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## Management Impacts on Stand Structure of Lakeshore *Phragmites* Reeds

*key words:* winter harvesting, burning, shoot density, biomass production, Lake Constance

### Abstract

Many lakeside *Phragmites australis* reeds are frequently harvested or burnt in winter for several purposes like extraction of raw material, natural preservation or facilitation of professional fishing or fish breeding. The question is, whether these practices support a sustainable development of the reeds. Data from a long term monitoring program at Lake Constance (Germany) demonstrate that culm morphology, stand structure and aboveground peak biomass are strongly influenced by the treatment. Winter harvested and burnt reeds exhibited higher culm densities (+76% of the untreated controls), and a higher peak biomass (+13%). The mean culm height was reduced by -13%. The percentage of insect infested shoots was 8.8% of the total shoot population, compared with 20.1% of the untreated controls. Consecutive harvesting treatments intensified these effects. In the first two years after the treatment had stopped the reed stands showed an 'overshoot' biomass production, and a strong trend towards the features of the untreated controls. The possible mechanisms (mechanical damage, frost kill of the growth tips and breaking of the apical dominance) are discussed. It is concluded that winter harvesting and burning treatments make the reeds more susceptible against some environmental hazards, and should therefore applied with precaution on the basis of a close examination of risks and benefits.

### 1. Introduction

Large wetland areas in Central Europe are covered with the common reed, *Phragmites australis* (CAV.) TRIN. ex STEUD. (Poaceae). In many cases these reeds are managed for different purposes by winter harvesting and burning or by summer mowing. Extraction of raw material (GRANÉLI, 1984; SCHUSTER, 1985; NEVEL *et al.*, 1997), improvement of wildlife diversity (DITLHOGO *et al.*, 1992; COWIE *et al.*, 1992; WARD, 1992; HAWKE and JOSÉ, 1996), facilitation of professional fishing and fish breeding, removal of organic matter and nutrients (SCHRÖDER, 1987) are the main objectives.

Many casual observations pointed out side effects like stand structure deterioration of the *Phragmites* reeds, spreading of undesired plant species, local extinction of reeds, and changes in reed breeding bird fauna. Hence, the use of reed belt management, in terms of sustainable development of wetlands, seems to be ambivalent, depending on specific aims, management practices, and ecological circumstances like substrate properties, hydrological regime and site specific stressors.

In this work the experimental results of winter harvesting and burning practice on the stand structure of lakeshore reedbeds at Lake Constance-Untersee are presented. The investigations included growth rate, morphology and density of *Phragmites* culms, and the biomass production of harvested and unharvested *Phragmites* reeds. The presumable consequences for the longterm stability of the reed beds and for the reed dwelling fauna are discussed.

## 2. Investigation Area

The Untersee is the western part of Lake Constance (SW-Germany, N-Switzerland), a shallow eutrophic prealpine lake with high annual water level fluctuations (c. 1.9 m on average), broad shelves and extended reed belts. 99.7% of the eulittoral reeds are formed by monospecific stands of *Phragmites australis*, a perennial grass with stout culms, c. 6–13 mm in diameter at the stem base, and c. 2.5–4.5 m in height. A dramatic die-back occurred between 1965 and c. 1980 when 37% of the lakeside reedbeds were lost (OSTENDORP, 1990).

Winter harvesting and burning were intended as countermeasure against organic matter and nutrient accumulation in the beds which was assumed to be the main reason for the reed decline (SCHRÖDER, 1987). Additionally, reeds were mown and burnt to increase the young fish population, and to facilitate bow-net fishing. Harvesting was done with different types of caterpillar vessels with an interchangeable mowing and chaffing device at the front. The work was usually carried out in winter, when the water level was low, and the ground deeply frozen. The chaffed straw and the litter were removed from the bed by hands or by machines. Burning was done mainly by local fishermen in early spring before tiller growth set on. The managed reeds formed the lake side edge or the central part of the reed belt. They were flooded during summer for c. 2–8 months up to a depth of 1.6 metres. The experimental fields were monitored for several years to examine the stand structure response of mown and burnt reedbeds in comparison with the untreated controls.

## 3. Methods

Investigations were performed along a total of 12 cross shore transects, 30 to 120 m in length, from the outer reed front to the mixed reeds at the landside edge where the former monospecific *Phragmites* reeds exhibited an understorey of *Carex* div. spp. and *Phalaris arundinacea* vegetation. Each transect consisted of 5 to 7 plots in regular distances, where stand structure measurements were done.

**Growth rate measurements:** On a subset of these plots c. 50 to 100 randomly selected tillers were labelled with plastic plates. Total height and number of leaves of each shoot were recorded weekly or fortnightly. The graph of the total shoot length against time gave a sigmoid curve of which the central part could be approximated by the linear regression function  $L(t) = r_L \times t + c$ . To find this regression curve for an individual shoot, all data points were initially included in the model, resulting in a bad fit with  $r < 0.98$  due to the sigmoid tails. Then data points were excluded pairwise from both tails of the data set until a correlation coefficient of  $r > 0.98$ , with  $n \geq 5$  data points was yielded.  $L$  is the time dependent length of a shoot,  $r_L$  is its growth rate (i.e. the mean daily shoot length increment during the linear growth phase),  $t$  is the time elapsed since the beginning of the year, and  $c$  is an additive term. The emergence date  $t_0$  was estimated as  $L(t) = 0 = r_L \times t_0 + c \rightarrow t_0 = -c / r_L$ . The date at which the maximum height was reached,  $t_{\max}$ , was computed from the regression line as  $L(t) = L_{\max} = r_L \times t_{\max} + c \rightarrow t_{\max} = (L_{\max} - c) / r_L$ .  $\Delta t = t_{\max} - t_0$  is the time interval of linear growth.

**Stand structure measurements:** Culm density ( $Z$ ) measurements and shoot sampling were done at the transect plots during winter time to avoid damage by the investigator. The locations were repeatedly sampled for several years depending on treatment, so that comparisons between treated/untreated sites for different years were possible. Three shoot classes could be distinguished: panicle bearing shoots, flowerless shoots, and insect infested shoots. It is assumed that the panicle bearing and the flowerless shoots can be parallelized with the 'primary shoots' (PSh) and the 'secondary shoots' (SSh), respectively (HASLAM, 1969a, b), whose formation is controlled by the vertical rhizome, and that the insect infested shoots (ISh) are either PSh or SSh, but are damaged by phytophagous arthropods later on during their development. ISh reveal a serious damage of the growth tip by (I) stem boring Lepidoptera larvae (mainly *Archanara geminipunctata* HAW., Noctuidae), which destroy the growth tip and the upper part of the shoot, and (II) apical gall forming arthropods (mainly *Lipara lucens* MEIG. and *L. rufitarsis* LOEW. [Chloropidae, Diptera], and *Stenotarsonemus phragmitidis* (v. SCHLECHTENDAL) [Tarsonemidae, Acari]). Other kinds of insect infestation (e.g. *Giraudiella inclusa* FR. [Cecidomyiidae, Diptera], *Hyalopterus pruni* (GEOFFR.) [Aphididae, Rhynchota]) do not induce such morphological changes, and are therefore not classed with the ISh.

**Culm biomass and peak standing crop:** About 10 to 15 shoots were selected from 5–8 counting plots of 0.36–1 m<sup>2</sup> each to give a stratified sample according to the share of each shoot class in the total population (within each shoot class, culms were taken randomly). The culms were clipped at ground level; stem length ( $L_S$ ), total number of leaves ( $N_{Lf}$ ), and stem mean diameter ( $D_m$ , measured at  $1/2 L_S$ )

were measured in the laboratory. Nonlinear calibration functions with different coefficients for different shoot classes were used to estimate the total biomass ( $W$ ) of an individual culm in late August when normally the maximum standing crop was reached. The individual total stem biomass ( $W_{\text{stem}}$ ) was estimated using the cylinder model  $W_{\text{stem}} = a \times D_m^b \times L_s^c$  with the mean diameter  $D_m$  and the stem height  $L_s$  as input variables. The coefficients were estimated by linear multiple regression of the linearized model  $\lg W_{\text{stem}} = \lg a + b \times \lg D_m + c \times \lg L_s$ . The total leaf biomass ( $W_{\text{leaves}}$ ) was estimated from a 2<sup>nd</sup> order polynomial model  $W_{\text{leaves}} = a \times W_{\text{stem}} + b \times W_{\text{stem}}^2$  (a no-intercept model was applied, since it fitted the data of low weight shoots more precisely than any intercept model). The total culm biomass  $W_{\text{culm}}$ , including leaves, leaf sheaths, and panicle if present, was calculated as  $W_{\text{culm}} = W_{\text{stem}} + W_{\text{leaves}}$ .  $W$  refers to a biomass which includes ash.

The peak standing crop (PSC) was calculated as the sum of standing crop values of each culm class which in turn was the product of mean density ( $Z$ ) and mean culm weight ( $W_{\text{culm}}$ ). PSC is regarded as a good estimate for the aboveground net primary production (NPP), since losses from grazing, shedding, and culm mortality are low (Kvet, 1971, Dykijova *et al.*, 1973).

No significant differences in stand structure could be detected between winter harvested and burnt reeds. Hence, the treatments are combined and compared with the untreated control in the following text.

## 4. Results

### 4.1. Tillering and Late Frost Killing

During autumn, new buds develop at the *Phragmites* rhizome and grow up near to the soil surface, or even reach a few centimeters height above ground, where the growth stops until next spring. Therefore, the date of emergence, calculated from the growth curve reflects the starting point of the growth which may deviate from the 'true' starting point by *c.* -2 days for tillers which have their tips above ground in early spring, and *c.* +2 days for below-ground buds. In Lake Constance reeds, the calculated date of emergence of the young shoots  $t_0$  was between 07 April and 31 May ( $n = 15$  stands in 1980 to 1984). At this time, the mean daily maximum temperature 5 cm below ground varied between +11.3 and +16.3 °C, and the mean daily minimum was between +5.9 and +9.7 °C. The absolute minimum temperature in the soil top layer did not fall below +2.7 °C (data from the German Weather Service [DWD] weather station at Constance).

Warm periods during which the young tillers start to grow may be followed by cold periods with night frosts. Even mild frosts of -0.2 to -1.7 °C destroyed the growth tip of shoots of more than 15 cm height. Frost damage was restricted to harvested and burnt reedbeds. In some cases, the extent of damage was greater on the landside section than near the water edge. A typical situation was recorded in 1984 on a harvested reedbed (see Fig. 1): the young shoots started to grow between 03 May and 08 May, reached a height of 15 to 30 cm, and were damaged during a cold weather period with frosts of -0.6 °C on 09 May to 10 May (temperature data from the DWD). 87% of all shoots were destroyed. After 22 days (mean date) 90% of them brought about 1.6 replacement shoots on average, coming out between the basal leaf sheaths of the dead primary shoots. They were significantly thinner than the 13% undamaged primary shoots ( $D_m = 4.41 \pm 0.85$  mm,  $n = 27$  vs.  $D_m = 7.96 \pm 1.08$ ,  $n = 13$ ,  $\alpha < 0.001$ , independent samples t-test). During the season, 37% of the replacement shoots were infested by gall forming insects (mostly *Lipara* sp.), the rest (63%) remained to be SSh in the sense that they did not develop a panicle in August. But 86% of the undamaged shoots effloresce into panicle bearing shoots, another 14% remained without a panicle. None of them were infested by parasites.

Frost damage may partly explain why winter harvested and burnt reeds exhibited higher densities of the total shoot population but not higher primary shoots densities (see Fig. 2). On the average of 9 pairs of harvested/unharvested reeds, the total shoot density measured in June increased by 29.3 m<sup>-2</sup> ( $\alpha < 0.05$  for  $H_A$ : difference  $\neq 0$ , paired t-test), i.e. a mean increase by 84% of the untreated controls.

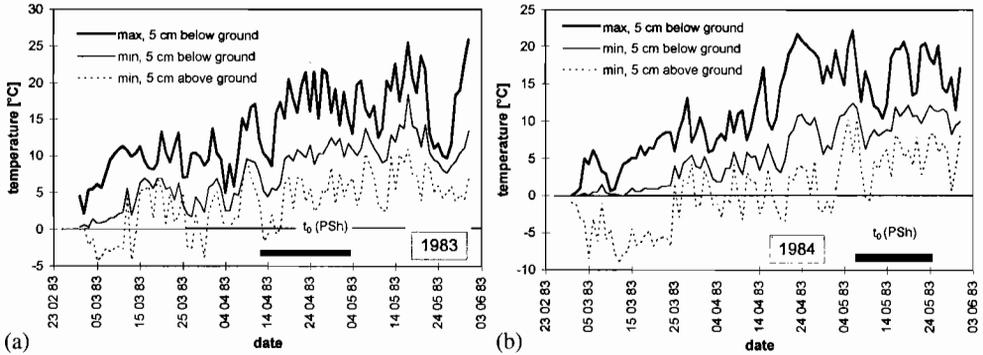


Figure 1. Air and soil temperature during springtime in (a) 1983 and (b) 1984, measured under standard conditions at the DWD weather station in Constance (daily maximum, 5 cm below ground level, daily minimum, 5 cm below ground, daily minimum, 5 cm above ground), and emergence period (PSh of harvested and untreated stands)

No frost damage was observed in 1983, since the shoots were not longer than 15 cm, so that the growing tip was near or below ground level. Serious damage was observed in 1984 due to the cold nights on 9<sup>th</sup> and 10<sup>th</sup> of May, as the shoots were 15 to 30 cm in height, and the growth tip was c. 10–20 cm above ground.

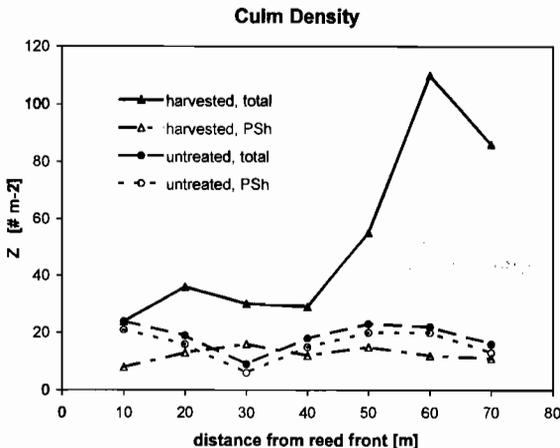


Figure 2. Culm densities of winter harvested reeds and untreated controls on June 11<sup>th</sup> 1981 at Lake Constance (primary shoots, total shoot population). Note the increase in secondary shoots in the landside part of the harvested area

#### 4.2. Growth Characteristics

The growth rate or mean daily increment of shoot length during the linear growth phase,  $r_L$  of individual culms ranged from 1.19 to 6.75 cm day<sup>-1</sup>. PSh exhibited significantly higher rates ( $4.93 \pm 1.13$  cm day<sup>-1</sup>, global mean of mean values from  $n = 13$  plots) than the SSh ( $4.10 \pm 1.31$  cm day<sup>-1</sup>,  $n = 12$  plots) ( $\alpha < 0.01$ , independent samples t-test). The ISh grew at a lower rate ( $3.71 \pm 1.73$  cm day<sup>-1</sup>,  $n = 7$  plots), but did not significantly differ from the other two culm classes at the  $\alpha = 0.05$  level. PSh from winter harvested and burnt reeds showed a significantly reduced growth rate ( $4.68 \pm 1.32$  cm day<sup>-1</sup>) compared to those from the control beds ( $5.47 \pm 0.91$  cm day<sup>-1</sup>) (Table 1); this was also the case for SSh ( $3.37 \pm 1.19$  vs.  $3.74 \pm 0.92$  cm day<sup>-1</sup>) but the difference was not significant.

Table 1. Growth characteristics of treated and untreated *Phragmites* reeds at Lake Constance-Untersee (global means  $\pm$  std.devs. of means from  $n = 4$  [secondary shoots, SSh], and  $n = 5$  [primary shoots, PSh] pairs of plots with 8 to 74 shoots in each plot. Statistics: paired t-test, differences of means between groups are not significant except for  $r_L$  in PSh [ $\alpha < 0.05$ ]).

	shoot class	treated	controls
growth rate	PSh	4.68 $\pm$ 1.32	5.47 $\pm$ 0.91
$r_L$ [cm day <sup>-1</sup> ]	SSh	3.37 $\pm$ 1.19	3.74 $\pm$ 0.92
emergence date	PSh	120 $\pm$ 12	122 $\pm$ 10
$t_0$ [days]	SSh	127 $\pm$ 15	120 $\pm$ 16
termination of linear growth	PSh	188 $\pm$ 5	190 $\pm$ 8
$t_{max}$ [days]	SSh	182 $\pm$ 7	183 $\pm$ 13
duration of linear growth	PSh	67.2 $\pm$ 12.7	68.8 $\pm$ 8.6
$\Delta t$ [days]	SSh	57.9 $\pm$ 15.6	60.2 $\pm$ 10.3

The mean date of shoot emergence,  $t_0$  ranged from 14 April to 31 May for individual stands (all culm classes pooled). In many cases an average PSh emerged a few days earlier (121  $\pm$  11 days mean date,  $n = 13$  plots) than a SSh (124  $\pm$  14 days,  $n = 12$  plots), and a ISH (127  $\pm$  18 days,  $n = 4$  plots); the differences of means were not significant. Treated reeds did not differ in mean  $t_0$  from the controls, neither for PSh nor for SSh.

The termination of growth,  $t_{max}$  was reached between 29 June and 19 July for PSh (189  $\pm$  7 days) and a few days earlier (184  $\pm$  9 days) for SSh ( $\alpha < 0.05$ ,  $n = 11$  plots, paired t-test). No significant differences were observed between harvested and untreated reeds for any culm class.

The mean duration of linear growth,  $\Delta t$  was significantly higher in PSh (68.6  $\pm$  10.0 d) than in SSh (59.8  $\pm$  11.1 days) ( $\alpha < 0.001$ ,  $n = 11$  plots, paired t-test).  $\Delta t$  means did not differ between treated and untreated reeds at the  $\alpha = 0.05$  level of significance (Table 1).

#### 4.3. Differences between Culm Classes of Full Grown Stands

PSh and SSh showed consistent morphological differences among all kinds of stands and treatments (Table 2). The SSh were significantly shorter, thinner, exhibited lower leaf numbers and a poorer biomass than the PSh from the same plot. ISH were shorter than the PSh since their shoot apex had been damaged or destroyed. Consequently, the biomass and the

Table 2. Culm morphology characteristics of primary shoots (PSh), secondary shoots (SSh), and insect infested shoots (ISH) in Lake Constance reeds (global means  $\pm$  std.devs. of means from  $n = 158$  to 206 plots). ISH comprise damage by *Archanaara*, *Lipara* and *Steneotarsonemus* (see text). Statistics: paired t-test; means followed by the same letter in the same row are different at the 0.01 % level of significance)

	PSh	SSh	ISH
stem height	3.16 $\pm$ 0.59	2.34 $\pm$ 0.58	2.29 $\pm$ 0.66
$L_S$ [m]	(a, b)	(a)	(b)
shoot mean diameter	7.66 $\pm$ 1.41	5.49 $\pm$ 1.41	7.80 $\pm$ 1.65
$D_m$ [mm]	(a)	(a, b)	(b)
total number of leaves	18.2 $\pm$ 1.8	15.6 $\pm$ 2.6	12.2 $\pm$ 2.5
$N_{Lf}$ [l]	(a, b)	(a, c)	(a, b, c)
total culm biomass	50.8 $\pm$ 20.3	20.2 $\pm$ 11.1	32.6 $\pm$ 17.6
$W_{culm}$ [g d.m.]	(a, b)	(a, c)	(a, b, c)

leaf number was reduced. The mean shoot diameter  $D_m$  did not differ significantly from those of the PSh. Presumably most of them started their growth as PSh before arthropod attack took place.

#### 4.4. Shoot Density, Shoot Class Composition, and Peak Standing Crop

The increased shoot density which had been observed in spring and early summer was kept to late summer at flowering time of *Phragmites* (Table 3). The density of the total shoot population was increased by 76% on average. The increase was mainly due to the 3-fold density of SSh, whereas the numbers of PSh and ISh did not significantly change. Consequently, the relative proportion of PSh and ISh in harvested and burnt stands was diminished, but the share of SSh nearly doubled (Table 3).

Table 3. Shoot density and peak aboveground standing crop (PSC) of harvested/burnt and untreated reeds at Lake Constance-Untersee, measured in Oct to Febr during low water period (global means  $\pm$  std.devs. of mean values from  $n = 13$  pairs of treated/untreated stands. PSC is corrected for shedded leaves using allometric calibration equations. Statistics: paired t-test. PSh – primary shoots, SSh – secondary shoots, ISh – insect infested shoots, TSP – total shoots population)

		treated		controls
culm density Z [m <sup>-2</sup> ]	PSh	18.1 $\pm$ 8.1	<i>n.s.</i>	14.6 $\pm$ 6.8
	SSh	22.7 $\pm$ 20.3	$\alpha < 0.05$	7.0 $\pm$ 5.6
	ISh	4.5 $\pm$ 4.0	<i>n.s.</i>	4.5 $\pm$ 3.9
	TSP	45.3 $\pm$ 24.4	$\alpha < 0.01$	25.9 $\pm$ 6.8
peak standing crop PSC [kg d.m. m <sup>-2</sup> ]	PSh	0.92 $\pm$ 0.47	<i>n.s.</i>	0.86 $\pm$ 0.33
	SSh	0.40 $\pm$ 0.24	$\alpha < 0.01$	0.20 $\pm$ 0.21
	ISh	0.11 $\pm$ 0.08	<i>n.s.</i>	0.21 $\pm$ 0.20
	TSP	1.42 $\pm$ 0.50	<i>n.s.</i>	1.26 $\pm$ 0.33
Z [%]	PSh	45.2 $\pm$ 16.6	<i>n.s.</i>	53.6 $\pm$ 23.5
	SSh	45.3 $\pm$ 13.9	$\alpha < 0.01$	25.0 $\pm$ 14.9
	ISh	8.8 $\pm$ 7.7	$\alpha < 0.05$	20.1 $\pm$ 12.1
PSC [%]	PSh	62.6 $\pm$ 16.4	<i>n.s.</i>	68.0 $\pm$ 20.5
	SSh	28.4 $\pm$ 14.1	$\alpha < 0.01$	14.8 $\pm$ 11.3
	ISh	9.0 $\pm$ 7.9	<i>n.s.</i>	17.2 $\pm$ 13.1

The mean peak aboveground biomass (PSC) of treated stands was by 13% higher than the biomass of the controls (Table 3). The contribution to the total biomass of the PSh and of the ISh did not significantly change, but the standing crop of the SSh doubled, reaching 0.40 kg d.m. m<sup>-2</sup>, i.e. 28.4% on average of the PSC of a treated stand.

#### 4.5. Culm Architecture in Harvested/Burnt Stands and in the Controls

An average shoot in a harvested or burnt stand was significantly shorter and thinner, and had a significant lower individual biomass than a mean shoot in the control (Table 4). This was mainly the effect of a changed proportion of culm classes in favour of the prevalence of shorter, thinner and lighter SSh (Table 2, and 3). However, the means of culm morphology traits within each shoot class were also affected: the PSh of treated stands were significantly shorter and lighter than the PSh of the control. They were also thinner, but the

Table 4. Shoot morphology of harvested/burnt and untreated reeds at Lake Constance-Untersee (global means  $\pm$  std.dev. of the mean values from 13 pairs of treated/untreated stands); see Table 3 for explanations.

		treated		controls	
stem height $L_s$ [m]	PSh	3.16 $\pm$ 0.45	$\alpha < 0.01$	3.48 $\pm$ 0.23	
	SSh	2.33 $\pm$ 0.53	n.s.	2.52 $\pm$ 0.28	
	ISh	2.29 $\pm$ 0.69	n.s.	2.51 $\pm$ 0.47	
	TSP	2.68 $\pm$ 0.65	$\alpha < 0.01$	3.09 $\pm$ 0.25	
shoot mean diameter $D_m$ [mm]	PSh	8.05 $\pm$ 1.00	n.s.	8.45 $\pm$ 0.63	
	SSh	5.74 $\pm$ 1.28	n.s.	6.09 $\pm$ 0.81	
	ISh	7.81 $\pm$ 1.50	$\alpha < 0.05$	8.82 $\pm$ 0.94	
	TSP	7.00 $\pm$ 1.22	$\alpha < 0.05$	7.92 $\pm$ 0.38	
total leaf number $N_{Lr}$ [l]	PSh	18.5 $\pm$ 1.5	n.s.	18.8 $\pm$ 1.4	
	SSh	15.7 $\pm$ 2.5	n.s.	15.9 $\pm$ 2.2	
	ISh	12.7 $\pm$ 2.9	n.s.	12.6 $\pm$ 2.3	
	TSP	16.7 $\pm$ 2.1	n.s.	16.8 $\pm$ 1.4	
total culm biomass $W_{culm}$ [g d.m.]	PSh	49.6 $\pm$ 11.1	$\alpha < 0.01$	62.4 $\pm$ 9.5	
	SSh	20.4 $\pm$ 10.8	n.s.	24.2 $\pm$ 6.3	
	ISh	30.5 $\pm$ 15.6	$\alpha < 0.05$	39.7 $\pm$ 12.8	
	TSP	35.7 $\pm$ 12.8	$\alpha < 0.01$	49.3 $\pm$ 2.4	

difference in mean diameter was not significant at the  $\alpha = 0.05$  level. The same trends were visible in SSh without being significant. Similarly, an average ISh was slightly shorter, significantly thinner and lighter in treated stands. The total number of leaves per culm remained unaffected by the treatment (Table 4).

#### 4.6. Effects of Multiple Harvesting

The results presented hitherto referred to a single harvesting or burning treatment. In a few cases the effects of a multiple treatment could be studied. One example is depicted in Figure 3. The data represent means of six plots along a transect, prior to the first winter harvesting ('0 harvest'), and after one, two, and three consecutive harvesting treatments.

There was a clear trend to an increased density of the total culm population, which started with 20.7 m<sup>-2</sup>, and finally reached 51.3 m<sup>-2</sup> on average (see Fig. 3a). This increase based on a rise in PSh density, mainly after the first treatment, and a continuous increase in SSh from 6.8 m<sup>-2</sup> to 27.3 m<sup>-2</sup>. Consequently, the percentage composition of the total culm population changed from a PSh dominated to a SSh dominated reed stand (see Fig. 3b). At the end, density and percentage contribution of SSh was higher than those of PSh.

The mean culm diameter decreased from 7.1 to 5.1 mm as the harvesting treatment was continued (see Fig. 3c). The same trend was observed for the PSh and the SSh up to the second harvesting, since no significant differences between the means of the second and the third treatment were discernible. The mean culm height of the total population showed a degressive trend with increasing harvesting frequency, which became clear after the second treatment (see Fig. 3d). This yielded also for the PSh, and less evident, for the SSh and the ISh. Again, the trend stopped for the PSh and the SSh after the second treatment. There was some parallelism in the trends of shoot diameter  $D_m$  and shoot height  $L_s$ , since both variables were well correlated.

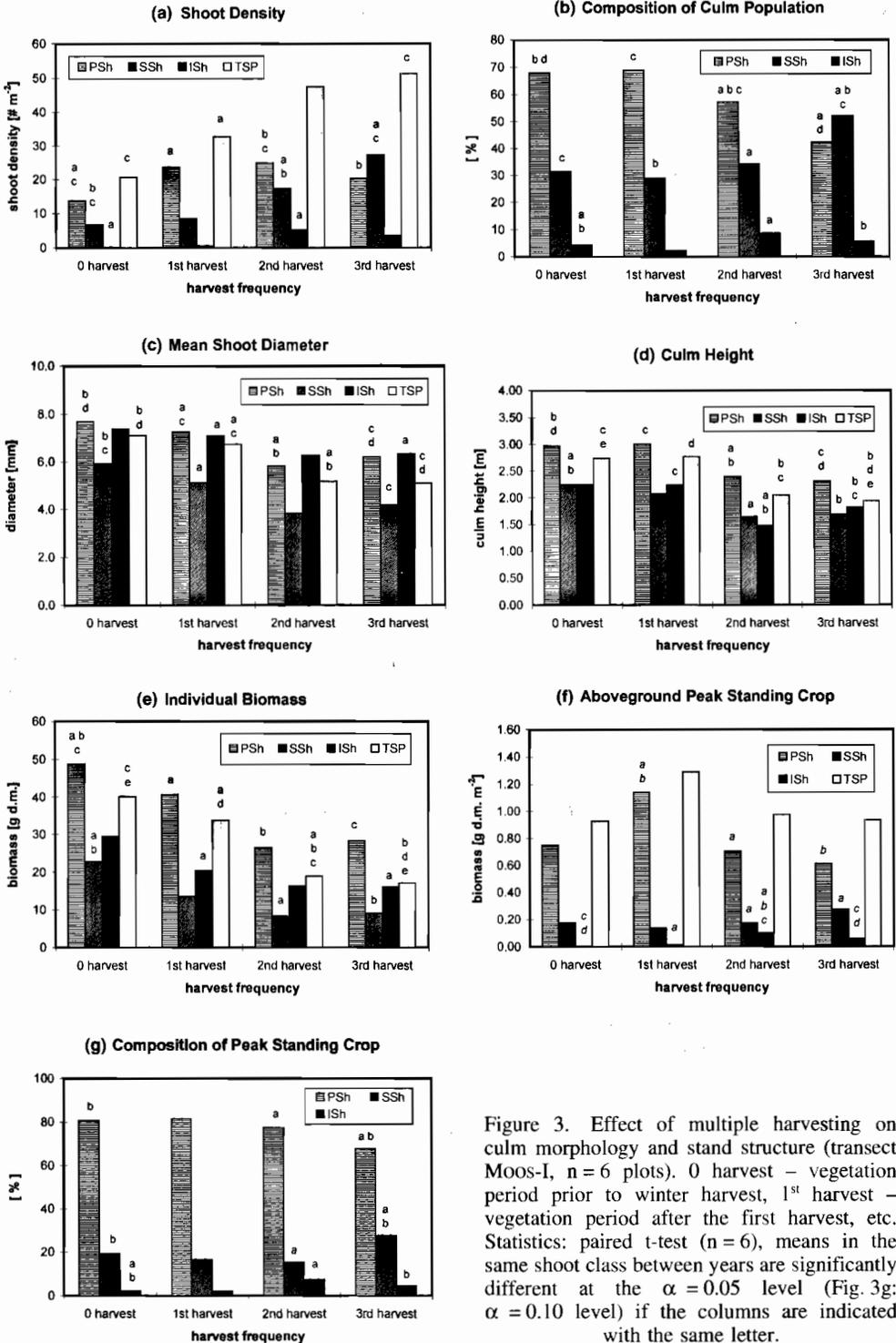


Figure 3. Effect of multiple harvesting on culm morphology and stand structure (transect Moos-I, n = 6 plots). 0 harvest – vegetation period prior to winter harvest, 1<sup>st</sup> harvest – vegetation period after the first harvest, etc. Statistics: paired t-test (n = 6), means in the same shoot class between years are significantly different at the  $\alpha = 0.05$  level (Fig. 3g:  $\alpha = 0.10$  level) if the columns are indicated with the same letter.

No trend was observed for the mean leaf number  $N_{Lf}$  of an individual culm, neither on the basis of the total culm population, nor for any shoot class (see Fig. 3e).

The individual biomass of an average culm,  $W_{culm}$  decreased in the course of consecutive harvesting treatments (see Fig. 3f). This was also the case within each shoot class. However, differences between the second and third treatment were not significant.

The PSC of harvested stands was somewhat higher after the first treatment, but dropped down to the initial value after two and three treatments (see Fig. 3g). This holds true also for the PSC of the PSh population, whereas the standing crop of the SSh population seems to increase after the second treatment. Not any difference of means was significant at the  $\alpha = 0.05$  level due to high intra-transectional variation, but some were significant on the  $\alpha = 0.10$  level. The percentage composition of the PSC was dominated by the biomass of the PSh irrespective of the harvest frequency. However, the share of PSh standing crop decreased from about 80% to 68%, and the share of SSh biomass increased from 15–19% to 28%, especially after the second treatment.

#### 4.7. Recovery of Culm Morphology and Stand Structure after a Twofold Treatment

At one site the stand structure development could be monitored for three years (1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup> recovery) after two consecutive burning treatments (see Fig. 4). In the season following the second burning treatment the stand exhibited the typical features discussed above, e.g. high shoot density (99.5 m<sup>-2</sup>), and a SSh dominated culm population (72.6%). The PSh and SSh were relatively thin and short (mean  $D_m = 6.2$  mm; mean  $L_s = 2.60$  m, and 3.4 mm, 1.66 m, resp.) with a low mean individual biomass (PSh:  $W_{culm} = 33.7$  g d.m., SSh:  $W_{culm} = 6.7$  g d.m.). The PSC of 1.24 kg d.m. m<sup>-2</sup>, however, was comparable to other treated stands.

In the three following years culm morphology and stand structure recovered, exhibiting trends towards the traits of untreated reeds. The total shoot density decreased continuously (see Fig. 4a), as the density and the percentage of the SSh did (see Fig. 4b). The share of PSh increased during the first two seasons. In the third season, however, many of the PSh suffered from insect attack, and were therefore identified as ISh. The mean shoot diameter and the mean culm height increased during the first and second recovery period, but there were little differences between the second and the third year (see Fig. 4c, d). The same trends were observed for mean  $N_{Lf}$  (see Fig. 4e) and mean  $W_{culm}$  in each shoot class (see Fig. 4f).

A strong increase in PSC was observed during the first two years of recovery, reaching 2.72 kg d.m. m<sup>-2</sup> (see Fig. 4g). The high PSC based mainly on a high PSh standing crop, whereas the share of the SSh biomass declined from 40% to about 15% (see Fig. 4h). This kind of 'overshoot' biomass production of *Phragmites* reeds one or two years after burning or harvesting treatments was observed at several management sites in the reed management program at Lake Constance.

#### 4.8. Reed Management and Yoda's Rule

A negative relation between mean individual biomass ( $W$ ) and culm density ( $Z$ ) is frequently found in *Phragmites* stands. The formal relation can be described by the 'ultimate thinning line' of Yoda's rule (YODA *et al.*, 1963; WHITE, 1980):

$$\lg W = \lg k - 1.5 \times \lg Z$$

The constant  $\lg k$  depends on growth form and species, and varies between 3.96 and 4.5 for *Phragmites australis* (MOOK and VAN DER TOORN, 1982; GRANÉLI, 1987). Figure 5 shows the position of a total of 129 reed stands at Lake Constance-Untersee in a  $\lg W/\lg Z$  plot

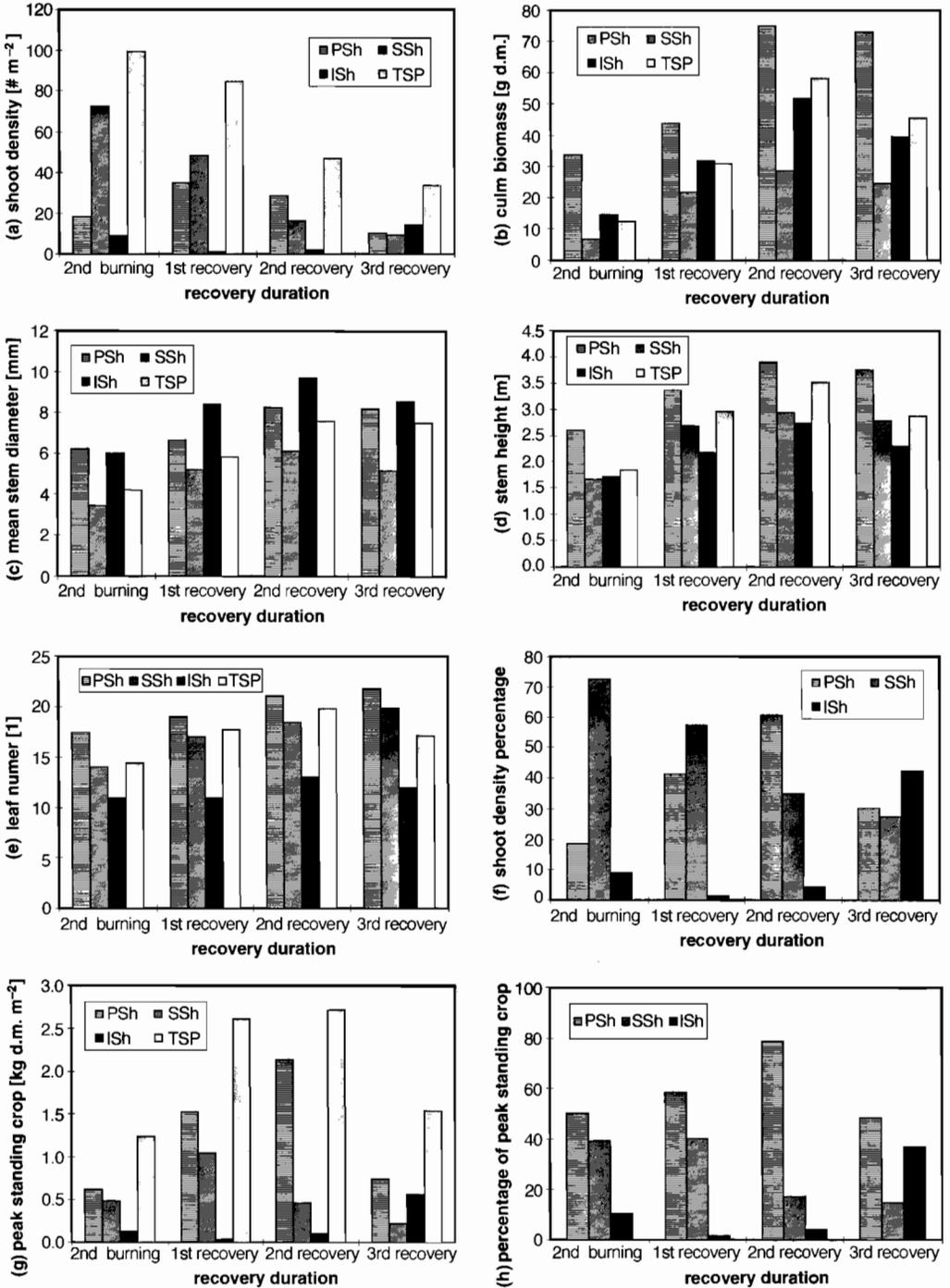


Figure 4. Effect of recovery from burning treatment on culm morphology and stand structure (transect Moos-II, n = 1 plot). 2<sup>nd</sup> burning – vegetation period after the second burning in series, 1<sup>st</sup> recovery – first vegetation period without burning in previous winter, etc.

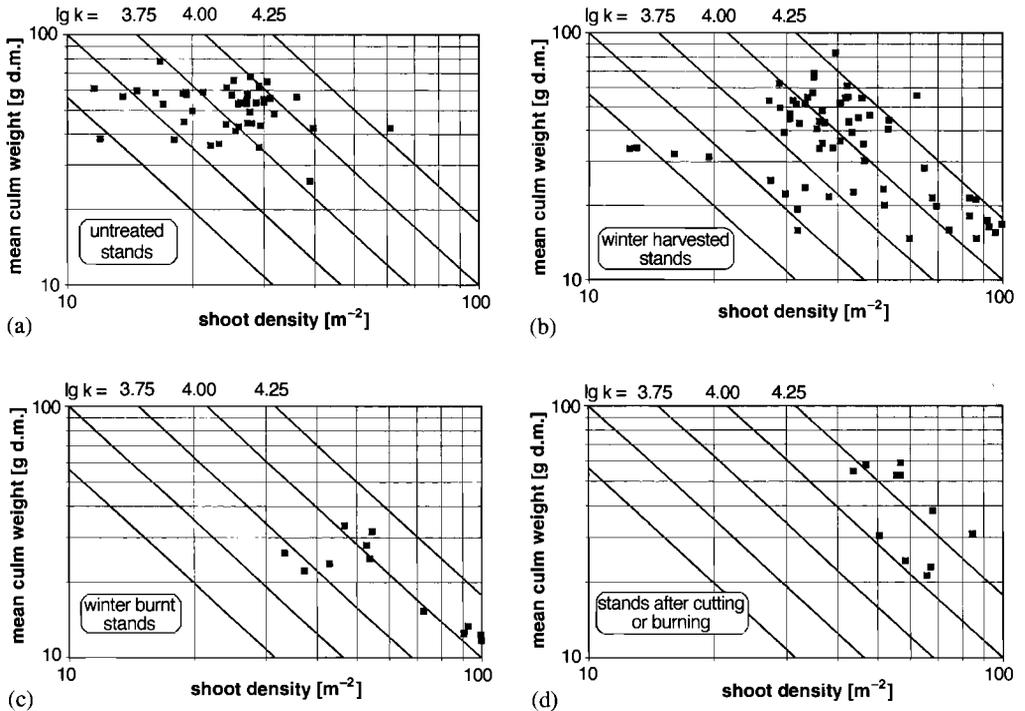


Figure 5. Shoot density and mean culm weight for (a) untreated reeds at Lake Constance-Untersee ( $n = 40$ ), (b) winter harvested ( $n = 63$ ) and (c) burnt reeds ( $n = 15$ ), and for reeds one or two seasons after the treatment has stopped (d) ( $n = 11$ ). Ultimate thinning lines with  $3.25 \leq \lg k \leq 4.25$  are also shown.

together with thinning lines with  $3.25 \leq \lg k \leq 4.25$ . Most of the data from typical reeds, unmown and unburnt for many years fell between  $\lg k = 3.25$  and  $4.00$  with high  $W_{\text{culm}}$  and medium  $Z$  values (see Fig. 5a). When these stands were subjected to a harvesting treatment a general shift towards a higher  $\lg k$  domain is observed, together with a general increase in  $Z$  and a decrease in  $W_{\text{culm}}$  (see Fig. 5b). The same trend holds for a burning treatment (see Fig. 5c). Maximum  $\lg k$  values between  $4.00$  and  $4.25$  were reached one or two years after the treatment had stopped (see Fig. 5d).

## 5. Discussion

At many European lakes large reed areas are regularly subjected to winter harvesting, mainly for economic purposes and for natural preservation. The question is, whether this kind of management supports the sustainable development of the reeds. Many studies have shown that winter harvesting is followed by a change in stand structure, e.g.

- increase in total culm density (GRANÉLI, 1989; INGRAM *et al.*, 1980; BJÖRNDAHL, 1985; COWIE *et al.*, 1992),
- decrease in mean culm height (HÜBL, 1966; INGRAM *et al.*, 1980; BJÖRNDAHL, 1985; COWIE *et al.*, 1992); in other cases no significant difference could be found (GRANÉLI, 1989)

- increase in peak standing crop (MAIER and SIEGHARDT, 1977; KRISCH *et al.*, 1979; INGRAM *et al.*, 1980; BÖRND AHL, 1985; GRANÉLI, 1989)
- lower percentage of insect infested shoots (KRISCH, 1980; VAN DER TOORN and MOOK, 1982; GRANÉLI, 1989)

Some other traits may be also affected, like leaf weight ratio ( $LWR = W_{\text{leaves}}/W_{\text{total}}$ ) (BJÖRND AHL, 1985), number of green leaves per shoot, and percentage of flowering shoots (GRANÉLI, 1989).

These findings are to a great part in agreement with the results presented in this study. Winter harvested (and burnt) reeds at Lake Constance consistently exhibit higher culm densities (+76% of the untreated controls,  $\alpha < 0.01$ ), and a higher peak biomass (+13%, n.s.). The culm height, averaged over all shoot classes is reduced by -13% ( $\alpha < 0.01$ ), and the percentage of insect infested shoots (ISh) is only 8.8% compared with 20.1% of the total shoot population of the untreated controls ( $\alpha < 0.05$ ). The total leaf number per shoot is not effected. The LWR might be positively affected, since thinner and shorter culms invest more biomass in the leaves and leaf sheaths than in the stem axis (OSTENDORP, unpubl.).

The mechanism by which these stand structure features are brought about, is not quite clear. GRANÉLI (1989) claims that a better light penetration in harvested reed beds in spring should be responsible for a decrease in early leaf shedding and shoot mortality, so that treated stands exhibit a higher percentage of panicle bearing shoots. In July, however, he found that the PAR profiles did not differ significantly between treated stands and the controls.

There is common wisdom that in early spring the microclimate on (large) harvested areas is harsher, e.g. late frosts may occur in clear and cloudless nights (GEIGER, 1962). Frost kills are therefore a common event on harvested and burnt reedbeds (HASLAM, 1972; KRISCH *et al.*, 1979; HAWKE and JOSÉ, 1996), as it was the case on many (but not all) test areas at Lake Constance. The untreated controls remained unaffected in any case.

Hence, there are at least four influence variables connected with harvesting and burning treatment, which might be responsible for the specific structure and morphology of treated *Phragmites* stands: mechanical stress by harvesting machines or temperature stress as the fire runs through the bottom litter layer, microclimatic factors (especially late frosts) in the tillering period, light penetration and PAR use efficiency of the canopy, and complex interactions between culm stature characteristics and phytophagous insect behaviour (oviposition of the females, mortality of the larvae, etc.). According to the results from Lake Constance reeds and literature data the following model is proposed:

In late summer and autumn, when the aboveground nutrients and carbohydrates are partly allocated to the underground storage organs, many buds develop at the vertical rhizomes to give tillers of a few centimetres length (HASLAM, 1969b). Presumably these tillers would come up to stout primary shoots (PSh) in the next season. As the beds are harvested by machines, many of these well developed tillers are destroyed either by the mowing device or by the wheels or creeper chains of the machine. The apical dominance of the growth tip over the nodial buds is broken, giving them a chance to shoot. The insertion of a replacement shoot on the destroyed tiller may be below or above ground surface, so that later on in the season it is identified as a secondary shoot (SSh) or as a lateral shoot by the investigator. Normally, one destroyed PSh-tiller is replaced by more than one SSh-tiller (Lake Constance: 1.6 on average), resulting in an increased total shoot density.

When late frosts occur on the harvested/burnt reedbeds, they destroy the growth tips of tillers more than c. 10 to 15 cm in aboveground height, since shorter tillers protect their growth tip belowground (s. RODEWALD-RUDESCU, 1974; Fig. 13). PSh-tillers have a greater chance of being damaged than the SSh-tillers, since they emerge earlier (Table 1). After a late frost event, a new cohort of SSh may develop as described above.

The growth rate of young *Phragmites* shoots rely on the nutrient and carbohydrate supply of the vertical rhizomes, even at the time when they have green leaves. There is some indication that the flux rate from the rhizome to the shoot is controlled by the basal diameter of the shoot (OSTENDORP, unpubl.). If this is true, the SSh should have a restricted access to the resources stored in the rhizomes. This may explain why SSh grow slower and for a shorter period than PSh do (Table 1).

The probability for a culm to get infested by arthropods depends strongly on its diameter (s. OSTENDORP, 1993 for a review), e.g. the final instars of the moth *Archanara geminipunctata* prefer stout culms, 6 to 7 mm in diameter; otherwise the larvae will not find sufficient space to complete the larval development and to pupate. The gall fly *Lipara lucens*, on the contrary, prefers thin shoots of 3–4.5 mm. Oviposition of the females is at maximum on shoots of 4 to 5 mm basal diameter, but larvae survival is best for thinner shoot (2–3 mm), presumably because plant defense mechanisms are not so effective. The last instar of *L. lucens* overwinters in the gall housing on the top of the dead shoot, and will be killed when the reed is harvested or burned during wintertide. It is plausible therefore that on harvested/burnt reeds the infestation rate by *Archanara* and by *Lipara* is reduced (VAN DER TOORN and MOOK, 1982; KRISCH, 1980; DITLHOGO *et al.*, 1992) (Table 3).

At the end of the growing season, harvested/burnt reeds reflect the sum of these influences and interactions, exhibiting denser stands of shorter and thinner culms with a lower biomass on average, (I) because the percentage of stout PSh is diminished in favour of small SSh, and (II) because in each shoot class means of height, diameter and individual biomass are lower (Table 4).

Nevertheless, means of the total peak biomass of treated stands are somewhat higher (without being significant for  $\alpha=0.05$ ). An improved PAR harvesting efficiency may contribute to this, and/or a higher exploitation of the nutrient and carbohydrate storage in the rhizome.

The 'ultimate thinning line' of Yoda's rule describes the maximum standing crop that can be produced by stands of the same species under varying combinations of shoot density and individual culm weight (HUTCHINGS, 1979). The concept was formulated for genetically distinct individuals (genets) of the same cohort which are subjected to intraspecific competition and subsequent density-dependent mortality of the individuals. GRANÉLI (1987) has shown that this concept can be applied to *Phragmites* reeds, though no 'self-thinning' occurs in well established stands. Evaluating hundreds of literature data through Europe he found that an ultimate thinning line of  $\lg k = 4.25$  is rarely passed, except for cultivated reeds in greenhouse and outdoor hydroponic cultures. The majority of the data from untreated reeds at Lake Constance lie between  $3.25 < \lg k < 4.0$ . Harvesting and burning lead to a shift of the central point of the data set towards the 4.25-thinning line (see Fig. 5). It is hypothesized therefore that treated stands are able to utilize resources better than untreated stands. Presumably, these resources are PAR and/or nutrients from the rhizome storage.

The changes in many stand structure traits of harvested/burnt *Phragmites* stands are reversible within two or three years after the management has stopped (Fig. 4). The early developing tillers are not damaged any longer, and regain the apical control over the subapical dormant buds. The nutrients and carbohydrate reserves stored in rhizomes have to support fewer but thicker shoots in the first growing period. Hence the total shoot density decreases, as well as the percentage of SSh, and the mean culm biomass increases within each shoot class. Recovering reed stands often exhibit a very high peak biomass, and the data points lie between the thinning lines  $\lg k = 4.0$  and  $4.5$ . This means that there must exist high amounts of resources which are available to the shoots, so that they can avoid intraspecific competition for a longer growth period than in treated reeds. The nature of these resources, however, is unclear.

## 6. Conclusion

Harvesting and burning management of lakeside reeds lead to a well defined change in culm morphology, stand structure, and biomass production. From the data presented here it can be concluded that managed reeds are more productive than untreated reeds. This may indicate that harvesting management is in agreement with the aim of sustainable wetland management. This hypothesis is supported by the finding that the effects of harvesting management are reversible within a relatively short period of time.

It should be noticed, however, that significant risks lay in winter cutting of lakeside reeds. First of all, the harvesting machine may crush the underground rhizomes and destroy near surface buds. Furthermore, the high percentage of secondary shoots makes a harvested and burnt stand more vulnerable to environmental hazards than an untreated stand: SSh grow slower, and high mortality may occur therefore in case of high flood events (OSTENDORP, 1991). They are more susceptible to mechanical stress like waves and washes, and contribute less to the mechanical stability of the stand as a whole (OSTENDORP, 1995). Finally, the reed breeding birds are sensitive to stand structure changes. Many species, especially marsh harrier, little crane, little grebe, great reed warbler, and bearded tit avoid cleared reed beds for breeding, whereas ground breeders like blue-headed wagtail and lapwing accept them as additional breeding habitats (s. OSTENDORP, 1993 for a review).

Summarizing these findings, there is reasonable doubt that winter harvesting might be a sustainable management philosophy at least for waterside reeds subjected to an array of natural stressors. The commercial reed harvesting in the Danube Delta, Romania, which began in the 1950s can be regarded as an example: here, the harvest tonnage reached 226,000 metric tons around 1963, and broke down to 75,000 tons ten years later. The mechanical damage to the reeds was one of the main factors that lead to the extinction of the reed-harvesting industry (NEVEL *et al.*, 1997). Hence, management schemes should critically balance benefits against risks.

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