital attributes, Noble & Slatyer 1980) under the conditions of intensive disturbance:

- Mobile turions and rooting shoot fragments, which allow the recolonization of disturbed sites (see also Kadono 1984).
- The possibility of regenerating the whole shoot complex from one single remnant bud, which can be regarded as the 'minimum reproductive unit' in *Potamogeton*.
- A perennating rhizome deep in the sediment, which provides a bud bank that cannot be

destroyed even by events catastrophic to all above-ground parts.

- Phenotypic plasticity, that is the possibility to produce opportunistically (Tomlinson 1982) shoots, internodes, leaves, or other plant parts of various sizes and shapes as a reaction to changes or forthcoming changes in the environment (see Mitchell & Rogers 1985).
- Synchronous shoot polymorphism, which will eventually lead to differential shoot mortality in case of destructive events. Thus, the combined aspects of maintenance, regeneration, and recolonization are likewise important.

Habitat templet and the occurrence of Potamogeton *species*

In Figure 1 a habitat templet is displayed to illustrate the ranges of occurrence of five *Potamogeton* species in relation to productivity of the habitat and disturbance. Productivity is a complex gradient, in which the availability of inorganic carbon, nitrogen, phosphorus, and light are involved. This axis defines the potential carrying capacity of the site. The disturbance axis indicates to which degree the potential carrying capacity is actually realized. A similar habitat templet was recently advanced by Taylor *et al.* (1990) from a theoretical point of view. It must be noticed that 'disturbance' is used in this context in the sense of Grime (1979; for a comprehensive discussion of the term, see Pickett *et al.* 1989).

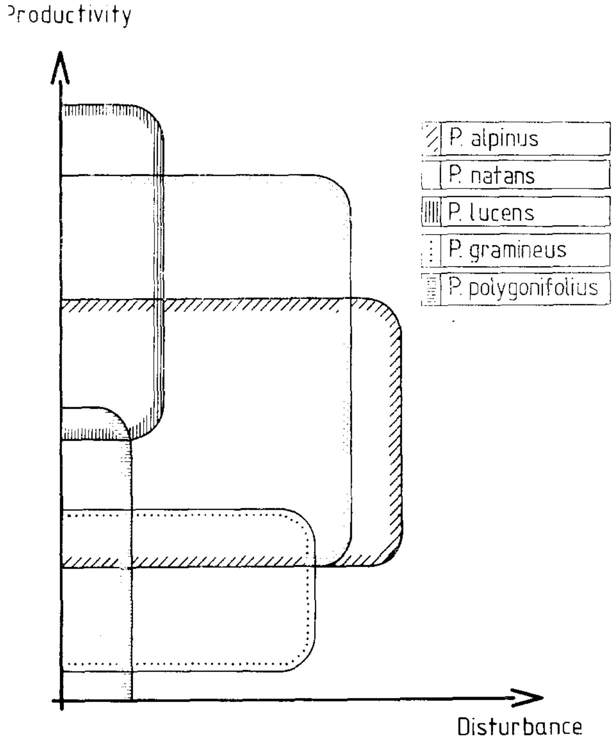

Fig. 1. Ecogram of preferential growth of various *Potamogeton* species with respect to productivity and disturbance regime in rivers.

In the diagram, *Potamogeton lucens* and *P. polygonifolius* occupy the area with low disturbance intensity. The original habitat distinction is still visible with *P. lucens* being restricted to productive habitats and *P. polygonifolius* to unproductive ones. The other three species can invade (or maintain themselves in) sites characterized by intensive and regular disturbance. The degree of disturbance that can be endured by the species can only be roughly estimated, but *P. alpinus* seems to have the highest tolerance. Also, in this species group the original habitat preference is visible. *P. gramineus* is restricted to the unproductive sites ('oligotrophic' conditions), while *P. alpinus* and more often *P. natans* can also be found in productive sites. In total, *P. natans* has the broadest range of habitat suitable for its growth. This is reflected by its overall high frequency in all kinds of water courses (see above).

Based on the figure, a selection of hypothetical trajectories of the development of some sites can be outlined. In 1946, already both productive and unproductive sites existed, with a clear majority of the unproductive ones. During the course of time, productivity increased in almost all sites that were not directly destroyed. But most of all, disturbance intensity increased in all sites. The potential gains and losses can easily be illustrated.

In hypothetical case 1, an undisturbed, unproductive site was suitable for the growth of *P. gramineus* and *P. polygonifolius*. An increase of disturbance alone will eliminate *P. polygonifolius*, while *P. gramineus* can maintain itself. This case rarely occurred in nature. In case 2, an unproductive site with intermediate disturbance is eutrophicated. *P. gramineus* will die out, while *P. alpinus* and *P. natans* are potential colonizers of this site.

In case 3, *P. polygonifolius*, *P. natans* and *P. alpinus* could coexist in a medium productive site without disturbance. An increase both in productivity and disturbance will lead to the elimination of *P. polygonifolius* and probably *P. alpinus*. In case 4, a productive site of low disturbance was colonized by *P. natans* and *P. lucens*. Here an increase of both productivity and disturbance will take the trajectory outside the area, in which viable strategies for broad-leaved species exist. These sites will be occupied by narrow-leaved species, or may even be completely devoid of macrophytes.

Discussion

Whether chemical or physical data explain more of the observed variation in aquatic communities depends on the scale of observation (small-scale studies in homogeneous areas vs. large-scale studies crossing geographical boundaries) and the choice of sampling sites (comparison among basic water types vs. comparison within one lake or one river system; cf. Wiens 1989). The occurrence of *Potamogeton* in rivers is regulated both by chemical and physical habitat factors, with chemical factors influencing the basic habitat choice (Kohler 1978; Haslam 1987; Carbiener *et al.* 1990) and physical factors influencing the within-river distribution (Wiegleb 1984a, 1988a; Haslam 1987; Dawson 1988). Competition has no influence on community structure, as necessary densities are rarely reached (Brux *et al.* 1988). Predation by herbivorous snails can play a role in certain cases (Brux & Wiegleb 1989).

In order to survive the drastic changes in habitat quality, *Potamogeton* species had to undergo drastic changes in ecological performance. This change surely was not achieved by genetic adaptation, as the main changes occurred within a period of appr. 10 years (water chemistry) or 25 years (river morphology). This would imply only a few generations possible, even if sexual reproduction had been successful. However, it is likely that the plants have crossed the gap between two adaptive peaks (Conrad 1990) by means of phenotypic reactions alone. Within each species those genotypes which survived had some predisposed structures (van Steenis 1981) suitable for maintaining themselves in the new habitat. These findings underline the importance of phenotypic plasticity both in the ecological and evolutionary context (Schlichting 1986; Stearns 1989; West-Eberhard 1989). This holds particularly for the monocotyledons with their special growth habit (Holttum 1955).

The rivers under study have been colonized by *Potamogeton* after the glaciation. At that time, natural disturbance caused by high spates and ice scour must have been normal events. Thus, only genotypes could invade these sites that were able to perform adequate life-cycles. Still now, the relation between disturbance tolerance and a northern-arctic distribution (*P. alpinus*, *P. gramineus*!) is visible. One may assume, that these genotypes survived by means of vegetative reproduction for several thousand years. So far, long-term survival of single genotypes can only be proved beyond doubt in some rare hybrids (e.g. *P. x undulatus* Wolfgang, *P. x spathulatus* Schrader ex Koch et Ziz), in which sexual reproduction can be excluded. They still grow in the same sites where they have been found more than 100 years ago, according to old floras and herbarium specimens.

The life history traits discussed above explain the performance of species along the disturbance gradient. The importance of this gradient has been stressed by various authors discussing macrophyte strategies (Van Wijk 1988; Day *et al.* 1988; Kautsky 1987, 1988; van Vierssen 1989; Murphy *et al.* 1990; Wiegleb & Brux 1991). The species' performance along the productivity gradient remains largely untouched, which shows the high degree of independence of the two axes. Most likely physiological traits are responsible for basic habitat selection, such as differential use of carbon and nitrogen sources, differential preference in sites of nutrient uptake (root vs. shoot), differential abilities of internal nutrient cycling (see comprehensive treatments in Hutchinson 1975; Raven 1981; Agami & Waisel 1986; Sondergaard 1988), and, last but not least, differential abilities to support their rhizomes with oxygen. Thus a predictive approach to the structure and dynamics of macrophyte communities would require a combined knowledge on the anatomical, morphological, and physiological properties of species during their whole life-cycle.

Conclusions

The results were mainly achieved by carefully studying the ecological performance of individual shoot complexes, which is a natural history approach. By means of this method we gained some insight into the mechanisms behind the changes at the population and community level (Wiegleb 1989). A comprehensive treatment should also include more ecophysiological information. In our case, physiological behaviour of the plants could only be inferred from literature data. Thus we cannot be sure whether there is also plasticity and polymorphism of physiological traits that influences the occurrence of genotypes.

We hope that at least some shoot complexes of *Potamogeton* will survive until our effort to preserve them from extinction will be successful. Plants for restoration of water courses and their flood plains have been repeatedly advanced (Dahl & Hullen 1989; Wiegleb 1991). Political effort is necessary for the implementation of these plans.

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