Zeitschrift: Bulletin of the Geobotanical Institute ETH

Herausgeber: Geobotanisches Institut, ETH Zürich, Stiftung Rübel

Band: 66 (2000)

Artikel: Mowing in early summer as a remedy to eutrophication in Swiss fen meadows : are really more nutrients removed?

Autor: Güsewell, Sabine / Zorzi, Alvaro / Gigon, Andreas

DOI: https://doi.org/10.5169/seals-377829

Mowing in early summer as a remedy to eutrophication in Swiss fen meadows: are really more nutrients removed?

SABINE GÜSEWELL, ALVARO ZORZI & ANDREAS GIGON

Geobotanisches Institut ETH, Gladbachstrasse 114, 8044 Zürich, Switzerland; guesewell@geobot.umnw.ethz.ch

Summary

1 Nutrient enrichment threatens plant species diversity in many wetlands. More frequent mowing is commonly recommended as a measure to enhance nutrient exports and thus to restore low-productive fen vegetation. While the effectiveness of the measure has repeatedly been verified in severely eutrophicated vegetation, it is still uncertain whether more frequent mowing is also recommendable for fens that are only moderately affected by eutrophication and still support characteristic fen plant communities.

2 To test the effect of more frequent mowing on the vegetation of fens in the Swiss lowlands, mowing experiments were established in 1995 or 1996 in three meadows in nature reserves near Zurich. All experimental plots were mown every year in September (traditional management, control treatment); treated plots were additionally mown in June. Total biomass yields, total amounts of exported N and P, and plant tissue N and P concentrations in late June or late August were compared between treatments in 1999 ($4^{th}/5^{th}$ treatment year). The same comparison was made for plots established in 1999 (1^{st} treatment year).

3 Both in the 1^{st} and in the $4^{th}/5^{th}$ treatment year, additional mowing in June did not affect total biomass yield, but this treatment slightly enhanced the amount of exported N (difference $\leq$ 29%) and significantly increased the export of P (difference $\leq$ 113%). The enhancement of nutrient exports was mostly due to higher nutrient concentrations in September in the treated plots.

4 The effect of additional mowing in June on N and P exports was higher in the 1^{st} than in the $4^{th}/5^{th}$ treatment year (e.g. for P 113% *vs.* 68%), suggesting that the effectiveness of the treatment decreases with time. However, comparison with data from 1997 ($2^{nd}/3^{rd}$ treatment year) showed that treatment effects on N exports fluctuated considerably among years, probably due to the impact of weather conditions on the water level and thus on nitrogen availability to the vegetation.

5 Additional mowing in June can be an effective measure to reduce the availability of nutrients. However, the magnitude of the effects on nutrient exports and biomass production is likely to depend on the nutrient limitation of each specific site.

Keywords: biomass yield, mowing regime, nutrient export, tissue nutrient concentrations, wetland management

Bulletin of the Geobotanical Institute ETH (2000), **66**, 11–24

Introduction

Nutrient enrichment is one of the main factors threatening the species diversity of wetland vegetation in central Europe (Klötzli 1986; Verhoeven *et al.* 1993). Causes of eutrophication include direct fertilisation (Bakker & Olff 1995), atmospheric inputs (Bobbink *et al.* 1998), agricultural run-off (Zelesny 1994), abandonment (Dierssen & Schrautzer 1997), flooding with polluted surface water (Koerselman *et al.* 1993) or drainage (Grootjans *et al.* 1996). Measures to prevent or remedy eutrophication must reduce inputs, enhance outputs or reduce the rate at which nutrients become available within the system (Koerselman & Verhoeven 1995). It has been suggested that management plans should primarily focus on the availability of the most limiting nutrient (Koerselman & Verhoeven 1995).

Many attempts have been made to prevent nutrient inputs into vegetation of high conservation interest (Marti & Müller 1994; van Duren *et al.* 1998), but this is often not completely possible for technical or financial reasons. Moreover, many nature reserves have already been eutrophicated during the last decades, with associated changes in productivity and plant species composition (Fojt & Harding 1995; Verhoeven *et al.* 1996; Bobbink *et al.* 1998). Their species diversity can only be maintained or restored if the eutrophication process is reversed through enhanced nutrient outputs (Pfadenhauer 1989; Klötzli 1991; Pfadenhauer & Klötzli 1996). The most commonly applied measures are mowing and topsoil removal. Topsoil removal may be most effective, but it is also work-intensive and destructive (D. Ramseier, pers. comm.), and therefore less suitable for large-scale application in nature reserves if the only purpose is to remedy eutrophication (but see Beltman *et al.* 1996).

Several experiments have addressed the effects of mowing regime on nutrient outputs (amounts exported with the hay), nutrient budgets or the productivity of the vegetation (Oomes & Altena 1987; Kapfer 1988, 1994, 1996; Gryseels 1989; Schwartze 1992; Oomes & van der Werf 1996; Prach 1996). Most of these experiments took place in severely degraded wetlands, e.g. drained and heavily fertilised fens, eutrophicated reedbeds or meadows abandoned for a long period of time. In these experiments the effects of mowing twice or three times a year were generally positive, with higher nutrient exports, reduced biomass production and enhanced species richness. The effects of frequent mowing are likely to be less favourable at sites that are only moderately eutrophicated and still support the plant communities to be protected. First, less nutrients will be exported since the productivity is lower. Second, plant species adapted to intensive management may be promoted at the expense of species adapted to extensive management (Höfner & Steiner 1987; Briemle & Ellenberg 1994; Kapfer 1994, 1996). Third, perennial species from nutrient-poor sites often rely on internal cycling of nutrients to cover a large fraction of their above-ground nutrient demands (Ganzert & Pfadenhauer 1986; Pfadenhauer & Lütke-Twenhöven 1986; Bernard *et al.* 1988; Aerts *et al.* 1999), and this cycling is prevented by frequent mowing. Additionally, reproduction by seeds may be inhibited (Schopp-Guth *et al.* 1996). Therefore, Kapfer (1987) recommended mowing fen meadows more than once a year only if their biomass yield exceeds 500 g m^{-2} or if characteristic fen species are absent. However, the proposed effects of more frequent mowing on moderately eutrophicated fens must be substantiated by experiments at appropriate sites to verify whether or not these recommendations can be considered a general rule.

Long-term mowing experiments were established in 1995 or 1996 in three litter fen meadows near Zurich (Switzerland). Treated plots, mown both in June and September, were compared to control plots, mown only in September, which is the traditional management of these meadows. Contrary to the experiments mentioned above, our sites were not used agriculturally nor heavily fertilised, but they have been subject to diffuse nutrient inputs and underwent a short period of abandonment before the traditional management was re-introduced for conservation purposes. Unfortunately, regular mowing in autumn has proved insufficient to restore the former mesotrophic conditions and the previous species richness documented, e.g. in Klötzli (1969). Therefore, governmental management guidelines recommend that eutrophicated fen meadows be mown in summer to export more nutrients (Bressoud *et al.* 1992). The aim of our experiments was to assess how additional mowing in early summer would affect nutrient exports.

Measurements of biomass yields and nutrient exports carried out in 1997 ($2^{nd}/3^{rd}$ year of the experiment) showed that 44% more nitrogen and 85% more phosphorus were exported when plots were mown in June compared to control plots (Güsewell 1998). However, such results may vary from year to year. In particular, the effect of additional mowing in summer might be highest in the 1^{st} year of treatment and then decrease progressively because biomass production is reduced in the treated plots (Güsewell 1998) until eventually the same amounts of nutrients are exported from treated and control plots. To test this idea, we determined yields and nutrient exports in 1999 in the experimental plots established in 1995 or 1996 as well as in new plots, mown in June for the first time in 1999. Our hypotheses were (1) that additional nutrient exports would be greater in the 1^{st}-year plots than in the $4^{th}/5^{th}$-year plots, and (2) that the results from 1997 (Güsewell 1998) would be intermediate.

Methods

STUDY SITES AND EXPERIMENTAL DESIGN

Experimental sites and the design have been described in Güsewell (1998). Briefly, sites were fens located on the Swiss Plateau near Zurich, at an altitude of 430–440 m a.s.l., with a long-term average temperature of 8–10 °C and average rainfall of 1000–1100 mm yr^{-1}. Soils were calcareous humic gleysols waterlogged or flooded in winter and early spring, and relatively dry in summer. The vegetation initially belonged to the phytosociological alliance Molinion (dominated by *Molinia caerulea* and various *Carex* species; nomenclature according to Lauber & Wagner 1996), but in some parts sites had become dominated by tall forbs and grasses and by *Phragmites australis* due to eutrophication (alliance Filipendulion). Experimental plots (10 x 10 m^2) were established in a randomised block design so as to include both Molinion and Filipendulion vegetation (two blocks for each type). All plots were mown yearly in early September as part of the normal management and the litter was removed soon after mowing. One plot per block was additionally mown in late June every year while the other plot, only mown in September, served as control plot. Additional mowing started in 1995 in two blocks (one per vegetation type), and in 1996 in the two others.

To compare the results of the long-term experiment with the response of the vegetation in the first year, biomass and nutrient exports were measured in plots that were mown in June only in 1999. Four pairs of 6-m^2 plots were established in patches of homogeneous vegetation with similar species composition and structure to those in the long-term experimental plots (one new pair per block). One randomly chosen plot per pair was mown in late June 1999 together with the long-term experimental plots, the second one served as control plot.

MEASUREMENT OF BIOMASS YIELDS AND NUTRIENT EXPORTS

To determine biomass yields, i.e. the total amount of biomass removed by either treatment, the above-ground biomass of the vegetation was sampled in all plots just before mowing. Thus, treated plots were sampled in late June and late August, but control plots only in late August. All vascular plants were clipped at approximately 2 cm above-ground level in three 0.16-m^2 quadrats per plot. Mosses were not sampled because they were sparse in all plots. Quadrats were arranged systematically at 1-m intervals within the experimental plots. In treated plots the same quadrats were clipped in June and in August so that the sum of both harvests actually represented the total yield of an individual quadrat.

All plant material was dried at 70 °C, weighed and ground. Total nitrogen and phosphorus were extracted using a modified Kjeldahl method (1h digestion at 420 °C with H_2SO_4 98% and a copper sulphate-titane oxide catalyst). Concentrations of N and P in the digests were determined colorimetrically on a flow injection analyser (*Tecator*, Höganäs).

Nutrient (nitrogen or phosphorus) exports in mg m^{-2} were then calculated as DW_{June} * $Concentration_{June}$ + DW_{August} * $Concentration_{August}$ (treated plots), and DW_{August} * $Concentration_{August}$ (control plots; DW, dry weight of the biomass in g m^{-2}; Concentration, tissue N or P concentration in mg g^{-1} DW)

NUTRIENT CONCENTRATIONS IN INDIVIDUAL PLANT SPECIES

To determine whether additional mowing in June over 4 or 5 years had affected the nutrient economy of individual plant species, nitrogen and phosphorus concentrations of the six most frequent species (*Carex acutiformis, Filipendula ulmaria, Lysimachia vulgaris, Molinia caerulea, Phalaris arundinacea* and *Phragmites australis*) were compared between treatments in late June 1999 in the long-term experiment. In treated plots, the plant material harvested to determine biomass yields was sorted to species before drying. Dry weight and nutrient concentrations were determined for the six species individually as described above. The remaining species were lumped together and their nutrient concentrations were also determined, so that nutrient concentrations of the whole sample could be calculated (needed for the calculation of nutrient exports and for comparison with the 1997 data). In the control plots, three 0.16-m^2 quadrats per plot were clipped and the six selected species were sorted. The remaining fraction was not analysed because this was unnecessary for the calculation of nutrient exports. Care was taken not to re-sample locations clipped in June during the August sampling in control plots, so that results on biomass yields were not affected by the June sampling.

DATA ANALYSIS

Means of the three samples per experimental plot were used for statistical testing. Data were log-transformed if necessary to obtain normally distributed residuals. Effects with type I error probabilities of 0.05–0.10 were

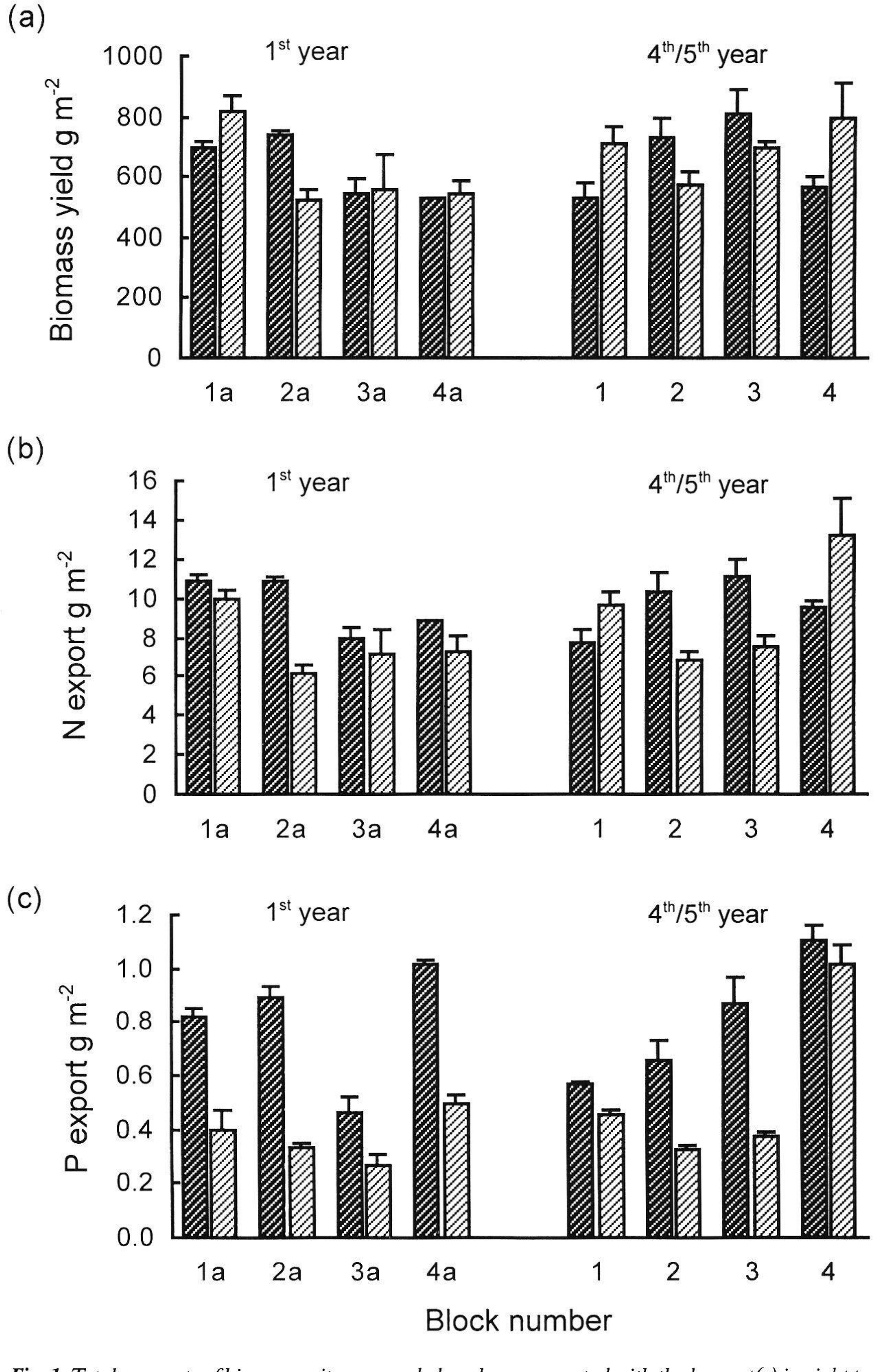

Fig. 1. *Total amounts of biomass, nitrogen and phosphorus exported with the harvest(s) in eight treated plots mown in June and September (dark shading) and eight control plots only mown in September (light shading). 1st year, plots mown in June in 1999 for the first time; 4th/5th year, plots mown in June yearly since 1995 or 1996 (means* ± SE, n = *3).*

Table 1. *Additional amounts of biomass, nitrogen and phosphorus (means ± SE) exported by mowing in June and September as a percentage of the amounts exported by mowing only in September, with the significance of differences (two-way ANOVA; factors treatment and block, only results for treatments shown). 1st year, plots mown in June in 1999 for the first time; 4th/5th year, plots mown in June yearly since 1995 or 1996. Significance levels: **, P < 0.01; °, P < 0.1; ns, P ≥ 0.1*

	Biomass		Nitrogen		Phosphorus	
	1st year	4th/5th year	1st year	4th/5th year	1st year	4th/5th year
Additional export (%)	5 ± 12	-2 ± 15	29 ± 16	12 ± 21	113 ± 19	68 ± 30
$F_{1,3}$	0.17 ns	0.16 ns	4.9 ns	0.30 ns	83.8 **	8.2 °

considered to indicate tendencies which might be relevant for conservation management.

Treatment effects on biomass yields and nutrient exports, as well as on nutrient concentrations in June or August were tested separately for the long-term plots and the new plots by means of two-way ANOVA with the factors treatment and block. The block effect was included in the model, but its significance was not tested for the statistical reasons explained by Sokal & Rohlf (1995, p. 347). Since the June nutrient concentrations in control plots had only been determined for six selected species, weighted average concentrations of these species were compared between treatments here. Nutrient concentrations in individual species were compared qualitatively because missing values (plots in which the species did not occur) prevented statistical testing.

Results

BIOMASS YIELDS AND NUTRIENT EXPORTS

Additional mowing in June did not increase total biomass yields: neither in the 1st nor in the 4th/5th treatment year did the amount of biomass harvested differ between treated and control plots (only mown in September; Fig. 1a, Table 1).

Additional mowing in June slightly increased the amount of nitrogen exported when the treatment was applied for the first time. In all four blocks N export was higher in treated plots than in control plots (Fig. 1b, Table 1). However, the difference between treatments varied considerably among blocks and was marginal in two of them, and thus, the treatment effect was not statistically significant ($P = 0.12$). After plots had been mown in June for 4/5 years, the total amount of N exported with the harvest was even lower than in control plots in two of the four blocks, and mean exports did not differ between treated and control plots.

Additional mowing in June markedly increased the export of phosphorus. In the 1st treatment year, the amount of P exported more than doubled ($P < 0.01$; Fig. 1c, Table 1). After 4/5 years of treatment, P exports from treated plots still exceeded those from control plots in all four blocks (on average 68% higher), but because the magnitude of the treatment effect varied considerably among blocks, this effect was only marginally significant ($P = 0.07$).

NUTRIENT CONCENTRATIONS

After 4/5 years of treatments, the N and P concentrations in the above-ground biomass of individual plant species in June did not differ consistently between treated and control

Table 2. *Nitrogen and phosphorus concentrations and their ratio (mean* ± SE, n = *4) in the above-ground plant biomass of plots mown in June and September and of plots mown only in September, determined (a) for individual plant species in late June and (b) for the whole vegetation in late June and late August of the 1st, 2nd/3rd and 4th/5th treatment year*

	Nitrogen ($mg\ g^{-1}$)		Phosphorus ($mg\ g^{-1}$)		N:P ratio	
	Treated	Control	Treated	Control	Treated	Control
(a) Individual species (4th/5th year, June)						
Carex acutiformis	14.3 ± 1.2	15.4 ± 0.6	1.33 ± 0.37	1.50 ± 0.34	11.9 ± 2.0	11.2 ± 1.8
Filipendula ulmaria	16.0 ± 0.4	14.0 ± 1.2	1.45 ± 0.17	1.34 ± 0.11	11.5 ± 1.2	10.5 ± 0.5
Lysimachia vulgaris	12.7 ± 1.1	12.3 ± 0.6	1.38 ± 0.32	1.36 ± 0.20	10.2 ± 1.3	9.5 ± 0.9
Molinia caerulea	11.8 ± 1.0	13.1 ± 1.3	0.98 ± 0.08	1.04 ± 0.10	12.1 ± 0.7	12.6 ± 0.2
Phalaris arundinacea [a]	15.8	13.9	2.12	1.82	7.5	7.6
Phragmites australis	14.4 ± 0.8	13.8 ± 0.6	1.25 ± 0.24	1.09 ± 0.20	12.4 ± 2.2	13.9 ± 2.0
(b) Whole vegetation						
1st year, June [b]	14.6 ± 0.6		1.39 ± 0.27		11.4 ± 1.6	
1st year, August [b]	17.7 ± 0.8	12.6 ± 0.8	1.08 ± 0.07	0.63 ± 0.07	17.4 ± 1.1	21.7 ± 1.1
2nd/3rd year, June [c]	15.4 ± 0.3	15.5 ± 0.3	1.26 ± 0.04	1.25 ± 0.04	12.8 ± 0.3	13.3 ± 0.3
2nd/3rd year, August [c]	16.9 ± 0.4	12.0 ± 0.4	1.47 ± 0.07	0.80 ± 0.07	12.1 ± 0.8	16.0 ± 0.8
4th/5th year, June [d, e]	13.0 ± 0.3	13.2 ± 0.3	1.21 ± 0.02	1.23 ± 0.02	11.3 ± 0.4	11.4 ± 0.4
4th/5th year, August [d]	18.3 ± 0.7	13.2 ± 0.7	1.05 ± 0.04	0.76 ± 0.04	18.2 ± 0.4	18.9 ± 0.4

[a] Only present in one block. [b] This study, new experiment. [c] Data from 1997 (Güsewell 1998).
[d] This study, long-term experiment. [e] Weighted average of the six species in (a).

plots (Table 2a). Moreover, for *Filipendula ulmaria* and *Lysimachia vulgaris* concentrations were higher in the treated plot of some block(s) and in the control plot of other(s), and differences between plots were often smaller than the variation among samples within plots (data not shown). Thus, even without statistical testing (cf. Methods), it was apparent that additional mowing in June had not affected the nutrient concentrations of individual plant species. Accordingly, nutrient concentrations of the whole vegetation in June (approximated by the weighted average of concentrations in the selected species) did not differ significantly between treatments (Tables 2b and 3).

Even in the absence of significant differences in N and P concentrations, differences in N:P ratios might have been significant, since the N:P ratio would not be affected by random variation in N and P concentrations as long as this variation is similar for both nutrients. Nevertheless, when compared for June, N:P ratios differed little between treatments, being higher in treated plots for three of the species and in control plots for the three other species (Table 2a), with large variation among blocks. Likewise, N:P ra-

*Table 3. Significance of differences in plant tissue nitrogen and phosphorus concentrations (mg g^{-1}) and N:P ratios between plots mown in June and September and plots only mown in September, tested with two-way ANOVA (factors treatment and block, only results for treatments shown). 1st year, plots mown in June in 1999 for the first time; 4th/5th year, plots mown in June yearly since 1995 or 1996. Significance levels: **, P < 0.01; *, P < 0.05; ns, P ≥ 0.1; -, not tested. For means and SE see Table 2*

	Nitrogen		Phosphorus		N:P ratio	
	1st year	4th/5th year	1st year	4th/5th year	1st year	4th/5th year
Late June: $F_{1,3}$	-	3.9 ns	-	1.2 ns	-	0.2 ns
Late August: $F_{1,3}$	26.3 *	37.8 **	48.9 **	19.5 *	77.0 **	0.9 ns

tios of the whole vegetation in June did not differ significantly between treatments (Tables 2b and 3).

In late August, N and P concentrations differed significantly between treated and control plots, both in the 1st year and in the 4th/5th year of treatment (Table 2b and 3). In the 1st year the difference between treated and control plots was greater for P than for N (in relative terms), and therefore N:P ratios were higher in control plots. N:P ratios did not differ between treatments in the long-term experiment because differences between treatments were approximately the same for N as for P.

Discussion

DIFFERENT EFFECTS OF ADDITIONAL MOWING ON BIOMASS, N AND P EXPORTS

The main results of this study are concordant with those of Güsewell (1998). In both studies, additional mowing in June did not enhance the total yield, but it did enhance the

Table 4. Published results on additional amounts of biomass, nitrogen, phosphorus and potassium exported by mowing more frequently (June/July and September/October) as a percentage of amounts exported by mowing only in September/October

			Additional export (%)			
Reference	Vegetation type	Year	Biomass	N	P	K
Kapfer (1987)	Calthion[1]	1982–85	22.5	55.1	60.0	10.6
	Calthion[1]	1982–85	-3.2	18.5	41.7	0.0
	Molinion	1982–85	16.7	27.9	22.2	33.3
Egloff (1986)	Molinion	1981	6.7	49.8	50.2	58.0
	Molinion	1982	-1.2	5.3	8.9	2.7
Schwartze (1992)	Wet grasslands[2]	1987	41.4	25.3	59.1	76.6
	Wet grasslands[2]	1988	33.2	35.0	76.1	22.3
	Wet grasslands[2]	1989	-0.73	10.2	not determined	

[1] Two different sites; data are means of 1982–1985.

[2] Means of ten sites supporting various plant communities (Cynosurion, Calthion, Magnocaricion).

exports of nutrients with stronger effects for phosphorus than for nitrogen. The higher nutrient exports from treated plots were due to higher nutrient concentrations in the hay of treated plots compared with control plots. Nutrient concentrations were higher for two reasons. First, nutrients were "diluted" in the increasing biomass between late June and late August in control plots, whereas treated plots were harvested for the first time in June before this "dilution". Second, nutrient translocation to below-ground parts already occurred in July or August in the control plots (see e.g. Warnke-Grüttner 1990) but not in the treated plots, where no senescence of the re-growth was observed until the second harvest at the end of August.

The additional exports of biomass, N and P found here were basically in the same order of magnitude as those determined by other authors in similar experiments, even though the range of values was broad (Table 4). In these other studies, additional mowing generally enhanced nutrient exports but did often not affect biomass yields, which is consistent with our results. However, in some of the studies total yield was enhanced more than the export of N, and in some other studies the export of N was enhanced more than the export of P (Table 4). Thus the specific effects of additional mowing on biomass yields, N and P exports depend on the site and vary from year to year, so that no general statement on their relative importance is possible.

TEMPORAL FLUCTUATIONS IN THE EFFECTS OF ADDITIONAL MOWING

Our first hypothesis, that treatment effects on the exports of N and P would be stronger in the 1st than in the 4th/5th year, was confirmed: In the 1st year, 29% more N and 113% more P were exported from the treated plots, whereas in the 4th/5th year only 12% more N and 68% more P were exported. However, this decrease in treatment effect was only for a small part due to reduced biomass production in the treated plots: the ratio of yield in treated plots to yield in control plots was only 7% higher in the 1st than in the 4th/5th treatment year. Higher nutrient concentrations in June, as well as greater differences in nutrient concentrations between treated and control plots in late August, also contributed to the stronger treatment effects in the 1st year (cf. Table 2). All these differences were slight, and only their cumulative effect resulted in a clear difference between the 1st and 4th/5th year of treatment.

Our second hypothesis that additional exports in 1997, the 2nd/3rd treatment year, would be intermediate between those for the 1st and for the 4th/5th year was only confirmed for phosphorus. For nitrogen, additional exports in 1997 were higher than those in 1999 in both 1st- and 4th/5th-year plots. Considerable fluctuations in the effects of additional mowing were also observed in other experiments (Kapfer 1988; Bakker & Olff 1995; Oomes *et al.* 1996). Weather conditions probably caused the fluctuation in our experiment. Spring 1999 was unusually wet, and our field sites were flooded until the end of June. This delayed the development of the vegetation, so that yields in June were relatively low, and a higher proportion of the annual growth occurred in July or August. Flooding probably also inhibited nitrogen mineralisation in these base-rich fens (Hauschild & Scheffer 1995), causing low N concentrations in the June biomass in 1999 compared with 1997, and therefore relatively low N exports with the first harvest of treated plots. Higher availability of N in the second part of the summer, after soils became aerated, caused higher N concentrations in August 1999 compared with August 1997. This primarily enhanced N exports from control plots, since biomass yields were much higher there. Higher N availability in July and August would also have strengthened limitation by P (Grootjans *et al.* 1986), which was reflected in lower P concentrations and higher N:P ratios in August (again comparing 1999 with 1997).

We conclude that the effect of additional mowing on the export of a specific nutrient strongly depends on the seasonal pattern of availability of that nutrient, which may be affected by weather conditions. Because of the resulting fluctuations in treatment effects, repeated sampling over several years is necessary to assess these effects with sufficient reliability, as has been shown elsewhere for effects on plant species composition (Bakker *et al.* 1996; Güsewell *et al.* 1998).

NO CLEAR EFFECTS OF ADDITIONAL MOWING ON NITROGEN AND PHOSPHORUS AVAILABILITY

Since additional mowing affected P exports more strongly than N exports in our experiment, this treatment might modify the relative availability of N and P to plants in the long term. According to Koerselman & Meuleman (1996), such a change should be reflected in a higher N:P ratio in the plant biomass, but contrary to this expectation, no difference in N:P ratios was found between treated and control plots in late June. Since N:P ratios are a rather rough indicator of nutrient limitation or relative nutrient availability (Wassen *et al.* 1995; Pegtel *et al.* 1996), the absence of difference only means that additional mowing had not yet depleted the nutrient pools sufficiently to cause a clear shift in nutrient limitation.

This negative result is not surprising for several reasons. First, the experimental plots had already been mown regularly in September before the experiments, so that plants probably had no extensive below-ground stores that could have been depleted by the treatment, contrary to unmanaged sites (e.g. Gryseels 1989). Second, total amounts of nutrients stored in the soil greatly exceeded the annual exports by mowing (Kapfer 1988; Bakker 1989; van Oorschot *et al.* 1997). Third, mineralisation rates, an important determinant of nutrient availability in fens (Koerselman & Verhoeven 1995) might even have been enhanced in treated plots after the June cut because of stronger fluctuations in soil temperature and humidity (Schwartze 1992). Finally, nutrient inputs to our sites remained unchanged, contrary to mowing experiments where treatments were concurrent with the cessation of fertiliser application (Egloff 1986; Olff *et al.* 1994; Pegtel *et al.* 1996). If our sites received sufficient P inputs, e.g. through run-off or ditch water, it seems plausible that even the significant effects of additional mowing on P budgets were in fact marginal, and that nutrient availability for the vegetation was hardly reduced by the treatment.

Treatment effects on K exports or K availability were not determined in this study. We assumed K not to be limiting at our sites because of their impermeable loamy soil, as K limitation normally occurs only on drained peat or permeable sandy soils (Koerselman & Verhoeven 1995; Kapfer 1996). Absence of K limitation was also suggested by the relatively high plant tissue K concentrations and low N:K ratios as determined in earlier studies at the same or nearby sites with similar vegetation (Brülisauer & Klötzli 1998; S. Güsewell, unpubl. data). At sites where additional mowing is likely to cause or strengthen K limitation, it might rapidly reduce the biomass production without enhancing the plant species diversity (Kapfer 1994, 1996; Oomes & van der Werf 1996; Oomes *et al.* 1996). Therefore, it is essential to determine K exports at potentially K-limited sites.

Consequences for management

The following conclusions can be drawn for the management of moderately eutrophicated fen meadows: more frequent mowing enhances nutrient exports, but the effect differs among nutrients. The enhancement of nutrient exports is still noticeable after several treatment years, but its magnitude tends to decrease over time and can moreover fluctuate considerably from year to year.

In this study, the additional export of P exceeded that of N in relative terms so that the measure would affect the biomass production more rapidly in P-limited than in N-limited vegetation. Since it has been suggested that biomass production in regularly mown prealpine fens is primarily limited by P (and possibly K) rather than by N (Egloff 1983, 1987; Zelesny 1994; Kapfer 1996), more frequent mowing seems appropriate to remedy eutrophication. However, additional nutrient exports are small compared with the pools, so that a return to oligotrophic conditions cannot be expected within a few years (Kapfer 1994, 1996). In this experiment, the rapidly reduced biomass production in treated plots (Güsewell 1998) was probably due to the direct effect of mowing on plant growth, and not to nutrient depletion in the soil. Therefore, it is to be expected that biomass production would increase again as soon as the treatment is discontinued. Whether continued mowing in June is, indeed, desirable at a particular site from the point of view of nature conservation also depends on various other aspects, such as possible damage to soils, disturbance, costs, and the direct effects of mowing on rare plant or animal species (Detzel 1984; Huemer 1996). These other aspects also need to be considered in decisions on the management of moderately eutrophicated fen meadows.

Acknowledgements

We are grateful to the nature conservation authorities of the Zurich Canton and to the landowners for allowing experiments to be carried out on private land in nature reserves, as well as to S. Bertschinger, T. Fotsch and T. Weber for mowing the experimental plots, and to A. Gerster, M. Hofbauer and R. Trachsler for assisting with laboratory work. We also thank F. Klötzli for advice in the initial phase of the experiment and J. Kollmann as well as three anonymous referees for their helpful comments on the manuscript. C. Bucher kindly improved the English text. The research was supported financially by the Swiss Federal Agency for Environment, Forest and Landscape (BUWAL).

References

Aerts, R., Verhoeven, J.T.A. & Whigham, D.F. (1999) Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology,* **80,** 2170–2181.

Bakker, J.P. (1989) Nature management by grazing and cutting. *Geobotany,* **14,** 1–400.

Bakker, J.P. & Olff, H. (1995) Nutrient dynamics during restoration of fen meadows by haymaking without fertiliser application. *Restoration of Temperate Wetlands* (eds. B.D. Wheeler, S.C. Shaw, W.J. Fojt & R.R. Allan), pp. 143–166. Wiley, Chichester.

Bakker, J.P., Olff, H., Willems, J.H. & Zobel, M. (1996) Why do we need permanent plots in the study of long-term vegetation dynamics? *Journal of Vegetation Science,* **7,** 147–156.

Beltman, B., van den Broek, T., Bloemen, S. & Witsel, C. (1996) Effects of restoration measures on nutrient availability in a formerly nutrient-poor floating fen after acidification and eutrophication. *Biological Conservation,* **78,** 271–277.

Bernard, J.M., Solander, D. & Kvet, J. (1988) Production and nutrient dynamics in *Carex* wetlands. *Aquatic Botany,* **39,** 125–147.

Bobbink, R., Hornung, M. & Roelofs, J.G.M. (1998) The effects of air-borne nitrogen pollutants on species diversity in natural and seminatural European vegetation – a review. *Journal of Ecology,* **86,** 717–738.

Bressoud, B., Broggi, M.F., Hintermann, U., Grünig, A., Marti, K., Schlegel, H. & Theis, E. (1992) Anforderungen beim Schutz der Flachmoore von nationaler Bedeutung. *Handbuch Moorschutz in der Schweiz Band II* (eds. Büro für Siedlungs- und Umweltplanung Zürich & Atelier Jäger Vaduz), Beitrag 1.1.2. BUWAL, Bern.

Briemle, G. & Ellenberg, H. (1994) Zur Mahdverträglichkeit von Grünlandpflanzen. *Natur und Landschaft,* **69,** 139–147.

Brülisauer, A. & Klötzli, F. (1998) Habitat factors related to the invasion of reeds (*Phragmites australis*) into wet meadows of the Swiss Midlands. *Zeitschrift für Ökologie und Naturschutz,* **7,** 125–136.

Detzel, P. (1984) Die Auswirkungen der Mahd auf die Heuschreckenfauna von Niedermoorwiesen. *Veröffentlichungen für Naturschutz und Landschaftspflege Baden-Württemberg,* **59/60,** 345–360.

Dierssen, K. & Schrautzer, J. (1997) Wie sinnvoll ist ein Rückzug der Landwirtschaft aus der Fläche? Aspekte des Naturschutzes sowie der Landnutzung in intensiv bewirtschafteten agrarischen Räumen. *Laufener Seminarbeiträge,* **1/97,** 93–104.

Egloff, T. (1983) Der Phosphor als primär limitierender Nährstoff in Streuwiesen (Molinion). Düngungsexperiment im unteren Reusstal. *Berichte des Geobotanischen Instituts ETH, Stiftung Rübel, Zürich,* **50,** 119–148.

Egloff, T. (1986) Auswirkungen und Beseitigung von Düngungseinflüssen auf Streuwiesen. Eutrophierungssimulation und Regenerationsexperimente im nördlichen Schweizer Mittelland. *Veröffentlichungen des Geobotanischen Instituts ETH, Stiftung Rübel, Zürich,* **89,** 1–183.

Egloff, T. (1987) Gefährdet wirklich der Stickstoff (aus der Luft) die letzten Streuwiesen? *Natur und Landschaft,* **62,** 476–479.

Fojt, W. & Harding, M. (1995) Thirty years of change in the vegetation communities of three valley mires in Suffolk, England. *Journal of Applied Ecology,* **32,** 561–577.

Ganzert, C. & Pfadenhauer, J. (1986) Seasonal dynamics of shoot nutrients in *Schoenus ferrugineus* (Cyperaceae). *Holarctic Ecology,* **9,** 137–142.

Grootjans, A.P., Schipper, P.C. & van der Windt, H.J. (1986) Influence of drainage on N-mineralisation and vegetation response in wet meadows. II. *Cirsio-Molinietum* stands. *Acta Oecologica,* **7,** 3–14.

Grootjans, A.P., Fresco, L.F.M., de Leeuw, C.C. & Schipper, P.C. (1996) Degeneration of species-rich *Calthion palustris* hay meadows: some considerations on the community concept. *Journal of Vegetation Science,* **7,** 185–194.

Gryseels, M. (1989) Nature management experiments in a derelict reedmarsh. II. Effects of summer mowing. *Biological Conservation,* **48,** 85–99.

Güsewell, S. (1998) Does mowing in summer reduce the abundance of *Phragmites australis* in fen meadows? *Bulletin of the Geobotanical Institute ETH,* **64,** 23–35.

Güsewell, S., Buttler, A. & Klötzli, F. (1998) Short-term and long-term effects of management on the vegetation of two calcareous fens. *Journal of Vegetation Science,* **9,** 861-872.

Hauschild, J. & Scheffer, B. (1995) Zur Nitratbildung in Niedermoorböden in Abhängigkeit der Bodenfeuchte (Brutversuche). *Zeitschrift für Kulturtechnik und Landesentwicklung,* **36,** 151–152.

Höfner, I. & Steiner, G.M. (1987) Auswirkungen von Mahd und Grundwasserentnahme auf ein Kopfbinsenmoor. *Erfassung und Bewertung anthropogener Vegetationsveränderungen* (eds. R. Schubert & W. Hilbig), pp. 75–91. Martin-Luther-Universität, Halle-Wittenberg.

Huemer, P. (1996) Frühzeitige Mahd, ein bedeutender Gefährdungsfaktor für Schmetterlinge der Streuwiesen (NSG Rheindelta, Vorarlberg, Österreich). *Vorarlberger Naturschau, Dornbirn,* **1,** 265–300.

Kapfer, A. (1987) Untersuchungen zur Renaturierung ehemaliger Streuwiesen im südwestdeutschen Alpenvorland – erste Tendenzen nach 4 Versuchsjahren. *Erfassung und Bewertung anthropogener Vegetationsveränderungen* (eds. R. Schubert & W. Hilbig), pp. 179–215. Martin-Luther-Universität, Halle-Wittenberg.

Kapfer, A. (1988) Versuche zur Renaturierung gedüngten Feuchtgrünlandes. Aushagerung und Vegetationsentwicklung. *Dissertationes Botanicae,* **120,** 1–144.

Kapfer, A. (1994) Erfolgskontrolle bei Renaturierungsmaßnahmen im Feuchtgrünland. *Schriftenreihe für Landschaftspflege und Naturschutz,* **40,** 125–142.

Kapfer, A. (1996) Regeneration artenreichen Feuchtgrünlandes im baden-württembergischen Alpenvorland - eine Bilanz nach 12 Versuchsjahren. *Veröffentlichungen Projekt "Angewandte Ökologie"*, **16**, 247–254.

Klötzli, F. (1969) Die Grundwasserbeziehungen der Streu- und Moorwiesen im nördlichen Schweizer Mittelland. *Beiträge zur Geobotanischen Landesaufnahme der Schweiz*, **52**, 1–296.

Klötzli, F. (1986) Tendenzen zur Eutrophierung in Feuchtgebieten. *Veröffentlichungen des Geobotanischen Instituts ETH, Stiftung Rübel, Zürich*, **87**, 343–361.

Klötzli, F. (1991) Möglichkeiten und erste Ergebnisse mitteleuropäischer Renaturierungen. *Verhandlungen der Gesellschaft für Ökologie*, **20**, 229–242.

Koerselman, W. & Meuleman, A.F.M. (1996) The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology*, **33**, 1441–1450.

Koerselman, W. & Verhoeven, J.T.A. (1995) Eutrophication of fen ecosystems: external and internal nutrient sources and restoration strategies. *Restoration of Temperate Wetlands* (eds. B.D. Wheeler, S.C. Shaw, W.J. Fojt & R.R. Allan), pp. 91–112. Wiley, Chichester.

Koerselman, W., van Kerkhoven, M.B. & Verhoeven, J.T.A. (1993) Release of inorganic N, P and K in peat soils; effect of temperature, water chemistry and water level. *Biogeochemistry*, **20**, 63–81.

Lauber, K. & Wagner, G. (1996) *Flora Helvetica*. Paul Haupt, Bern.

Marti, K. & Müller, R. (1994) *Pufferzonen für Moorbiotope. Schriftenreihe Umwelt 213*. BUWAL, Bern.

Olff, H., Berendse, F. & de Visser, W. (1994) Changes in nitrogen mineralization, tissue nitrogen concentrations and biomass compartimentation after cessation of fertilizer application to mown grassland. *Journal of Ecology*, **82**, 611–620.

Oomes, M.J.M. & Altena, H.J. (1987) Changes in the vegetation of extensively used agricultural grassland caused by cutting date and cutting frequency. *Erfassung und Bewertung anthropogener Vegetationsveränderungen* (eds. R. Schubert & W. Hilbig), pp. 75–91. Martin-Luther-Universität, Halle-Wittenberg.

Oomes, M.J.M. & van der Werf, A. (1996) Restoration of species diversity in grasslands: The effect of grassland management and changes in ground water level. *Acta Botanica Gallica*, **143**, 451–461.

Oomes, M.J.M., Olff, H. & Altena, H.J. (1996) Effects of vegetation management and raising the water table on nutrient dynamics and vegetation change in a wet grassland. *Journal of Applied Ecology*, **33**, 576–588.

Pegtel, D.M., Bakker, J.P., Verweij, G.L. & Fresco, L.F.M. (1996) N, K and P deficiency in chronosequential cut summer-dry grasslands on gley podzol after cessation of fertilizer application. *Plant and Soil*, **178**, 121–131.

Pfadenhauer, J. (1989) Gedanken zur Pflege und Bewirtschaftung voralpiner Streuwiesen aus vegetationskundlicher Sicht. *Schriftenreihe des Bayerischen Landesamtes für Umweltschutz, München*, **95**, 25–42.

Pfadenhauer, J. & Lütke-Twenhöven, F. (1986) Nährstoffökologie von *Molinia coerulea* und *Carex acutiformis* auf baumfreien Niedermooren des Alpenvorlandes. *Flora*, **178**, 257–166.

Pfadenhauer, J. & Klötzli, F. (1996) Restoration experiments in middle European wet terrestrial ecosystems: an overview. *Vegetatio*, **126**, 101–115.

Prach, K. (1996) Degradation and restoration of wet and moist meadows in the Czech Republic: general trends and case studies. *Acta Botanica Gallica*, **143**, 441–449.

Rodewald-Rudescu, L. (1974) *Das Schilfrohr* (Phragmites communis *Trinius*). Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Schopp-Guth, A., Maas, D. & Pfadenhauer, J. (1996) Influence of management on the seed production and seed bank of calcareous fen species. *Journal of Vegetation Science*, **5**, 569–578.

Schwartze, P. (1992) Einfluss unterschiedlicher Pflegemassnahmen auf Vegetation, Stickstoffverfügbarkeit und Aufwuchs nordwestdeutscher Feuchtgrünlandgesellschaften. *Dissertationes Botanicae*, **183**, 1–204.

Sokal, R.R. & Rohlf, J. (1995) *Biometry*. Freeman, New York.

Van Duren, I.C., Strykstra, R.J., Grootjans, A.P., ter Heerdt, G.N.J. & Pegtel, D.M. (1998) A multidisciplinary evaluation of restoration measures in a degraded *Cirsio-Molinietum* fen meadow. *Applied Vegetation Science*, **1**, 115–130.

Van Oorschot, M., Robbemont, E., Boerstel, M., van Strien, I. & van Kerkhoven-Schmitz, M. (1997) Effects of enhanced nutrient availability on plant and soil nutrient dynamics in two English riverine ecosystems. *Journal of Ecology,* **85,** 167–179.

Verhoeven, J.T.A., Beltman, B. & de Caluwe, H. (1996) Changes in plant biomass in fens in the Vechtplassen area, as related to nutrient enrichment. *Netherlands Journal of Aquatic Ecology,* **30,** 227–237.

Verhoeven, J.T.A., Kemmers, R.H. & Koerselman, W. (1993) Nutrient enrichment of freshwater wetlands. *Landscape Ecology of a Stressed Environment* (eds. C.C. Vos & P. Opdam), pp. 33–59. Chapman & Hall, London.

Warnke-Grüttner, R. (1990) Ökologische Untersuchungen zum Nährstoff- und Wasserhaushalt in Niedermooren des westlichen Bodenseegebiets. *Dissertationes Botanicae,* **148,** 1–214.

Wassen, M.J., Olde Venterink, H.G.M. & de Swart, E.O.A.M. (1995) Nutrient concentrations in mire vegetation as a measure of nutrient limitation in mire ecosystems. *Journal of Vegetation Science,* **6,** 5–16.

Zelesny, H. (1994) Vegetationskundliche und nährstoffökologische Untersuchungen im Übergangsbereich von Mehrschnitt-Wirtschaftsgrünland zu Streuwiese im Württembergischen Alpenvorland. *Dissertationes Botanicae,* **211,** 1–243.

Received 22 February 2000
Revised version accepted 11 May 2000