

EM-Algorithm as a tool for structure analysis of stands of the common reed (*Phragmites australis*)

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ABSTRACT

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The frequency distributions of morphometric and mechanical properties of randomly sampled stalks of seven reed stands at Lake Constance-Untersee are analysed by the Estimation-Maximisation Algorithm. The aim was to look for composed (bimodal) distribution indicating at least two different stem types. In each stand, between one and nine parameters are found to give a bimodal distribution. The two stem types are 'flowering shoots' and 'non-flowering shoots'. The means of nearly all parameters investigated are different at the 1% level of significance. The flowerless shoots are identical with 'secondary shoots' and the flowering shoots refer to terminal (= 'primary') shoots. The separation of stem types allows investigation of the stand structure and the influence upon it by 'rhizome-internal' and 'external' factors in more detail.

1. INTRODUCTION

The common reed (*Phragmites australis* (Cav.) Trin. ex Steud., Poaceae) is a ubiquitous species in central Europe, colonising a wide range of habitats, i.e. lake shores, fenland, brackish tidal marshes and dumping places, provided there is sufficient water in the subsoil. The stature of the reed stalks varies from very short (ca. 0.5 m, on inland saline soils) to very tall culms (ca. 5 m, on fertile sediments of lake shores and estuaries (Rodewald-Rudescu, 1974). However, even within a stand of limited area one can find a remarkable variability in the performance of the individual stalks. The

question arises whether the variability within stands can be described by a simple relation to which other parameters can be reduced.

The basis of a comparison of the symmorphology and the structure between different populations is the analysis of frequency distributions of morphological properties. There have been several efforts to use skewness and kurtosis of a distribution of morphometric variables for an ecological interpretation. Ernst (1983, p. 51) postulated that growth parameters of plants will be normally distributed if the plants grow under optimal conditions. If stressed, they would show a negative skewed distribution. Haslam (1970a) investigated the distribution of stalk length in several reed stands. She differentiated 'dominant, dense stands' with a negative skewness and 'restricted sparse stands' with a negative kurtosis. Crook et al. (1983) found in stands which were affected by the 'reed die-back' negative skewed or even bimodal frequency distributions of the stalk length. However, the form of the distribution could change in course of the season. These findings are often based only on the interpretation of histograms and not on statistical tests.

In this paper the hypothesis that, at least, simple parameters such as length, diameter, and number of leaves are normally distributed was re-investigated with improved statistical methods. The suspicion was that values of skewness and kurtosis, reported in previous studies, which differ greatly from those of a normal distribution, do not necessarily contradict this hypothesis but may indicate that the sample chosen was such that two (or more) subpopulations were superimposed, whereby the morphometric properties of each are normally distributed. By means of the E(xpectation)-M(aximisation) Algorithm (Dempster et al., 1977) it is possible to separate different subpopulations according to a maximum-likelihood criterion. Then the hypothesis of a composite distribution is tested against the hypothesis of a simple distribution. If the hypothesis of a composite distribution is adopted, each sub-distribution is tested for normality. In this way we tried to get some information about the subpopulations, if any exist.

2. MATERIAL

This paper analyses the frequency distributions of a total of 18 parameters measured on seven reed stands. The data were collected for other scientific purposes concerning the reed decline and the reed management (Ostendorp, in preparation). The reed stands chosen are monospecific lake-side stands of *Phragmites australis* (*Phragmitetum typicum*, sensu Lang, 1967) in Lake Constance, Untersee. The frequency distributions of the following parameters are analysed:

L	stalk length (m)
D_m	stalk diameter in the middle of the stalk (mm)
D_b	stalk diameter at the stalk basis (mm)
n_{bl}	number of leaves per stalk
m_t	total biomass of a stalk (dry matter) (g)
dL/dt	maximum rate of growth (cm day^{-1})
t_0	beginning of maximum growth (days since year's begin)
t_{\max}	termination of maximum growth (days since year's begin)
Δt	duration of maximum growth (days)
$2s/D$	ratio of stem wall thickness s (% of stem diameter D_m in the middle of the stalk)
z	specific density of the stem (incl. lumen) (g cm^{-3})
ρ	specific density of the stem wall tissue (excl. lumen) (g cm^{-3})
E_1	Young's modulus (= modulus of elasticity) (based on a stick model) (N cm^{-2})
E_2	Young's modulus (based on a tube model) (N cm^{-2})
S_1	critical breaking strength (based on a stick model) (N cm^{-2})
S_2	critical breaking strength (based on a tube model) (N cm^{-2})
M_E	bending stiffness (N cm^2)
M_S	breaking strength (N cm^2)

[For definition, measurement and evaluation of these parameters see Ostendorp (1982)]. Only intact stalks are considered here but not stalks with insect galls. Stalks were clipped off at the base, quantitatively or at random, within several test fields of 0.36 m^2 each. Measurements were taken in the laboratory. All parameters except t_0 , t_{\max} , Δt , and dL/dt refer to fully grown stalks.

3. METHOD

Let us assume that we have N different observations x_i ($i = 1, 2, \dots, N$) for an item. The observations are drawn from k different populations but there is no a priori information about which observation is drawn from which population. The problem is to estimate the moments of the distributions of the observations, the probabilities p_{ij} with which a specific observations x_i belongs to population j , and the relative size of the populations λ_j :

$$\lambda_j = \frac{1}{N} \sum_{i=1}^N p_{ij} \quad \text{with} \quad \sum_{j=1}^k \lambda_j = 1$$

The idea of the EM-Algorithm (Dempster et al., 1977) is to separate this complex problem of estimation into two parts which are easily solvable. In an *estimation* step the moments of the distributions are estimated under the assumption that the probabilities p_{ij} were known. In a second *maximisation* step the estimators for p_{ij} are calculated by use of the Bayesian formula for

conditional probabilities under the assumption that the moments of the distributions are known:

$$\hat{p}_{ij} = \frac{\lambda_j f(x_i | p_{ij} = 1)}{\sum_{m=1}^k \lambda_m f(x_i | p_{im} = 1)}$$

where $f(\cdot)$ is the conditional density for x_i under a given presumption about the corresponding population and $\sum_{j=1}^k \hat{p}_{ij} = 1$.

The E- and M-steps are repeated in turn until convergence is achieved. Under the assumption that the observations are independently normally distributed with mean \bar{x} and variance σ^2 , the corresponding conditional densities are easily calculated:

$$f_{ij} = f(x_i | p_{ij} = 1) = (2\pi)^{-1/2} \sigma^{-2} \exp\left(-\frac{1}{2} u_i^2 / \sigma^2\right)$$

where $u_i = x_i - \bar{x}$. In most cases, convergence was achieved after 50 to 100 iterations.

The method was implemented on a mainframe computer as well as on a IBM-compatible personal computer. A brief description of the program is available on request from the authors.

4. RESULTS

The efficiency of the EM-Algorithm can be demonstrated by the frequency distribution of stalk length shown in Fig. 1. The data have been published by Kauppi et al. (1983). The distribution curve is negatively skewed ($s_k = -0.976$), and the hypothesis of normality of the overall distribution is rejected (χ^2 -test: $\alpha < 0.001$). Instead of supposing a more complicated distribution, we assumed that the sample taken ($n = 1066$ fully grown stalks) consist of two subpopulations, that is to say G_1 'short stalks' and G_2 'tall stalks'. A normal distribution is presupposed for each subsample. The EM-Algorithm computes estimates of the means and the variance of G_1 and G_2 as well as the share of each subsample. The null hypothesis ('homogeneous population') can be tested by means of a likelihood-ratio test. For the overall sample, the log of the likelihood value gives -374 ; for two different subsamples, the sum of the log likelihood values is $+98$. The test statistic is minus two times the difference of the two likelihood values. Thus:

$$\hat{\chi}^2 = -2(-374 - 98) = 944 \gg \chi_{1;0.001}^2 = 10.8$$

The null hypothesis can therefore be rejected at the 0.1% level. The parameters of each frequency distribution are:

$$G_1: \bar{x}_1 = 2.16, \quad \pm s_{x_1} = 0.35$$

$$G_2: \bar{x}_2 = 2.60, \quad \pm s_{x_2} = 0.14$$

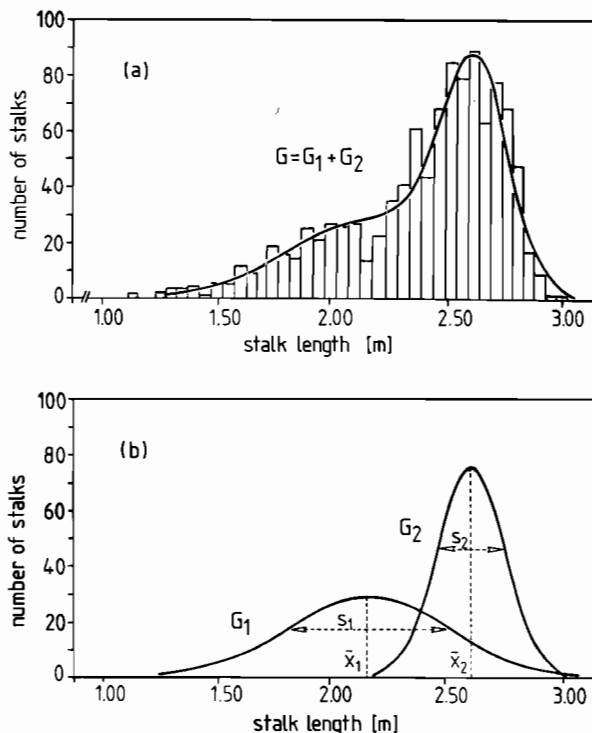


Fig. 1. Application of the EM-Algorithm to the distribution of stalk height in a Finnish reed stand. (a) Histogram: data from Kauppi et al., 1983; solid – computed distribution according to EM-Algorithm. (b) Splitting of the empirical distribution into the sub-distributions G_1 and G_2 by the EM-Algorithm.

The two distributions can be superimposed by addition, yielding the computed distribution of the overall sample shown in Fig. 1a. The computed overall distribution fits the original data very well: the null hypothesis (computed distribution = empirical distribution) cannot be rejected even at the 10% level (nonparametric Kolmogorov–Smirnov test). Hence it can be demonstrated that the reed stand investigated by Kauppi et al. is very likely composed of two different stalk populations.

The results of Lake Constance–Untersee data are given in Table 1: seven reed stands with a total of 18 variables have been analysed by means of the EM-Algorithm. It is clearly demonstrated that, for the most part, a composed frequency distribution can be assumed. This implies the existence of (at least) two different stalk populations within a stand. There is at least one variable in each stand that creates a partition into the two groups. The variables L and m_t are the most appropriate ones for demonstrating the existence of groups.

TABLE 1

Application of the EM-Algorithm – results

Stand	Kind of stress/ treatment	Sample size	Separating variables	Non separating variables
MOD I	not seriously damaged by mechanical factors	104	$L^{***}, m_t^{***}, E_1^{***},$ $E_2^{***}, S_1^{***}, S_2^{***},$ M_E^{***}, M_S^{***}	$z, \rho, 2s/D, D_m,$ n_{b1}
MOD II	mechanically damaged by waves and drifting matter	172	D_m^{***}	–
MOD IIIa	not mechanically damaged	101	$L^{***}, m_t^{**}, n_{b1}^{***}$	D_m
MOD IIIb	mechanically damaged by waves and drifting matter	113	m_t^{***}	L, D_m, n_{b1}
MO XI 40 m	mowed in winter	160	L^{***}, D_m^{***}	–
MO XVII 25 m	mowed in winter	59	$L^{***}, D_m^{***}, n_{b1}^{***},$ $m_t^{***}, D_b^{***}, dL/dt^{***}$ $t_0^{***}, t_{max}^{***}, \Delta t^{***}$	–
MO XVII 35 m	untreated reference to MO XVII 25 m	29	$L^{***}, n_{b1}^{***}, m_t^{***},$ $t_0^{***}, t_{max}, \Delta t^{***}$	$D_m, D_b, dL/dt$

The reed stands investigated (the denotations used here refer to other publications), each sample size (n = number of stalks), and the variables for which the algorithm yields a partition or no partition are given; levels of significance at which the null hypothesis (homogeneity of the distribution) can be refused (likelihood-ratio test): * – 5%, ** – 1%, *** – 0.1%

As the data support the view that each stalk population consists of two subpopulations, one may look for a dichotomous variable that simply describes the two subpopulations. During the field work, it was noticed that stalks without a panicle were small and performed weakly with respect to all properties observed compared with panicle-bearing culms. Hence, it was examined whether the variable 'stalk-type' (panicle-bearing vs. non-panicle-bearing) could be the variable required.

The arrangement of splitting the population by (1) the EM-Algorithm, and (2) by the variable 'stalk type' was checked as follows: after partition of an empirical distribution by the EM-Algorithm, each individual stalk i shows a distinct probability p_i to be an element of the subpopulation 1 and a probability q_i ($q_i = 1 - p_i$) to belong to the subpopulation 2. Let subpopulation 2 be the one with the greater mean regarding a certain variable. For

all reed stands and all variables, yielding a partition by the EM-Algorithm, the number of stalks n was computed, for which the following holds:

$p \geq 0.5$ and stalk without panicle: n_1

$q \geq 0.5$ and stalk with panicle: n_2

$p < 0.5$ and stalk without panicle: n_3

$q < 0.5$ and stalk with panicle: n_4

If EM-Algorithm and variable 'stalk type' split the population identically, one has to expect that $n_1 + n_2 = n_{\text{tot}}$ and $n_3 + n_4 = 0$ (n_{tot} number of all stalks examined). The value of η gives the degree of congruence between the two methods if the partition is not identical:

$$\eta = \frac{n_1 + n_2}{n_{\text{tot}}} < 1$$

The results are given in Table 2. In twelve of the 42 cases the EM-Algorithm failed to give a statistically significant splitting into subpopulations. High degrees of congruence can be achieved for 20 of the remaining 30 cases ($\eta > 0.8$): the partition by the variable 'stalk type' closely follows the partition created by the EM-Algorithm. Very high η -values are provided by the variables L and, to a lesser extent, m_t . Relatively low η -values were computed for the growth parameters dL/dt , t_0 , t_{max} and Δt . Hence, these variables are less suitable for the description of subpopulations.

The EM-Algorithm can be also used to isolate outliers. The existence of outliers has to be assumed if the splitting into two subpopulations is significant and one subpopulation represents only a small part of the sample (say 1 to 5%). For the data set analysed here, an identification of outliers and, hence, a partition into 'wrong' subpopulations was found for the variables E_1 and E_2 (reed stand MOD I), m_t (MOD IIIa) and t_{max} (MO XVII 35 m). Yet, the partition could be improved only in the case of t_{max} by elimination of the outliers.

5. DISCUSSION

The morphological characteristics of animal or plant populations are commonly investigated by one of the following three statistical techniques: ordination methods such as principal components, discriminant function analysis, or analysis of variance. These methods require a priori information about the existence of two (or more) subpopulations and the discriminating qualities. This information is, however, not always available [see, for example, the data given by Kauppi et al. (1983)]. In such cases, the procedure suggested here, which is based upon the EM-Algorithm, leads to the desired

TABLE 2

Degree of congruency (η) between splitting by the EM-Algorithm and by the variable 'stalk type', respectively

	MOD I	MOD II	MOD IIIa	MOD IIIb	MO XI 40 m	MO XVII 25 m	MO XVII 35 m
Stalks without panicles	$n = 35$	100	17	88	121	37	9
Stalks with panicles	$n = 69$	72	84	25	39	22	20
L	96%	-	99%	No partition	99%	88%	90%
D_m	No partition	83%	No partition	No partition	96%	90%	No partition
D_b	-	-	-	-	-	90%	No partition
n_{b1}	No partition	-	92%	No partition	-	81%	76%
m_t	95%	-	22%	96%	-	80%	86%
E_1	36%	-	-	-	-	-	-
E_2	36%	-	-	-	-	-	-
S_1	85%	-	-	-	-	-	-
S_2	82%	-	-	-	-	-	-
M_E	92%	-	-	-	-	-	-
M_S	93%	-	-	-	-	-	-
dL/dt	-	-	-	-	-	59%	No partition
t_0	-	-	-	-	-	75%	79%
t_{max}	-	-	-	-	-	68%	61%
Δt	-	-	-	-	-	75%	90%

The variables z , ρ and $2s/D$ are omitted because no partition could be found; the η values have been computed without regard of outliers, except in $t_{max}/MO XVII 35 m$ when one outlier has been eliminated; the number of measured stalks is given.

results. This method makes full use of the shape of the empirical distribution and does not require any additional information. Furthermore, the variances can be different in the two (or more) subpopulations. The EM-Algorithm as a tool for exploring distributions which are composed of a number of superimposed normal distributions is used here in a univariate context; generalisation to the multivariate case is possible.

Statistical analysis of the literature and our own measurements have demonstrated that even monospecific plant populations of simple architecture like *Phragmites* stands consist of two (or more) subpopulations represented by different stalk types. The EM-Algorithm led to a highly significant

TABLE 3

Differences between the stalk classes 'panicle-bearing-shoots' and 'non-panicle-bearing shoots'

		Means and standard deviations		
		Stalks with panicle	Stalks without panicle	Significance
stalk length	L (m)	3.16 ± 0.59	2.34 ± 0.58	***
stalk diameter	D_m (mm)	7.66 ± 1.41	5.49 ± 1.41	***
number of leaves	n_{bl} (-)	18.2 ± 1.8	15.6 ± 2.6	***
stalk biomass	m_t (g dry weight)	50.8 ± 20.3	20.2 ± 11.1	***
stem wall thickness	$2s/D$ (%)	14.4 ± 1.0	15.2 ± 1.7	*
specific density (stem)	z (g cm ⁻³)	0.180 ± 0.014	0.150 ± 0.021	***
spec. density (stem wall)	ρ (g cm ⁻³)	0.678 ± 0.049	0.537 ± 0.065	***
Young's modulus	E_1 (10 ³ N cm ⁻²)	878 ± 103	622 ± 128	***
Young's modulus	E_2 (10 ³ N cm ⁻²)	1907 ± 246	1301 ± 267	***
breaking strength	S_1 (10 ³ N cm ⁻²)	21.7 ± 2.3	15.9 ± 3.7	***
breaking strength	S_2 (10 ³ N cm ⁻²)	47.2 ± 5.1	33.1 ± 7.1	***
bending stiffness	M_E (N cm ²)	17765 ± 11962	3745 ± 3378	***
breaking strength	M_S (N cm)	1030 ± 567	300 ± 218	***
max. growth rate	dL/dt (cm day ⁻¹)	4.93 ± 1.13	4.10 ± 1.31	**
beginning	t_0 (day)	120.7 ± 10.7	123.7 ± 13.8	—
termination	t_{max} (day)	189.1 ± 6.5	184.0 ± 9.0	*
duration	Δt (day)	68.6 ± 10.0	59.8 ± 11.1	***

Global means \pm sd; $n = 13$ to 204 reed stands; levels of significance, see Table 1

partition for a great variety of variables. The two subpopulations can be simply characterised as 'stalks with a panicle' and 'stalks without a panicle'. The performance of the non-panicle-bearing shoots is consistently weaker compared to the panicle-bearing shoots (Table 3); only the wall of the stem is slightly thicker (variable $2s/D$). Furthermore, the proportions of stalks are significantly different: the L/D_m -ratio is lower for flowerless shoots, but the ratio 'biomass of leaves/total biomass of the shoot' is higher (0.27 vs. 0.22, Ostendorp, unpublished data). Haslam (1970b) found the number of nodes to be lower in non-panicle-bearing culms. Krolikowska (1971) showed that the transpiration of this stalk type was the 1½-fold of the flowering shoots. The stem tissue of flowerless stalks contains more ash, nitrogen and phosphorus (Mochnacka-Lawacz, 1974).

The consistent differences regarding a great set of properties justifies looking at the subpopulations as two distinct stalk classes. This implies the need to discuss their (different) origins. As in many cases the diameter at the stem basis is different, it is postulated that the properties 'panicle-bearing' and 'non-panicle-bearing' is controlled by the rhizomes (Ostendorp, in preparation).

The stalks which had been subjected to insect attack (e.g. *Lipara* sp., Diptera, Chloropidae; *Archanara geminipunctata*, Lepidoptera, Noctuidae) form a third class. But, in contrast to the first two classes, the shortened stem axis and the lowered stem diameter are subsequent effects of the insect infestation. If the stalks had not been infested, they would have developed into either flowering or non-flowering shoots, belonging to one of the first two classes. By means of the D_b -distribution in each class, one can estimate the possibility that an infested stalk with a known D_b can be fitted in one of them. In the reed stand MO XVII 25 m (15 stalks damaged by *Lipara* sp.), 13 stalks fell into the group G_1 (weak stalks) and only two belonged to G_2 (stout stalks). In contrast, in the adjacent stand MO XVII 35 m (23 stalks damaged by *Archanara geminipunctata*), five stalks were of the G_1 -type and 18 of the G_2 -type. In this latter stand, the G_1 -type stalks were infested more than average, and in the former stand they were damaged less than average. The ecological behaviour of each of the two insect species is assumed to be the cause of the differential infestation ratio (Vogel, 1984).

The ratio of G_1 -type to G_2 -type culms is different for different reed stands. High values occur particularly in winter-mowed or burned reeds [on average, 18.1 to 22.7 stalks m^{-2} (Ostendorp, unpublished data)] and in stands which suffered from waves and drifting matter (cf. MOD IIIb in Tables 1 and 2); in stands without mechanical damage the ratio drops below 0.1. It is postulated that the enhanced occurrence of G_1 -type stalks is controlled by the damage to the apical meristems by mowing, burning, grazing, drifting matter, and frost. Hence, the G_1 class seems to be identical with the 'secondary (= lateral) shoots' [sensu Haslam (1969, 1970a, b)] that compensate the 'primary (= terminal) shoots' which had died off. Whether this overlap is quantitative needs to be demonstrated by subsequent research.

6. SUMMARY

The subject of the paper was to investigate the hypothesis that the morphometric properties of a stalk population of the common reed (*Phragmites australis*) are normally distributed. In contrast to previous studies the possibility that a random sample could be composed of two or more subsamples belonging to different subpopulations was explicitly taken into account. It can be demonstrated that neglecting the possibility of superimposed distributions can result in an erroneous rejection of the normality hypothesis. The statistical procedure used here is based on the Expectation-Maximisation Algorithm. This method exploits the shape of the empirical distribution and does not require a priori information about the discriminating properties of the subpopulation.

The algorithm computed the means and variances of each subpopulation and a likelihood-ratio test was used to test the hypothesis of heterogeneity against the null hypothesis of homogeneity of the sample. In 30 of a total of 42 cases the homogeneity assumption was rejected. Hence, it was concluded that most of the lakeside reed stands at Lake Constance consist of at least two different shoot populations. The culm types could be characterised as panicle-bearing or flowering shoots and non-flowering shoots without a panicle. Non-flowering shoots were the weaker ones in all respects. It was assumed that the discrimination against the non-flowering shoots is controlled by the rhizome. The proportion of this class of shoots was high in stands which had been previously damaged by frost, waves, drifting matter, waterfowl grazing etc.; this indicated that flowerless shoots are identical with 'secondary' (= lateral) shoots which recover 'primary' (= terminal) shoots lost by mechanical damage. The separation of (at least) two stem types allows a more detailed investigation of the stand structure of reed and the influence upon it by 'rhizome-internal' and 'external' factors.

7. ZUSAMMENFASSUNG

In der vorliegenden Untersuchung wurde die Hypothese der Normalverteilung ausgewählter morphometrischer Eigenschaften einer Halmpopulation des Schilfs (*Phragmites australis*) überprüft. Im Gegensatz zu anderen Studien wurde die Möglichkeit explizit in Betracht gezogen, daß eine Zufallsstichprobe aus mehreren Unterstichproben zusammengesetzt sein könnte, die jeweils aus unterschiedlichen Grundgesamtheiten stammen. Es konnte gezeigt werden, daß die Vernachlässigung dieser Möglichkeit zu einer irrtümlichen Zurückweisung der Normalitätsannahme führen kann. Das hier benutzte statistische Verfahren stützt sich auf den 'Expectation-Maximisation-Algorithmus'; es wertet allein die Form der empirischen Häufigkeitsverteilung aus und bedarf keiner a priori Information über die diskriminierenden Eigenschaften etwaiger Subpopulationen.

Der Algorithmus berechnet die Mittelwerte und Varianzen von Merkmalen einer jeden Subpopulation. Mit einem Likelihood-Ratio-Test wurde die Alternativhypothese (Heterogenität) gegen die Nullhypothese (homogene Verteilung) geprüft. In 30 von 42 Fällen konnte eine signifikante Trennung erzielt werden, so dass anzunehmen ist, dass sich die meisten Schilfbestände aus (mindestens) zwei verschiedenen Halmpopulationen zusammensetzen. Die beiden Halmgruppen lassen sich als 'rispentragende Halme' und 'rispenlose Halme' beschreiben. Die rispenlosen Halme sind in fast allen untersuchten Eigenschaften schwächer ausgebildet als die rispentragenden Halme des gleichen Bestandes. Vermutlich wird die Benachteiligung ihrer Wuchsleistung durch das Schilfrhizom gesteuert. Besonders hoch ist ihr

Anteil in mechanisch belasteten Beständen; dabei ist die Klasse 'rispenlose Halme' weitgehend identisch mit den 'Sekundärtrieben' (= Lateraltriebe), die die durch mechanische Schädigung, Frost, Wellenschlag, Treibgut und Beweidung verloren gegangenen 'Primärtriebe' (Terminalsprosse) ersetzen. Die Unterscheidung von (mindestens) zwei verschiedenen Halmtypen erlaubt eine detailliertere Untersuchung der Bestandsstruktur von Schilfröhrichten und ihrer Beeinflussung durch 'rhizom-interne' und 'externe' Faktoren.

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