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Effects of water level variations on the dynamics of the reed belts of Lake Constance

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Abstract

Following the extreme flood at Lake Constance in 1999 the reed belts of the shore of Baden-Württemberg lost approximately 30 ha (24%) of their lakeside reed beds. This loss is comparable with the situation in the late 1960s, when approximately 40 ha died back due to the extreme flood in 1965 and due to the high spring water levels in the subsequent years. In the time period between the extreme floods of 1965 and 1999, the reed areas expanded to nearly 85% of their original area before 1965.

As a consequence of the extreme flood in 1999 a loss of 44% of the above ground biomass of 1998 occurred. One third of this loss was regenerated in the subsequent years 2001 and 2002. Similar results were obtained for the calculation of the biofilm area provided by the submerged culm parts of the reed stands. A loss of 47% of the biofilm surface area was estimated. By 2002 only one fifth of the lost area had been regained. This reflects the fact that the regeneration of the lakeside stands at lower elevation levels proceeds much more slowly than that of the inner stands on higher elevation levels, which con-tribute less to the submerged surface areas of the reed stands.

Simulations of the extreme flood event of 1999 show a strong association with the results of the aerial photo interpretation. This confirms the concept of the model and supports the hypothesis that water level fluctuations play a major role in the reed dynamics of Lake Constance. The results demonstrate the close interaction of hydrological processes with dynamics of biota, thus the necessity of an ecohy-drological approach for the understanding and for the sustainable management of littoral ecosystems.

Key words: ecohydrology - hydrological variations - vegetation dynamics - Phragmites australis - flood tolerance - growth model.

1. Introduction

In recent decades a large decrease in lake shore reeds has been observed on many central European lakes (Ostendorp 1989; van der Putten 1997; Brix 1999). Lake Constance has also been affected by this decline. The main factorial complexes resulting in reed decline, apart from direct damage by hu-man use of lake shores, are mechanical damage by waves and flotsam, grazing pressure of waterfowl, musk and Nutria (Coypu) and eutrophication (Ostendorp 1989). Furthermore, genetic diversity in clone structures is discussed as a factor influencing reed decline (Koppitz, Kühl 2000). In particular eutrophication was often held responsible for the decline (Klötzli, Grünig 1976; Schröder 1979, 1987). Less is known about the influence of water level fluctuations. Reeds play important ecological roles (Ostendorp 1993a, b), for example as a structural element and nutritional plant for a highly specialized fauna and as protection against lake shore erosion. They also promote "self cleaning" of the water through the enhancement of the microbial decomposition of organic substances.

The extreme flood of 1999 on Lake Constance, the third largest since regular level readings on Lake Constance began in 1816/17 (Jöhnk *et al.* 2004), led to a large population decline in aquatic reeds (Schmieder *et al.* 2002; Ostendorp *et al.* 2003). The physiological mechanisms of flood damage have been described by Koppitz (2004).

This work explores the following questions: (1) What regeneration processes can be seen in the years immediately after the extreme flood of 1999?, (2) How could the recent changes be rated in the long term reed dynamic of Lake Constance, especially in comparison with the changes after the extreme flood of 1965?, (3) How will the populations develop in the future, taking the expected climatic changes into consideration?, (4) How can the interaction between water level on Lake Constance and reed growth be modeled on a spatial level?

2. Material and methods

Study area

Lake Constance is the largest northern prealpine lake. It draws approximately 80% of its yearly water influx from the alpine area. It is distinguished from most other prealpine lakes, in that its yearly pattern is close to a natural water level pattern. In spring (March-June) the level of Lake Constance increases by approximately 2m due to the snow melt and precipitation (Dienst 1994; Luft, Vieser 1990; Jöhnk *et al.* 2004). The detailed water level records, that have been made since 1816/17, allow investigations into medium and long term trends in lake levels, as well as an accurate comparison of the time pattern of single flood events, with the typical growth curve of reeds on different elevation levels. The inves-tiga-

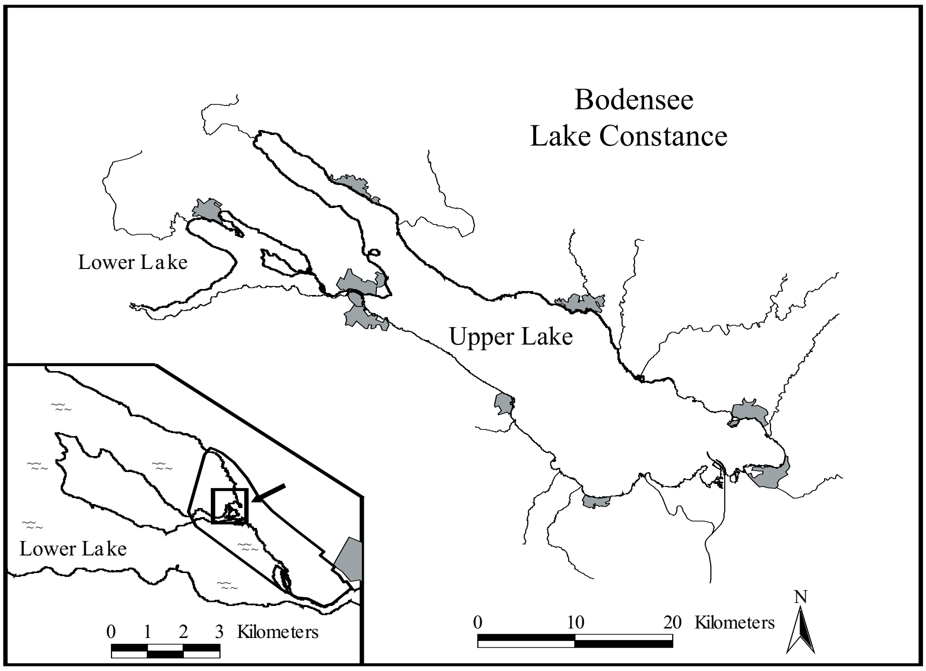

Fig. 1. Map of the study area of Lake Constance. The investigated part of the shoreline is shown as thick line; the box marked by the arrow in the map inlet indicates the area shown in Fig. 10.

tion area was the Lake Constance shore, in Baden-Württemberg (Fig. 1). The investigated reed-populated shore sections have a total length of 43 km.

Changes in reed areas after the extreme floods of 1965 and 1999

In order to measure changes in aquatic reed areas after the extreme flood, two series of color infrared (CIR) aerial photographs with a 1:5 000 scale were made on 2000 July 22nd and 2002 July 20th. In ad-dition to these two series, which contained approximately 150 aerial photographic images, aerial pho-tographs from 1993 (Schmieder 1998) and 1999 (IGKB 1999) were used for comparison with the con-dition before the extreme flood. For three lakeshore sections (Giehrenmoos in nature reserve Wollmat-inger Ried, the shore north of Konstanz-Litzelstetten and for the Stockach Aach river mouth) addi-tional panchromatic aerial images from March 21th 1962, as well as color aerial images from July 7th and August 15th 1967 (Lang 1973) and from 1978 July 11th and July 14th (Lang 1981) were evaluated.

From the aerial images from 1962 and 1999, the areas of the previous year's reed population were digitized, as the new reed generation had not yet grown. The grades of damage were defined using the first qualitative evaluation of the aerial image series from July 22th 2000 and on-site observation as follows (see Schmieder *et al.* 2002): G1=undamaged, G2= lightly damaged, G3=clearly damaged, G4=heavily damaged, G5=extremely damaged. The land side border of the aquatic reed population was defined at an altitude of 395.30 m a.s.l. for the Untersee (lower lake) and 395.70 m a.s.l. for the Obersee (upper lake) (see Schmieder *et al.* 2002). The elevation line was derived from the digital bathymetric map of Lake Constance (Braun, Schärpf 1994).

The methods of stereoscopic evaluation and the processing of digital vector data in a geographical information system (GIS) are described in detail in Schmieder *et al.* (2002).

The reed areas of three shore sections for which data were available for 1961, 1967 and 1978 (see Schmieder *et al.* 2003) were extrapolated to the total area of reed populations in Baden-Württemberg in order to compare the changes in total area with the total area figures from 1993, 1998 and 2000. This allowed the comparison of the effects of the extreme floods of 1965 and 1999. The length of these three shore line sections is 2.01 km in total. This comprises approximately 5% of the total inves-tigated reed populated shore length of 43 km. The average relative changes in the 1993-2000 period in the three shore line sections were found to be roughly equivalent to the relative changes in the total area. Thus it was assumed that the three shore line sections are also representative of the total reed populated shore length in the previous years (Böcker *et al.* 2003).

From the aerial image series of 2000 the total areas as well as the areas of different grades of reed damage were digitized. In the 2002 series only the different grades of damage were digitized. The 2002 total area was determined using the areas of the five grades of damage from 2002: within the GIS, the relative sizes of areas of different grades of damage in comparison to the total were deter-mined geometrically. Consequently, the 2002 total sizes of areas of different grades of damage were weighted using the 2000 relative sizes to obtain the 2002 total area (details in Böcker *et al.* 2003).

Estimation of above ground stand biomass and biofilm area

Through the combination of the results from the aerial photographic evaluation and field investigation of selected monitoring areas (Schmieder *et al.* 2002), the total above ground biomass of the reeds on the Untersee (lower lake) for 1998, 2000 and 2002 was calculated. In order to do this the average population biomass of different grades of damage was multiplied with the relative area of the respec-tive grade of damage for one year and summed over all degrees of damage. For 1993 and 1998 the means of the biomass of undamaged to slightly damaged populations (G1 and G2) were used to esti-mate the total population biomass.

The aquatic reeds are allocated an important role with regard to the ecological function of biological "self cleaning" of the shallow water zone (Ostendorp 1993a, b). The surfaces of submerged culm sec-tions that can be colonized by bacterial growth (hereinafter referred to as biofilm area) play an essen-tial role.

In order to estimate the biofilm area, i.e. the surface area of the submerged culm sections, a combined data set of a digital elevation model (grid cells of 5m x 5m, elevation resolution of 20 cm) and the ge-ometries of the areas of the different grades of damage from the respective year was generated. In re-spect to the reference point of the average annual lake level, the length of the submerged culm sections (H) was determined for each grid cell of the combined data set. Using the mean culm diameter of culms from each individual grade of damage (D=2r, averaged over all different culm classes), meas-ured on field trips, the average submerged culm surface area (O) of a culm in its respective elevation level was calculated using the formula [$O = 2\ \Pi\ r\ H$]. Multiplied with the average number of reed culms per m2 and with the total area of a reed population of a specific grade of damage at the appropri-ate elevation level, one obtains the biofilm surface area of the respective class of reed damage. Summation of all damage classes yields the total biofilm area of aquatic reed. The biofilm area of the ground sediment and the reed litter surface are neglected in this calculation.

Simulation of the interaction between annual reed growth pattern and annual lake level time series - the reed growth model (RGM)

The extreme flood of 1999 damaged reed populations, as it occurred very early in the growth phase of the reeds. In case of normal annual water level pattern, the top leaves of the reed culm rise above the surface of the water. If this is not the case, growth inhibition occurs, which can cause the culm to die off if it remains submerged for a long time. One can assume that in order for a reed to survive, the three top most leaves of the culm have to rise above the water. That is, the distance between the water surface and the height of the third leaf has to be greater than zero.

The reed growth model (RGM) simulates the growth curve of reed culms, depending on the elevation level and the individual water level time series for predetermined growth parameters (a detailed de-scription of the model can be found in Böcker *et al.* 2003). The culms are considered quasi-independently. For a given elevation level and a given grade of damage the growth of a large number of culms with randomly chosen growth parameters from the admissible variability of the chosen grade of damage were simulated. The behavior of such culm clusters with given growth parameters and culm density allows an evaluation and classification of the population into a new specific damage class at the end of each growth period.

In order to verify the simulation model and to evaluate values and fluctuations of the parameters used, data from a monitoring program were used (Böcker *et al.* 2003). The growth and leaf generation of single reed culms from different places with varying damage grades were measured and statistically analyzed over a time period of approximately 150 days. From this, with the help of a linear growth model, the parameters for the length increment rate and the development of the leaf numbers were determined.

The temporal change of the distance between the third leaf and the culm top was determined using a polynomial approach. A logistic growth model derived from this monitoring data was used in the de-velopment of the simulation model.

For the modeling, four grades from the five grades of damage from the extensive classification of reed populations were used (damage grade 5 was only used to describe irreversibly destroyed reed, because most areas of this damage grade did not contain any culms). The growth parameters (growth rates, etc) were calculated for these grades of damage. For the model calculations a more fine-grained classifica-tion of the damage grade was used (1.0, 1.1,... 3.9, 4.0), so that the transition between different damage grades becomes smoother. The elevation level of the individual reed stands, i.e. pixels from a digital elevation model, has a resolution of approximately 10 cm. For Lake Constance, which has a maximum water level fluctuation of approximately 4 m, 42 individual elevation levels were used.

In order to simulate the growth behavior in relation to an annual water level time series, the behavior in relation to 42 elevation levels and 41 grades of damage must be determined. Thus for every simu-lated year 1722 calculations with different input parameters have to be carried out. For every annual water level time series, the model results in the calculation of the corresponding transition rules for the grades of damage from beginning to end of the growth period. These are then saved as a table. These tables contain the grade of damage (the relative culm density), which one obtains with the given eleva-tion level and the start grade of damage at the end of a water level year. This procedure only needs to be carried out once for each individual annual water level time series. To obtain simulations for a cer-tain sequence of annual water level time series the transition rules for each water year simply have to be chained. A spatial GIS-simulation of reed development can be carried out by applying such a table of transition rules belonging to an annual water level time series to all pixels, i.e. reed stands. For every pixel, which is assigned a specific grade of damage and elevation level, the corresponding table entry (new grade of damage at the end of the year) is used to update its grade of damage at the end of the growth period of the water year in use.

The model scheme is graphically illustrated in Fig. 2. A simulation run of the growth model for an individual culm is shown in Fig. 3. Each stand was given an elevation level and a grade of damage. The growth parameters and their flucuations were determined using the damage grade. Per stand, that is per pixel in a GIS-system, 1 000 individual culms were calculated. For each culm the growth pa-rameters were randomly taken from a normal distribution. The growth iteration begins on day 100, that is on the 10th of April, and it ends on day 250, on the 27th of September. This time window encloses the whole growth phase of a reed culm. In the temporal pattern of growth the

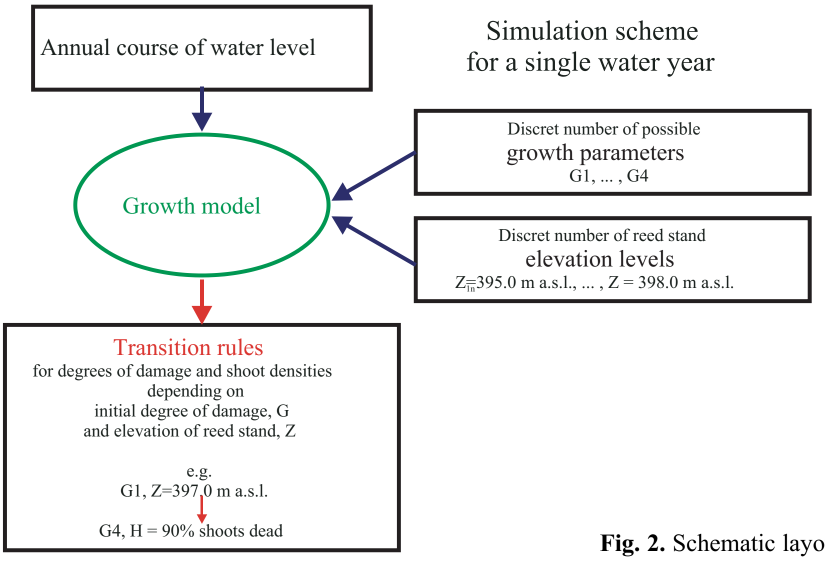

Fig. 2. Schematic layout of the growth model.

water level changes, so that in certain circumstances culms may be submerged beyond the third leaf. In this case, it is assumed, that growth rate is reduced. The longer the culm is submerged, the greater the growth inhibition, at the end leading to the death of the reed culm. At the end of a growth phase many culms may have died, possibly as a result of flood damage. The new damage grade of the population is then determined from the number of surviving culms and their lengths, i.e. the biomass of the stand. This value represents an entry for the transition rule of a certain damage grade on a fixed elevation level within a certain annual water level time series.

3. Results

Changes in total reed area after the extreme floods of 1965 and 1999

The changes in the total surface areas during the recent decades show a high dynamic and a clear cor-relation with the hydrological variations (Fig. 4). From the approximately 135 hectares of aquatic reeds that existed in 1961, by 1967 40 hectares had died as a result of the extreme flood of 1965. Total as well as relative area loss of aquatic reeds as result of this extreme event was higher than that caused by the extreme flood of

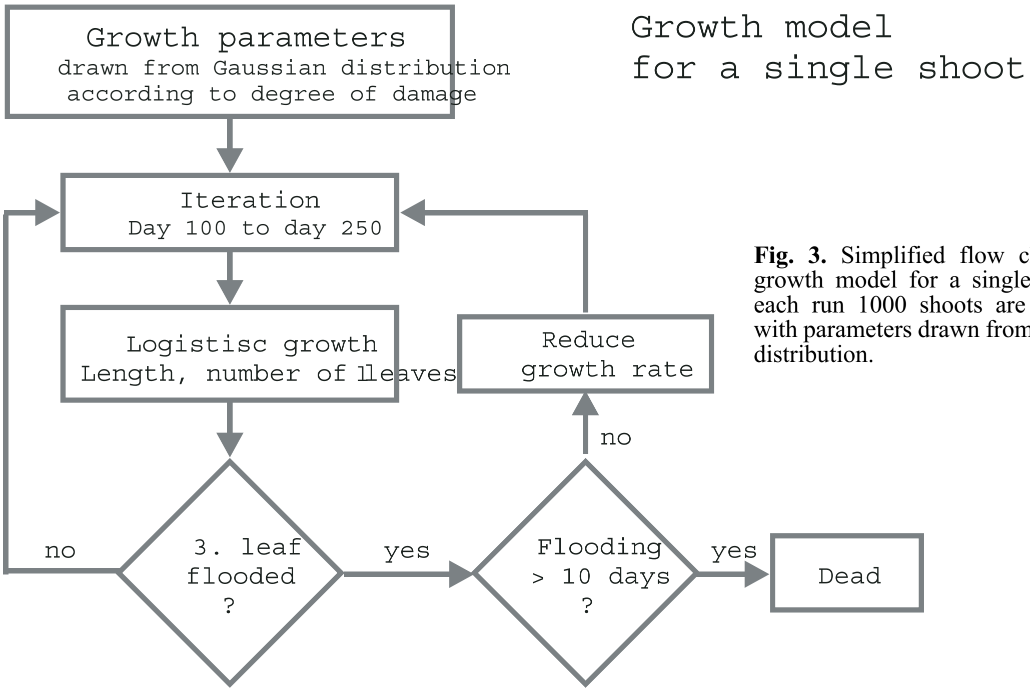

Fig. 3. Simplified flow chart of the growth model for a single shoot - in each run 1000 shoots are cal-culated with parameters drawn from a Gaussian distribution.

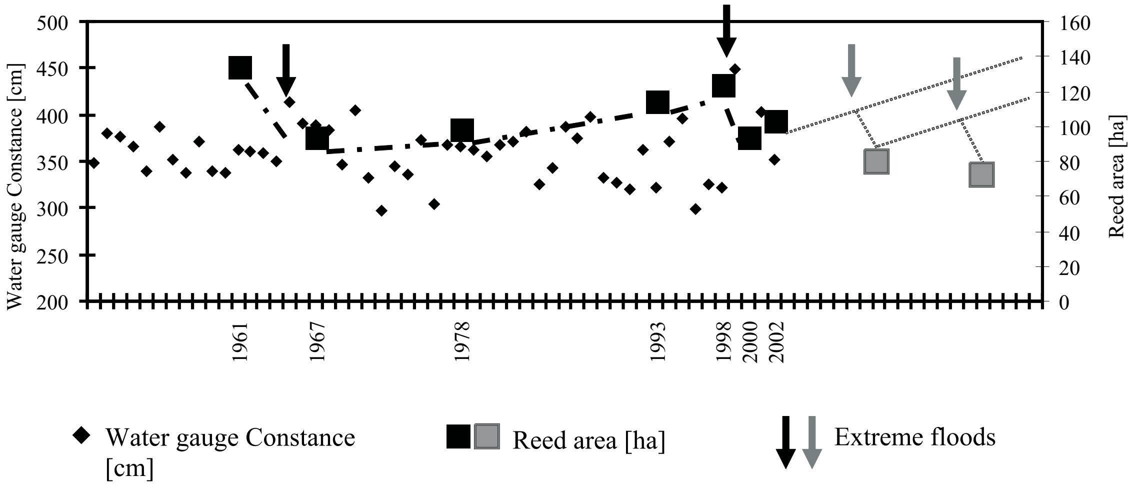

Fig. 4. Reed areas of the years 1961, 1967, 1978, 1993, 1998, 2000 and 2002 in comparison with the annual mean water levels (May and June) of the time period 1951 - 2002 and prediction (grey colour) of the areas in case of a higher frequency of extreme floods in the future.

1999, with a loss of approximately 30 hectares (Table I). On average, for the time period 1961 to 1967 a mean land-side shift of the lake-side reed border of 9.4 m was calculated, whereas the regression of the lake-side reed border between 1998 and 2000 was merely 6.9 m. In the time period between the extreme floods the reeds spread out again. The spreading accelerated with increasing temporal distance from the extreme year of 1965. Above all, in the time period from 1993 to 1998 the reed area on the Baden-Württemberg shore of Lake Constance had greatly increased by 9.3 hectares in size. However, after more than 30 years the aquatic reeds could only spread to 85% of their original area of 1961.

In 2000 nearly 30% of the aquatic reed areas of 1998 were heavily (G4) or extremely (G5) damaged as a result of the extreme flood of 1999 (Fig. 5). Nearly 30% were clearly damaged (G3), while approxi-mately 40% were only slightly damaged or not damaged at all.

In 2002, the relative surface of the higher damaged populations (G3, G4, G5) was less than in 2000, whereas in the main the heavily damaged areas (G4) decreased in favor of the less damaged areas (Fig. 5). Whilst in the Obersee the extremely damaged areas decreased, these areas increased slightly in the Untersee. In contrast to this, areas which appeared undamaged (G1) increased considerably, especially in the Untersee, so that in total there was a clear recovery of the slightly to heavily damaged popula-tions (G2 to G4), whereas the proportion of extremely damaged and often totally killed off areas (G5) hardly changed.

Total above ground biomass and biofilm area of the aquatic reed populations in 1998, 2000 and 2002

Comparing the changes in the total above ground biomass in the period from 1998 to 2002 (Fig. 6), with the changes in the reed areas (Section. 4.1), the impact of the extreme flood with respect to the total biomass is much higher. Whereas the area losses amounted to 24%, the extreme flood caused a 44% loss in total above ground biomass in the time period from 1998 to 2000. From 2000 to 2002 a recovery (35% of the losses) can clearly be seen.

From the combination of relative areas of the different damage grades and their corresponding culm density and with the help of the elevation levels of the stands, the submerged culm surface area avail-able for formation of microbial

Table I. Reed areas of the years 1961, 1967, 1978, 1993, 1998 and 2000, and the changes in the time periods between the investigated years.

Year	Reed areas [ha]	Difference		Shift of the reed front	
		[ha]	[%]	[m]	per year [m]
1961	134.8				
		-40.3	-29.9	-9.4	-1
1967	94.5				
		4.7	5.0	1.1	0.1
1978	99.2				
		15.8	15.9	3.7	0.2
1993	115.0				
		9.2	8.0	2.1	0.4
1998	124.2				
		-30.2	-24.3	-7.0	-3
2000	94.0				
		9.3	9.9	2.2	1.1
2002	103.3				

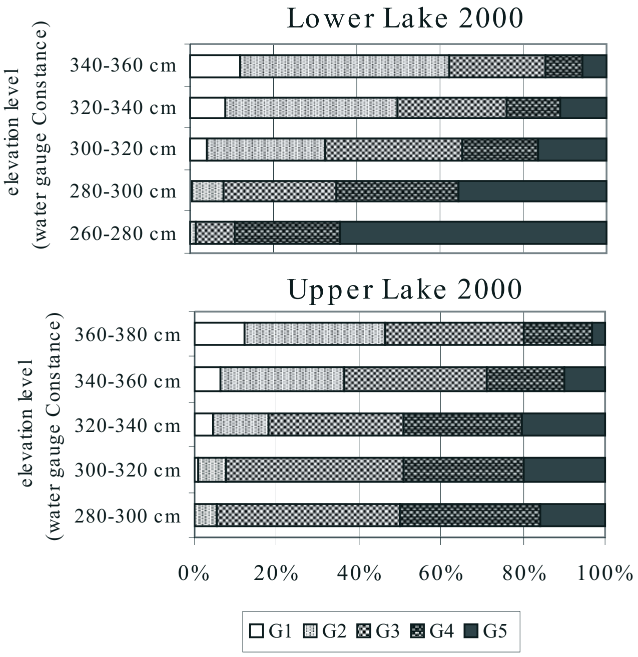

Fig. 5. Percentage of areas of different damage degrees (G1 to G5) in the years 2000 and 2002.

biofilms was calculated for certain water levels (Fig. 7).

Compared with the changes in the above ground biomass the percentage of decline of the biofilm area as a result of the extreme flood was similar in its order of magnitude (-47%). However, the regenera-tion of these surfaces (19% of the losses) in the years after the extreme flood was clearly lower than the regeneration of the population biomass. This reflects the spatial situation of the population structure, where the recovery took place mostly in populations on a high elevation level. The populations on a low elevation level, which are more important for the biofilm area, showed only a small tendency to recover.

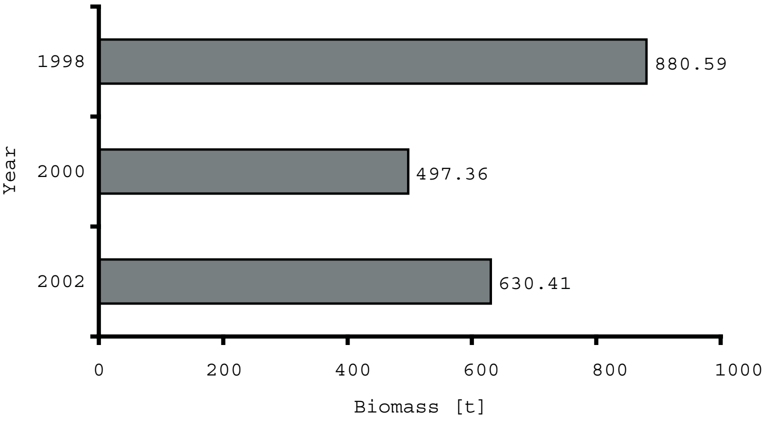

Fig. 6. Changes in total biomass of reed areas between 1998 and 2002.

Simulation of the extreme flood of 1999 using RGM

In Fig. 8 the modeled growth patterns for culm clusters of the four grades of damage G1, G2, G3 and G4 are compared with the measured values. The simulation values shown in the figure represent the average and the onefold standard deviation. The model parameters fitted to the measurements yield simulation results encompassing the bandwidth of measured data for all four cases. This verifies the validity of the model and the chosen parameters.

In the simulation of the extreme flood of 1999, discontinuities in the logistic curves stand out (Fig. 9). There was damage in all three chosen elevation levels. Especially at an elevation level below 396 m a.s.l., the grade of damage of undamaged populations (G1) increases to heavily damaged (G4). It is clearly recognizable that the reaching of the high water mark coincides with reed death. Only the lar-ger culms, which protrude out of the water surface, could continue to grow. This led to a shift in the length distribution towards larger values, and with this to a jump in the pattern of the curve. Afterwards, the reed length distribution of the reduced surviving populations is no longer normally distrib-uted, so that the standard deviation given for the simulated results cannot be trusted unconditionally.

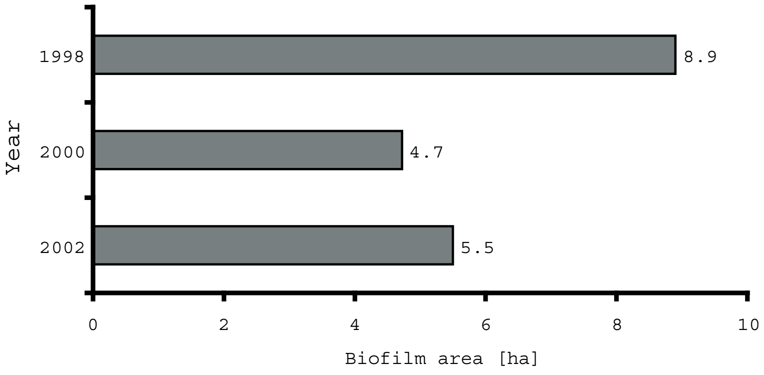

Fig. 7. Changes in total biofilm area of reed areas between 1998 and 2002.

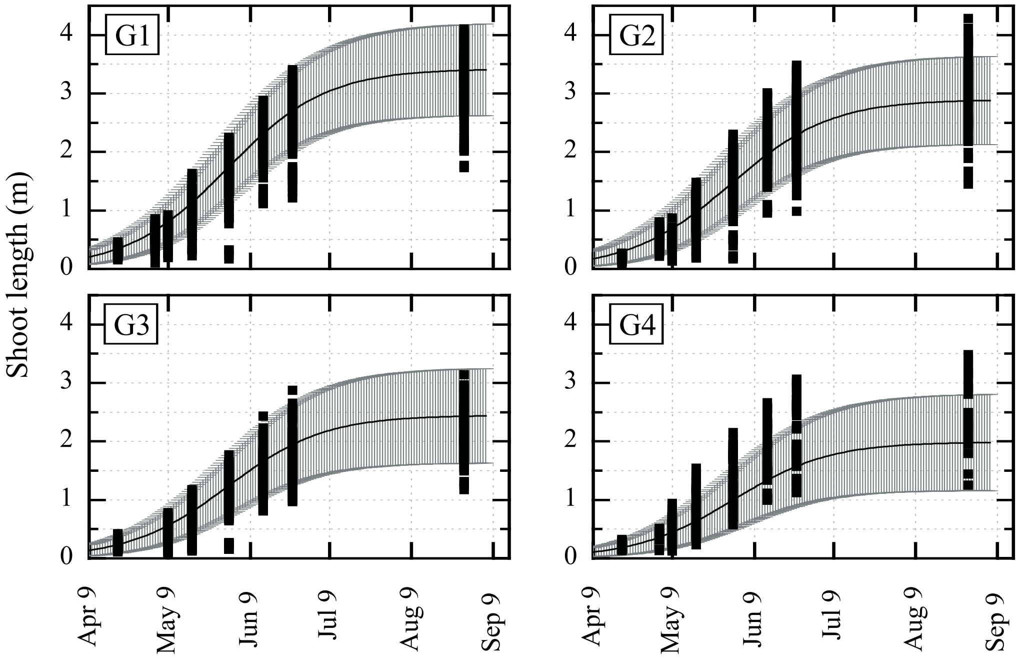

Fig. 8. Simulations with logistic growth model and comparison with field measurements for reed stands with different degrees of damage, G1 - G4. Shown are mean pattern and standard deviations for shoot length.

The cartographic visualisation of the simulation results for the geometrics of 1998 reed populations within the geographical information system resulted in a picture similar to the grades of damage of the aquatic reeds obtained from the evaluation of aerial images (Fig. 10). In particular, the lakeside popu-lation on low elevation level experienced heavy to extreme damage, that declines landwards, with in-creasing elevation level. While the simulation results at different elevation levels were homogenous, the evaluation of aerial images was more heterogeneous.

4. Discussion

The aquatic reeds of Lake Constance, which is not regulated, show a dynamic development, which is characterized by an advancing and receding lakeside reed front. On a local scale these processes are caused by certain local stresses (mechanical damage from waves and flotsam, grazing by water birds or mammals, insect infestation). On a larger regional scale, this dynamic is primarily influenced by hydrological conditions (Ostendorp 1990). The results of this study have shown, that in the recent dec-ades the spatial dynamics of the reed populations have shown a clear association with water level fluc-tuations. The large reed declines from 1961 to 1967 and 1998 to 2000 were primarily caused by the early and large floods of 1965 and 1999. The populations expanded again during the period between the extreme floods. There are clear parallels between the floods of 1965 and 1999 and their conse-quences. In 1965 the maximum water level was 24 cm less than in 1999; however, the water levels in the main growth phase of the reed culm were very similar. In addition, in both extreme years there were storms during the high water phase, which further harmed the already damaged reeds. The GIS-analyses of the population areas for the time period 2000 to 2002 are supported by simultaneous inves-tigations on population structure, culm morphology and deposits in rhizomes in 50 monitoring areas (Schmieder *et al.* 2002; Ostendorp *et al.* 2003). It was not the maximum water level that determined the level of damage in 1999, but its early occurrence. In May and June the growing culms could not win the race against the increasing water levels.

The culms were submerged and oxygen transport in the rhizome ceased. An anaerobic metabolism started (Koppitz 2004), which led to the total depletion of stored carbohydrates in many rhizome sec-tions (Ostendorp in preparation). In the following years, the damaged stands had weaker culms and, in consequence, a greater sensitivity towards natural stresses, such as early water level rise, wind and waves (Schmieder *et al.* 2002). In 1965 and 1999 the water levels were above average in spring. This increased the impact of the extreme floods.

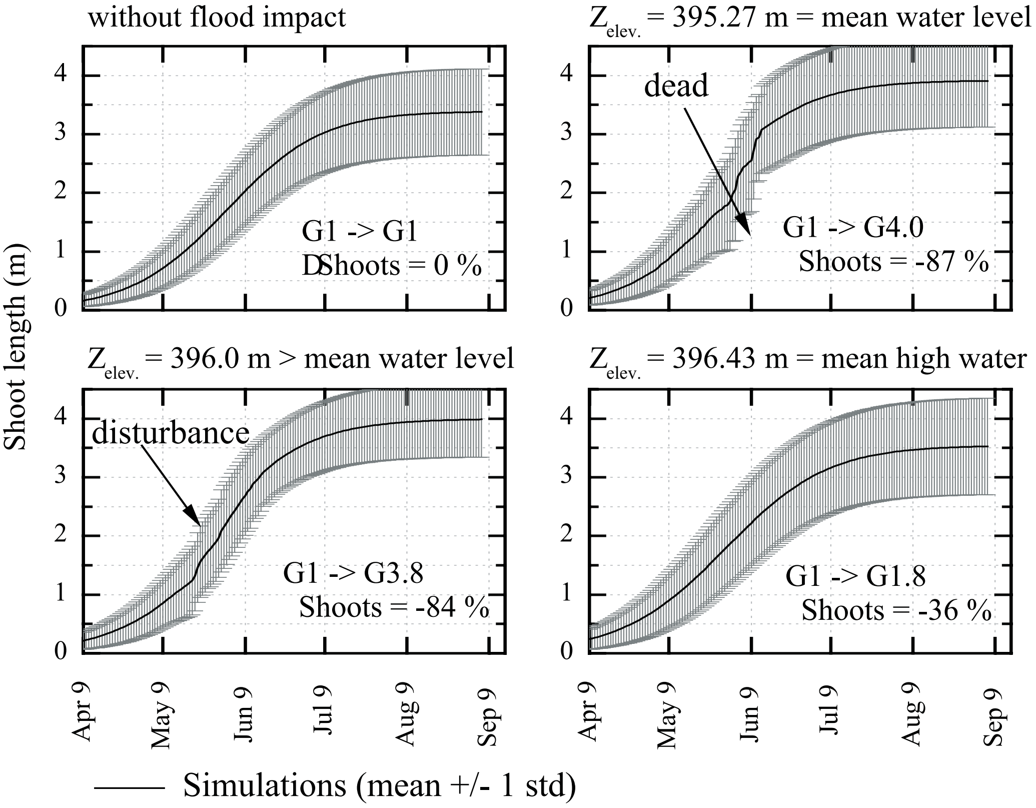

Fig. 9. Simulations for reed with a G1 degree of damage. Shown is the development of shoot length for four cases: without flood impact (top left) and reed stand elevation at mean water level (top right), above mean water level (bottom left) and at mean high water level (bottom right), respectively.

The relative losses in above ground biomass caused by the 1999 flood greatly exceeded the percentage decrease of the aquatic reed area. The changes in culm morphology in reed populations as a result of the flood reflect this fact. Whilst the aerial photo evaluations of damage grades only gave conclusions concerning the culm densities, the field data collected shows that the weakness of the surviving culms increased with increasing damage grade, which results in less above ground biomass (Schmieder *et al.* 2002; Ostendorp *et al.* 2003). Combination of aerial photo evaluation and field data measurements allow precise statements about the effects of the extreme flood of 1999 on the vitality of the reeds.

The relative decrease in biofilm area on the submerged culm sections as a result of the extreme flood of 1999 is comparable in its order of magnitude with the decline in the population biomass above ground. However, the relative increase of the biofilm area in the time period of 2000-2002 is clearly less than that of the biomass. This is reflected in the changes in population structure. The populations on a higher elevation level could regenerate relatively quickly. However, most of populations on the low elevation levels, which provide the largest fraction of submerged culm surface, were heavily to extremely damaged and subsequently died off completely (Dienst *et al.* 2004). The long-term losses of the reeds growing in low areas could have lasting effects on the important ecological functions attrib-uted to aquatic reeds (the self cleaning ability and the protection of the open water from polluting substances) (Ostendorp 1993a, b). During the vegetation period the loss of surface structures might be at the least partially compensated for by submerged macrophytes, which quickly colonized dead reed areas (personal observations).

The effects of extreme floods on the aquatic reeds of Lake Constance can be simulated by the me-chanical growth model RGM. The simulation of the extreme flood of 1999 corresponds very well with the damage that actually occurred, which highlights the sensitivity of the model. The model also con-firms the yearly water level development as a primary factor for the reed dynamics. The larger hetero-geneity of the actual flood damage in the individual elevation levels in comparison with the simula-tions can be explained by co-factors that possibly change sensitivity towards floods. With increasing damage grade, an increased attack rate by the reed beetle (*Donacia clavipes*) can be seen (Schmieder *et al.* 2002; Ostendorp *et al.* 2003). The differences in rhizome carbohydrate reserves among popula-tions or

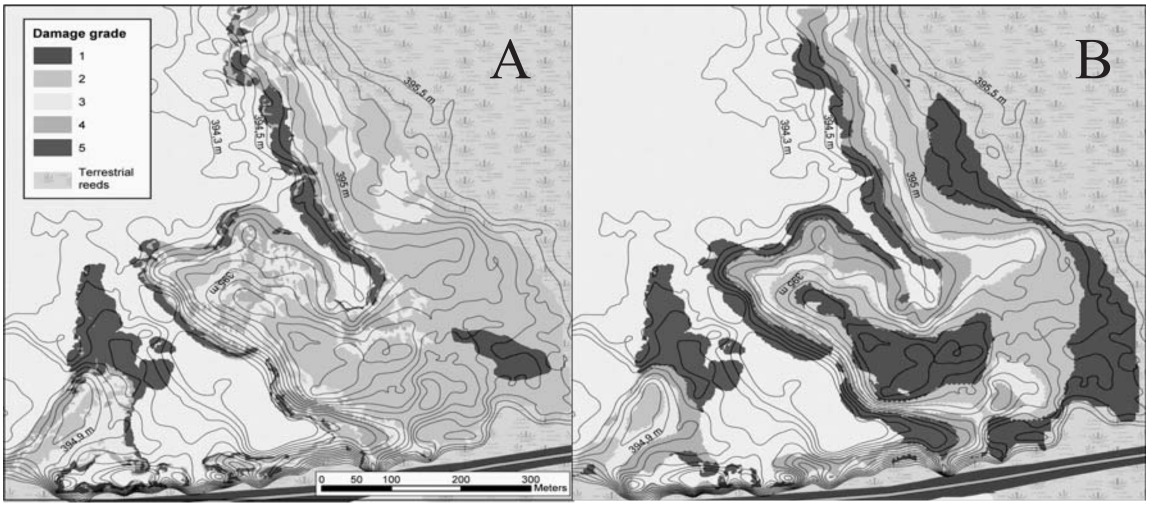

Fig. 10. Map of the classification from aerial photos (A) in comparison with the model simulation of the extreme flood in 1999 (B).

mechanical stress factors from storm events and flotsam could also play a role.

The regeneration of populations after such extreme events can also be simulated on the basis of a se-ries of annual water level patterns. However, populations that have been killed off entirely are not in-cluded in the growth model. Thus the recolonization of dead reed areas, from, for example, vital land-side populations, cannot be simulated with the model. For this subject a GIS based extension of the model is planned.

With the help of GIS, the simulation results can spatially be transferred onto the aquatic reed popula-tions and represented cartographically. Using different scenarios regions can be discovered, in which, for example, the danger of a total reed population loss by frequent extreme floods is particularly high. Thus the developed model allows the estimation of the effects of future extreme events.

For the middle to long term prognosis of the Lake Constance reeds it is critical how the heavily dam-aged areas develop and whether a lakeside expansion is possible. Both are dependent on the develop-ment of the water levels in the future. The low water year of 2003 - the high water mark lay only slightly over the long term mean water mark - could at least in the short term give an expansion boost. However, investigations in 1984 and 1992 on the lakeside reed border of western Lake Constance have shown, that, at the most, an average lakeside reed expansion of 0.5 m is possible, even in favor-able years (Pier *et al.* 1993). The available aerial photo evaluations gave an average expansion of merely 0.4 m per year in the hydrologically favorable years between 1993 and 1998. The regeneration of the reed front that regressed by 7m between 1998 and 2000 will take at least 20 years, even under favorable conditions. The low water year 2003 favored the colonisation of the dried up areas with cat-tail (*Typha latifolia* L.), so that the reeds in many areas achieved the extent that they had before the extreme flood (Dienst unpubl.). They provide, at least for the short term, protection against erosion. The next years will show whether the Typha-reeds will keep their hold, or whether they will be dam-aged by floods or replaced by Phragmites- reeds.

The investigations on Lake Constance have shown how natural water level fluctuations affect the reed dynamics, and they have also considerably extended discussion about the causes of reed decline on central European lakes (Ostendorp 1989; Van der Putten 1997; Brix 1999). However, as the majority of the lakes in the prealpine area have a regulated water level, the results can thus only partially be transferred.

Even though the effects of the extreme floods are dramatic for reed populations and the species that are directly dependent on them, like for example the great reed warbler (*Acrocephalus arundinaceus* L.) (Woithon, Schmieder 2004), the natural water level fluctuations with their extreme events are very important for structural diversity and biodiversity in the littoral zone. Plant communities, like those of the Littorelletea communities (Dienst, Strang 1999), are directly dependent upon water level fluctua-tions. Water level regulation has caused their disappearance from the majority of prealpine lakes. The importance of water level fluctuations for the species variety of shore vegetation has been emphasized by Hill *et al.* (1998). They compared the shore vegetation between regulated and unregulated lakes in New Scotland, Canada. Plant communities on the regulated lakes were less diverse and contained more exotic species; rare species in general were completely absent. According to Hill *et al.* (1998) the water level fluctuation that is optimal for shore vegetation is 1 to 2 m.

Wilcox (1995) also mentions that water level fluctuations are vital for the wetland areas of Lake Huron, as they maintain the cycle of succession processes and wetland diversity. High water levels periodically eliminate competitive terrestrial plants. When the water levels decline, less competitive species can quickly colonize the free areas using seeds or other surviving organs and can, at the least, complete one life cycle and replenish their diaspore bank, before being displaced by more competitive plants. The height, frequency, seasonal occurrence, and duration of the extreme events play an impor-tant role for the fluctuations of the biota. The experiences on Lake Constance confirm these conclusions. The results demonstrate the close interaction of hydrological processes with dynamics of biota, thus the necessity of an ecohydrological approach (Zalewski *et al.* 1997) for the understanding and for the sustainable management of littoral ecosystems is apparent.

How should we classify the extreme flood of 1999 in the long-term water level time series of Lake Constance? Whilst the number of large flood events decreased in the second half of the last century (Dienst 1994; Luft, Vieser 1990), at the moment there appears to be a tendency towards floods taking place earlier in the year (eg. also in 2000 and in 2001). It is possible that climate change has caused this. Climate change has become evident in the Lake Constance area (Beniston, Jungo 2002). Mild and short winters allow the water levels to increase earlier in the year. It must be feared that the more fre-quent and stronger appearance of floods means that the reeds will never again expand to their previous large population sizes.

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