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Autor: Güsewell, Sabine / Klötzli, Frank
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Measuring the abundance of *Phragmites communis* Trin. in wet meadows - a methodological investigation

SABINE GÜSEWELL & FRANK KLÖTZLI

Geobotanisches Institut ETH, Stiftung Rübel, Zürichbergstrasse 38, 8044 Zürich, Switzerland

Summary

1 Increasing abundance of *Phragmites communis* Trin. is a potential threat to rare species in Swiss wet meadows that should be considered in nature conservation management. Therefore, efficient methods to measure the abundance of *Phragmites* are required. Aboveground biomass, leaf area index and nutrient contents are convenient abundance criteria. They can be estimated with simple morphological field measurements and more detailed measurements on harvested shoots. We investigated correlations and variability of several morphological traits and nutrient concentrations in 14 wet meadows, in order to determine the most appropriate morphological traits and the best sampling design.

2 Culm length, culm diameter, leaf size and leaf number were positively correlated with each other and with the density of shoots. However, the relationships among these variables differed depending on sites and time. Nutrient concentrations in culms or in leaves did mostly not relate to shoot size.

3 The shoot density (number per unit area) varied strongly even on a small spatial scale and changed up to 236% between two consecutive years. The mean culm length of a plot changed up to 42% in the same period, and the mean diameter up to 59%. The direction and the intensity of change differed among and within sites.

4 The abundance of *Phragmites* is assessed most efficiently by measuring the density of shoots and the culm length along transects perpendicular to gradients in abundance. Regression parameters for estimating biomass or leaf area index should be established separately for each site and investigation period; calibrations can be done with about 20 shoots. Plots containing 20–30 shoots appeared suitable for determining the density and size of the shoots in the field; about ten such plots (200–300 shoots) will lead to a standard error of 10% on shoot density in a homogeneous site.

5 To detect either a spread of *Phragmites* or a conceivable management effect on its abundance, continuous long-term investigations on permanent plots will be necessary.

Keywords: biomass, morphology, sampling design, fluctuations, spatial variation, wetlands

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Introduction

Common reed (*Phragmites communis* Trin.) is a worldwide distributed tall grass with outstanding ecological and economic significance (Rodewald-Rudescu 1974). Conse-

quently, this species has been extensively studied during the last decades, but almost exclusively in more or less monospecific stands, e.g. lakeshore reed belts or artificial reedbeds. However, more attention is now being paid to the occurrence of *Phragmites* in fens and wet meadows, where it is spreading and possibly displacing rare and endangered plant species (Ellenberg & Klötzli 1967; Klötzli 1986; Marti & Müller 1993; Brülisauer 1996). This spread should be considered in nature conservation management; strongly invaded sites might, for instance, be mown more frequently (Bressous *et al.* 1992). Measuring the abundance of *Phragmites* accurately and efficiently is necessary for taking such decisions.

Abundance measurements should be related to the tendency of *Phragmites* to spread and to suppress other plant species; suitable criteria are aboveground biomass *(AB),* leaf area index *(LAI),* and nutrient concentrations of shoots. The aboveground biomass in late summer is approximately equal to the aboveground production (error of 5–15% according to Graneli 1984). Biomass production is generally considered the best measure of the overall performance of species. The aboveground biomass is also a good predictor for competitive effects on other plants (Gaudet & Keddy 1988). Measuring belowground biomass is not practicable because it requires extensive and destructive sampling (Ondok & Kvet 1978). The leaf area index indicates the amount of light absorbed by *Phragmites* and thus its shading effect on smaller plants (Dykyjová 1971; Hirose & Werger 1995). Nutrient concentrations in shoots may indicate nutrient availability of the site (Wassen *et al.* 1995). Increased nutrient availability is assumed to give *Phragmites* a competitive advantage over other wet meadow species (Klötzli 1986; Brülisauer 1996).

Whenever direct and destructive measurement of the three above criteria is too time-consuming (especially *LAI*) or problematic (e.g. in permanent plot research), non-destructive estimation methods based on morphological measurement are preferable. Appropriate measurements and sampling design depend on the correlations of morphological traits and on their spatial and temporal variability. Therefore, we investigated these aspects in 14 wet meadows to answer the following questions:

(1) Can shoot density (shoot number per unit area) be used to monitor changes in the dominance of *Phragmites*?
(2) If not: which additional variable(s) should be measured?
(3) Which sample size and which sampling design is needed in the field measurements and in the calibrations to obtain sufficiently accurate estimations?

Material and methods

STUDY SITES

The 14 study sites were wet meadows in the Swiss "Mittelland", i.e. the region between the Alps and the Jura range, at an altitude of 400–550 m a.s.l. (Table 1). The long-term average annual temperature of the area is 8–10 °C, the average annual rainfall 900–1400 cm. 1995 was a particularly warm year with high precipitation, whereas 1996 was near average in temperature but dry.

The soils at the study sites have developed on glacial sediments or on lake gyttia and are mostly rich fen peat soils. The groundwater table is at or above soil surface in winter, and can drop to 1 m or more below surface in summer (Klötzli 1969). The vegetation types are given in Table 1. Most sites were subject to eutrophication, thus original communities (alliances Molinion and Caricion davallianae)

Table 1. Characteristics of the study sites with abbreviations used in the text, coordinates as defined by the Swiss topographic map, altitude in meters a.s.l., and vegetation types after Klötzli (1969)

Lake	Label	Coordinates	Altitude	Vegetation type*
Neuenburgersee	N1	563400 / 197100	430	Caricion davallianae
	N2	569900 / 203000	430	Magnocaricion
Katzensee	K1	680550 / 254100	436	Molinion/Filipendulion
	K2	680525 / 253700	440	Filipendulion/Phragmition°
	K3	680425 / 254025	438	Filipendulion/Phragmition°
Greifensee	G1	692350 / 247875	437	Car.dav./Filip./Phragmition°
	G2	691950 / 247650	437	Magnocaricion
	G3	692500 / 247800	437	Calthion/Filipendulion
	G4	692550 / 247750	437	Caricion davallianae
Zürichsee	Z1	702350 / 229050	408	Molinion
	Z2	702300 / 229200	408	Caricion lasiocarpae
	Z3	709700 / 229600	406	Molinion
Pfäffikersee	P1	702300 / 244575	538	Molinion
	P2	702300 / 244575	538	Caricion davallianae

* Only alliances are given because vegetation was heterogeneous in most sites.
° Eutrophic terrestrial reedbeds.

were increasingly replaced by tall species of the alliances Filipendulion, Magnocaricion and Phragmition (Boller-Elmer 1977; Klötzli 1986). Wet meadows were traditionally mown by farmers in autumn or winter. In the study sites this management had either been maintained or resumed about ten years ago, except in the sites N1, N2, G4 and K1, which had been subjected to mowing experiments (Buttler 1992). In those four sites measurements were carried out on the established permanent plots. Unless otherwise stated, only the winter-cut plots were included in the analyses. The other sites were chosen to represent different degrees of invasion by *Phragmites*. Plots for morphological measurements were arranged systematically on two or more parallel transects through each site. Biomass samples were taken either on or close to these plots.

MEASUREMENTS AND DATA ANALYSIS

Relations between morphological traits

Culm length and basal diameter were measured in August 1995 or 1996 for all *Phragmites* shoots within 93 1-m^2 plots in six of the sites. The culm length was measured from the soil surface to the base of the panicle, if present, or to the base of the uppermost leaf. The basal diameter was determined in the middle of the second internode. In addition, shoots within three adjacent 1-m^2 plots were counted. The mean shoot number in these four plots was taken as shoot density and the percentage of shoots with panicle as fecundity. We assessed correlations between pairs of variables with Pearson coefficients *(r)* and used analyses of covariance to test whether regression lines differed among sites.

All shoots in 51 1-m^2 plots were harvested in June, July or August 1996 at five of the sites. We measured the length and the diameter of culms and counted all well-developed leaves, including dry ones. The length and width of the largest leaf were also measured for some samples. The shoots were dried at 70 °C and weighed individually. We calculated correlations among morphological traits and compared the fit of various regres-

sion models for the estimation of shoot biomass. On the one hand, we used different independent variables (culm length, culm diameter, leaf number and their combinations), on the other hand we applied three different models for each independent variable, i.e. (a) simple regression model, (b) model allowing regression parameters to differ among sites and months, and (c) model allowing regression parameters to differ among plots and months. We also used analyses of covariance to test the significance of parameter differences (a) among sites, and (b) among months.

A total of 33 shoots was harvested arbitrarily in July 1996 in six of the sites (5–7 shoots per site). We measured culm length and diameter, determined the length, the width and the area of all leaves, using a LI-3100 area meter (Li-Cor Inc., Lincoln Nebraska, USA), and calculated linear regressions for the estimation of leaf areas.

Temporal variation

In 54 plots of 1m^2, shoot density, mean culm length, and mean basal diameter were measured in two consecutive years (1995 and 1996). Fecundity, as the percentage of flowering shoots, was only measured in 20 plots. We tested differences between years using the Wilcoxon test for each site and each variable. The relative mean change of each variable in each site was calculated as

$$\Sigma_j (x_{j96} - x_{j95}) / \Sigma_j x_{j95},$$

where x_{jk} = value of the variable in plot j in year k.

Spatial variation

Large-scale variation was studied qualitatively by comparing the 93 plots mentioned above. Small-scale variation was studied in four large plots of 9 m^2 to 20 m^2, divided into contiguous quadrats of 25 x 25 cm^2. We counted the shoots in each quadrat, grouped adjacent quadrats into blocks of 2, 4, 9, 16, 24 and 36, and calculated the total shoot numbers in each block. The coefficient of distribution *(CD)*

$$CD = \frac{Variance\ of\ (total)\ shoot\ numbers}{Mean\ (total)\ shoot\ number},$$

calculated for the single quadrats and for each block size, was used to measure the degree of spatial aggregation; *CD* is 1 for a random distribution, and >1 for a contagious distribution (Greig-Smith 1952, 1983). The standard error of *CD* was calculated after Greig-Smith (1952) as $\sqrt{2/N-1}$, and a t-test was applied to test the significance of non-randomness.

Variability of nutrient concentrations

In August 1995, all shoots were harvested within two 1-m^2 plots in the site K1 and two plots in the site G4. One plot per site had already been mown in June. Shoots were sorted according to culm length, grouped into size classes of five shoots, dried, ground and analysed for total N, P and K. Additionally, eight plots were sampled in July or August 1996. Shoots were again grouped according to the culm length, but in order to obtain size classes as homogeneous as possible, the shoot number was 3–7 per group. Shoots were divided into leaf blades, leaf sheaths and culms, and the fractions were analysed separately. Total N and P were extracted by a modified Kjeldahl method (Skalar Methods 155-432/503-324) and analysed colorimetrically on a continuous flow analyser; K was extracted with 20% hydrochloric acid after dry digestion and analysed by atomic absorption. All of the extractions and measurements were carried out at FAL (Reckenholz, Zürich). We tested with two-way ANOVA (factors "plant part" and "shoot group") whether nutrient concentrations differed

Table 2. Correlations and results of analyses of covariance for pairs of morphological traits of Phragmites communis*: (a) measured on single shoots in June, July or August (n =486), and (b) determined for 1-m² plots in August* (n =*93). Given are Pearson correlation coefficients and the significance of differences in regression lines among sites* (n =*8 in a, 6 in b) / among months* (n =*3 in a); * , significant differences in regression slopes; ° , significant differences in intercept; * /°, P < 0.05; ** /°°, P < 0.01; *** /°°°, P < 0.001; ns, P > 0.05*

(a) Single shoots	Culm length	Basal diameter	Leaf number	Leaf width
Basal diameter	0.87 * / ***			
Leaf number	0.62 *** / ***	0.52 *** / ***		
Leaf length	0.81 ** / ns	0.74 ° / °	0.56 *** / *	0.79 * / *
(b) 1-m² plots	Culm length	Basal diameter	Shoot density	
Basal diameter	0.91 **			
Shoot density	0.35 ***	0.17 **		
Fecundity	0.86 *	0.80 °°°	0.06 ***	

among plant parts. The dependence of nutrient concentrations on shoot size was tested with the regression model D_{conc} = *constant* + D_{length} + *plot x* D_{length}, where D_{conc} and D_{length} were differences between the concentration (culm length) in the size class and the mean concentration (culm length) for the plot. If the interaction term was significant, we tested the dependence of D_{conc} on D_{length} for each plot separately, using Bonferroni probabilities.

Results

Correlations between morphological traits

The traits related to the size of individual *Phragmites* shoots were all positively correlated (Table 2a). The correlation was strongest between culm length and diameter (r = 0.87) and between culm length and maximal leaf length (r = 0.81). Either slope or intercept of linear regressions differed among sites and among months for most pairs of variables. Consequently, correlations between traits were stronger when calculated separately for each site. The correlation of culm length and diameter, for instance, reached 0.92.

Traits related to whole plots (shoot density, shoot fertility, and mean shoot size) were also positively correlated (Table 2b), but all correlations with density were weak; again did regression parameters differ among sites.

Estimation of aboveground biomass

Aboveground biomass *(AB)* could be estimated either directly for a whole plot, or as the sum of biomass estimated separately for each shoot in the plot. For the direct estimation a loglinear relation was established between the mean shoot dry weight *(DW)* of a plot and the product of mean culm length and mean basal diameter: *log (dry weight) = -1.97 + 1.04 x log (length x diameter),* r^2 = 0.94; *AB = shoot density x mean DW.*

Table 3. *Regression models, regression fit and analyses of covariance for the estimation of shoot biomass (dry weight) based on shoot morphology; r^2, adjusted multiple squared r (r^2_{all}, for simple models; $r^2_{s/m}$, for models with grouping factor sites and months; $r^2_{p/m}$, for models with grouping factor plots and months); $P_{site/month}$, significance of differences in regression parameters among sites / months; symbols for levels of significance as in Table 2*

Simple regression model	r^2_{all}	$r^2_{s/m}$	$r^2_{p/m}$	P_{site}	P_{month}
log (DW) = -2.4 + 1.2 x log (diameter x length)	0.95	0.97	0.98	***	***
log (DW) = -2.9 + 1.8 x log (length)	0.88	0.92	0.96	***	ooo
log (DW) = -0.89 + 2.5 x log (diameter)	0.80	0.91	0.93	***	***
log (DW) = -1.05 + 1.8 x log (leaf number)	0.39	0.61	0.65	**	ooo

Using this equation, we estimated *AB* for the 93 plots in which length and diameter had been measured, and plotted this estimate against the shoot density (Fig. 1). A regression yielded: *log (AB) = -0.61 + 1.17 x log (shoot density)*, $r^2 = 0.88$. Thus, if only an approximate ranking of *Phragmites* abundance was needed, the shoot density would have been sufficient. However, a large range of biomass was found at densities of 20–60 shoots m^{-2}, which is typical for reed-invaded wet meadows; at these densities, shoot density could hardly be used to estimate *AB*.

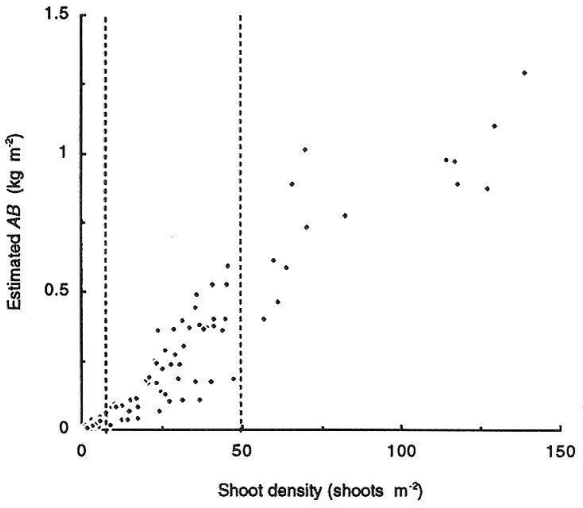

Fig. 1. *Relation between shoot density and estimated aboveground biomass* (AB) *in 93 1-m^2 plots. The dashed lines indicate the limits of shoot density classes according to Marti & Müller (1993). Despite a strong overall correlation between density and* AB, *a large range of biomass was found within each class.*

Various models with 1, 2 or 3 independent variables were used to estimate the biomass of individual shoots (cf. Table 3). The best fit was obtained with both length and diameter as predictor variables. This could be done either through a multiple regression or through a simple regression on the product of culm length and diameter. Both models fitted equally well (i.e. similar r^2 and standard error), but the simple regression had more stable coefficients. Taken separately, culm length yielded a better fit than basal diameter and leaf number. Leaf number hardly improved the regression fit when added to culm length; r^2 increased by less than 1%. Regression parameters (either slope or intercept) differed both among sites and among months, and consequently the regression fit (r^2) was improved by up to 0.26 by including a grouping factor (sites and months or plots and months) in the model. Thus, in practice *AB* estimations will be more accurate if calibrations are performed separately for each site or for each part of a site and for each time period.

ESTIMATION OF LEAF AREA INDEX

The most accurate estimation of *LAI* would consist in measuring length and width of all leaves in a plot, estimating individual area as *leaf area = 0.53 x leaf length x leaf width* ($r^2 = 0.99$; $n = 292$), and adding up leaf areas over all shoots. However, the sampling effort would be prohibitive. Since mean and maxi-

mal leaf size were strongly correlated, it appeared possible to measure only the area of the largest leaf of each shoot; i.e. *mean per-leaf area = -2.5 + 0.85 x maximal leaf area* (r^2= 0.98; n=33); $LAI = \Sigma_{all\ shoots}$ *mean per-leaf area x leaf number).* A further simplification consisted in estimating the mean per-leaf area from squared culm length: *mean per-leaf area = 9.4 + 10.2 x (culm length)*^{2} (r^2 = 0.83; n = 33). If leaf numbers had not been counted, the total leaf area would have to be estimated directly from culm length or diameter: *total leaf area = 43 + 120 x (culm length)*^{2} (r^2 = 0.71), and: *total leaf area = 35 + 10 x (basal diameter)*^{2} (r^2 = 0.59). As for shoot biomass, the best fit was obtained with culm length, but there was no advantage in using both length and diameter (r^2 = 0.71). In any case, a considerable loss of precision would result from excluding leaf numbers.

TEMPORAL VARIATION

The differences in shoot density and shoot size between consecutive years were considerable in those plots studied during two consecutive years: shoot density changed up to 236%, culm length up to 42% and basal diameter up to 59% (Fig. 2). Yet, these differences were inconsistent across plots within sites, across sites, and across variables. In each site one or two variables changed significantly among years, but which variables did change depended on the site. For each variable the average relative change was positive in some

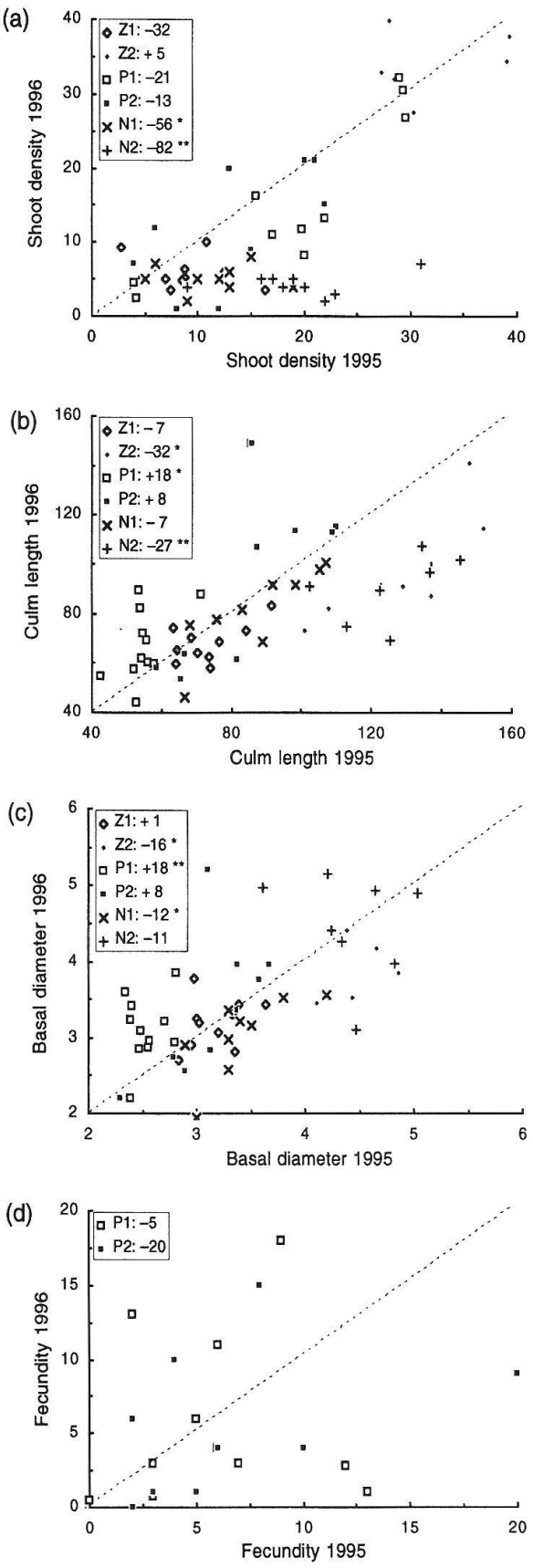

Fig. 2. *Fluctuations of (a) shoot density, (b) culm length, (c) basal diameter, and (d) fecundity in 54 1-m*^{2} *plots between two consecutive years, illustrating the differences among and within sites in direction and amount of change. Dashed lines correspond to unchanged abundance; legends include mean changes of sites (percent of the 1995 mean), and the significance of changes tested with the Wilcoxon signed rank test (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).*

sites and negative in others, and the same held for plots within sites. An increase of culm length was usually associated with an increase of basal diameter in all six sites (rank correlation r_s = 0.12–0.93). Conversely, changes of shoot density were either positively or negatively correlated with changes in culm length or diameter (r_s = -0.68–0.78). These results suggest large and unpredictable year-to-year fluctuations in shoot density, size and fecundity.

SPATIAL VARIATION

Spatial variation occurred at different scales, i.e. among sites, among plots within sites, and within plots. Sites differed not only in average shoot density and size, but also in the variances among plots and in the shape of distribution: both progressive gradients and sharp limits occurred (Fig. 3).

Within plots, shoot distribution was contagious. In all four plots investigated by contiguous quadrats the variance of shoot numbers per quadrat was significantly greater than the mean shoot number (CD = 1.6–2.4, $P <$ 0.001). The CD hardly changed with block size up to blocks of about 20 shoots (Fig. 4). In larger blocks, the CD increased steadily in the sites K2 and G4, whereas it decreased in K1, and reached a maximum at a block size of 49.9 shoots (16 quadrats) in K3. The relatively constant CD found at the smaller block sizes suggested that the accuracy of shoot density estimation depended on the total number of shoots counted, regardless of shoot density and of the number of subplots. Indeed, from

$CD = s^2/\bar{x}$ follows that $s = \sqrt{CD \times \bar{x}}$,

and hence $s/\bar{x} = \sqrt{CD}/\sqrt{\bar{x}}$.

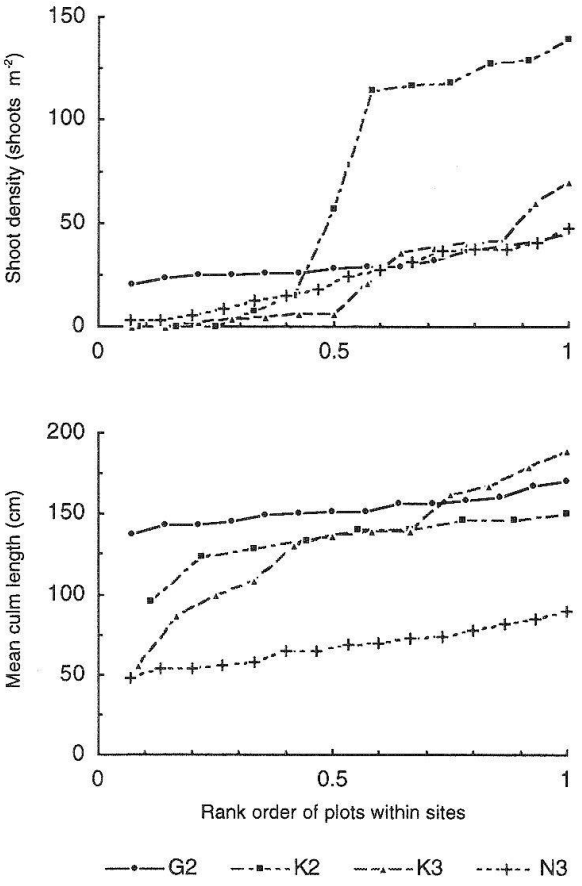

Fig. 3. Distribution of shoot density and culm length among 1-m² plots within four of the study sites (cf. Table 1), indicating differences in the range of abundances and in the steepness of gradients in invasive Phragmites *stands.*

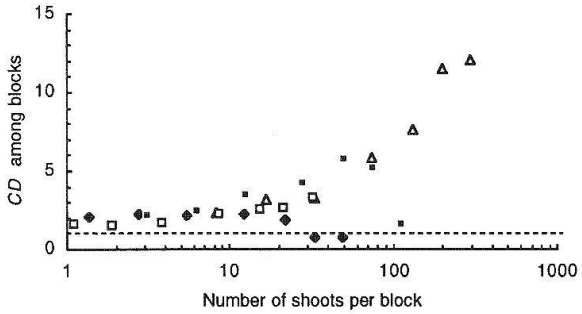

Fig. 4. Spatial variability of shoot densities (CD, *coefficient of distribution) in relation to the number of shoots counted. The dashed line* (CD = *1) corresponds to randomly distributed shoots; higher* CD *indicate spatial aggregation. Site symbols (cf. Table 1):* ◆, *K1;* △, *K2;* ■, *K3;* □, *G4.*

Table 4. Coefficients of variation (CV) *of nutrient concentrations measured in different groups of shoots sampled within the same plots. Data are ranges of* CV *(in %) calculated for 4–8 different plots*

Nutrient	Whole shoots	Blades	Sheaths	Culms
N	1.8 – 15.6	4.9 – 8.1	7.7 – 19.2	2.3 – 24.0
P	7.8 – 23.3	0.0 – 19.3	13.3 – 29.6	39.2 – 173.2

If shoots were counted in n subplots with m shoots per plot, shoot density would be estimated with a relative standard error of $\sqrt{CD}/\sqrt{n\,m}$. According to our data, 200–300 shoots would have to be counted to estimate the density with a relative standard error of 10%. For verification *CD* was also calculated for the 93 plots in which shoots had been counted on 4 adjacent 1-m^2 subplots. Most plots had indeed a *CD* between 1 and 3, but *CD* values up to 10 also occurred at various shoot densities; therefore, large errors will sometimes be made in determining the shoot density.

The size of shoots also varied strongly within plots, with coefficients of variation of 40–100% for shoot dry weight, 15–47% for culm length, 15–40% for basal diameter, and 5–32% for leaf number (data from the 51 plots used for biomass sampling). Thus, the mean of a sample of e.g. 10 shoots would be estimated with an average standard error of 21% for dry weight, 9% for culm length, 8% for basal diameter and 6% for leaf number. Again, these errors would differ strongly from plot to plot.

Nutrient concentrations

The concentrations of total nitrogen (N) and total phosphorus (P) varied among different plant parts, i.e. leaf blades had higher concentrations than culms and sheaths ($P < 0.001$). Shoots from plots mown in June had higher P and K concentrations than shoots from unmown plots ($P < 0.05$), while no significant difference was found for N. Concentrations of N and P were unrelated to shoot size in whole shoots and in individual plant parts, except N concentration in leaf blades, which appeared to be higher in large shoots ($P < 0.01$). The variance among shoot classes within plots approximated therefore the variance that would have been found among samples of five shoots randomly harvested within each plot. Coefficients of variation among shoot classes, calculated for each plot (Table 4), suggested that 20–30 shoots would normally estimate mean N and P concentrations with a standard error of 10%, whereas K measurements were subject to much larger errors.

Discussion

A method for assessing the abundance of *Phragmites* in wet meadows must be adapted to the growth form of this plant and to the objective of the study. In the context of nature conservation the mere presence of *Phragmites* is not an assessment criterium in itself, as low or medium abundance of *Phragmites* is common in wet meadows. Therefore, the specific degree of abundance has to be considered, particularly the aboveground biomass *(AB)* and the leaf area index *(LAI)*.

Abundance measurement based on shoot density

The relationship between shoot density and *AB* or *LAI* is variable, because the average size of shoots varies strongly among sites, within sites and among years, and because its relation to shoot density may be either posi-

tive or negative. A negative relation between shoot density and *AB* has been found in monospecific *Phragmites* stands under optimal site conditions, where intraspecific competition limits shoot growth (Graneli 1984). In terrestrial mixed stands, however, interspecific competition and nutrient availability are limiting (Haslam 1971). As a result, we found the density and the average size of shoots to be positively correlated, and thus shoot density may be used as a measure of abundance, provided the differences are large enough. The four density classes defined by Marti & Müller (1993), i.e. <10 shoots m^{-2}, 10–50, >50, or "monospecific stands" fullfill this requirement, as a change towards a higher class is likely to reflect a real increase of biomass (cf. Fig. 1). However, a large range of abundances may be found in the class 10–50. Therefore, this classification does not reflect the more subtle changes in abundance, which would be essential to detect a spread or a management effect. For an exact assessment of the abundance of *Phragmites*, not only shoot counts, but also morphological measurements are necessary.

SELECTION OF MORPHOLOGICAL VARIABLES FOR ABUNDANCE ESTIMATION

Size proportions of *Phragmites* shoots often vary among different ecotypes (e.g. Dykyjová 1978). However, the morphological variables measured in this study were strongly correlated to each other. This is probably due to the relatively small range of soil conditions in the study sites, whereas the ecological amplitude of *Phragmites* is high. Moreover, the size proportions of *Phragmites* shoots appear to be insensitive to varying light conditions (Ekstam 1995). The relatively constant proportions found in wet meadows imply that a single morphological variable describes the shoot size fairly well.

We found culm length to be the best predictor for both shoot biomass and leaf area. Basal diameter has often been preferably used as shoot size variable because of its good correlation with other morphological traits (van der Toorn & Mook 1982), because it is relatively independent of short-term environmental fluctuations (Haslam 1970), and because of its ecological significance (Ostendorp 1993). Moreover, in a dense and high reed stand culm diameter is generally easier to measure than culm length or leaf number. In our sites, however, culm length could be measured more easily and accurately than basal diameter, and was better correlated with other morphological traits (cf. Graf 1996; Hills & Murphy 1996).

Regarding the ecological significance, while the diameter is important for wintering insects or nesting birds (Ostendorp 1993), the possible suppressive effect of *Phragmites* on endangered plant species is more likely to depend on the height of the plant (Gaudet & Keddy 1988). Thus, if only one trait is measured, culm length should be preferred to basal diameter. If a second trait is measured, the choice depends on the criterium to be assessed. In our study, measuring basal diameter did improve estimates of biomass, but did not impove estimates of leaf area. Counting leaf number, on the other hand, increased the accuracy of estimates of leaf area, but had no effect on estimates of biomass. Therefore, the variables to measure in a field study are either a combination of culm length and culm diameter (for *AB* assessment), or a combination of culm length and leaf number (for *LAI* assessment), or culm length on its own.

SAMPLING DESIGN FOR FIELD MEASUREMENTS

The abundance of *Phragmites* is often heterogeneous within a site. Both sharp limits and progressive gradients occur, and sites differ

strongly in the variability and distribution of shoot densities. These differences may reflect different causes of spreading. Some factors (e.g. atmospheric N deposition) may influence whole sites, others (e.g. local inflow of nutrient- and oxygen-rich water through drainage ditches) affect only parts of the site. It is therefore important to describe the exact pattern of spread, rather than comparing site means. A random distribution of plots within sites is not efficient in revealing such patterns, and a site stratification is arbitrary if gradients are progressive (cf. Greig-Smith 1983). Most suitable is a systematic design with transects perpendicular to the steepest abundance gradient, sampled either by contiguous plots or at fixed intervalls (Ondok & Kvet 1978). Several parallel or perpendicular transects allow to detect two-dimensional gradients.

The plot size should be adapted to the small-scale variation in the size and density of the shoots. Ondok (1971) reported clusters of 20 x 40 cm^2 to 40 x 80 cm^2, but he noted that the cluster size was inversely related to the average shoot density and that aggregation was weaker in sparse stands. The latter is consistent with our results, which revealed no clear cluster limits. Plots with 20–30 shoots appeared suitable to determine the shoot density in the sites investigated. This number corresponded to 1 m^2 in moderately invaded sites, and to 0.25–0.5 m^2 in severely invaded ones. Ten plots of that size would usually allow an assessment of shoot density with a standard error of 10%.

SAMPLING DESIGN FOR CALIBRATIONS AND NUTRIENT ANALYSES

Despite the strong correlations between pairs of morphological variables, regression parameters differed among sites and months. Sites with strong gradients of *Phragmites* abundance should therefore be stratified into sampling plots with similar shoot size; separate calibrations should be calculated for each plot. If field measurements are carried out in different parts of the growing season (e.g. for a growth analysis), new calibrations are needed approximately monthly. Other authors used 50 (Kauppi *et al.* 1983) or even 100 shoots (Ulrich & Burton 1985) for their calibrations, but in this study 20 shoots provided reliable estimates of regression parameters at the plot level.

Nutrient concentrations were as variable as the shoot size, but mostly unrelated to it. The higher N concentrations in leaves of large shoots compared with those in leaves of small shoots of the same plot may be a strategy that enables leaves which receive more light to assimilate more efficiently (Hirose *et al.* 1988). Hirose *et al.* (1988) found that N concentrations in *Lysimachia vulgaris* differ vertically along the shoots. Our results suggest that the same holds for *Phragmites,* and that exact comparisons of nutrient concentrations are possible only for given plant parts (e.g. leaf blades) and for a given position in the shoot (Allen & Pearshall 1963). The failure of previous investigations to establish a relation between the dominance of *Phragmites* and nutrient concentrations (Boller-Elmer 1977; Zelesny 1994; Brülisauer 1996) might partly be due to the fact that only whole shoots were analysed. However, such detailed measurements are probably of small indicative value for nature conservation, and too expensive for a routine abundance assessment.

SAMPLING DESIGN FOR THE ASSESSMENT OF TEMPORAL DYNAMICS

It is often difficult to determine whether *Phragmites* is really spreading in a site, since trends in abundance occur slowly and are difficult to differentiate from the strong annual fluctuations which result from differences in

climatic or hydrological conditions (Haslam 1972). Moreover, changes are inconsistent within sites, differing even between close plots. The strong within-site heterogeneity, both spatial and temporal, would make systematically arranged permanent plots more efficient than a random selection of different plots each year (Weber *et al.* 1995). A nested sampling design (e.g. four contiguous 1-m^2 plots) would allow a distinction between divergent evolutions within sites and purely local fluctuations.

The marked spatial and temporal patterns found in this study are not particular to *Phragmites:* high mobility and strong fluctuations have been described for many species in a large number of vegetation types (van der Maarel 1996). Whether a trend proves significant or not is often a matter of the scale applied (Zobel & Masing 1987). This ambiguity does not make it impossible or useless to assess changes in the abundance of *Phragmites,* but it means that (a) any statement about an increase or decrease in abundance must be related to a definite spatial and temporal scale with reliable error estimations, (b) establishing a progressive increase of abundance may require many years of repeated measurements, and (c) any rating of abundance changes as "improvement" or "deterioration" must be based on spatially and temporally explicit aims of nature conservation. Moreover, additional measurements will be necessary, depending on the context of the investigation. Indeed, predictions about future changes of abundance may require measurements of environmental factors (cf. van Hulst 1980). The assessment of management techniques should include an assessment of the impact of management on endangered plant and animal species (e.g. Klieber *et al.* 1995). Finally, the causes of the spread of *Phragmites* cannot be fully understood without addressing the underlying social, economical and political factors (Finlayson 1994). Thus, measuring the abundance of *Phragmites* must be part of a broader monitoring programme in order to help preventing a further degradation of the last Swiss wet meadows.

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