



Dynamics of common reed (*Phragmites australis* Trin.) in Swiss fens with different management

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Abstract

Dynamics of common reed (*Phragmites australis* Trin.) in Central Europe have so far mostly been investigated in connection with studies on reed 'die-back' along lake shores. However, there has recently been increasing concern about reed expansion at terrestrial sites, such as fens and wet grasslands. In this paper we report on the results of four separate studies which monitored reed dynamics in Swiss fens with various mowing regimes over a period of 4 to 15 years. The first study compared unmown plots with plots mown in winter in a triennial rotation; the second one included unmown plots, plots mown in summer, and plots mown in winter; the third one compared plots mown in June and September with plots only mown in September; the fourth study investigated only plots mown in September. Shoot number and shoot size were recorded in permanent quadrats. In all studies the performance of *P. australis* fluctuated without trend or tended to decrease during the period investigated. The decreasing tendency concerned shoot size rather than shoot number, and within a given study it was stronger for plots with initially taller shoots. The various mowing regimes did hardly influence these changes. Mowing in winter every three years reduced shoot size in the year after mowing, but not on the long term. Mowing every year in late summer reduced the shoot size compared with unmown plots on the short term, but this effect almost disappeared on the long term, after mowing had become biennial. Mowing in June (in addition to in September) caused no noticeable effects. We conclude that other factors (e.g. weather conditions, competition, or population processes) are more important than management in determining the abundance of *P. australis* in the fen communities investigated here, although long-term effects of mowing in summer still need more investigation. As a practical consequence it is suggested that at sites which are not strongly dominated by *P. australis*, as most of those investigated here, reducing the performance of this species should not constitute a major target of nature conservation management, nor can its dynamics be used as an indicator for management success before underlying causes are better understood.

Introduction

Dynamics of common reed (*Phragmites australis* Trin.) was the object of numerous investigations during the last decades. Reed monitoring can be motivated by economic or by scientific interests. Economic interests are relevant where reed is harvested for industrial use (Granéli, 1990; Haslam, 1995) or where it impedes other human activities (Husák 1978; Khat-

tab and El-Gharably 1990). From a scientific point of view, reed-environment or reed-herbivore interactions have been found particularly interesting (Klötzli, 1971; Mook and Van der Toorn, 1985; Tschamtké, 1988). In addition, many studies on reed dynamics have been carried out in the context of wetland management for nature conservation (Bibby and Lunn, 1982; Gryseels, 1989a, b; Ostendorp, 1995), their pur-

pose being often to assess how human impacts directly or indirectly affect this dynamics.

Two opposite trends gave rise to concern in this context. In Central Europe most studies were related to the problem of reed 'die-back' along lake shores (Ostendorp, 1989; Van der Putten, 1997). They quantified changes in reed populations (Stark and Dienst, 1989; Krumscheid et al., 1989; Schmieder and Pier, 2000, this volume), searched for causal relationships (Klötzli, 1971, 1974; Boar et al., 1989; Fuchs, 1993; Krauss, 1993; Cízková et al., 1996; Van der Putten, 1997), or evaluated the effectiveness of measures for protection or restoration (Klötzli and Züst, 1973; Ostendorp, 1995).

At the same time there has also been increasing concern about reed encroachment in areas where this species was formerly absent, such as freshwater marshes in parts of the USA (Marks et al., 1994), or about increasing dominance in areas where *P. australis* had long been present with only low abundance, e.g. fens and wet grasslands in Central Europe (Klötzli, 1986; Güsewell and Klötzli, 1998). Reed expansion is generally considered undesirable in nature reserves because stands dominated by *P. australis* generally have lower plant species richness than the initial marsh or fen vegetation (Wheeler and Giller, 1982; Güsewell and Klötzli, 1998; Keller, 2000). Also, the tall growth form of *P. australis* makes invaded wetlands unsuitable for animal species requiring an open vegetation structure.

In opposition to reed die-back, which has been extensively investigated and well-documented in scientific literature, detailed studies on reed expansion in fens or wet grasslands are scarce. Available evidence for this expansion is rather qualitative and contained in unpublished studies or reports (e.g. by Marti and Müller, Zürich, 1993). Likewise, the assumption that reed expansion is triggered by eutrophication or abandonment is plausible given the biology of this species (De Kroon and Bobbink, 1997) and has also been supported by field surveys (Briemle and Ellenberg, 1994; Brülisauer and Klötzli, 1998), but not yet demonstrated in experimental work. Finally, the recommendation to restore reed-invaded fen meadows by mowing in summer (Bressoud et al., 1992; Van Diggelen et al., 1996) is, again, based on circumstantial evidence and still needs experimental confirmation (Güsewell, 1998).

In this contribution we report on the results of four studies of reed dynamics in calcareous fens or wet grasslands of the Swiss Plateau. Two of the studies

were undertaken in the eighties as part of a broader monitoring programme in a large wetland nature reserve. The two others started in 1995 specifically to investigate reed dynamics in fen meadows. Our aim was to address the following questions:

- How does the performance (shoot number and size) of *P. australis* change at these sites?
- How does mowing at different times and frequencies affect the performance of *P. australis*?

We further examine whether reed dynamics appears to depend on site conditions, in particular nutrient availability or water level, within the range found at our study sites. Finally we draw some conclusions for management and monitoring.

Methods

Field sites

Reed dynamics was investigated in several wetlands of the 'Plateau', the lowland part of Switzerland (Central Europe), at an altitude of 430–550 m (Figure 1). The average annual temperature of the area is 8–10 °C (winter mean temperature around 0 °C, late frosts until April), the average annual rainfall is 900–1200 mm.

Two studies were carried out on the southern shore of Lake Neuchâtel, a meso-eutrophic lake in the western part of the Swiss Plateau. A large wetland area called 'Grande Cariçaie' developed here after the lake level had been lowered by about 3 m in 1869 (Buttler et al., 1985). This wetland is separated from the higher lying farmland by a forested slope and a fringe of alluvial forest, and therefore well-protected against nutrient run-off. Soils are all highly calcareous and consist of gleysols bearing an organic material layer of various thickness. Some parts of the wetland are frequently inundated by lake water and support high-productive reed or tall-sedge vegetation. Other parts are isolated from the lake by a forested ridge or by higher elevation, and fed by rainwater, small rivulets, run-off from the slope, or groundwater. These sites are water-logged in winter and fairly dry in summer (groundwater level up to –100 cm) and support various types of mesotrophic rich-fen communities. Shallow ponds with eutrophic floating or emergent vegetation occur locally on the lakeward side of the wetland. Study 1 encompassed most of these vegetation types, with two large experimental sites extending from the edge of the alluvial forest to the lakeside (Cheyres; coordinates on the Swiss national grid:

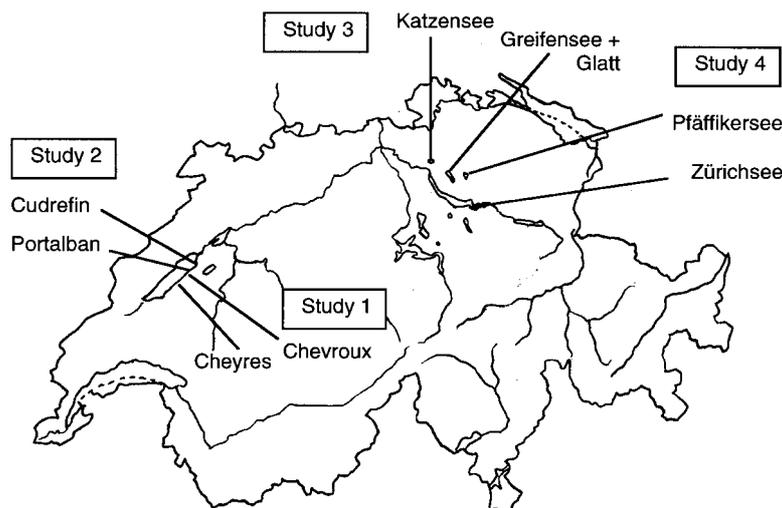


Figure 1. Location of the study sites on the Swiss Plateau.

550°800 / 186°300 and Chevroux; 560°000 / 194°500). Study 2 took place at two fairly dry locations: Cudrefin (569°900 / 203°000), dominated by various small *Carex* species, and Portalban (563°400 / 197°100), dominated by *Schoenus nigricans* and *Cladium mariscus*. All sites had been unmanaged for at least 20 years before the beginning of the experiments. The zone surrounding the experimental plots of study 2 remained unmown throughout the experiment.

The two other studies investigated fen meadows (size: 1–3 ha) near Zürich in the north-eastern part of the Swiss Plateau. Sites are part of lakeside wetlands, except the site 'Katzenssee', located in a swampy basin. Soils range from peat to humic gleysols and are all base-rich. They are water-logged in winter and fairly dry in summer (groundwater level –50 to –100 cm). Most sites receive nutrients from adjacent intensively used farmland. Depending on these inputs the vegetation ranged from mesotrophic to eutrophic types and included characteristic plant communities of rich fens or litter meadows as well as tall-herb stands (alliances *Caricion davallianae*, *Molinion*, and *Filipendulion*, respectively). All sites had been mown yearly in September or October for several years before monitoring started, but some sites had gone through a period of abandonment earlier. Study 3 was carried out at three locations: 'Greifensee' (692°550 / 247°750), dominated by *Molinia caerulea* and various *Carex* species; 'Katzenssee' (680°550 / 254°100), dominated by *Molinia caerulea*, *Carex acutiformis*, *C. panicea*, *C. elata*, *Juncus subnodulosus* and various tall forbs,

and 'Glatt' (691°950/247°650), dominated by *Phragmites australis*, *Carex acutiformis*, *Phalaris arundinacea* and *Solidago gigantea*. Study 4 monitored two pairs of adjacent meadows dominated by *Molinia caerulea* near lakes Pfäffikersee (702°200 / 244°600) and Zürichsee (702°300 / 229°100), the drier ones (P1, Z1) with small *Carex* species, the wetter ones (P2, Z2) with *Schoenus ferrugineus* (nomenclature according to Lauber and Wagner, 1996).

Field design and sampling

Study 1: Mowing in winter every three years

Large parts of the 'Grande Cariçaie' have been mown every three years in winter (October–March) since 1984 as part of an ongoing large-scale management scheme. To this end the wetland area (350 ha in total) was subdivided in plots of 2–3 ha, and a third of these plots was mown every year with a special caterpillar-machine, which immediately removed the litter. To assess the effects of mowing on the vegetation and particularly on *Phragmites*, two unmown control areas were designated in Cheyres (3.2 ha) and in Chevroux (44.9 ha) when management started. Pairs of permanent quadrats (3 m × 5 m) with comparable species composition were arbitrarily placed in the mown zones and the control areas, so as to represent all vegetation types. Additional quadrats were placed in the mown zone of Cheyres where some wet vegetation types occurred without being represented in the control area. The abundance of *Phragmites* was recorded every year in September or October by counting all living shoots

in three subplots of 1 m² (randomly selected within the permanent quadrats every year) and measuring the length and basal diameter of ten shoots. These shoots were selected by 'blindly' taking shoots at 3–5 points within the permanent quadrat. This procedure overestimates the mean shoot size since poorly developed shoots tend to be excluded, but it yields comparable results among years. In 1991, records were carried out by a different investigator who sampled shoots randomly, including poorly developed ones; these records were not included in data analysis.

Study 2: Mowing in summer or in winter

Three blocks, each with three experimental plots (11 × 11 or 13 × 13 m²), were established in 1982 in Cudrefin and in Portalban, respectively. One plot per block was mown in summer (August), one in winter (January–February), and one was left unmown. Treatments were allocated randomly within blocks. Mowing was carried out with a portable machine, and the litter was removed manually. Management was annual from 1982 to 1987, and biennial since then (Buttler, 1992; Güsewell et al., 1998). The diameter of all living reed shoots was measured in early August every year from 1983 to 1987 and from 1995 to 1997 within three permanent 1-m² quadrats which had been randomly placed along the line bordering a 5 × 5 m² subplot in the centre of each experimental plot. Shoot length was also measured from 1995 to 1997 for biomass estimation (see below).

Study 3: Mowing in June in addition to mowing in September

This mowing experiment started in 1995 and comprised in total six blocks (1–3 per location), each with three experimental plots (10 × 10 m²). All plots were mown yearly in September by farmers who removed the litter soon after mowing, except in particularly wet years. One plot per block was additionally mown in late June every year, one plot every two years, and one was never mown in June. The additional mowing was carried out with a portable machine, and the litter was removed mechanically at the driest site (Greifensee), manually at the two others. Twelve permanent quadrats (1 m²) were placed in the central part of each experimental plot. Shoots were counted in all quadrats; their length and diameter were measured in three of the quadrats. At site 'Glatt' additional mowing started only in 1996 (due to the destruction of the plots established in 1995) and the treatment 'additional mowing every two years' was missing because

the remaining homogeneous area was too small for three plots. Therefore, this site (one block) was excluded from the analysis of treatment effects, but its control plot was included in the calculation of mean trends in plots without additional mowing.

Study 4: Mowing in September

Between 6 and 10 permanent quadrats (1 × 1 m²) were placed along two parallel transects within each site. Transects followed gradients in the abundance of *P. australis*, i.e. reached from a zone with higher abundance to a zone with lower abundance. We chose to place our quadrats on such transitions because change, if any, seemed most likely to occur here. The length and diameter of all shoots was determined in each quadrat in 1995, 1997 and 1998. Because six of the quadrats at site P2 were not recorded in 1998, they were excluded from data analysis.

All studies: measurements and biomass estimation

In all studies shoot length was measured from soil surface to the base of the uppermost leaf (at the base of the panicle, if present). The basal diameter was measured in the middle of the internode situated at approximately 1/4 of the shoot length (studies 1 and 2) or in the middle of the second internode (studies 3 and 4) – trials showed very similar results for the two procedures (Güsewell, unpublished). The aboveground biomass of *P. australis* (gm⁻²) was estimated as a log-linear function of the product of shoot number, mean shoot diameter and mean shoot length (Güsewell and Klötzli, 1998). Biomass could not be estimated for study 1 since no shoots had been sampled here to determine the regression parameters. In study 2, aboveground biomass had been determined by direct sampling in 1983–1986, but only in two blocks per location (Buttler, 1987); the aboveground biomass of the other species was also sampled (Güsewell et al., 1998).

Data analysis

Mean values per permanent quadrat (studies 1 and 4) or per experimental plot (studies 2 and 3) were used for data analysis. Shoot numbers were square-root transformed, and aboveground biomass was log-transformed, whereas shoot length and diameter met the requirements for parametric tests without transformation. Since tendencies may be relevant for management, we considered (cautiously) even marginally significant trends or treatment effects ($p < 0.1$)

Response function analysis (Mead, 1988) was used in all studies to analyse trends in the performance of *P. australis* during the period investigated. For each permanent quadrat (studies 1 and 4) or experimental plot (studies 2 and 3) a linear regression against years was calculated with each variable (first year of the study = 0, second year = 1 etc.). The slopes of the regression lines represented the mean change per year. T-Tests were performed on these slopes to test for significant trends. In studies 2 and 3, only data from control plots were used for these t-tests, and two-way analyses of variance (factors treatment and block) were performed to test for significant treatment effects on the direction or rate of change.

In study 1 treatment effects could not be tested statistically because the unmown plots were not replicated within locations; mown and unmown plots were only compared qualitatively. Quadrats from the mown zone in Cheyres that had no equivalent in the unmown zone were excluded from this comparison. In order to examine whether the triennial mowing regime caused short-term fluctuations (i.e. three-years cycles) in reed performance we averaged for each quadrat all values measured in either the first, second or third year after mowing. The effect of time was then tested with univariate repeated measures Anova (Greenhouse Geisser adjustment). In study 2 short-term effects of mowing (1983–1986) appeared likely to differ from long-term effects (1983–1997) because different processes could be at work (e.g. stimulation of shoot sprouting after litter removal versus depletion of belowground reserves) and because the mowing regime changed from annual to biennial after 1986. Short-term effects were analysed as described before, whereas for long-term effects the difference between the mean of the first two years (1983–1984) and the mean of the last three years (1995–1997) was used as ‘slope’ in the response function analysis.

Finally we also examined whether the rate of change (given by the regression slopes) depended on reed performance at the start of the study (approximated by the intercept of the regression to avoid excessive deviations due to annual fluctuations). For this exploratory analysis we pooled data from the different locations within each study and did not carry out statistical tests because their validity would have been questionable after pooling.

Table 1. Short-term effects of mowing every three years in winter on the performance of *Phragmites australis* at the two locations of study 1: Mean shoot number and size in the mown permanent quadrats ($n = 6$) in the first, second and third year after mowing, as well as s.e. and significance of differences calculated with univariate repeated measures Anova (p). Shoot numbers were square-root transformed.

	Year after mowing	Sqrt shoot number	Shoot length	Basal diameter
Cheyres	1	3.3 ± 0.1	163.8 ± 3.2	4.91 ± 0.08
	2	3.4 ± 0.1	173.8 ± 3.2	4.71 ± 0.08
	3	3.0 ± 0.1	183.5 ± 3.2	4.97 ± 0.08
	p	< 0.1	< 0.01	< 0.1
Chevroux	1	3.8 ± 0.1	197.5 ± 3.5	5.66 ± 0.06
	2	3.6 ± 0.1	212.3 ± 3.5	5.74 ± 0.06
	3	3.5 ± 0.1	206.7 ± 3.5	5.81 ± 0.06
	p	ns*	< 0.05	ns

* ns = not significant ($p > 0.1$).

Results

Study 1: Mowing in winter every three years

The performance of *P. australis*, measured as the number and size of living shoots, fluctuated considerably among years at both locations and with both treatments (Figure 2). The effects of mowing could not be tested for significance (cf. methods), but it is apparent on Figure 2 that reed dynamics in mown and unmown plots did not differ to any significant extent: not only were there no obvious differences in long-term trends; even mid-term fluctuations were generally similar. A short-time effect of mowing was found when comparing values of shoot length measured one, two or three years after mowing: shoots were significantly shorter in the year after mowing than in subsequent years (Table 1). These cycles were not apparent in Figure 2 because the different plots were mown in different years. The shoot number was lowest and the basal diameter highest in the third year after mowing, but differences between the first and second year after mowing were not consistent, and effects were only weakly significant (Cheyres) or not significant (Chevroux). Nevertheless, all together these fluctuations suggest that mowing did have a certain impact on reed performance, but that two years without treatment were sufficient for recovery, thus preventing long-term effects.

As regards overall long-term trends, the number of shoots and their basal diameter generally tended to decrease, although this was only partly significant

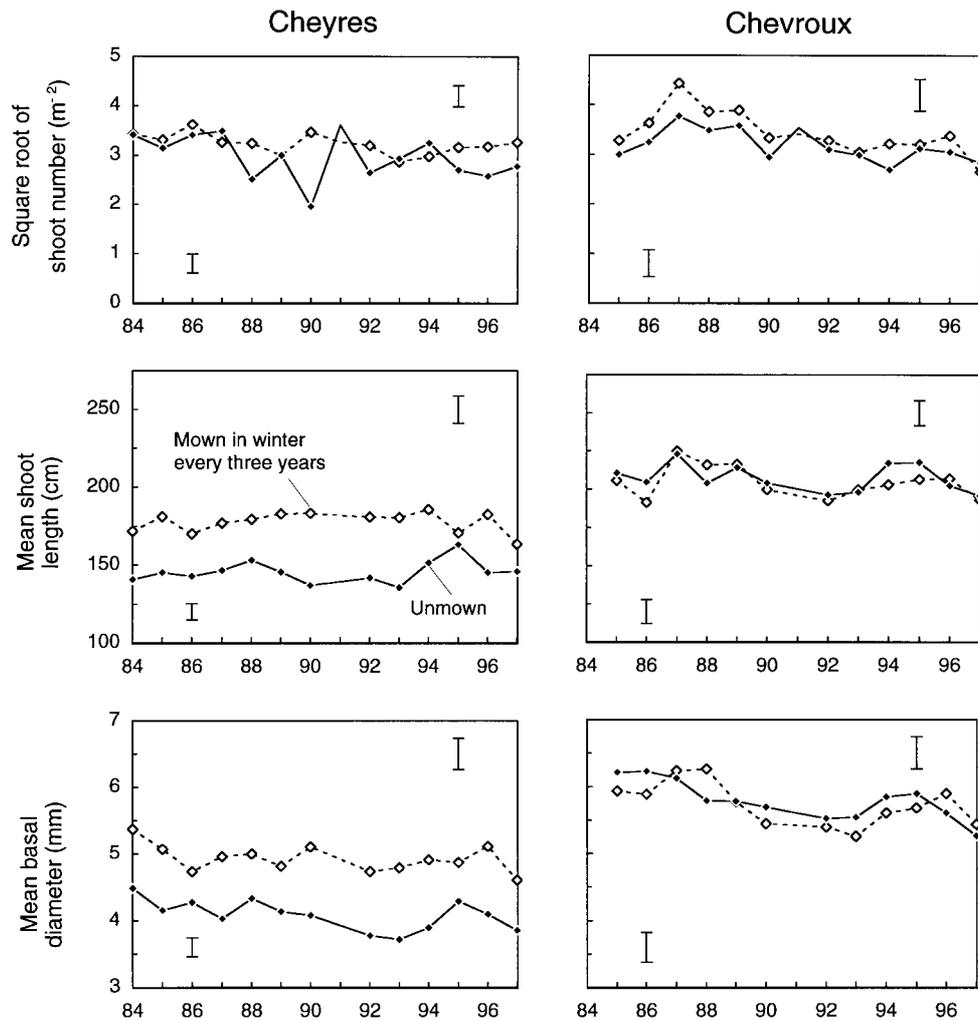


Figure 2. Mean changes in the performance of *Phragmites australis* at the two locations of study 1, in plots mown in winter every three years (dotted lines) or unmown (full lines). Data are means of values measured in 6 permanent quadrats per plot. Error bars are \pm s.e. for the comparison of years within treatments; bars in the upper right corner: mown plots, bars in the lower left corner: unmown plots.

Table 2. Mean annual change (= mean slope of linear regressions against years \pm s.e.) and significance of trends in the performance of *Phragmites australis* at the two locations of study 1, in plots mown every three years in winter or unmown ($n = 6$). Changes in shoot number were calculated after square-root transformation.

		Sqrt shoot number	Shoot length	Basal diameter
Cheyres mown	mean \pm se	-0.024 ± 0.011	-0.079 ± 1.11	-0.022 ± 0.04
	p	<0.1	ns	ns
Cheyres unmown	mean \pm se	-0.043 ± 0.019	0.422 ± 0.73	-0.030 ± 0.02
	p	<0.1	ns	ns
Chevroux mown	mean \pm se	-0.076 ± 0.038	-0.847 ± 1.27	-0.045 ± 0.043
	p	ns	ns	ns
Chevroux unmown	mean \pm se	-0.044 ± 0.027	-0.694 ± 0.66	-0.056 ± 0.020
	p	ns*	ns	<0.05

* ns = not significant ($p > 0.1$).

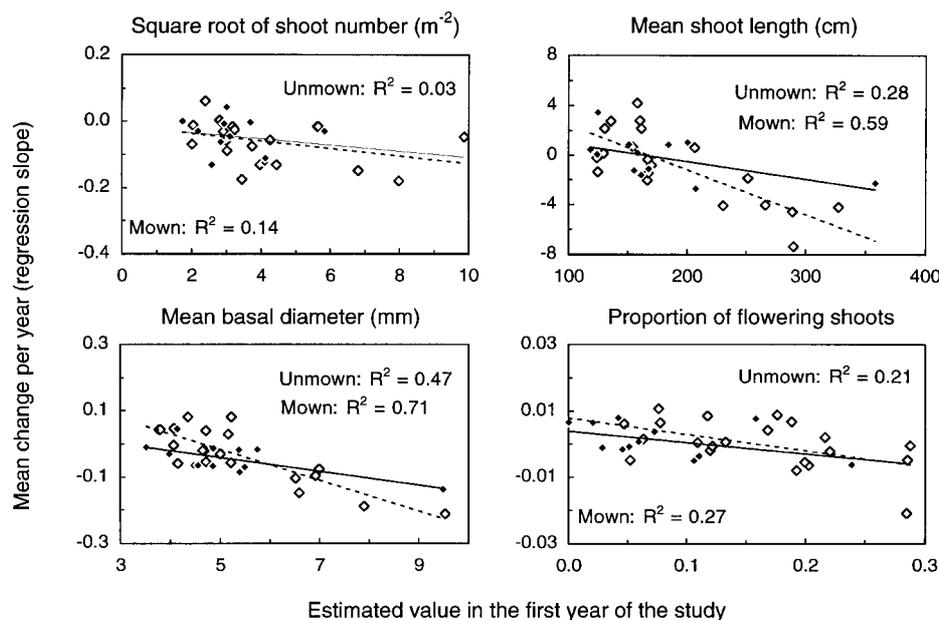


Figure 3. Relation between changes in the performance of *Phragmites australis* (regression slope) and its performance in the first year of the study (regression intercept) in each of the permanent quadrats of study 1. Open symbols: mown plots, closed symbols: unmown plots.

(Table 2). The low significance of long-term trends was due to considerable differences among plots: while a marked decrease occurred in some of them, others experienced little change, and in a few cases even an increase in the measured variables. These differences in the rates of change (regression slopes) were related to the initial values, especially as regards shoot size. In all plots that had tall shoots at the beginning of the study mean shoot length decreased in the course of time, whereas it could either increase or decrease in plots with initially smaller shoots (Figure 3). The relation between initial size and change over time seemed to be more pronounced for the mown than for the unmown plots, but this difference must be considered cautiously because in the case of unmown plots there was only one plot with high initial shoot length, which therefore determined to a large extent the relation. Similar results as for shoot length were obtained for the basal diameter. No such difference was found for the number of shoots, nor for the proportion of flowering shoots, i.e. the (weak) relation between initial values and change hardly differed between treatments (Figure 3).

Study 2: Mowing in summer or in winter

During the first four years of the experiment, shoot diameter significantly decreased in summer-mown

plots compared with the two other treatments at both locations (Figure 4, Table 3). The number of shoots was subject to considerable fluctuations, particularly in the unmown plots (Figure 4). It seemed to increase in summer-mown compared with winter-mown plots, but this only appeared clearly in 1986. There was no consistent difference in trends between mown and unmown plots during the period 1983–1986. In spite of the weakly significant treatment effect on regression slopes found for Cudrefin, the results rather suggest that fluctuations in shoot numbers were too strong at these sites to allow any conclusions about treatment effects to be drawn after a four-year period.

On the long term, mowing in summer every two years appeared to reduce both the shoot number and the basal diameter compared with unmown plots in Cudrefin (Figure 4, Table 3). Mowing in winter apparently had similar effects as mowing in summer on shoot number, while changes in basal diameter rather resembled those in the unmown plots. Basically the same trends were observed in Portalban, but treatment effects were not significant. Again fluctuations were considerable, particularly in the control plots. Nevertheless it appeared that the aboveground biomass of *P. australis* decreased in the mown plots between 1984 and 1997 contrary to unmown ones. During the same period the biomass of the other species increased slightly in the mown plots and much more in the un-

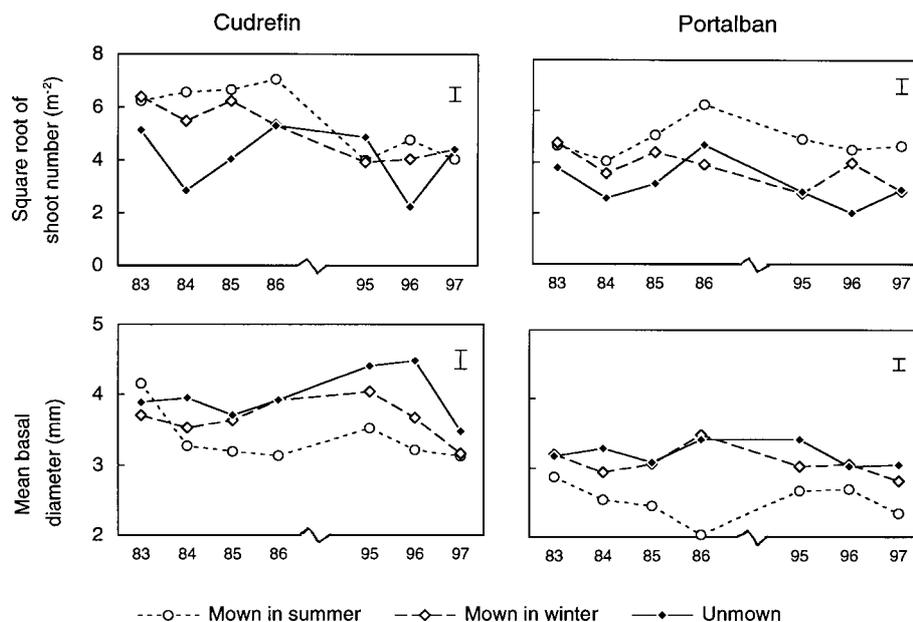


Figure 4. Mean changes in the performance of *Phragmites australis* in plots mown in summer, mown in winter, or left unmown at the two locations of study 2. Data are means of values measured in 3 experimental plots per location and treatment. Error bars are \pm s.e. for the comparison of years within treatments.

Table 3. Effect of mowing in summer or in winter on the performance of *P. australis* in study 2. Data are mean squares and significance levels of two-way analyses of variance performed (a) on the mean annual change of the variables between 1983 and 1986 (slopes of regression against years, 'short term') or (b) on the difference between means of 1983–84 and means of 1995–97 ('long term'). Changes in shoot number were calculated after square-root transformation.

	df	Sqrt shoot number				Basal diameter			
		Cudrefin		Portalban		Cudrefin		Portalban	
		MS	p	MS	p	MS	p	MS	p
(a) Short-term (1983–1986)									
Treatment	2	0.221	<0.1	0.082	ns	0.128	<0.01	0.113	<0.01
Block	2	0.049	ns*	0.061	ns	0.002	ns	0.009	ns
Residual	4	0.042		0.075		0.002		0.005	
(b) Long-term (1983–84 versus 1995–97)									
Treatment	2	1.441	<0.1	0.659	ns	0.320	<0.05	0.003	ns
Block	2	0.127	ns	0.978	ns	0.018	ns	0.016	ns
Residual	4	0.226		0.711		0.024		0.014	

* ns = not significant ($p > 0.1$).

mown ones (Güsewell et al., 1998). As a result the degree of dominance of *P. australis* (its fraction in aboveground biomass) decreased with all treatments to approximately the same extent (Cudrefin: 29–61% *P. australis* in 1984–86 and 13–30% in 1996–1997; Portalban: 13–29% in 1984–86 and 8–11% in 1997).

Because the sites had been unmown for 20 years or more before the beginning of the study, we assumed long-term trends in the control plots to be similar to long-term trends outside the experimental plots, where

areas of several ha continued to be unmown. Shoot number and diameter fluctuated without obvious trend in Cudrefin, in spite of the slightly negative mean slope for shoot number (-0.37 y^{-1} , $t = -3.02$, $p < 0.1$, based on square roots). In Portalban a (weak) decreasing tendency was found for both the shoot number (-0.53 y^{-1} , $t = -4.38$, $p < 0.05$), and the basal diameter (-0.07 mm y^{-1} , $t = -3.03$, $p < 0.1$).

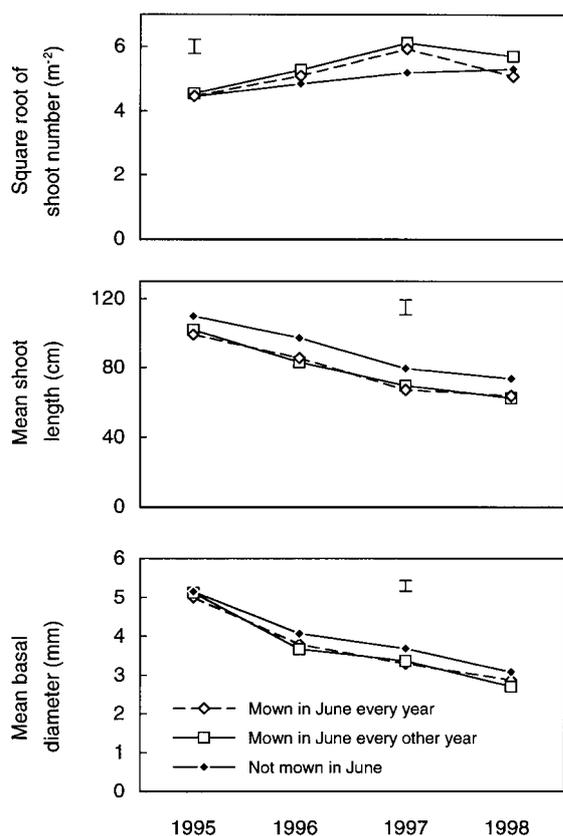


Figure 5. Mean changes in the performance of *Phragmites australis* in plots with or without additional mowing in late June at two of the three locations of study 3 (site 'Glatt' excluded, $n = 5$ plots, cf. text). Error bars are \pm s.e. for the comparison of years within treatments.

Study 3: Mowing in June in addition to mowing in September

The shoot number of *P. australis* increased and its shoot size (length and diameter) decreased from 1995 to 1998 in the experimental plots (Figure 5). Tested with the data from plots only mown in September (normal management of the sites; $n = 6$), all these trends were significant (shoot number: $+2.5 \text{ y}^{-1}$, $t = 3.97$, $p < 0.05$, shoot length: -12.7 cm y^{-1} , $t = -5.82$, $p < 0.01$, basal diameter: -0.6 mm y^{-1} , $t = -13.26$, $p < 0.001$). Taken together, the changes in shoot number and size resulted in an average decrease in aboveground biomass of 16% per year ($t = -4.23$, $p < 0.05$; $n = 5$).

Additional mowing in June did virtually not affect the trends: For none of the variables did regression slopes differ among treatments ($p > 0.1$ for all tests). In contrast, trends differed among blocks for shoot length ($p < 0.01$) and for the number of shoots ($p <$

0.1). Plotting trends against initial values, we found a clear relation for shoot length – stronger decrease when shoots were initially taller – but not for the number of shoots (Figure 6).

Study 4: Mowing in September

The number of shoots decreased at all four sites from 1995 to 1998, but trends were (weakly) significant only at the two sites near Lake Zürichsee, Z1 and Z2 (Figure 7, Table 4). Shoot length and basal diameter decreased at the Zürichsee sites (diameter only at site Z2); at sites P1 and P2 (lake Pfäffikersee) changes were not significant. Aboveground biomass, as estimated from this data, decreased slightly near Lake Zürichsee and did not change significantly near Lake Pfäffikersee. As in studies 1 and 3 the change in shoot length was negatively correlated with the mean shoot length in 1995, whereas no such correlation was found for the number of shoots (Figure 6).

Discussion

The two main results of this study – overall tendency of *Phragmites australis* to remain stable or decrease in abundance, rather than to increase, and weakness or absence of mowing effects – were rather unexpected since they contrasted with the contention that *P. australis* currently tends to spread in Swiss fens or wet grasslands, particularly abandoned ones. We will first discuss the reliability of these results and search for explanations, and then try to draw some conclusions for the management and monitoring of fen meadows.

Absence of spread

No increase in the performance (shoot number or shoot size) of *P. australis* was detected in this study. However, before concluding that the species did actually not spread, we need to examine whether our investigations were really appropriate to detect trends. The measured variables (shoot number, shoot length and basal diameter), are strongly correlated with other traits that might be considered better measures of performance or competitive ability, such as aboveground biomass (Güsewell and Klötzli, 1997), date of emergence and rate of shoot elongation (Ostendorp, 1991), leaf area index (Szajnovski, 1973), light interception (Güsewell and Edwards, 1999). This means that measuring these other variables would hardly have revealed different or more significant trends. Monitoring

Table 4. Mean annual change (= mean slope of linear regressions against years \pm s.e.) and significance of trends in the performance of *Phragmites australis* at the four locations of study 4. Changes in shoot number were calculated after square-root transformation, and changes in the estimated biomass after log-transformation.

	<i>n</i>	Sqrt shoot number	Shoot length	Basal diameter	Log estim. biomass
Pfäffikersee P1	9	-0.15 \pm 0.16 ns*	-0.46 \pm 3.22 ns	-0.02 \pm 0.10 ns	-0.01 \pm 0.07 ns
Pfäffikersee P2	5	-0.10 \pm 0.25 ns	3.25 \pm 3.67 ns	0.02 \pm 0.11 ns	-0.03 \pm 0.07 ns
Zürichsee Z1	10	-0.18 \pm 0.08 <0.1	-3.87 \pm 0.69 <0.001	0.03 \pm 0.03 ns	-0.08 \pm 0.02 <0.01
Zürichsee Z2	6	-0.23 \pm 0.10 <0.1	-12.55 \pm 1.48 <0.001	-0.16 \pm 0.06 <0.1	-0.12 \pm 0.02 <0.001

* ns = not significant ($p > 0.1$).

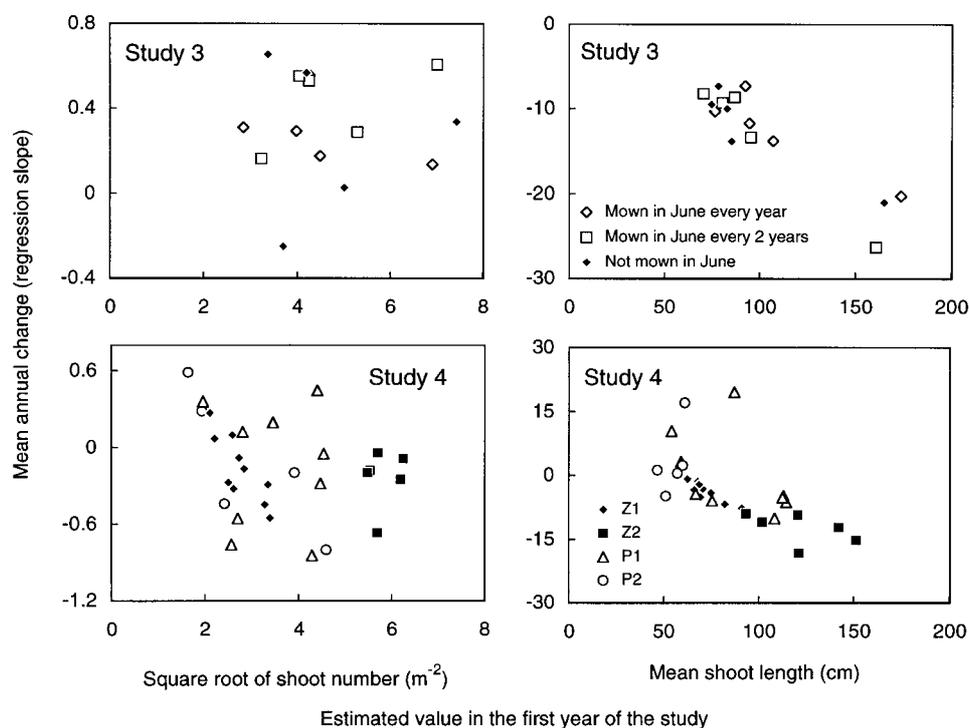


Figure 6. Relation between changes in the performance of *Phragmites australis* (regression slope) and its performance in the first year of the study (regression intercept), in study 3 and in study 4. All plots were mown every year in September, and some plots of study 3 were mown additionally in June. Z1, Z2: Zürichsee; P1, P2: Pfäffikersee.

reed in permanent quadrats reduced the error variation due to spatial heterogeneity, but did not totally suppress it, since shifts in small-scale spatial patterns in shoot number or shoot size occur from year to year (Güsewell and Klötzli, 1997). This could lead to important standard errors for the mean regression slopes, so that only some trends appeared signific-

ant. However, the visual inspection of the graphs suggests that the lack of significance was generally due to weak trends rather than to strong small-scale spatio-temporal variation.

An important limitation of studies 3 and 4 was their short duration. In study 1, where a long time series was available, the measured variables (mean per location

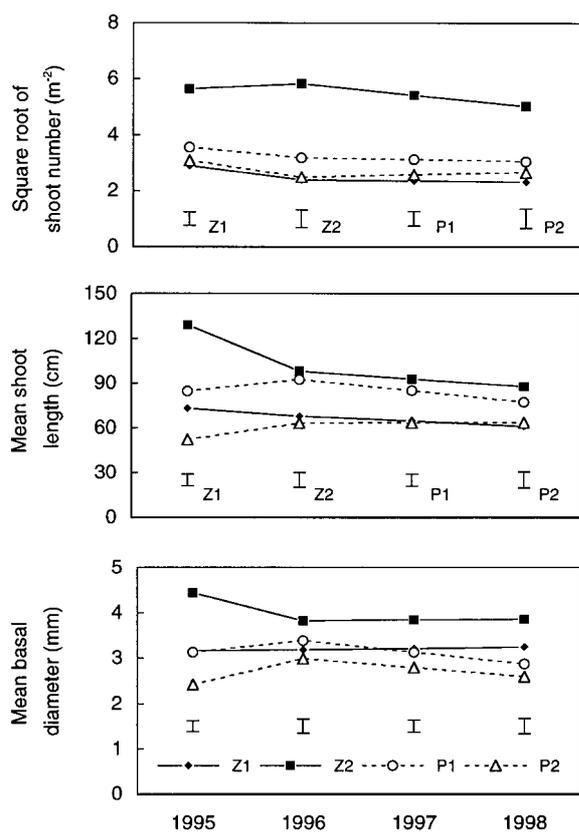


Figure 7. Mean changes in the performance of *Phragmites australis* at the four locations of study 4 (Z = Zürichsee, P = Pfäffikersee; $n = 5$ to 10 plots per location). Error bars are \pm s.e. for the comparison of years within each location.

and treatment) could increase or decrease consistently at yearly intervals over periods of five to eight years before the trend reversed. For example, the basal diameter in unmown plots of Chevroux decreased from 1988 through 1993, but increased again afterwards, and the 1996 value was almost as high as the 1988 value. Causes for such fluctuations might be worth closer investigation. Weather conditions certainly play an important role (Haslam, 1970, 1975): several consecutive years with unfavourable weather may lead to the depletion of belowground reserves and, therefore, to the persistence of a decreasing trend for one or more years even after weather conditions became favourable again (Haslam, 1975). Similar fluctuations as in study 1 might have been at the origin of some changes found in the three other studies, where trends and mid-term fluctuations could not be distinguished. Contrary to 1995, the late winter 1996 was fairly cold and dry, and drought together with severe late frost

occurred in April 1997. Frost generally increases the shoot number and reduces the mean shoot size because killed primary shoots are replaced by several secondary ones (Haslam, 1969; Van der Toorn and Mook, 1982). In monodominant reed stands the aboveground biomass can be unaffected or even enhanced after frost (Haslam, 1972), but more frequently it is reduced (Mook and Van der Toorn, 1982), and the latter is particularly likely to occur in mixed stand where the associated delay in growth will give to the other species a competitive advantage over *P. australis*. Thus, the negative trend found at most locations in the region of Zürich (studies 3 and 4) may be simply due to differences in early spring temperature. The trend should be confirmed for at least ten other years before it can be interpreted as an actual decrease in the performance of *P. australis* at these sites, and even longer time series would be needed if the observed decrease proves to be actually a fluctuation due to weather conditions within a long-term increasing trend.

The relatively small number of locations investigated certainly also constrained the validity of our results. It could be that *P. australis* increased at other locations while it did not at those under study. Marks et al. (1994) mention that in the USA *P. australis* can grow as a subdominant species for several years at a newly colonised site before it starts to expand and become dominant. This behaviour is found with many invasive plant species (Kowarik, 1995). An additional constraint in studies 1 and 4 was that plots were located on ecological gradients (water level, nutrient status). If there had been sufficient replication to analyse dynamics separately for different parts of the gradients, changes might have been much clearer in some parts. Such a distinction would be particularly important to study the causes underlying observed dynamics, since the response of *P. australis* to changes in nutrient supply or water level is likely to depend on the set of initial site conditions (e.g. Buttery and Lambert, 1965; Haslam, 1971, 1972; Cízková-Koncalová et al., 1996; Clevering, 1998).

In conclusion, our data does not exclude the possibility that *P. australis* does spread in fens or wet grasslands of the Swiss Plateau. More extensive sampling will be needed before such conclusions can be drawn. However, the results indicate that the spread, if any, must either be confined to some sites, none of them having been included in our investigations, or be slow enough to be undetectable in short- or mid-term studies, and can therefore certainly not be considered dramatic.

Weakness of mowing effects

Mowing appeared to have only little effect on the performance of *P. australis* in our experiments. Most above remarks concerning the reliability of results also apply here, although fluctuations due to weather conditions would only have affected the results if they interacted with treatment effects. Such interactions are, indeed, conceivable in studies 1 and 2. Frost has generally more severe effects at mown sites due to litter removal (Krisch et al., 1979; Mook and Van der Toorn, 1982). Another problem was that in study 1 the unmown control area in Cheyres was confined to the drier part of the wetland and had, therefore, no quadrats with high initial shoot size. Given the negative relation between trends and initial size, this might have influenced the results. Nevertheless, we think that the problem was minor since results were basically the same in Chevroux, where the mean initial shoot size did not differ between treatments.

The clearest effect was found in the short-term data of study 2, where mowing in summer increased the number of shoots and reduced their size (diameter) compared with the two other treatments. This typical reaction of *Phragmites australis* to mechanical damage (Haslam, 1969, 1970) is normally associated with a decrease in aboveground biomass production (Mook and Van der Toorn, 1982). Reduced biomass after mowing in summer has been reported by various authors. For example, Haslam (1970) mentions 40% lower biomass in the year after mowing in July and 15% lower biomass after mowing in August, and even greater reductions if stubbles are flooded after mowing. Other authors report significant reduction in the percentage cover after mowing in summer (Gryseels, 1989b; Briemle et al., 1991; Marks et al., 1994). The effect is attributed to the depletion of belowground reserves of nutrients and carbohydrates (Granéli, 1990), or to the enhanced competitive ability of other species (George, 1992).

Surprisingly, in our study 2 the short-term effects of mowing in summer on *P. australis* disappeared or became much weaker on the long term. The fact that mowing became biennial after 1986 may undoubtedly have contributed to this result. Nevertheless, if mowing in summer during three consecutive years had severely affected *P. australis*, mowing every two years for ten other years would have been expected to maintain, or even to strengthen these effects. If the sites had been subject to enhanced nutrient inputs, *P. australis* might (since 1986) have taken up and stored enough

nutrients in the years without mowing to compensate for losses. However, the absence of marked changes in species composition and in biomass production in the experimental plots between 1983 and 1997 (Güsewell et al., 1998) indicates that eutrophication did not occur.

Equally surprising was the absence of effect of additional mowing in June in study 3. A detrimental effect would have been expected here even more than in study 2, since rhizomes are maximally depleted in late June (e.g. Granéli et al., 1992). A possible explanation is that mowing in summer reduced the biomass of the other species at the study sites (Güsewell, 1998), and this may have reduced their competitive effect on *P. australis* (Hürlimann, 1951; Haslam, 1971).

In study 1, where plots were mown in winter every three years, no detrimental treatment effects were expected since this mowing regime has widely been recommended as the optimal one for the maintenance of vigorous reed stands (Klötzli and Züst, 1973; Granéli, 1990; George, 1992), except where resistance against mechanical stress (the action of waves) is decisive for survival (Ostendorp, 1995). Rather than detrimental effects, growth promotion might have been expected with periodic mowing in winter owing to the removal of litter (Granéli, 1989, 1990; George, 1992) or to the repression of strong competitors (Gryseels, 1989a). However, no considerable litter accumulation occurred in the unmown plots, and the main competitors at the study sites – *Carex* species – were apparently not affected by the periodic winter mowing (pers. obs.). This, together with possible mechanical damage due to the weight of the mowing machine, may explain the absence of promotion through mowing in our study.

Possible role of site conditions

Dependence of reed dynamics on site conditions has been suggested by various authors. Moderate nutrient enrichment, particularly as regards nitrogen, is considered a major factor enhancing the performance and competitive ability of *P. australis* (Marks et al., 1994; Brülisauer and Klötzli, 1998; Güsewell and Edwards, 1999). At first sight results from our studies 3 and 4 rather suggested the opposite: changes in the mean shoot size (length or diameter) appeared to be negatively related to the initial shoot size. Tall shoots indicate nutrient-rich conditions at terrestrial sites, while the water level seems to play a minor role within the range found in fens or wet grasslands (Haslam, 1970; Güsewell and Klötzli, 1998;

Brülisauer and Klötzli, 1998). This suggests that the decreasing tendency for mean shoot size was stronger where the productivity was higher. We can imagine three explanations for this rather surprising fact. One possibility is that there has been a short-term increase in performance in nutrient-enriched parts of the sites, which is now reversing. In that case the decrease could be expected to be stronger where the previous increase was stronger. A second possibility is that weather conditions, which we thought to be responsible for the overall trends observed between 1995 and 1998, affect *P. australis* more where the species dominance is higher, and therefore competition by other species lower. A third possibility would be that stronger competitors have started to repress *P. australis* in the more productive plots, as suggested by Buttery and Lambert (1965), Haslam (1971), George (1992) and others. However, this last possibility seems very unlikely because the 'more productive' plots were still much less productive than those mentioned by these other authors, and actually, no spread of potential strong competitors (e.g. *Glyceria maxima*, *Agrostis stolonifera*, *Juncus subnodulosus*) was observed. As to the two other possibilities, they remain speculative as long as the factors determining reed dynamics at terrestrial sites have not been studied in more detail.

In study 1, mean shoot size was related to the water level: the tallest shoots were found in the wetter quadrats. The decreasing tendency for quadrats with tall shoots might therefore be indicative of a succession towards drier site conditions, as hypothesized for the 'Grande Cariçãie' by Buttler (1987). This succession is also suggested by the species composition of the permanent quadrats (Le Nédic and Güsewell, in prep.). Furthermore, our data provided some (rather weak) evidence that the negative relation between initial shoot size and change in shoot size was more pronounced in the mown plots. This might indicate a detrimental effect of mowing at the wettest sites in contrast to drier ones, which would be consistent with the results of other authors (e.g. Ostendorp, 1991; Rolletschek et al., 2000, this issue).

Practical implications

To monitor reed dynamics at terrestrial sites, various authors have recommended to determine shoot number and shoot size yearly in a sufficient number of permanent quadrats (e.g. Marks et al., 1994; Güsewell and Klötzli, 1997). Our investigations, particularly those from study 3, confirm the importance

of measuring shoot size in addition to shoot number: increasing shoot number can be associated with decreasing aboveground biomass, so that surveys based solely on shoot number may suggest trends opposite to the reality.

The problem with permanent quadrats is their low efficiency. They require much sampling effort and, if so, will reveal even small trends e.g. due to weather conditions; however, these trends may be irrelevant for nature conservation. Concomitantly, only a restricted number of sites can be monitored in this way, and those in which *P. australis* actually increases may not be included. On the other hand, monitoring at longer time intervals may produce unreliable results because measurements may be carried out in a year with particular meteorological conditions. A combination of quadrats monitored yearly at a few locations, and quadrats monitored occasionally at more locations might provide an efficient strategy, since the first could be used to correct results obtained in the latter for short-term fluctuations. In such a monitoring programme it would be important to consider separately and with sufficient replication the range of ecological conditions occurring in the study area.

In considering the implications of our results for management it is important to realise that controlling the performance of *P. australis* was not the primary target of management at our sites. When winter mowing was established in the 'Grande Cariçãie', the main aims were to prevent, or at least to slow down, the succession towards drier vegetation types and scrub encroachment, and to promote species richness (Buttler, 1987). As discussed above, the decreasing performance of *P. australis* in the wetter parts, particularly in the mown plots, might indicate that the first aim has not been reached. However, this is uncertain because mechanical damage might also have influenced the results. The second aim, promoting species richness, has been achieved, since species numbers remained constant or even increased in the mown permanent quadrats, whereas they decreased in the unmown ones (Le Nédic and Güsewell, in prep.). The fact that triennial mowing in winter has been able to promote species richness contrasts with the results obtained elsewhere (e.g. Rosenthal, 1992) and is probably related to the mesotrophic site conditions prevailing in most parts of the 'Grande Cariçãie' (Buttler, 1987).

Species richness was also promoted by mowing (regardless of the date) in study 2 (Buttler, 1992; Güsewell et al., 1998) and by additional mowing in June in study 3 (Güsewell and Zorzi, unpubl.). It is

not surprising that the impacts of mowing on the performance of *P. australis* and on species richness were uncoupled. Even though there is an overall negative relation between performance of *P. australis* and species richness in Swiss fen meadows (Güsewell and Klötzli, 1998), this relation is mostly due to differences in plant communities along gradients in the performance of *P. australis*, and not to the presence or performance of *P. australis* itself (Güsewell and Edwards, 1999). This means that if the aim of management is to maintain or enhance species richness, there is no need to strive for a low performance of *P. australis*, and also, that species numbers needs to be monitored directly to assess management success, the abundance of *P. australis* being an unsuitable indicator.

We wish to stress that the practical implications proposed here are only valid in situations such as described in this study, i.e. without dramatic increase in the performance of *P. australis*. They do *not* hold in situations where *P. australis* spreads aggressively and suppresses the established vegetation, as reported from some parts of the US (Keller, 2000, this issue). An important question would be how to distinguish between 'benign' and potentially 'aggressive' dynamics in an initial phase. To answer this question, reed dynamics at terrestrial sites and its relation to site conditions as well as to management require more careful investigation. Without more detailed knowledge on these relations it is questionable whether the performance of *P. australis* can be used as an indicator of management success in fens or wet grasslands.

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