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Management of *Phragmites australis* in Swiss fen meadows by mowing in early summer

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Abstract

Mowing experiments were carried out from 1995 to 2001 in Swiss fen meadows to investigate whether the abundance of *Phragmites australis* is reduced by mowing in early summer in addition to mowing in autumn. Experimental plots of 100 m^2 were established in three fen meadows that are mown every year in September; treated plots received an additional cut in late June either every year or every two years. Until 1997, the additional cut had no effect on the above-ground biomass of *Phragmites* (monitored every year in late June). As from 1998, the biomass of *Phragmites* was 25–30% lower in the plots with annual June cut than in the control plots. However, the pooled biomass of all other plant species decreased similarly, so that the degree of dominance of *Phragmites* was not reduced. An additional June cut every two years had no effect on the biomass of *Phragmites*. In June 2001, the shoots of *Phragmites* were smaller in annually June-cut plots than in control plots, but allometric relationships between shoot length and diameter, shoot growth from June to August, and nitrogen and phosphorus concentrations of shoots did not differ between June-cut and control plots. The additional June cut increased the total export of N with the hay by 18%, and that of P by 50% in 2001. These additional nutrient exports were smaller than those found in the first years of the experiment and not larger for *Phragmites* than for the remainder of the vegetation. Together, the results suggest that a depletion of below-ground stores caused *Phragmites* to decrease after several years of additional mowing in June. Eighty further permanent quadrats in fen meadows with normal management (mown annually in September) were surveyed in 1995–96 and in 2001. The above-ground biomass of *Phragmites* increased during this time in 49 out of 80 plots, with a mean relative difference of +35.5%. Thus, even if additional mowing in early summer only slightly reduced the performance of *Phragmites* compared to plots mown only in September, this treatment might help to prevent the species from spreading under the current conditions in Swiss fen meadows.

Introduction

Phragmites australis (common reed) is a widespread species in European lowland fens. It is often the dominant species at permanently flooded sites, but generally only sparse to moderately abundant when the water table is lower because its shoot density and size are restricted by limited water and nutrient supply, competition or management (Haslam, 1970, 1973). Increased nutrient supply or the abandonment of regular management can cause *Phragmites* to become dominant in fens where it used to be sparse (Gigon and Bocherens, 1985; Klötzli, 1986; van Diggelen et al., 1996). This development is regarded as undesirable in nature conservation areas as it often reduces the species richness of the vegetation and causes the disappearance of rare plant species (Roman et al., 1984; Marks et al., 1994). Herbicides are commonly used to restore reed-invaded marshes in the USA (Ailstock et al., 2001). However, if the spread of *Phragmites* occurs in fens of high conservation value (Güsewell and Klötzli, 1998), it is preferable to reduce the performance of this species without negative impacts on the established vegetation through an appropriate management regime (see also Wilson and Clark, 2001).

The effects of management (mowing, grazing or burning) on the performance of *Phragmites* and its ability to suppress other plant species are known to depend on the type and timing of measures. Mowing or burning in winter does generally not affect stands of *Phragmites* negatively and may even contribute to their conservation (Granéli, 1990; Buttler, 1992; Güsewell et al., 2000a). By contrast, mowing in summer or autumn can reduce *Phragmites*, particularly if the measure is associated with flooding (Weisner and Granéli, 1989; Hellings and Gallagher, 1992). At nutrient-rich sites, mowing twice during the summer may be necessary for a substantial reduction of *Phragmites* (Gryseels, 1989b; Schütz and Ochse, 1997). Grazing by cattle or horses can cause a drastic reduction in the abundance of *Phragmites* within only two or three years (van Deursen and Drost, 1990; Rozé, 1993).

Fen meadows in north-eastern Switzerland were traditionally mown in late autumn or winter, after nutrients and carbohydrates have been translocated from above-ground to below-ground parts. Soils were nutrient-poor, and the vegetation low-productive and species-rich (Ellenberg, 1996). Currently, fen meadows have become more productive, and they are mostly mown in September for conservation. The effect of mowing in September on the nutrient economy of plants depends on their phenology: plants lose a smaller fraction of their nutrients if they senesce already towards the end of the summer (Warnke-Grüttner, 1990). Compared to most other species in fen meadows, *Phragmites* has resorbed a higher fraction of N and P from the above-ground biomass by the end of August (Güsewell, 1998). By removing a smaller fraction of the plant's nutrient pools, mowing in early September might provide *Phragmites* an advantage over the other species. Indeed, the abundance of *Phragmites* has increased in many fen meadows mown in September during the last few decades (Marti and Müller, unpublished report). It has been proposed that sites where *Phragmites* spreads should be mown in early summer (June–July), when nutrient contents of *Phragmites* shoots are maximal. However, no published evidence has so far confirmed that this management regime is effective in reducing *Phragmites*.

Mowing experiments carried out from 1995 to 1997 in fen meadows near Zurich showed that an additional cut in late June did indeed enhance the losses of N and P relatively more for *Phragmites* than for the other species (Güsewell, 1998). Nevertheless, the shoot biomass of *Phragmites* was not affected by the treatment, and its share in total biomass even increased (Güsewell, 1998; Güsewell et al., 2000a). A possible reason is that the additional exports of nutrients and assimilates were compensated for by the mobilisation of below-ground reserves. In this case, the shoot biomass of *Phragmites* should decrease after several years of additional mowing in June, when below-ground reserves have become depleted.

To test this hypothesis, the mowing experiments were pursued for a total of seven years and monitored regularly to assess the long-term effects of additional mowing in June. Furthermore, the effects of mowing on shoot growth and nutrient exports were re-investigated in the last year of the experiment (2001) to test the hypothesis that the effect of additional mowing in June on nutrient exports would decrease with time (due to decreasing biomass of *Phragmites*) and would no longer differ between *Phragmites* and the other species (Güsewell, 1998; Güsewell et al., 2000a). Finally, additional permanent quadrats established in 1995 or 1996 at sites mown in September were re-surveyed in 2001 to assess whether the shoot biomass of *Phragmites* generally shows an increasing tendency under the current management of fen meadows.

Methods

Study sites and experimental design

The three experimental sites are fen meadows 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; they are waterlogged from late autumn to spring but relatively dry in summer. The vegetation is heterogeneous in response to local differences in water table and nutrient supply and belongs to the alliances Molinion, Caricion davallianae, Filipendulion or intermediate community types (Güsewell and Edwards, 1999). Swiss fen meadows have traditionally been mown by farmers in order to use the material as litter in stables. This management was discontinued at most sites after 1950 but resumed during the eighties

Table 1. Vegetation of the six experimental blocks: vascular plant species composition in June 2001 and above-ground biomass in control plots in late August 2001 (total and *Phragmites australis*). Nomenclature according to Lauber and Wagner (1996). Data are means (SD) of 2–3 samples.

Site	Block	Main vascular plant species (species with cover ≥5% and/or numerous shoots)	Biomass ($g\ m^{-2}$) Total	Phragmites
Greifensee [1]	1	*Ajuga reptans, Carex acutiformis, Equisetum palustre, Filipendula ulmaria, Holcus lanatus, Lysimachia vulgaris, Phragmites australis, Poa trivialis*	599.2 (68.5)	305.2 (n.a.)
	2	*Ajuga reptans, Carex acutiformis, C. flava, C. hostiana, C. panicea, Equisetum palustre, Holcus lanatus, Lotus uliginosus, Lysimachia vulgaris, Molinia caerulea, Phragmites australis*	522.2 (93.8)	102.4 (23.0)
	3	*Carex acutiformis, C. elata, C. flava, C. hostiana, C. lasiocarpa, C. panicea, Lysimachia vulgaris, Lythrum salicaria, Mentha aquatica, Molinia caerulea, Phragmites australis, Potentilla erecta, Succisa pratensis*	583.7 (98.4)	142.2 (24.8)
Katzensee[2]	4	*Carex acutiformis, C. panicea, Deschampsia caespitosa, Equisetum palustre, Filipendula ulmaria, Juncus effusus, J. conglomeratus, Lotus uliginosus, Lysimachia vulgaris, Phragmites australis*	538.3 (70.4)	99.8 (58.8)
	5	*Carex acutiformis, C. elata, C. panicea, Deschampsia caespitosa, Equisetum palustre, Filipendula ulmaria, Juncus subnodulosus, Lysimachia vulgaris, Mentha aquatica, Molinia caerulea*	573.7 (102.8)	25.0 (9.0)
Glatt[3]	6	*Agrostis gigantea, Calamagrostis epigeios, Carex acutiformis, Deschampsia caespitosa, Galium elongatum, Phalaris arundinacea, Lythrum salicaria, Phragmites australis*	673.2 (3.6)	132.0 (13.0)

[1] Coordinates 692’550/247’750. [2] Coordinates 680’550/254’100. [3] Coordinates 691’950/247’650 (Swiss National Grid).

for nature conservation. During the seven years of the experiment, the sites (including the experimental plots) continued to be mown every year in September as part of the normal management; the plant material was removed soon after mowing.

Experimental plots (10 m × 10 m, n = 18) were established in a block design with six blocks (Table 1). One plot per block was mown in late June every year, a second plot was mown in June every two years, and the third (control) plot was never mown in June. The June cut (at approximately 5 cm height) was carried out mechanically if sites were dry enough, and manually otherwise. In two extremely wet years, mowing had to be postponed until early July. Treatments started in 1995 for blocks 1, 2, 4 and 5, and in 1996 for blocks 3 and 6. Due to disturbance in the first year, the plot mown in June every two years was lost from block 6. Some data were collected only for the control plots and those mown in June every year; the latter will then simply be called the ‘June-cut plots’.

Three 4-m^2 permanent quadrats were established in the central part of each experimental plot. Plot corners were marked permanently with metal pipes in the soil, which were searched every spring using a metal detector. Permanent quadrats were then located from plot corners. The absence of permanent above-ground marks enabled a normal management of the sites in September (using agricultural machines) and avoided that visitors or birds would be attracted.

Measurements

The performance of *Phragmites* was recorded in all permanent quadrats every year from 1995 through 2001 in late June, right before the first cut of treated plots. The number of shoots taller than 20 cm was counted in the entire quadrat, whereas the culm length and basal diameter of all shoots were measured in a 1-m^2 subquadrat. Culm length was measured from the soil surface to the base of the uppermost leaf (inflorescences being infrequent), and the basal diameter was measured in the middle of the second internode; means of all shoots in the subquadrat were used in data analysis. The above-ground biomass of *Phragmites* in each permanent quadrat was estimated by multiplying the shoot number m^{-2} by the mean shoot biomass (in g). The mean shoot biomass (in g) was estimated from the mean length (in cm) and mean diameter (in mm) of all shoots within a quadrat using the relationship established by Güsewell and Klötzli (1997):

$$\log \text{mean biomass} = -1.97 + 1.04 \cdot \log (\text{mean length} \cdot \text{mean diameter})$$

Figure 1. Experimental plots at site Katzensee in June 2001, showing a quadrat (4 m^2) left unmown within a June-cut plot.

The same measurements were carried out again at the end of August 2001 to estimate the biomass of *Phragmites* exported by the September cut as well as the growth of *Phragmites* shoots between June and August (in the control plots) or the re-growth of young shoots in the June-cut plots. To compare both the growth of undisturbed shoots and the re-growth of young shoots between June-cut and control plots, one 4-m^2 quadrat was left unmown in the border zone of each June-cut plot in June 2001 (Figure 1), and one 4-m^2 quadrat was mown in June 2001 in the border zone of each control plot. Measurements in the central part (1 m^2) of these additional quadrats were identical to those in permanent quadrats.

After the August measurements, the shoots of *Phragmites* were harvested, dried for 24 h at 70 °C and weighed to determine their biomass. A total of 180 shoots from all sites and treatments was weighed individually, while the other shoots were pooled and weighed per quadrat. Data from this sampling were used to examine whether allometric relationships between shoot length, diameter and biomass had been altered in the June-cut plots.

To compare the effects of mowing on *Phragmites* to those on the remainder of the vegetation (hereafter called 'the other species'), the whole vegetation was clipped about 1 cm above ground level in three 0.16-m^2 quadrats per experimental plot in the last days of June and of August 2001, i.e. just before the mowing. Care was taken to sample different quadrats at the second date. Bryophytes were not sampled because their biomass was minor compared to that of vascular plants, and their height was generally < 1 cm. The plant material was sorted into *Phragmites* and other species, dried at 70 °C, weighed and ground. Total nitrogen and phosphorus were extracted using a modified Kjeldahl method (1h digestion at 420 °C with 98% H_2SO_4 and a copper sulphate-titanium oxide catalyst). Concentrations of N and P in digests were determined colorimetrically on a flow injection analyser (Tecator, Höganäs, Sweden).

Field survey

To determine how the biomass of *Phragmites* changed under the normal management for a larger number of sites in fen meadows, eighty of the 4-m^2 plots surveyed by Güsewell and Klötzli (1998) in August 1995 or 1996 were re-surveyed in August 2001. As in the former survey, shoots were counted in the whole plot and measured in one quarter of it, and the above-ground biomass was estimated as described for the mowing experiment.

Data analysis

Data were log-transformed to obtain normally distributed errors, except shoot numbers which were square-root transformed. In all statistical analyses, blocks were random factors, i.e. the tests showed whether treatments or species had consistent effects across the various vegetation types occurring in these fen meadows, as represented by the six experimental blocks. Treatment means and standard errors reported in tables or graphs are the back-transformed results of these analyses, so that standard errors indicate how much treatment effects varied among blocks (rather than variation among individual samples). Since the errors were asymmetric after back-transformation, the positive (larger) errors are reported.

The effects of mowing in June on the number, size and biomass of *Phragmites* shoots were analysed in two ways: using final values, i.e. means from 2000 and 2001, and using the change, i.e. differences between means from 1995/1996 and those from 2000/2001. Means from two years were taken to reduce the effects of short-term fluctuations; they were calculated separately for each of the three permanent quadrats per experimental plot. Block 6 was excluded from this analysis because it had no plot June-cut every two years.

At the site Katzensee, part of the area was not mown in autumn 2000 because it was flooded. The 2001 data from the four permanent quadrats affected by this unplanned abandonment were excluded from the analysis of long-term change, but they were used to examine the effects of short-term abandonment on the performance of *Phragmites* by comparing them with data from neighbouring quadrats that were mown normally in autumn 2000.

Data from the 80 re-surveyed plots were analysed with paired t-tests to determine whether on the whole, *Phragmites* had increased or decreased between the two surveys. The relationship between log-transformed biomass in 1995–96 and in 2001 was described by a model 2 regression line (Sokal and Rohlf, 1995): the slope was determined with principal component analysis, and the intercept was calculated from the slope and the means of both variables.

The growth of *Phragmites* shoots between June and August was quantified by expressing the August values as percentage of June values (100% = no change). The log-transformed percentages were then tested for differences between June-cut and control plots, separately for the growth of undisturbed shoots and for the re-growth of shoots after the June-cut.

The total biomass exported by mowing in a year (yield) was the sum of DM_{June} and DM_{August} in June-cut plots, and equal to DM_{August} in control plots (DM = dry mass of the above-ground biomass in g m^{-2}). The export of a nutrient (N or P) was calculated as $DM_{June} \cdot Conc_{June} + DM_{August} \cdot Conc_{August}$ for June-cut plots, and as $DM_{August} \cdot Conc_{August}$ for control plots (Conc = tissue N or P concentration in mg g^{-1} DM). These calculations were done per experimental plot, using the mean biomass and N or P concentration either of *Phragmites* or of the remainder of the vegetation. In the case of *Phragmites*, the biomass used in these calculations was the value estimated from the shoot counts and measurements done in permanent quadrats (see above). This was because the total area on which shoots were counted (12 m^2 per experimental plot) was much larger than the area on which biomass was harvested (0.48 m^2), which seemed preferable because the shoot number of *Phragmites* in small quadrats is very variable (Güsewell and Klötzli, 1997).

Results

Changes in Phragmites *biomass between 1995 and 2001*

The shoot number, shoot size and above-ground biomass of *Phragmites* all changed considerably in the course of the experiment (Figure 2). The shoot number fluctuated without consistent temporal trend or response to treatments (Figure 2a). For the shoot diameter, shoot length and biomass (Figure 2b-d), a period of decrease (1995–1998) was followed by a period of stabilisation or increase (1998–2001). The final values (2000–2001) of shoot length and diameter differed significantly among treatments, with lower values in the plots additionally June-cut every year

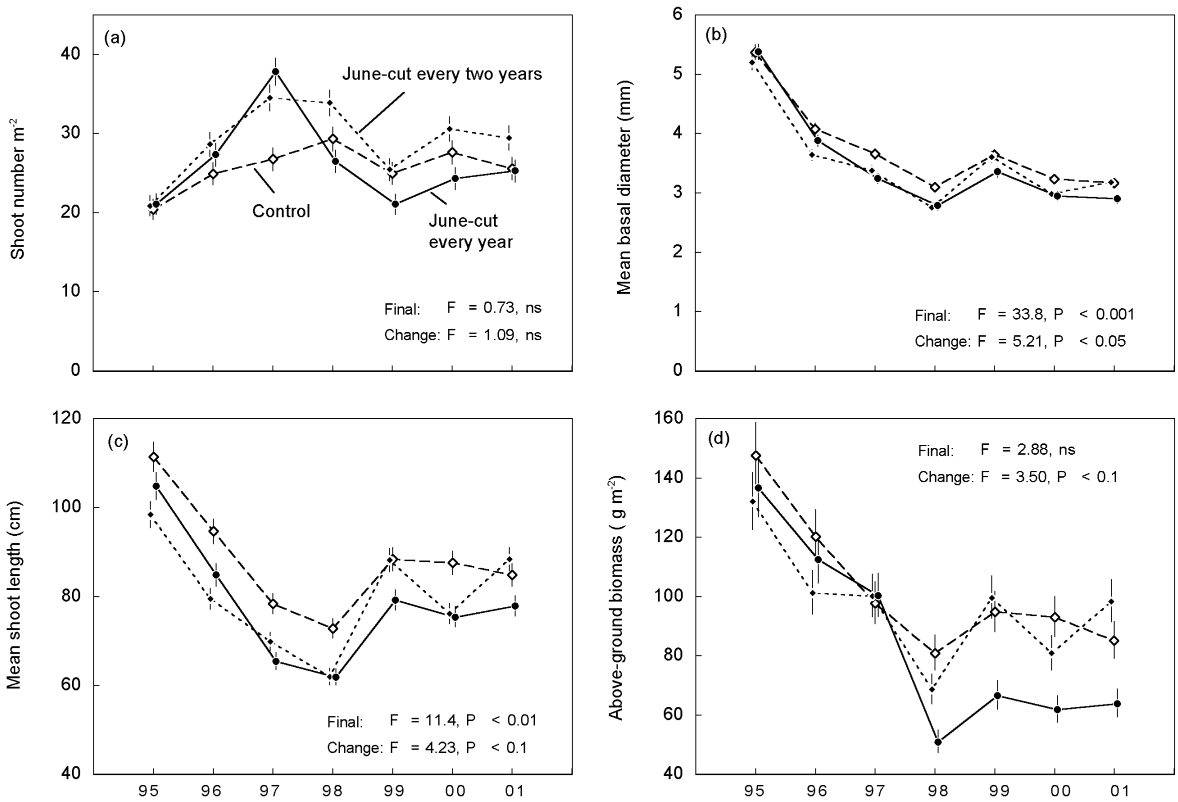

Figure 2. Changes in (a) shoot number, (b) mean shoot diameter, (c) mean shoot length and (d) above-ground biomass of *Phragmites australis* between 1995 and 2001 under the three experimental treatments. Data are means (±SE) of the six experimental blocks. Within each graph, results of Anova testing for differences among treatments are given. Tests of 'Final' data compared the mean values of 2000–2001 among treatments, whereas tests of 'Change' compared the differences between mean values of 1995–1996 and those of 2000–2001. *F*-ratios and significance levels are given (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; $^{\circ}$, $p < 0.10$; ^{ns}, $p > 0.1$).

than in the control plots (mown only in September; Figure 2b,c). Plots that were June-cut every two years did not differ consistently from the two other treatments. The differences between June-cut and control plots were already apparent as tendencies in 1995 and/or 1996, so that the change between initial and final values differed less clearly among treatments than the final values themselves. With the above-ground biomass, two phases of the experiment are apparent (Figure 2d): until 1997, there were no treatment effects, but as from 1998, the biomass was 25–30% lower in the plots June-cut every year than in the control plots. This treatment effect was marginally significant if it was tested using the change between initial and final biomass, whereas final biomass itself did not differ significantly due to considerable variation among blocks.

Short-term abandonment considerably enhanced the performance of *Phragmites australis* at the site Katzensee, where four permanent quadrats were not mown at all in 2000 due to flooding (Table 2): shoot number and shoot size increased between 2000 and 2001, leading to a 87.2% increase in above-ground biomass. This contrasted with neighbouring quadrats, which were mown normally in 2000, and in which a decrease in shoot number and shoot size resulted in a 21.8% reduction in biomass between 2000 and 2001.

In a larger set of plots mown annually in autumn (field survey, $n = 80$), the difference in the above-ground biomass of *Phragmites* between 1995–96 and 2001 varied widely, ranging from a 76% decrease to a 900% increase (Figure 3). The change was positive in 49 plots and negative in 27. Positive changes were most frequent among plots with low initial biomass, as indicated by the positive intercept and the slope smaller than 1 of the regression line (Figure 3). Overall, the biomass of *Phragmites* was significantly higher in 2001 than in 1995–96 ($t = 3.21$, $p = 0.002$), with a

Table 2. Effects of short-term abandonment on the performance of *Phragmites australis:* mean differences (+ SE, n = 4) between measurements from June 2000 and those from June 2001 in permanent quadrats left unmown due to wetness in autumn 2000 or normally mown (control) at the study site 'Katzensee'.

Mean difference in . . .	Unmown in 2000	Mown in 2000
Shoot number (m^{-2})	+2.00 (2.16)	–0.02 (0.22)
Mean shoot length (cm)	+27.22 (7.70)	–8.95 (2.79)
Mean basal diameter (mm)	+0.43 (0.21)	–0.26 (0.08)
Above-ground biomass (g m^{-2})	+87.2% (39.0%)	–21.8% (4.3%)

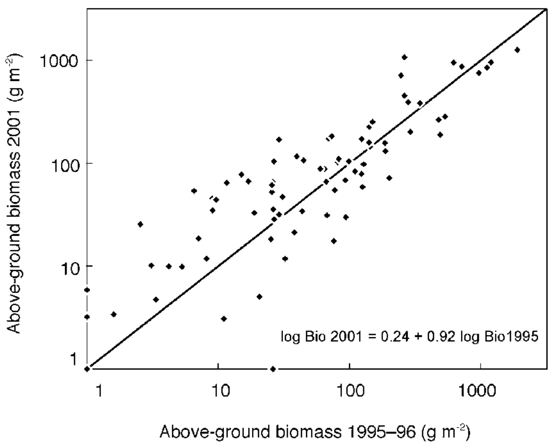

Figure 3. Relationship between the above-ground biomass of *Phragmites australis* determined in late August 1995/96 and late August 2001 in 80 plots in fen meadows (logarithmic scale); the line (1:1) corresponds to same biomass in both years.

mean difference of +35.5%. This increase in biomass was not due to a change in shoot number but due to an increase in shoot diameter (+0.52 mm, t = 8.46, $p <$ 0.0001).

Biomass of Phragmites *and other species in 2001*

The above-ground biomass of *Phragmites* did not differ significantly between June-cut and control plots in 2001, although it was on average 26% lower in June-cut plots (Figure 2d). By contrast, the biomass of the other species was significantly lower in June-cut plots (283±12 g m^{-2}) than in control plots (338±14 g m^{-2}, $p < 0.05$), as was total above-ground biomass (408±12 g m^{-2} vs. 481±14 g m^{-2}, $p < 0.05$). The share of *Phragmites* in total biomass did not differ between June-cut plots and control plots. In the 0.16-m^2 quadrats (border zone of the experimental plots), *Phragmites* represented on average 32±2% of total biomass in June-cut plots, and 30±2% in control plots. In the permanent quadrats, the biomass of *Phragmites* was lower than in the border zone and only represented 14.2% (June-cut) and 16.5% (control) of total biomass, if the latter was assumed to be similar to that in the border zone.

Morphology and growth in summer 2001

Relationships between mean shoot diameter and mean shoot length in the permanent quadrats in June 2001 did not differ among the three treatments (Figure 4a). The relationship between the length and the diameter of individual shoots in late August 2001 did not differ between control plots and the quadrats which were left unmown in June 2001 within June-cut plots. The shoots re-grown after the cut of June 2001 were shorter relative to their diameter than the undisturbed shoots, but the slope of the relationship was the same (Figure 4b).

Between June and August 2001, the shoots of *Phragmites* in control plots increased in length by 24.6% (Table 3a). Simultaneously, shoot mortality reduced the shoot number by 5.3%, so that the above-ground biomass increased less (+18.8%) than the mean biomass of individual shoots. In the quadrats left unmown within June-cut plots, the increase in length between June and August 2001 was significantly smaller than in the control plots, i.e. only +10.2% (Table 3a). However, the shoot number increased by 3.9%, and the overall relative increase in biomass (+20.8%) did therefore not differ significantly from that in the control plots. The biomass of the other species increased by 27.7% between June and August in the control plots, and only by 7.1% in the unmown quadrats of June-cut plots, but this difference was not statistically significant (Table 3a).

Table 3. Growth of *Phragmites australis* and of the remainder of the vegetation ('other species') between late June and late August 2001 (a) in quadrats that were not mown in June 2001 and (b) in quadrats that were mown at the end of June 2001. Data are means (+SE, n = 6) of values in late June and in late August for experimental plots cut in June and September ('June-cut') or only in September ('control'). August values are then given as percentage of June values, and these percentages are compared between June-cut and control plots with Anova. Significance levels are ***, $p < 0.001$; *, $p < 0.05$; ^{ns}, $p > 0.1$.

		Shoot number (m^{-2})	Shoot length (cm)	Biomass (g m^{-2})	
		Phragmites	*Phragmites*	*Phragmites*	Other species
(a) Growth in quadrats not mown in June 2001					
June	June-cut	32.0 (0.3)	95.4 (0.7)	129.1 (3.5)	277.3 (16.8)
	Control	24.8 (0.2)	77.9 (0.6)	76.1 (2.0)	337.9 (20.4)
August	June-cut	33.4 (0.4)	105.1 (0.8)	156.1 (4.2)	297.2 (18.0)
	Control	23.8 (0.2)	97.1 (0.7)	90.5 (2.4)	431.3 (26.1)
Aug. (% of June)	June-cut	103.9	110.2	120.8	107.1
	Control	94.7	124.6	118.8	127.7
ANOVA	*F*-ratio, *p*	12.3*	68.6***	0.1^{ns}	2.2^{ns}
(b) Re-growth after mowing in June 2001					
June	June-cut	22.6 (5.5)	73.7 (6.6)	54.3 (13.7)	286.8 (24.9)
	Control[a]			60.1 (15.1)	334.7 (29.0)
August	June-cut	6.3 (3.0)	30.5 (2.7)	5.8 (1.5)	115.8 (10.0)
	Control[a]			2.9 (0.7)	112.3 (9.7)
Aug. (% of June)	June-cut	31.4	41.4	10.7	40.4
	Control[a]			2.1	33.5
ANOVA	*F*-ratio, *p*			3.8^{ns}	1.4^{ns}

[a] Shoot number and shoot length not determined.

The re-growth of *Phragmites* after mowing in June 2001 was extremely poor in four of the six blocks, with biomass in late August reaching only 0–6% of the values from June (Table 3b). June-cut plots and the mown quadrats within control plots did not differ in this respect. The re-growth of the other species ranged from 20% to 50% of June values and did not differ between the June-cut plots and the mown quadrats within control plots (Table 3b).

Nutrient concentrations and exports

Nutrient (N and P) concentrations of the above-ground biomass in June 2001 did not differ between June-cut and control plots, nor did they differ between *Phragmites* and the other species (Table 4). In late August 2001, concentrations of both N and P were much higher in the regrowth of June-cut plots than in the senescing biomass of control plots, and this difference was greater for *Phragmites* than for the other species: June-cutting caused a 110% higher N concentration and a 273% higher P concentration in the biomass of *Phragmites*, compared to 59.8% (N) and 72.9% (P) in the biomass of other species (Table 4).

The total amount of biomass exported by mowing was 11% lower in June-cut plots than in control plots (Table 5). This difference was primarily caused by the lower exports of *Phragmites* biomass, while the exports of biomass of other species did not differ. The total export of N was 17.8% larger in June-cut plots than in control plots; this difference was entirely due to a larger export of N with the biomass of the other species. The total export of P was 49.5% larger in June-cut plots than in control plots; both *Phragmites* and the other species contributed to this difference.

Discussion

The results of this experiment suggest that additional mowing in June affected the performance of *Phragmites australis* through effects on various processes, viz. shoot growth, insect herbivory, plant-internal cycling of assimilates and nutrients, and nutrient export with the hay. In contrast to other mowing experiments in reed stands (e.g. Gryseels, 1989a,b; Cowie et al., 1992), effects of mowing on litter accumulation were not relevant here because all plots were

Table 4. Mean concentrations of nitrogen and phosphorus in late June and late August 2001, determined in the above-ground biomass of *Phragmites australis* and of the remainder of the vegetation ('other species'), in experimental plots cut either in June and September ('June-cut') or only in September ('control'). Data are means (+SE), n = 6. The effects of treatments, species (*Phragmites* vs. other) and their interaction were tested with Anova (F-ratios and significance levels are given; ***, $p < 0.001$; *, $p < 0.05$; ^{ns}, $p > 0.1$).

		Nitrogen (mg g^{-1})		Phosphorus (mg g^{-1})	
		late June	late August	late June	late August
June-cut	*Phragmites*	14.64 (0.37)	21.90 (0.96)	1.09 (0.03)	1.94 (0.06)
	Other species	14.25 (0.36)	20.32 (0.89)	1.24 (0.04)	1.47 (0.05)
Control	*Phragmites*	15.04 (0.38)	10.36 (0.46)	1.12 (0.03)	0.52 (0.02)
	Other species	14.73 (0.38)	12.71 (0.56)	1.35 (0.04)	0.85 (0.03)
ANOVA	Treatment	0.57^{ns}	396.30***	1.52^{ns}	280.90***
	Species	0.33^{ns}	0.73^{ns}	2.76^{ns}	1.17^{ns}
	Treat × Species	0.02^{ns}	10.54*	0.99^{ns}	156.80***

Table 5. Exports of biomass, nitrogen and phosphorus through mowing (g m^{-2}), determined in 2001 in experimental plots mown either in June and September ('June-cut') or only in September ('control'). Total exports (all vascular plant species) were subdivided into those with *Phragmites australis* and those with the remainder of the vegetation ('other species'). Data are means (+SE), n = 6. The significance of differences between June-cut and control plots was tested with Anova (**, $p < 0.01$; *, $p < 0.05$; °, $p < 0.10$; ^{ns}, $p > 0.1$).

		Exports (g m^{-2})		ANOVA
		June-cut	Control	F ratio, p
Biomass	Total	502.4 (16.6)	561.1 (18.5)	5.68°
	Phragmites	69.2 (9.5)	106.4 (14.5)	5.67°
	Other species	401.8 (20.9)	428.6 (22.3)	0.83^{ns}
Nitrogen	Total	8.0 (0.2)	6.8 (0.2)	19.89**
	Phragmites	1.1 (0.2)	1.1 (0.2)	0.00^{ns}
	Other species	6.4 (0.4)	5.5 (0.3)	4.96°
Phosphorus	Total	0.65 (0.02)	0.43 (0.02)	61.58**
	Phragmites	0.08 (0.01)	0.06 (0.01)	6.39°
	Other species	0.53 (0.03)	0.36 (0.02)	21.60**

mown in September, so that no litter accumulated in any treatment. The effects of additional mowing differed according to the time scale at which they were considered: immediate effects (within the same season), short-term effects (after one or two years), and long-term effects (after more than five years).

Effects of additional mowing on shoot growth

After the June cut, the shoots of *Phragmites* were not only thinner and shorter than those with undisturbed growth, but also shorter relative to their diameter (and biomass). This could in principle reduce the ability of *Phragmites* to compete against other species (cf. Gaudet and Keddy, 1988; Hills and Murphy, 1996), but as the height of the other plant species was also low after the June cut (Güsewell, 1997), the altered shoot diameter–culm length relationship was unlikely to contribute to the reduction of *Phragmites*. After several years of mowing in June, shoot size was reduced without change in the diameter-length relationship.

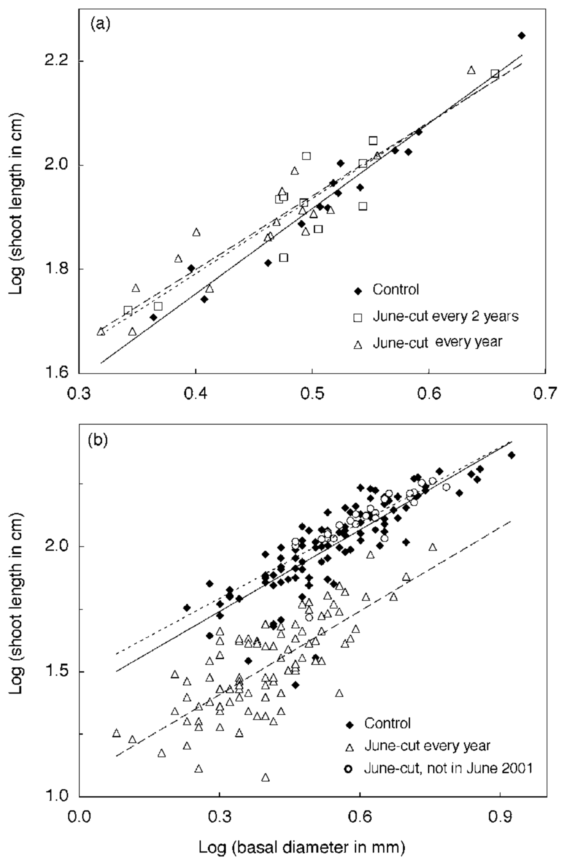

Figure 4. Allometric relationships between shoot diameter and shoot length: (a) mean values per plot in June 2001, (b) values for individual shoots in August 2001 ('June-cut, not in June 2001' means the quadrats left unmown in 2001 within the June-cut plots, cf. Figure 1).

The same was found by other authors who compared mown with unmown *Phragmites* stands (van der Toorn and Mook, 1982; Ostendorp, 1991, 1995).

The number of shoots per unit area was slightly (1995–97) or strongly (2001) reduced in the re-growth after mowing, which differs from other studies showing enhanced shoot numbers after disturbance (e.g. van der Toorn and Mook, 1982; Tscharntke, 1990; Cowie et al., 1992). Most of these studies concerned unmanaged, highly productive reed stands, where shoot density is regulated by competition for light, and where enhanced light supply after disturbance stimulates dormant buds of side shoots (Tscharntke, 1999). In contrast, there were very few side shoots in the re-growth of my June-cut plots. The shoot number in June was enhanced in the June-cut plots during the first few years of the experiment, but in the longer term, the enhancement was reversed; the same occurred in calcareous fens of western Switzerland (Güsewell et al., 2000a).

The combined effects of mowing in June on shoot size and on shoot number caused the above-ground biomass to be drastically reduced in the re-growth, unaffected in the short term (1995–1997), and slightly reduced in the longer term (1998–2001). This supports my initial hypothesis that *Phragmites* compensated the losses caused by additional mowing through the mobilisation of below-ground stores until available reserves were depleted. The appearance of treatment effects in 1998 suggests that the depletion was reached after three years, and that subsequent shoot growth was no longer supported by below-ground stores but had to rely on current-year assimilation. Similarly, Granéli et al. (1992) found that in an aquatic reed stand, one third of the main nutrients (N, P, K) stored in the rhizomes was used every year for above-ground growth, and that the annual turnover rate of rhizomes was 30%. Guthruf et al. (1993) estimated that some 30% of the carbohydrates stored below ground in a terrestrial reed stand were translocated to above-ground parts in spring.

The translocation of assimilates and nutrients from below-ground to above-ground plant parts is mostly complete by the end of June (Granéli et al., 1992). Later in the growing season, biomass production depends on current-year assimilation. Thus, the proposed depletion of below-ground stores should not affect the growth of shoots between late June and late August. Indeed, the relative increase in biomass of undisturbed shoots from late June until late August did not differ between our June-cut and control plots, which further supports the depletion hypothesis.

Effects of regular versus irregular mowing in September

The overall tendency of *Phragmites* biomass to increase, as observed in the field survey, may be an indication that the current management is not sufficient to prevent an increase of *Phragmites* in the long term, as also found in northern Germany by Schütz and Ochse (1997). However, long-term observations at other sites in Switzerland showed that the abundance of *Phragmites* may fluctuate considerably, with periods of continued increase or decrease as long as 5–6 years (Güsewell et al., 2000a). It cannot be excluded that the positive change in mean biomass between 1995–96 and 2001 was only part of a fluctuation. In addition, even if there has actually been an overall increase, this only concerned quadrats with low initial abundance. Thus, it might be that sites where *Phragmites* is absent or very sparse will progressively be colonised, but that this will not lead to a general shift towards vegetation strongly dominated by *Phragmites* under the current, moderately eutrophic conditions.

The quadrats left unmown in September 2001 at site 'Katzensee' showed that a strong increase of *Phragmites* must be expected as soon as management is discontinued in fen meadows. Relative to the biomass in June 2000, abandonment caused a more than 100% increase in biomass in 2001 (+87% vs. –22%). Even occasional short-term abandonment might therefore provide *Phragmites* a competitive advantage over years. In an experiment close to my site 'Greifensee', strips of a fen meadow were left unmown once every fifth year on a rotational basis (Bosshard et al., 1988); a 17% increase in the frequency of *Phragmites australis* was observed over a period of 14 years (M. Winteler, unpublished data). Regular management is therefore essential if the dominance of *Phragmites* is likely to become a problem.

Interactions between mowing and insect damage

The re-growth of *Phragmites* shoots after the June cut was much lower in 2001 than in 1997 (11% vs. 37%; Güsewell, 1998). In fact, re-growth in 2001 was closely similar to that in 1997 at the site 'Katzensee' (32–49% of June biomass), and extremely poor at the two other sites (0–6%). This was related to insect damage, most probably due to an outbreak of the moth *Archanara geminipunctata* (Lep. Noctuidae; T. Tscharntke, pers. comm.). At site 'Greifensee', almost 100% of the shoots were damaged. Shoot were attacked both in June-cut and in control plots, but the impact was probably stronger on the younger and thinner shoots on the re-growth. Insect damage must therefore be taken into account in the assessment of management effects as it may cause these effects to differ considerably from year to year. Outbreaks of *Archanara geminipunctata* occur periodically in reed stands (Tscharntke, 1990), and other sites of the region were also affected in 2001 (author's observation). *Archanara geminipunctata* is being considered as a potential agent for biological control of *Phragmites* in the USA and Australia (Tscharntke, 1999). The results from this study suggest that control might be most effective if the action of insects was associated with mowing.

Effects of mowing on nutrient concentrations and exports

Nutrient concentrations in June 2001 did not differ between treatments nor between *Phragmites* and the other species, and they were quite similar to those obtained in June 1997 (Güsewell, 1998) and in June 1999 (Güsewell et al., 2000b). This indicates that the additional June cut did not cause an increased nutrient deficiency in *Phragmites*. Nutrient concentrations in late August strongly differed between June-cut and control plots; the difference between the two treatments clearly exceeded differences observed in 1997 and 1999, especially in *Phragmites*. Nevertheless, the intensity of treatment effects on nutrient concentrations did not generally increase with time: From the first to the fifth year of the experiment, the difference in N concentration between June-cut and control plots remained the same (+40%), and the difference in P concentration rather decreased (+71% in the first year, +83% in the third, +38% in the fifth, Güsewell, 1998; Güsewell et al., 2000b). The causes of such changes in treatment effects remain to be investigated; differences in weather conditions might be involved (Güsewell et al., 2000b; Olde Venterink et al., 2001).

During the seven years of the experiment, the effects of the additional June cut on total N exports fluctuated without consistent trend, whereas the effects on P exports decreased progressively: the relative increase in N exports due to mowing in June was 29% in the first year, 44% in the third, 12% in the fifth, and 18% in the seventh; the relative increase in P exports was 113% in the first year, 85% in the third, 68% in the fifth and 50% in the seventh (Güsewell, 1998; Güsewell et al., 2000b). The effects of the June cut on nutrient exports decreased more strongly with time for *Phragmites* than for the other species: In 1997, 90% more N and 181% more P were exported with *Phragmites* in June-cut plots than in control plots (Güsewell, 1998). In 2001, no additional N and only 50% more P were exported. This may have been partly related to the insect outbreak and the resulting poor re-growth after June cut. If so, the results from 2001 underestimated the additional nutrient exports for 'normal' years.

Conclusions

The effects of the additional cut in late June on *Phragmites australis* were strongly time-dependent, partly due to internal factors (depletion of below-ground stores) and partly due to external factors (insect outbreaks or variation in weather conditions). Some fluctuations could not (yet) be related to obvious internal or external factors. This shows the importance of including several years of observation in an assessment of management effects (Tilman, 1989). However, a regular monitoring can have effects on the vegetation itself. Thus, the fact that the biomass of *Phragmites* in 2001 was systematically lower in the permanent quadrats than in the border zone of the experimental plots strongly suggests an effect of the frequent walking around the permanent quadrats. Long-term studies must be careful to avoid such effects.

The results of this study suggest that the biomass of *Phragmites* slowly increases with the normal management of fen meadows (mowing in September), and that no fast or drastic reduction of this species can be expected from an additional cut in June, at least at base-rich and rather productive sites such as those investigated here. The effects of additional mowing were rather weak; they appeared only after several years, and *Phragmites* was not affected more than the remainder of the vegetation. Additional mowing every two years even had no effect at all. It seems that these treatments can be more effective at sites that are less productive or otherwise unfavourable for *Phragmites* (P. Sturm, pers. comm. and U. Weber, unpublished report). Grazing would certainly reduce *Phragmites* more rapidly than mowing (van Deursen and Drost, 1990; Rozé, 1993), but the trampling damage would probably outweigh the benefit of reducing *Phragmites* (A. Gander, pers. comm.). Actually, since the biomass of *Phragmites* increases only slowly under the current management with mowing in September, the effect of an additional cut in June might be just sufficient to compensate this increase. Whether or not such a measure is recommendable would to a large extent depend on the effects of the additional cut on the botanical and faunistic diversity of these fen meadows (e.g. Klieber et al., 1995; Radlmair and Laußmann, 1997; Vinther & Hald, 2000; Bergamini et al., 2001), which should therefore be investigated separately.

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