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Susceptibility of Lakeside *Phragmites* Reeds to Environmental Stresses: Examples from Lake Constance-Untersee (SW-Germany)

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With 3 Figures and 2 Tables

Key words: Lake shore vegetation, *Phragmites australis*, die-back of reeds, mechanical stress, flooding stress, model

Abstract

The lakeside border of *Phragmites* reeds is under the control of many environmental factors, among which the flooding height and the degree of mechanical load by waves and washes are the most prominent. Examples from Lake Constance-Untersee show that the reed front retreats under enhanced stresses. Models are presented that describe the susceptibility of lakeside reeds to mechanical damage and to flooding events. A monitoring programme which ran from 1984/85 to 1992/93 showed a slow lakeward progression of the reeds in a decade of abnormally low water conditions.

Introduction

The Common Reed, *Phragmites australis* (CAV.) TRIN. ex STEUD. (Poaceae) is a world-wide distributed grass with a wide ecological amplitude (RODEWALD-RUDESCU 1974; CONERT 1983). At the shallow-sloped shores of many European lakes it forms monospecific belts which often cover many hectares, or even square kilometres. The landside border of pure *Phragmites* reeds is controlled by the competitive power of trees and bushes, and by human impacts (wet meadow use, construction of lake walls, land fills, etc.). The factors that determine the lakeside reed front are much less clear: presumably a specific combination of mean and/or maximum flooding height, or flood frequency, mechanical stress by waves and drifting matter, grazing by coypus, muskrats and waterfowl, and sediment quality (e.g. redox conditions and oxygen consumption capacity) plays an important role (COOPS et al. 1994, 1996; WEISSNER 1987, 1991).

The importance of these factors becomes obvious by analysing extreme events which have led to a destabilization of the lakeside reed front and to an extensive reed decline, as it was the case at Lake Constance. In this paper a concise summary of the factors of reed die-back is given, and two models which describe the susceptibility of *Phragmites* to mechanical and flooding stress are discussed. Most of the details have been published elsewhere (e.g. OSTENDORP 1990, 1991 b, 1992, 1995 a).

Investigation area

The investigations were performed at Lake Constance-Untersee, the shallow eutrophic lower lake basin of Lake Constance, with extended lake shores (10.2 km^2 littoral area between 394.0 and 396.0 m a.s.l., mean width 143 m, mean slope angle 0.80°). 99.7% of the fringing reeds consists of (nearly) monospecific *Phragmites australis* stands, covering a total of 295 hectares (German territory only). The sublittoral zone is overgrown with submerged macrophytes, mainly *Chara* spp., *Potamogeton* spp. and filamentous algae (e.g. *Cladophora* sp.), which are often uprooted by waves during storms in autumn, and washed onto the shore (OSTENDORP 1991 a, 1992).

The yearly course of the lake level of Lake Constance mainly depends on the discharge of the Alpenrhein river, so that in June and July the water level reaches its maximum, and it drops down gradually to the yearly minimum in February and March (mean water level = 395.09, mean low water = 394.35, mean high water = 396.23 m a.s.l., period 1937–1987, water gauge station Berlingen, LUFT et al. 1990). The annual course of the water level is modified by episodic high flooding events which occur after heavy rainfall in the prealpine mountains. Flood disasters with water levels higher than 396.65 m a.s.l. have frequently happened during this century, but they have been less frequent in the last decade (for the last time in 1987; DIENST 1994). Normal-

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ly, they are restricted to the period from June to August covering the second half of the growth period of *Phragmites australis*. Westerly winds prevail changing from WNW in spring and summer to WSW in winter. Strong winds and storms are rare and occur mainly from October to April, in seasons when the water level is low.

Dynamics of the lakeside reeds at Lake Constance-Untersee

In the late 1960s a serious decline of lakeside reeds was effected by professional fishermen. This was the starting-point of a series of investigations into the causes and circumstances of the die-back (SCHRÖDER 1979, 1987; OSTENDORP 1990, 1991 a, b, 1992). After decades of more or less continuous lakeward progression the decline began at several locations between 1954 and 1962. By far the strongest decline happened between 1962 and 1967, so that by 1967 18% of the fringing *Phragmites* reeds (69 hectares, 1954 = 100%) were lost. In the following years another 5% died back (Table 1). The outermost reed stands (394.0–394.5 m a.s.l.) were the most affected (–75%), whereas the landside fringe (395.5–396.0 m a.s.l) lost only 19% of its area by 1954. Due to the lakeside losses the mean depth penetration line of *Phragmites* shifted from 394.49 ± 0.13 m a.s.l. to 394.95 ± 0.22 m a.s.l. A detailed evaluation of the temporal pattern of the decline showed that it was the summer of 1965 which was characterized by extreme meteorological and hydrological events. The water level in June was the fifth highest since the beginning of water mark records in 1817, and events with squalls and strong winds of 6° Beaufort and more were by 36% more frequent than on average in the period between 1959 and 1984.

In the winter of 1984/85 a monitoring programme was started to record the reed front dynamics at representative shore sections with a high spatial and temporal resolution (PIER et al. 1993; OSTENDORP et al. 1996). 10 sets of data are currently available comprising up to 51 test sections of 25 m length each. The data demonstrate that many lakeside reeds have spread anew since the middle of the 1980s. The high progression rates between 1984/85 and 1987/88 with 4.3 to 15.5 cm a^{-1} were followed by a regression of –4.8 cm a^{-1} on average in 1988/89. Since that time a continous advance has been observed with mean rates between 11.4 und 49.2 cm a^{-1}. For wind and wave exposed stands individual progression rates were lower than the average in all years of all stands.

The data of this monitoring programme and of the dramatic decline around 1965 led to the hypothesis that mechanical stresses to the lakeside reed front and the maximum flooding height during summer are among the most important factors determining the dynamics of the fringing reeds in Lake Constance-Untersee.

Significance of extreme flooding events

The rhizomes of lakeside reed stands are buried in the waterlogged sediment. Hence, in spring and early summer the young shoots must grow through a water column of varying height. By its architecture, *Phragmites australis* is a terrestrial plant which lacks any adaptations to submersed carbon assimilation. Consequently, the photosynthesis will be arrested if the leaves are waterlogged (RODEWALD-RUDESCU 1974: 81). The culms react on prolonged submergence with an accelerated growth, but finally die as soon as the carbohydrate reserves in the rhizomes are exhausted. Additionally, the limitation of the oxygen supply to the rhizomes by the submerged green parts of the culms may play an important role since the anoxic glucose metabolism yields by far a lower energy gain than the oxic respiration (BRÄNDLE & CRAW-

Table 1. Decline of fringing *Phragmites* reeds at Lake Constance-Untersee 1954–1983: reed bed area lost in the period 1954/c. 1983. Total reed bed area was 265 hectares (= 87% of the littoral area) for the landside reeds in 1954, and 114 hectares (= 18% of the littoral area) for the lakeside reeds.

	Period				
	1954–1964	1965–1967	1968–1972	1972–1978	1978–1983
Landside reeds:					
Decline	36 ha (41%)		8 ha (9%)		0 ha (0%) (?)
Main causes	land fills, boating places, camping sites etc.		land fills, boating places, camping sites etc.		?
Lakeside reeds:					
Decline	10 ha (11%)	23 ha (26%)	4 ha (5%)	4 ha (5%)	3 ha (3%)
Main causes	?	flood disaster, storms, hailstorm in summer 1965	mechanical damage by macrophyte wash, bank erosion		winter harvesting and burning of reeds

FORD 1987; BRÄNDLE 1991). Therefore, it is assumed that growing *Phragmites* shoots must not be completely flooded for longer than 3 days, or must not be flooded higher than to a critical culm length L_{crit}, so that at least two expanded leaves are left unflooded.

The degree of threat to lakeside *Phragmites* reeds by floods can be estimated if the following parameters are known: (I) the critical length (L_{crit}) as a function of time t, (II) the water mark (W) as a function of time, and (III) the elevation of the ground of the *Phragmites* stand relative to the zero-mark of the water gauge (W_0):

critical submergence for culm i: $W_i(t) \geq L_{crit}(t) + W_0$ (1)

critical length of a culm: $L_{crit} = L_{tot} - m\,(L_{tot} - L_0)^n$ (2)

L_{crit}: critical culm length; L_{tot}: total culm length; L_0: maximum length of leafless young shoots for which submergence is irrelevant (since they do not photosynthesize); m, n: coefficients which must be determined empirically by fitting the regression curve (in this study: m = 8.97, n = 0.34, L_0 = 40 cm).

The total length can be estimated as:

$$L_{tot} = r_L\, t + a \qquad (3)$$

r_L: linear growth rate [cm d^{-1}], a: coefficient, t: time [d]. The beginning of the linear growth ($L_{tot} = 0$) is then $t_0 = -a / r_L$. Table 2 gives some examples from Lake Constance-Untersee.

By means of this model the effects of two floods, 1965 and 1987, on the growth of *Phragmites* were investigated (OSTENDORP 1991 b). The growth rate had been known from many measurements at Lake Constance-Untersee. The water level was taken from daily water mark records at the water gauge station at Berlingen. The elevation of the reed front in the years before 1965 was reconstructed by using the still existing stubble fields of the former reedbeds verified by aerial photographs from 1962.

According to this model the following situation was reconstructed: In the first two months of the growth period (from the beginning of May to the beginning of July) in 1965 about two thirds of lakeside culms were submerged over several weeks ($W > L_{crit} + W_0$). This must have led to a die off of all these culms. Additionally, the flood peak at the end of June was accompanied by strong winds and hail storms so that many of the taller culms which had successfully competed with the rising water level were destroyed. In 1987 the maximum water level was only a few centimetres below of that of 1965, but the flood began to swell three weeks later. Hence, the *Phragmites* shoots got a good start for growing and the great majority of them was able to grow faster than the rising water level ($W < L_{crit} + W_0$). It must be noted, however, that the lakeside reed front was at a higher elevation (W_0) than before the great die-back in 1965. The model applied to the situation in 1987 postulated that nearly no culm losses were to be expected, a result which could be verified by field observations. Fortunately, no mechanical threat occurred during the growing season, as it was the case in 1965. Although the current year's culm generation was not impaired directly, the flood in 1987 had a delayed effect on the subsequent reed generation: a retreat of the reed front by –4,8 cm a^{-1} on average was observed during the growth period of 1988, evidenced by the reed front mapping.

Looking at the period of 1984/1994 as a total, this was a decade with low summer high water levels interrupted by one extreme event in July/August 1987, only. There has not been such a closed period of six years with extreme low summer water levels since the beginning of water mark records at Lake Constance in 1817, as it was the case between 1989 and 1994. OSTENDORP et al. (1996) found a significant negative correlation between the flooding height of a *Phragmites* stand in May and its mean progression/regression rate. It is understandable, therefore, that in years with low summer water levels reed stands below the mean water level are able to spread lakewards, whereas in years with high floods they are not or even undergo a retreat.

Table 2. Growth parameters of *Phragmites* shoots at Lake Constance-Untersee. - D_b: shoot basal diameter [mm], a, r_L: coefficients according to the regression model L_{tot} [cm] = a + r_L t [d], t: time from the beginning of the year [d], t_0: emergence date [d], t_{max}: time at which L_{max} is reached [d]; means ± std.dev's; (# – insect infested shoots are included; significance: n.s. – not significant, * – $\alpha < 0.05$, *** – $\alpha < 0.001$).

	Primary shoots (n = 62)	Secondary shoots (n = 50)
D_b, [mm]	8.24 ± 1.58	5.17 ± 0.94
a, [cm]	–603 ± 164	–443 ± 162
r_L (mean ± std.dev.), [cm d^{-1}]	4.77 ± 1.0	3.52 ± 0.95
t_0, [d]	125 ± 12	123 ± 17
t_{max}, [d]	193 ± 7	184 ± 11
a – dependence on D_b	a = –242 – 43.9 · D_b, r = 0.424***	a = –328 – 22.3 · D_b, r = 0.130, n.s.
dto, total culm population #	a = –242 – 46.5 · D_b, r = 0.522***, n = 166	
r_L – dependence on D_b	r_L = 1.94 + 0.343 · D_b, r=0.541***	r_L = 1,79 + 0.334 · D_b, r = 0.331*
dto., total culm population #	r_L = 1.79 +0.381 · D_b, r = 0.658***, n = 164	

Significance of macrophyte wash

A detailed evaluation of selected series of aerial photographs demonstrated that the reed belt at Lake Constance-Untersee suffered losses at least up to the end of the 1970s, i.e. for a long time period after the extreme flood event in 1965. Therefore, other factors than high water levels must be responsible.

The 1970s had been a period of pronounced eutrophication before, in the 1980s, waste water purification measures became effective. Due to the high nutrient level submerged macrophytes and filamentous algae became very abundant (LANG 1981). In late summer and autumn when the water level drops, and strong winds occur, macrophytes and macroalgae were uprooted by wind-induced waves, and washed ashore in dense clumps, thereby damaging *Phragmites* culms mechanically. From 1981 to 1983 between 7.5 and 14.2% of the reed covered shoreline was affected by strong macrophyte washes. The heaps mainly consisted of *Cladophora* sp., *Chara* sp. and *Potamogeton* spp., accompanied by drift wood and floating rubbish. Clumps with a high proportion of *Chara* were shown to bring about the strongest mechanical damage; *Cladophora*-dominated clumps were not so effective (OSTENDORP 1992). The degree of wash, i.e. the height of the heaps, and their lateral extension, depends on numerous factors, but, over a couple of years, a certain degree of load seems to be characteristic for each shore section.

The macrophyte clumps which had been laid down over and around the lower sections of *Phragmites* stems were compacted as the water level dropped in autumn, and decomposed anaerobically. It was hypothesized that reduced chemical compounds can accumulate which may be harmful to *Phragmites* (SCHRÖDER 1987). This hypothesis was tested in laboratory and field assays, but clearcut results have not yet be obtained (OSTENDORP 1992). Hence, the main threat to the reeds by macrophyte and macro-algae washes is the mechanical impact.

Since the end of the 1980s submerged water plants have become gradually less abundant, presumably due to the reduced phosphorus level in the pelagic water of Lake Constance which in turn reflects the success of waste water purification efforts in the catchment area. Shoreline mappings from 1986 to 1991 at Lake Constance-Obersee (KRUMSCHEID-PLANKERT 1992), and 1994/95 at the Untersee (PIER, unpubl.) confirm the visual impression that the intensity of macrophyte wash is much lower now.

Mechanical damage and 'power of mechanical resistance' of *Phragmites* stands

A significant correlation was found between the amount of drifting matter which had been washed ashore, and the difference in culm density of front standing reeds between two subsequent years: the culm numbers will decrease if the stands have been affected by medium or severe washes (OSTENDORP 1992). Similarly, PIER et al. (1993) found low progression rates for wind and wave exposed stands on step sloped shores.

The degree of mechanical damage in a given situation depends on numerous factors which can be grouped into (i) factors connected with the wave energy at the reed front, (ii) amount of submerged macrophytes and filamentous algae, and their behaviour during the process of uprooting, transporting by the waves, and being washed ashore, and (iii) factors which determine the 'power of mechanical resistance' of reed stems (OSTENDORP 1995 a).

BINZ-REIST (1989) published an impressive attempt to bring the physical interactions between winds, waves, drifting matter and *Phragmites* stems into a mathematical model. This model allows the estimation of the wave height (as a measure for wave energy) at which a *Phragmites* culm of given geometric and elastic properties will be bent or broken. However, many input variables must be measured with sufficient precision to take advantage of his model. This makes it unattractive for its use in an ecological and practical context.

As an alternative, a model was developed that focuses the visco-elastic properties of a stem (OSTENDORP 1995 a). This model allows a prediction which of two *Phragmites* stands with a known stand structure (e.g. culm density) and a known symmorphology (e.g. mean stem diameter) will lose more culms or more biomass as a consequence of a mechanical threat that is the same for both stands. Input variables are stem diameter, stem wall thickness (to compute the moment of inertia J), the modulus of elasticity E, the breaking stress S of representative culms, and the culm density of the stand.

Using the modulus of elasticity E and the moment of inertia J, the bending stiffness for a single stem is $M_E = E \cdot J$. M_E is a measure for the external bending force which a single stem can encounter for a given deformation. The model postulates for a *single stem* i that the probability for this stem not to fail under a given impact of wave ⊕ drifting matter action is a monotonous function of $M_{E(i)}$:

$$pmr_{(i)} \text{ (power of mechanical resistance of a single stem)} \propto M_{E(i)} \qquad (4)$$

This means that each stem will fail (i.e. bent or broken) if its bending stiffness falls below a critical M_E value. This "critical value" can be estimated from the maximum distance between the cumulative M_E distribution curves for damaged and undamaged culms.

The deformation forces that a reed *stand* can tolerate are assumed to be proportional to the sum of the $pmr_{(i)}$ values of all culms i affected by the forces at the same time.

PMR (power of mechanical resistance of a reed stand)

$$\propto \hat{M}_E = \sum_{i=1}^{n} E_i \cdot J_i \qquad (5)$$

1,..., n: culms affected at the same time. – For simplicity the number n of culms is set to be the culm density (m^{-2}). For a reed stand the model postulates that, for a given strength of mechanical impact, the percentage of failing culms (or destroyed biomass, respectively) is proportional to M_E.

Considering the complexity of the impact of external forces and of the visco-elastic reaction of a stem section, it becomes clear that these models can be valid only in a stochastic sense. That means, on the level of single culms the statement of the model is true for only a part of all cases, and on the level of reed stands the regression curve will show a notable variance.

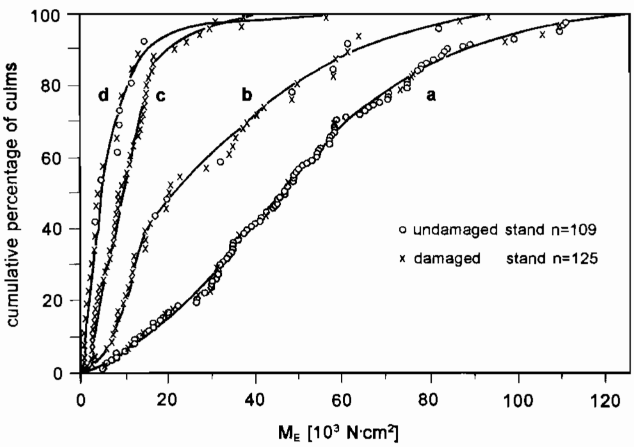

Fig. 1. Test of the pmr model on the level of individual stems: cumulative frequency of bending stiffness M_E of stems from 10 damaged and 10 undamaged test plots (see Fig. 2). **(a)** upright stems; **(b)** bent stems; **(c)** stems bent down to the water surface; **(d)** broken stems. The cumulative frequency distributions from the pairs a/b, b/c, and c/d belong to different data populations (Kolmogorov-Smirnov test, $\alpha < 0.01$).

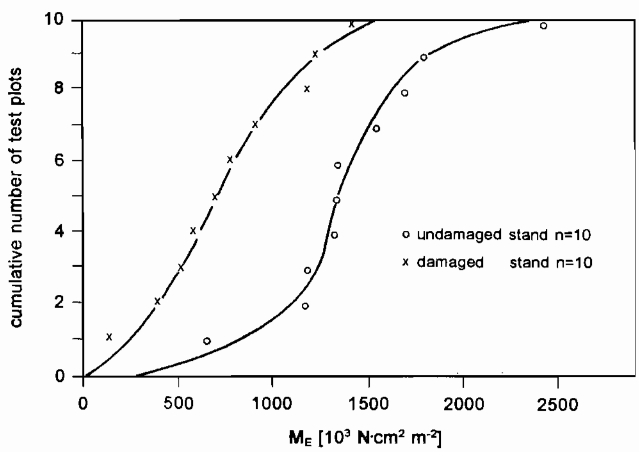

Fig. 2. Test of the PMR model on the level of the whole *Phragmites* stands: cumulative $\hat{M}_E$ values of 10 damaged and 10 undamaged test plots which had been affected by the same wave and drifting matter impact. The cumulative frequency distributions belong to different data populations (Kolmogorov-Smirnov test, $\alpha < 0.01$).

The validity of the model was tested using three *Phragmites* stands from the Lake Constance-Untersee shore. One example is given in Figs. 1 and 2. Each stand had been exposed before to a damaging wave ⊕ drifting matter impact with a constant strength along the shore section considered. However, the stands differed by their culm density and by the morphology of the culms. The pmr model referring to single stems, yielded 82% true predictions, when the pair a+b *vs.* c+d is considered (Fig. 1). Similarly, the cumulative frequency distributions over $\hat{M}_E$ were significantly different for severely damaged and undamaged stands, respectively (Fig. 2). A positive correlation was found between M_E and the share of damaged culms (and damaged biomass, respectively).

Hence, the potential degree of endangering of *Phragmites* stands by mechanical impacts can be predicted on the basis of stand structure, culm morphology and visco-elastic properties of the stem alone. It is concluded that *Phragmites* stands with a high proportion of thin and weak secondary shoots should have higher biomass losses due to a mechanical impact of given strength than a stand which is mainly composed of stout primary shoots. Secondary shoots are the replacement for young primary shoots (or for the terminal buds from which they emerge) that have been destroyed by various stressors in the foregoing season. The most important stressors at Lake Constance are the mechanical damage by waves and washes, grazing by water fowl and infestation by the moth *Archanara geminipunctata* (Noctuidae, Lepidoptera). A positive feed-back might be the consequence: a *Phragmites* stand, once seriously damaged, will develop a stand structure in the next season which makes it more susceptible to mechanical threats. And, if the mechanical stress happens again, the weakening of the stand structure will be accentuated, and finally the stand will die back.

Discussion

From aerial photographs, early investigations and models presented in this paper, the history of Lake Constance-Untersee reeds can be divided into four periods (Fig. 3):

(1) period until c. 1954 – progression period, during which the lakeside reed front advanced by dozens of metres. It is hypothesized that in the first half of the century (i) the high frequency of floods, (ii) the low nutrient content of the water and the sediments, and (iii) the mechanical damage by commercial reed harvesting limited the progression rate of *Phragmites* reeds. In the period between 1870 and 1940, 3.3 "damaging" floods (i.e. flood crest at 396.65 m a.s.l. or above) happened per decade on average; in contrast, the period of 1938–1954 exhibited only two weak floods. By 1960 the lake reached an eutrophic state with c. 50 mg $P_{soluble}$ m^{-3} (turnover period). Presumably, the commercial reed harvesting had the same effects on the reed as the winter harvesting

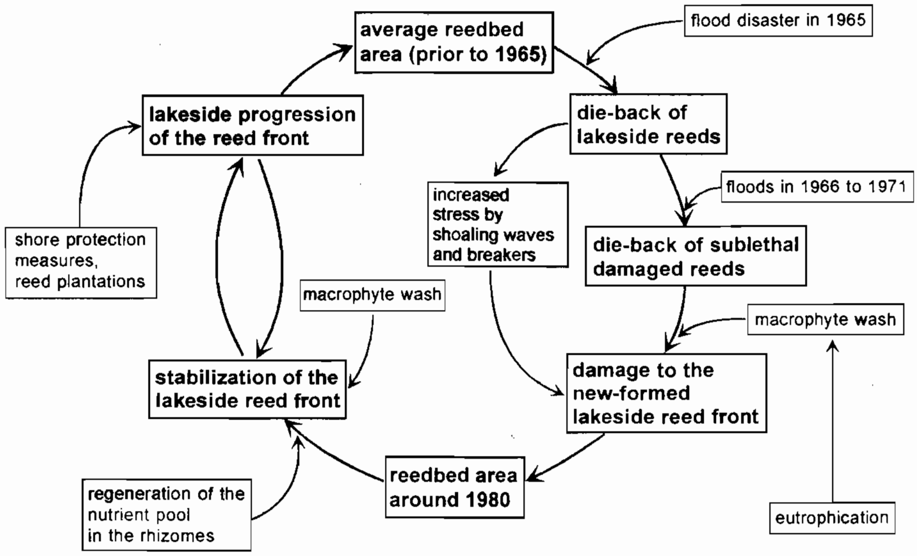

Fig. 3. Schematic overview over the development of lakeside reeds at Lake Constance-Untersee.

in modern times: a shift towards a stand structure with high proportions of secondary shoots, and a weakening of the mechanical properties of *Phragmites* stems (OSTENDORP 1995 b).

(2) period between 1954 and 1967 – regression period induced by extreme hydrological and meteorological events resulting in the extinction of large lakeside reed areas at the end of this period, and in a landward shift of the present day reed front. The chronology of these events can be traced back in full detail (OSTENDORP 1990): the main stressors have been a flooding for weeks in the summer of 1965, and wind induced waves and drifting matter.

(3) period between 1968 and the beginning of the 1980s – stagnation phase, where some of the damaged reeds recovered, and others died back. Extreme floods were not important any longer (one event in 19 years). As new stressors (i) washes of macrophyte and filamentous algae came up supported by the high nutrient level of the pelagic water body (c. 100 mg $P_{soluble}$ m^{-3}, turnover period), and (ii) to a minor extent bank erosion at the reed front.

(4) period from the middle of the 1980s onwards – progression phase favoured by the fact that the importance of two stressors had abated: (i) the abundance of drifting matter at the reed front (especially *Cladophora* mats), (ii) the mean summer water level was well below the average of the period of 1937/1987, so that low lying reedbeds were able to expand lakeward.

These results encourage the prognosis that the fringing *Phragmites* reeds at Lake Constance-Untersee will expand under the present conditions, and one day they will take up the area they had in 1954. This should not be mistaken as a cyclic process. Rather, human impact on landscape, like the construction of reservoirs in the Alpenrhein catchment area, diverting water into other catchment areas, the manipulation of the outflow threshold of the lake, etc., may have effects on the hydrological regime of Lake Constance (LUFT 1993), and, thereby, on the dynamics of the littoral communities. Presently, the consequences for the equilibrium between diverse stresses and the stability of the lakeside reed front, and for its future development are not predictable, not even in the fundamentals.

References

BINZ-REIST, H.-R. (1989): Mechanische Belastbarkeit natürlicher Schilfbestände durch Wellen, Wind und Treibzeug. Veröff. Geobot. Inst. ETH Zürich **101**: 1–536.

BRÄNDLE, R. (1991): Flooding resistance of rhizomatous amphibious plants. In: M.B. JACKSON, D.D. DAVIES & H. LAMBERS (eds.), Plant life under oxygen deprivation, pp. 35–46. The Hague.

– & CRAWFORD, R.M.M. (1987): Rhizome anoxia tolerance and habitat specialization in wetland plants. In: R.M.M. CRAWFORD (ed.), Plant life in aquatic and amphibious habitats, pp. 397–410. Oxford.

CONERT, H.J. (1983): *Phragmites*. In: Illustrierte Flora von Mitteleuropa (founded by G. HEGI), 3rd. ed., Vol. **1**/3: 126–133. Berlin, Hamburg.

COOPS, H., GEILEN, N. & VAN DER VELDE, G. (1994): Distribution and growth of the helophyte species *Phragmites australis* and *Scirpus lacustris* in water depth gradients in relation to wave exposure. Aquatic Botany **48**: 273–284.

– VAN DEN BRINK, F.W.B. & VAN DER VELDE, G. (1996): Growth and morphological responses of four helophyte species in an experimental water-depth gradient. In: H. COOPS (ed.), Helophyte zonation: impact of water depth and wave exposure. pp. 47–61. Nijmegen.

DIENST, M. (1994): Die Wasserstände des Bodensee-Obersees von 1893 bis 1992. Schrr. VG Bodensee **112**: 147–162.

KRUMSCHEID-PLANKERT, P. (1992): Uferrenaturierung und Röhrichtschutz. – Abschlußbericht zum Entwicklungs- und Erprobungsvorhaben "Wiederansiedlung von Schilfbeständen am Bodensee" im Auftrag des Bundesministeriums für Umwelt, Naturschutz und

Reaktorsicherheit, Bonn. Research Report, 2 Vols. Limnologisches Institut, Universität Konstanz.

LANG, G. (1981): Die submersen Makrophyten des Bodensees – 1978 im Vergleich mit 1967. Ber. IGKB **26**: 1–64.

LUFT, G. (1993): Langfristige Veränderungen der Bodensee-Wasserstände und mögliche Auswirkungen auf Erosion und Ufervegetation. Limnologie Aktuell **5**: 51–75.

– VAN DEN EERTWEGH, G. & VIESER, H. (1990): Veränderungen der Bodensee-Wasserstände von 1887 bis 1987. Handbuch Hydrologie Baden-Württemberg 6.2. Karlsruhe.

OSTENDORP, W. (1990): Die Ursachen des Röhrichtrückgangs am Bodensee-Untersee. Carolinea **48**: 85–102.

– (1991 a): Zur Geschichte der Uferröhrichte des Bodensee-Untersees. Schrr. VG Bodensee **109**: 215–233.

– (1991b): Damage by episodic flooding to *Phragmites* reeds in a prealpine lake: proposal of a model. Oecologia **86**: 119–124.

– (1992): Shoreline algal wash as a factor in reed decline in Lake Constance-Untersee. Hydrobiologia **242**: 165–174.

– (1995 a): Estimation of mechanical resistance of lakeside *Phragmites*-reeds. Aquatic Botany **51**: 87–101

– (1995 b): Effect of management on the mechanical stability of lakeside reeds in Lake Constance-Untersee. Acta Oecologica **16**: 277–294.

– STARK, H., KRUMSCHEID-PLANKERT, P. & PIER, A. (1996): Dynamics and restoration of lakeside reedbelts in a prealpine lake (Lake Constance, Germany). Proc. 2nd Int. Symp. on Habitat Hydraulics, Québec, June 1996, Vol. B, pp. 753–765. Québec.

PIER, A., DIENST, M. & STARK, H. (1993): Dynamics of reed belts at Lake Constance (Untersee and Überlinger See) from 1984 to 1992. Limnologie Aktuell **5**: 141–148.

RODEWALD-RUDESCU, L. (1974): Das Schilfrohr – *Phragmites communis* TRIN. Die Binnengewässer **27**: 1–302. Stuttgart.

SCHRÖDER, R. (1979): The decline of reed swamps in Lake Constance. Symp. Biol. Hung. **19**: 43–48.

– (1987): Das Schilfsterben am Bodensee-Untersee, Beobachtungen, Untersuchungen und Gegenmaßnahmen. Arch. Hydrobiol., Suppl. **76**: 53–99.

WEISSNER, S.E.B. (1987): The relation between wave exposure and distribution of emergent vegetation in a eutrophic lake. Freshwater Biology **18**: 537–544.

– (1991): Within-lake patterns in depth penetration of emergent vegetation. Freshwater Biology **26**: 133–142.

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