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Does mowing in summer reduce the abundance of common reed (*Phragmites australis*)?

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Summary

1 Common reed (*Phragmites australis* Trin.) has recently spread in fen meadows of the Swiss Plateau, where it might reduce species richness and displace typical fen species.

2 Mowing experiments were carried out in two fens near Zurich to investigate whether mowing in June (in addition to the usual September cutting) is an effective measure to reduce the abundance of *Phragmites*. Changes in the number and size of *Phragmites* shoots were monitored during three years. The aboveground biomass and nutrient concentrations of *Phragmites* and of all other vascular plant species ("other species") were determined in the third year of the experiment.

3 The additional June cutting had no significant effect on shoot number and size, and, therefore, on the aboveground biomass of *Phragmites* during this period. The biomass of *Phragmites* did not differ between treatments, but the biomass of the other species was lower in plots with additional June cutting. Due to this additional cutting, 90% more N and 181% more P were, on an average, removed with *Phragmites*, but only 30% more N and 64% more P with the other species. Thus, the nutrient economy of *Phragmites* was stronger affected than the nutrient economy of the rest of the species.

4 The availability of nutrients and interspecific competition are probably decisive for the long-term treatment effects. Further monitoring is needed to evaluate whether mowing in June and September will eventually reduce the abundance of *Phragmites* by depleting its belowground reserves. However, the results of this study indicate that other means (e.g. grazing) are necessary for a short-term control.

Keywords: cutting experiment, cutting regime, management, nature conservation, nutrient economy, wetlands

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Introduction

Common reed (*Phragmites australis* Trin.) is a world-wide distributed tall grass species of great economic and ecological importance (Haslam 1973a,b; Rodewald-Rudescu 1974). Many reed stands are managed to increase their production and to regulate the size of

shoots (Haslam 1973a; Granéli 1984), to enhance their mechanical resistance on lake shores (Klötzli 1974; Ostendorp 1995), or to maintain favourable habitat conditions for reed-dwelling birds and insects (Bibby & Lunn 1982; Tschardtke 1992). On the other

hand, *Phragmites* can be a troublesome weed invading various cultures, e.g. rice or cane (Izatt 1979), fishponds and channels (Husák 1978), coastal areas (Hellings & Gallagher 1992), or freshwater wetlands such as fens (Biewer 1994). Many fen meadows of the Swiss Plateau have recently been affected by a spread of *Phragmites* (Klötzli 1986; Marti & Müller 1993), which is considered undesirable as it is associated with a decrease in species richness and the disappearance of typical fen species (Güsewell & Klötzli 1998). Even though it is not yet clear to what extent *Phragmites* is actually responsible for these changes (Güsewell & Klötzli 1998), managers of wetlands nature reserves often seek to control *Phragmites* at sites where its abundance has increased (Egloff 1984; Bressous *et al.* 1992).

Different techniques have been applied to control *Phragmites*. Good results are normally obtained by spraying herbicides (Glyphosate or Dalapon) followed by mowing or burning (Izatt 1979; Jones & Lehman 1987). Mowing or burning followed by deep flooding is another option (Husák 1978; Demina 1979; Hellings & Gallagher 1992). Such "drastic" measures are suitable in species-poor vegetation types strongly dominated by *Phragmites*, but not in fen meadows, where other species have to be preserved. To control *Phragmites* at such sites, measures based on the traditional management, to which the protected species are adapted, would be more adequate. In Switzerland, lowland fen meadows have traditionally been mown in late summer or autumn (Egloff 1984). It is generally assumed that mowing earlier in summer (June–July) will reduce the abundance of *Phragmites* (Egloff 1984; Bressous *et al.* 1992). Indeed, in fens or wet grasslands that have been regularly mown in summer for a long time little or no *Phragmites*

occurs (van Diggelen *et al.* 1996). Yet, management experiments provided little direct evidence for the effectiveness of this treatment so far. *Phragmites* was either not present at the experimental sites (Wolf *et al.* 1984; Bakker & de Vries 1985; Kapfer & Pfadenhauer 1986; Oomes & Altena 1987; Rosenthal 1992), or changes in its abundance were not related to treatments (Finckh 1960; Rowell *et al.* 1985; Egloff 1986).

To be an effective control of *Phragmites*, mowing in June (in addition to September) should reduce its aboveground biomass through a decrease in the number or size of shoots. Moreover, the aboveground biomass of *Phragmites* should be reduced more strongly than that of the other species present at the site, so that the dominance of *Phragmites* decreases. To produce such an effect, the additional mowing in early summer should affect the nutrient economy of *Phragmites* more than that of the species to be preserved. To determine whether additional mowing in early summer actually produces these effects, experiments have been carried out in two fen meadows of the region of Zurich since 1995. This contribution presents results after the first three years of management.

Methods

STUDY SITES AND EXPERIMENTAL DESIGN

The two experimental sites are fens located on the Swiss Plateau near Zurich, at an altitude of 430–440 m a.s.l. The long-term average annual temperature of the area is 8–10 °C, the average annual rainfall 1000–1100 mm. Soils are calcareous humic gleysols, with strongly decomposed and humified peat in the top soil ("Anmoor"). Due to fluctuations of the groundwater table, soils are waterlogged in winter, but relatively dry in summer.

Site "Greifensee" (Swiss National Grid 692'550/247'750) is a wet meadow near lake Greifensee, dominated by *Molinia coerulea* and various *Carex* species; *Phragmites* is moderately abundant (nomenclature follows Hess *et al.* 1991). A ditch draining nutrient-rich water from the adjacent farmland runs through the site. Along this ditch the vegetation is highly productive, dominated by *Phragmites*, *Carex acutiformis*, *Holcus lanatus* and various tall forbs. Site "Katzensee" (680'550/254'100) is situated in the "Allmend Katzensee", a flat swampy basin. The vegetation is dominated by *Molinia coerulea*, *Carex acutiformis* and various tall herbs in the drier parts, and by *Carex panicea*, *Carex elata*, *Juncus subnodulosus* and tall herbs in the wetter parts. Both sites had been mown yearly in September for at least five years before the experiments started.

The experiment followed a block design with blocks 1–3 at site "Greifensee" and blocks 4–5 at site "Katzensee". Each block consisted of two plots (10 x 10 m²). Both plots were mown yearly in early September and the litter was removed soon after mowing. The treated plots were additionally mown in late June. Treatments started in 1995, except for block 3, where they only started in 1996. To monitor the effects of treatments on the abundance of *Phragmites*, twelve 1-m² permanent quadrats were established per experimental plot. Quadrats were arranged systematically in three groups of four quadrats (i.e. three 4-m² quadrats) to minimize trampling and edge effects.

FIELD AND LABORATORY TECHNIQUES

The abundance of *Phragmites* in all plots was recorded in late June and late August or early September 1995, 1996 and 1997. The late summer measurements will hereafter be referred to as "September" measurements. The

number of shoots taller than 20 cm was counted in all twelve 1-m² quadrats per plot ("shoot density"). The culm length and the basal diameter of all shoots were measured in one randomly chosen quarter of each 4-m² quadrat. Culm length was measured from the soil surface to the base of the uppermost leaf, or to the base of the panicle for flowering shoots. The basal diameter was taken in the middle of the second internode. Mean values per experimental plot were used for data analysis.

The aboveground biomass of all vascular plants except *Phragmites* (hereafter called "other species") was harvested in the last days of June and of August 1997, i.e. just before the mowing. To avoid confusion, the second sampling will again be called the "September" sampling. Block 2 could not be sampled for lack of time. The biomass was clipped at ground level in three 0.16-m² quadrats per plot. Mosses were not sampled because they were sparse at all sites. Care was taken in the control plots to sample new quadrats at the second date. The plant material was dried at 70 °C, weighed and ground. Total N and P were extracted using a modified Kjeldahl method (1h digestion at 420 °C with H₂SO₄ 98% and a copper sulphate-titane oxide catalyst). Concentrations of N and P were determined colorimetrically on a flow injection analyser (TECATOR, Höganäs, Sweden).

The biomass of *Phragmites* in the permanent quadrats was estimated non-destructively through field measurements and calibrations based on Güsewell & Klötzli (1997). For calibrations 20–40 shoots per experimental plot were harvested outside the permanent quadrats in late June 1996 and within the permanent quadrats in late August or early September 1996. The relationship between weight and length of individual shoots was

Table 1. Effect of an additional cutting in June on shoot density and size of *Phragmites australis* measured in late June and in early September from 1995 to 1997. Data are mean squares and the significance of effects based on repeated measures ANOVA. See text for details on calculations

Source	df	Late June			Early September		
		Density	Length	Diameter	Density	Length	Diameter
Treatment	1	149.30 ns	0.1 ns	0.03 ns	0.06 ns	0.25 ns	0.04 ns
Error	3	59.90	125.3	0.50	0.29	0.70	0.19
Year	1	166.57 <0.01	1586.1 <0.1	0.58 ns	0.70 <0.1	1.30 <0.05	0.01 ns
Error	3	4.20	202.1	0.22	0.10	0.05	0.00
Treat x year	1	69.97 ns	0.55 ns	0.01 ns	0.01 ns	1.09 ns	0.05 <0.05
Error	3	29.08	8.22	0.06	0.04	0.28	0.00

used to estimate the biomass of *Phragmites* in 1996. The relationship between the mean shoot weight and the product of mean shoot length and mean basal diameter was used to estimate the biomass in 1995 and 1997 (cf. Güsewell 1997).

To determine nutrient concentrations in *Phragmites*, 20–40 shoots were harvested per experimental plot in the last days of June and August 1997 (outside the permanent quadrats in June) and analysed as described for the “other species”.

DATA ANALYSIS

To analyse how the additional June cutting had influenced changes in the density and size of *Phragmites* shoots from 1995 to 1997, the 1995 data were used as a baseline, i.e. they were subtracted from the 1996 and 1997 data. The resulting differences were then analysed with univariate repeated measures ANOVA (factors treatment, df = 1, year, df = 1, and block, df = 3). Block 3 was not included in this analysis because mowing in June had only started in 1996. As significant “year x block” interactions occurred, “year” effects were tested against these interactions, and “treatment x year” interactions were tested against the residual error term. Aboveground biomass, nutrient concentrations, total nutri-

ent contents and the contribution of *Phragmites* to the aboveground biomass were all log-transformed to stabilize error variances; they were analysed with two-way ANOVA with the factors “treatment” and “block”, but only the “treatment” effect was tested (Sokal & Rohlf 1995, p. 347). Effects with type I error probabilities of 0.05–0.10 were considered to indicate tendencies not confirmed yet, but still relevant for conservation management.

Results

DENSITY AND SIZE OF *PHRAGMITES*

During the three years of the experiment, shoot density increased and shoot size decreased (Fig. 1), but this trend was independent of the additional mowing in June; differences between 1995 and the two subsequent years did not differ between treated plots (with additional June cutting) and control plots (Table 1). Shoot density in June, however, seemed to increase in treated plots compared with the controls (Fig. 1a). Thus, the additional mowing in June had certainly not reduced the abundance of *Phragmites*, and had possibly increased it.

Large differences in shoot size were found between treated and control plots in August (Fig. 1b) because shoots of different age were

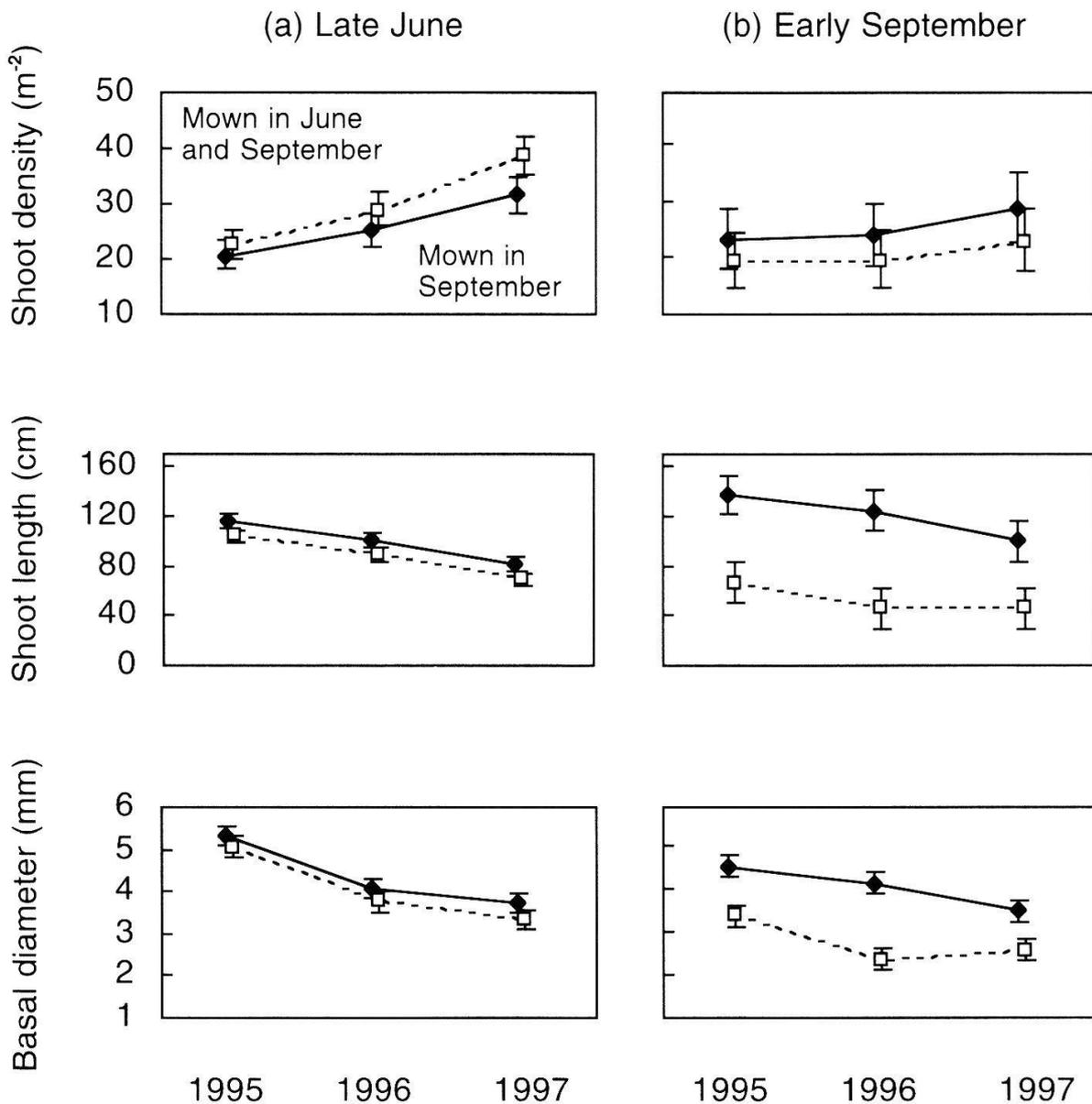


Fig. 1. Changes in mean density, length and basal diameter of *Phragmites* shoots (a) in late June, and (b) in late August–early September from 1995 (start of the experiment) to 1997. Dashed lines: plots mown in June and September. Solid lines: plots only mown in September. Error bars indicate standard errors of comparisons between treatments within each year (Mead 1988, p. 397).

compared: shoots had emerged in spring in the control plots, but only in July in the treated plots. However, these differences did not increase from 1995 to 1997. The significant “treatment x year” interaction for shoot diameter in August (Table 1) reflected a fluctuation, not an increasing treatment effect (cf. Fig. 1b). This means that the ability of *Phragmites* to regenerate after the June cutting

did not decrease in the treated plots during the investigation period.

ABOVEGROUND BIOMASS OF *PHRAGMITES* AND OF THE OTHER SPECIES

To determine how additional mowing in June affects the aboveground biomass, one can either consider regeneration after mowing, i.e. the biomass reached at the end of the same

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Table 2. Effect of an additional cutting in June on aboveground biomass and total nutrient contents ("standing stock") of *Phragmites australis*, and all other species, measured in late June 1997.

		Biomass	Nitrogen	Phosphorus
<i>Phragmites</i>				
Mean (g m ⁻²)	Treated plots	86.28	1.43	0.11
	Control plots	74.06	1.22	0.09
ANOVA results	$F_{1,3}$	0.91	1.68	3.92
	Significance (<i>P</i>)	ns	ns	ns
Other species				
Mean (g m ⁻²)	Treated plots	245.25	3.71	0.30
	Control plots	313.88	4.80	0.38
ANOVA results	$F_{1,3}$	15.67	32.32	19.52
	Significance (<i>P</i>)	<0.05	<0.05	<0.05

growing season, or the biomass produced during the following year(s).

Within the same growing season, mowing in June affected the aboveground biomass of *Phragmites* more strongly than that of the other species: the biomass of *Phragmites* at the end of the summer was only 37% (SE = 8%) of the biomass before mowing (end of June), compared with 61% (SE = 6%) for the other species. This difference could not be attributed to a seasonal effect, as the biomass of *Phragmites* and the biomass of the other species increased by the same factor (26–27%) from June to August in the control plots. Consequently, *Phragmites* regenerated poorly after mowing compared with other species.

Conversely, additional mowing in June during two years did not affect the aboveground biomass reached by *Phragmites* in June 1997 (third year), nor the amounts of nutrients stored in this biomass (Table 2a), whereas the biomass and nutrient contents of the other species were reduced (Table 2b). As a result, the contribution of *Phragmites* to the aboveground biomass in June 1997 was higher in treated plots than in the controls (29% vs. 21%; $F = 7.03$, $P < 0.1$).

NUTRIENT ECONOMY OF *PHRAGMITES* AND THE OTHER SPECIES

Mowing in June during two years did not lead to lower nutrient concentrations in the aboveground biomass of treated plots compared with controls: neither for *Phragmites* nor for the other species did nutrient concentrations in June 1997 differ between treatments (Table 3a). Nutrient concentrations in early September were markedly higher in treated plots than in the controls, particularly for phosphorus (Table 3b), because in the treated plots shoots were much younger.

Mowing in June and September removed more nutrients than mowing only in September, even though the total biomass exported by mowing (adding together both harvests in the treated plots) was the same with both treatments (Table 4a). On an average, mowing in June and September removed 44% more N and 85% more P than mowing in September only. The greater nutrient export in treated plots was mainly due to the higher nutrient concentrations in September. Differences between treatments were stronger for *Phragmites* than for the other species: on an average, mowing in June and September re-

Table 3. Effects of an additional cutting in June on nutrient concentrations in the aboveground biomass of *Phragmites australis*, and all other species in the third year of the experiment

		N (June)	N (Sept)	P (June)	P (Sept)
<i>Phragmites</i>					
Mean (mg g ⁻¹)	Treated plots	16.76	17.36	1.32	1.51
	Control plots	16.54	11.69	1.26	0.64
ANOVA results	$F_{1,3}$	0.02	56.98	1.27	113.86
	Significance (<i>P</i>)	ns	<0.01	ns	<0.01
Other species					
Mean (mg g ⁻¹)	Treated plots	15.19	16.86	1.28	1.89
	Control plots	15.32	12.56	1.28	1.27
ANOVA results	$F_{1,3}$	0.20	28.65	0.22	45.38
	Significance (<i>P</i>)	ns	<0.05	ns	<0.01

Table 4. Effects of an additional cutting in June on the export of biomass and nutrients through mowing, and the relative contribution of *Phragmites australis* to this export in the third year of the experiment

		Biomass	Nitrogen	Phosphorus
Total export				
Mean (g m ⁻²)	Treated plots	537.11	8.53	0.70
	Control plots	495.70	5.96	0.38
ANOVA results	$F_{1,3}$	1.02	20.83	33.05
	Significance (<i>P</i>)	ns	<0.05	<0.05
Contribution of <i>Phragmites</i>				
Mean (%)	Treated plots	21.89	22.95	22.42
	Control plots	18.76	18.12	14.61
ANOVA results	$F_{1,3}$	2.36	2.83	25.79
	Significance (<i>P</i>)	ns	ns	<0.05

moved 90% more N and 181% more P than mowing in September only for *Phragmites*, but only 30% more N and 64% more P for the other species. The contribution of *Phragmites* to the export of phosphorus was, therefore, higher in the treated plots than in the controls, and the same tendency (though not significant) was found for nitrogen (Table 4b). Thus, the nutrient economy of *Phragmites* appeared to be more strongly affected by an additional cutting in June than the nutrient economy of the other species.

Discussion

IMPACT OF MOWING ON THE NUTRIENT ECONOMY OF *PHRAGMITES*

In its main habitat, aquatic sites, *Phragmites australis* experiences virtually no interspecific competition, but in regularly managed fen meadows, there are many competitors, and *Phragmites* emerges later in the year than most of them (Hürlimann 1951; Buttery & Lambert 1965; Haslam 1971). To be successful under these conditions, *Phragmites* must

grow rapidly in early summer despite the shading and the root competition of species that have developed earlier. Carbohydrates and mineral nutrients stored in belowground parts during previous growing seasons make such a fast growth possible. Additional mowing in late June was expected to remove the carbohydrates and mineral nutrients that were supplied to the shoots in spring (Fiala 1976; Hocking 1989; Granéli 1990; Granéli *et al.* 1992), i.e. to deplete the belowground reserves, and thus, to reduce the competitive ability of *Phragmites* (e.g. Rodewald-Rudescu 1974; Egloff 1984).

In the present study, mowing in June and September did, indeed, remove significantly more nutrients than mowing only in September. The carbohydrate economy was not investigated, but in plots that had been mown in June, N and P concentrations were still as high in early September as in late June. This suggested that *Phragmites* was still growing, and that most assimilates produced during August were used for growth, whereas they would have been stored in the rhizomes if plots had not been mown in June (Fiala 1976; Granéli *et al.* 1992; Guthruf *et al.* 1993).

ABSENCE OF SHORT-TERM TREATMENT EFFECTS

In view of the impact of additional mowing in June on the nutrient economy of *Phragmites*, a negative effect on shoot size, aboveground biomass or nutrient contents could be expected. However, no such effect was observed during the period of investigation. Changes in shoot density and shoot size observed in treated plots between 1995 and 1997 did not differ from those observed in the controls. They were, therefore, unrelated to management, whereas differences in ground-water level and weather conditions (e.g. dry spring 1996, severe late frosts in April 1997)

probably had an impact (Haslam 1972). Since the biomass of the other species was, on an average, reduced by the additional mowing, the contribution of *Phragmites* to total aboveground biomass was even increased, suggesting that the species had actually been promoted by this treatment.

The most obvious explanation for the absence of significant treatment effects was the limited duration of the experiment. In long-term management experiments, time lags of up to ten years were observed between a change in management and changes in the abundance of certain species (Olf & Bakker 1991; Grootjans *et al.* 1996). Rhizomatous geophytes like *Phragmites* seem particularly able to respond with a delay because they only use a fraction of their belowground reserves for the annual growth (Granéli *et al.* 1992), and therefore stores will take several years to be depleted.

However, mowing did significantly reduce the abundance of *Phragmites* within one or two years in other experiments. There are several possible reasons for the stronger treatment effects observed in those studies:

- Some of the experiments were carried out at unmanaged sites (Gryseels 1989; Briemle & Ellenberg 1994), where the accumulated litter of *Phragmites* probably excluded other species (Haslam 1971; George 1992). Litter removal allowed other species to invade and to compete against *Phragmites*.
- Some experiments were conducted on waterlogged soils. Removing the culms reduces the supply of oxygen to the belowground parts (Brix 1990; Armstrong & Armstrong 1988). The subsequent anoxia causes important losses of carbohydrates from rhizomes (Cízková-Koncalová *et al.* 1992), which may strongly affect the plant (Weisner & Granéli 1989).

- In aquatic stands, stubbles were flooded after mowing, and rhizomes began to rot (Husák 1978); salt water proved to be particularly detrimental (Hellings & Gallagher 1992).
- In highly productive terrestrial stands, *Phragmites* was displaced by certain grass species, e.g. *Agrostis stolonifera* or *Glyceria maxima*, which are more tolerant to mowing in summer than *Phragmites* (George 1992; Rodwell 1995).

UNCERTAIN LONG-TERM TREATMENT EFFECTS

Assuming that *Phragmites* would strongly decrease once its belowground reserves are depleted, it would be interesting to estimate the time needed for this depletion. Unfortunately, this is hardly possible without field measurements of belowground biomass and its turnover. Direct measurements at the experimental sites are needed because the belowground biomass of *Phragmites* as well as its production and decay vary considerably among sites (Fiala 1976; Hocking 1989; Granéli *et al.* 1992; Cízková *et al.* 1996). Due to the depth of the rhizomes and roots of *Phragmites* at terrestrial sites and to their spatial variability (Kvet 1973; Ondok 1978), such measurements would have been both unreliable and destructive and were omitted in this study.

Moreover, internal nutrient cycling is not particular to *Phragmites*, but typical for the dominant species in fen meadows (Kuhn *et al.* 1982; Ganzert & Pfadenhauer 1986; Bernard *et al.* 1988; Marti 1994). Consequently, other species are likely to be affected by nutrient depletion as much as *Phragmites*. In this experiment, additional mowing in June removed more nutrients from *Phragmites* than from the other species. However, this result is probably mainly due to the fact that, in opposition to *Phragmites*, the other species had a

lower June biomass in the treated plots than in the controls. Without this difference in June biomass, the additional nutrient removal through the mowing in June would have been even lower for *Phragmites* than for the other species because *Phragmites* regenerated poorly after the first cut.

The long-term effect of mowing is likely to depend on the nutrient status of sites. Experiments by Rosenthal (1992) show that even mowing twice a year may be insufficient to reduce invasive rhizomatous species in nutrient-rich fen meadows. However, according to Briemle & Ellenberg (1994), *Phragmites* is more sensitive to mowing than the species investigated by Rosenthal (1992). It might, therefore, decrease in plots mown in June for a longer time. The vertical distribution of nutrients in the soil is also important: an inflow of nutrient-rich groundwater at a depth within reach of *Phragmites* roots, but not of roots of smaller species (Boller-Elmer 1977; Klötzli 1986), might enable *Phragmites* to take up more nutrients than other species. It might then retain the initial advantage apparent in this study.

CONSEQUENCES FOR MANAGEMENT

To evaluate whether mowing in June and September or another form of management is more suitable for the conservation or restoration of reed-invaded fen meadows, effects of other possible treatments on *Phragmites*, on the other species and on site productivity need to be considered.

The control treatment in the present study, i.e. mowing once a year in September, is likely to be milder than mowing twice a year and seems therefore preferable for the typical plant species of fen meadows (cf. Briemle & Ellenberg 1994). However, this treatment exports relatively few nutrients because aboveground biomass in late summer repre-

sents only part of the annual production (e.g. Bernard *et al.* 1988), and because translocation of nutrients to belowground parts already starts in July or August in many dominant plant species (e.g. Warnke-Grüttner 1990). Moreover, the total nutrient contents (biomass x nutrient concentrations) in the control plots of the present study indicated that *Phragmites* had already translocated a greater fraction of nutrients to rhizomes than the other species before the September cutting. This is consistent with results of Warnke-Grüttner (1990) and suggests that the management currently practised in most fen meadows is rather unsuitable if the aim is to prevent a spread of *Phragmites* (Hürlimann 1951; Rosenthal 1992; Schütz & Ochse 1997).

More frequent mowing, i.e. three or four times a year, might be more effective in reducing dominant species like *Phragmites* (Rosenthal 1992) and in lowering site productivity than mowing twice a year. This kind of management would probably lead to undesirable changes in species composition, i.e. promote species adapted to frequent mowing (Kapfer & Pfadenhauer 1986). Kapfer (1987) and Klötzli (1991) recommended to only apply it if biomass production exceeds 500 g m⁻² or if no rare or characteristic fen species are present at a site.

Several studies have shown that grazing can be a very effective measure to reduce *Phragmites* because this species is selectively eaten by cattle or horses and severely affected by trampling (van Deursen & Drost 1990; Roze 1993; Walther 1994). This management has now also been implemented in certain Swiss fens, using highland cattle (Hasler 1996a,b). One important drawback of grazing is that it removes much less nutrients than mowing (Bakker 1989; Marrs 1993). Moreover, other species (e.g. orchids) are likely to suffer from trampling as well. A combination of mowing

and short periods of grazing when the soil is dry might be a suitable, but rather labour-intensive solution.

Since each of the possible alternative treatments presents certain drawbacks, mowing in June and September might still be a suitable management for reed-invaded fen meadows, even if short-time success cannot be expected and long-term effects still need to be evaluated. At least, this mowing regime leads to a considerably higher nutrient export than mowing in September only, to a lower aboveground biomass and a more open vegetation structure during most of the summer. These effects are probably more important for species richness and for the rare species of fen meadows than a possible (future) reduction of *Phragmites* (Güsewell & Klötzli 1998).

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