

Abundance of common reed (*Phragmites australis*), site conditions and conservation value of fen meadows in Switzerland

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SUMMARY

The abundance of *Phragmites australis* (Trin.) has increased in many fen meadows of the Swiss Plateau. The vegetation of 241 4-m² plots was surveyed to determine how the abundance of *Phragmites australis* was related to site conditions and to the botanical conservation value. The aboveground biomass of *P. australis* (ABP) ranged from 0 g to 1270 g dry weight m⁻². ABP was positively correlated to the nitrogen indicator value of the vegetation, but uncorrelated to the soil moisture indicator value. The abundance of 55 of 85 plant species was significantly related to ABP. High ABP was, on an average, associated with low conservation value in terms of species richness, number of rare or endangered species, and proportion of typical mire species. Strong differences were, however, found between plots with tall-herb vegetation (alliance *Filipendulion*) and plots dominated by heathgrass or small sedges (alliances *Molinion* and *Caricion davallianae*). The conservation value of *Filipendulion* plots was low and decreased significantly with increasing ABP. The conservation value of *Molinion* and *Caricion* plots was generally high and not related to ABP. Nevertheless, the current spread of *P. australis* might reduce the conservation value of *Molinion* and *Caricion* meadows in three ways: (1) a direct impact of shading is likely to become apparent only after several years; (2) if *P. australis* spreads into a site together with tall herbs, the loss of conservation value will be greater than if only tall herbs invade; and (3) if the presence of *P. australis* increases nutrient availability, it may indirectly cause the spread of tall herbs and the resulting loss of conservation value. Thus, spread of *P. australis*, spread of tall herbs and increased productivity are strongly related to each other and must be considered together when changes in the vegetation of fen meadows are evaluated.

Key-words: biodiversity, competition, eutrophication, invasive plants, wetlands.

INTRODUCTION

Fen meadows of the alliances *Molinion* and *Caricion davallianae* are vegetation types of outstanding conservation value because of their species richness and their high proportion of rare and endangered species (Wheeler 1988; Landolt 1991). Their area in western Europe has been reduced to a small fraction of the original extension during

this century, due mainly to the increase of intensive agricultural use (Hampicke *et al.* 1991; Oomes & Van der Werf 1996). Despite legal protection, the remaining sites have mainly been degraded through eutrophication (Klötzli 1986), abandonment (Müller *et al.* 1992), changes in hydrology (Fojt & Harding 1995) or invasion by alien plant species (Voser-Huber 1983). One of the changes currently observed in Swiss lowland fen meadows is a spread of *Phragmites australis*. The dominance of this species appears to increase even in nature reserves, where the traditional management, mowing in late summer or autumn, is still in practice (Klötzli 1986; Leupi 1987; Marti & Müller 1993).

Referring to a spread of *P. australis* as a threat for nature conservation may seem surprising after the concern that was caused by reed 'die-back' on Central European lake-shores (e.g. Ostendorp 1989; Van der Putten 1994). This apparent contradiction is explained by the different ecological character of lake shore reed belts and wet meadows. In reed belts, the presence of *P. australis* is limited by various abiotic site factors such as water depth (Hürlimann 1951), wind and waves (Klötzli 1974), or toxic substances in the sediment (Armstrong *et al.* 1996), and its density and height are limited mainly by intraspecific competition (Haslam 1971a; Graneli 1987). Reed is weakened and finally dies if changes of site conditions deplete or damage its shoots or rhizomes (Klötzli & Züst 1973b; Cizkova-Koncalova *et al.* 1992). This 'die-back' is rated negatively, because it results in shoreline erosion and a loss of habitat for waterfowl (Ostendorp 1993). Conversely, site conditions in fen meadows (and other wet terrestrial ecosystems) are generally favourable to *P. australis* (Hürlimann 1951). Its productivity is lower than in aquatic stands, but it is more resistant to stress factors (Guthruf *et al.* 1993). The presence and abundance of *P. australis* in terrestrial habitats are mainly limited by interspecific competition for light and nutrients (Haslam 1971b), and *P. australis* tends to spread if changes of site conditions give it a competitive advantage (Marks *et al.* 1994). This spread in fen meadows is considered a threat to nature conservation because *P. australis* is expected to displace specialized, rare and endangered plant species, and to reduce biodiversity through increased shading (Biewer *et al.* 1994; Onimaru & Yabe 1996). Therefore, conservationists seek to reduce its abundance through special management (Bressous *et al.* 1992).

However, surprisingly little is known about the real extent of the problem (Leupi 1987). In particular, precise records of the abundance of *P. australis*, that would allow determination of where and how much this species is spreading, are scarce. The factors that cause *P. australis* to spread and the patterns of its abundance are not well understood (Leupi 1987; Marti & Müller 1993). Also, it has not yet been established whether *P. australis* actually affects the plant species composition of invaded fen meadows in a way that significantly reduces their botanical conservation value.

In this paper we present the results of a vegetation survey in 11 fen meadows in wetland reserves of the Northeast Swiss Plateau that are considered to be affected by the spread of *P. australis*. We surveyed the current abundance of *P. australis* and investigated its relation to ecological indicator values of the vegetation as well as to indices of conservation value. The aim of the study was to assess whether a further spread of *P. australis* was likely to affect the conservation value of fen meadows.

MATERIALS AND METHODS

Study sites

The abundance of *Phragmites australis* (Trin.) and the species composition of the

Table 1. Characteristics of the study sites with the coordinates of the Swiss topographic map, the number of plots investigated in each vegetation type (C: *Caricion*, M: *Molinion*, F: *Filipendulion*), the shoot densities of *Phragmites australis* (shoot number m⁻²), and the species richness of the vegetation (species number in 4-m² plots)

| Lake | Site | Coordinates | Number of plots | | | Shoot density | | Species number | |
|--------------|------|---------------|-----------------|----|----|---------------|-------|----------------|-------|
| | | | C | M | F | Mean | Range | Mean | Range |
| Katzensee | K1 | 680-55-253-70 | — | — | 14 | 16 | 0-140 | 19 | 14-24 |
| | K2 | 680-45-254-05 | — | — | 12 | 45 | 0-70 | 15 | 8-24 |
| Greifensee | G1 | 692-35-247-90 | — | 6 | 20 | 20 | 1-83 | 21 | 14-29 |
| | G2 | 691-95-247-65 | — | — | 24 | 31 | 20-45 | 12 | 9-17 |
| | G3 | 692-50-247-80 | — | — | 16 | 18 | 1-46 | 17 | 6-27 |
| | G4 | 692-55-247-75 | 7 | 14 | 6 | 27 | 14-60 | 25 | 11-38 |
| | G5 | 691-95-247-95 | 18 | 6 | — | 16 | 1-43 | 21 | 14-30 |
| Zürichsee | Z1 | 702-35-229-05 | 7 | 21 | 9 | 10 | 1-49 | 26 | 14-36 |
| | Z2 | 702-30-229-20 | 12 | 2 | 4 | 27 | 8-60 | 19 | 13-33 |
| | Z3 | 709-70-229-60 | — | 15 | — | 20 | 3-48 | 36 | 30-41 |
| Pfäffikersee | P1 | 702-20-244-60 | 28 | — | — | 23 | 0-59 | 24 | 9-36 |

vegetation were investigated in 11 wet meadows in nature reserves near Zürich, Switzerland, at an altitude of 400–540 m (Table 1). The long-term average annual temperature range was 7–9°C, and the average annual rainfall was 1000–1400 mm. All sites were part of lakeside wetlands, except K1 and K2, located in a swampy basin. The soils were mainly base-rich peat soils; more acidic conditions were found in parts of sites Z1 and Z2, and humic gleysols at sites G1, G3, G4 and Z3. The meadows were mown yearly in September or October, but some of them had been left abandoned for several years before 1985–90. Most sites received nutrient inputs from the surrounding farmland, since they were bordered by fertilized grasslands or crop fields or traversed by drainage ditches.

A series of 2 × 2-m² plots were arranged on parallel transects at each site. Between 12 and 37 plots were investigated at each site, depending on the size of the meadows. If a plot would have been disturbed by ditches or foot paths, or if inhomogeneity was apparent in the vegetation, the plot was shifted by 0.5 m or 1 m to obtain (visually) undisturbed and homogeneous conditions. Additional plots were inserted at intermediate positions if particularly steep gradients in the abundance of *P. australis* occurred locally. The sites K1 and K2 were very similar; therefore, they were treated as one site in data analysis.

Measurements and estimations

The species composition of the vegetation in each of the 241 2 × 2-m² plots was investigated in 1995 (five sites) or in 1996 (six sites). Abundance and dominance of all vascular plant species in the plots was recorded between late May and early July using the Braun–Blanquet scale (Dierschke 1994).

The abundance of *P. australis* was recorded in mid-August of the same year by counting the number of shoots taller than 20 cm per 2 × 2-m² plot, and by measuring the culm length and the basal diameter of all shoots in the front left quarter (1 m²) of the plots. Culm length was measured from the soil surface to the base of the uppermost

leaf, or to the base of the panicle for flowering shoots, respectively. Basal diameter was taken in the middle of the second internode. The aboveground biomass of *P. australis* (ABP, dry weight in g m⁻²) was calculated as the product of shoot density (mean shoot number m⁻²) and mean dry weight per shoot (g). The latter was estimated from mean culm length (m) and mean basal diameter (mm) according to Güsewell & Klötzli (1997):

mean dry weight per shoot = $1.07 \times (\text{length} \times \text{diameter})^{1.04}$

Data analysis

Classification of the vegetation. Different vegetation types were found in the meadows investigated. To analyse data separately for each type, we classified the 241 vegetation relevés with the minimum variance clustering procedure provided by the statistical software MULVA 5 (Wildi & Orlóci 1996). Only 85 species (of 203) that were present in at least nine plots and in at least three sites were included in the calculations. The Braun-Blanquet scale was transformed to a rank scale from 0 to 6 and 'similarity ratios' were used as a measure of resemblance. The groups formed by the cluster analysis were attributed to phytosociological alliances by comparison with the vegetation tables in Klötzli (1969) and Wildi & Klötzli (1978).

Abundance of P. australis. The 241 plots surveyed represented a gradient from low to high abundance of *P. australis*. The abundance was expressed as the aboveground biomass of *P. australis* (ABP), using a logarithmic scale. Relations between ABP and other species were described as 'response curves' or as 'increase (or decrease) along the ABP gradient'. Such 'response curves' merely described statistical relationships. A spatial pattern, a temporal change or a causal relation was not necessarily implied.

Response curves of species. To describe how the abundance of individual plant species changed along the *Phragmites* gradient, we used a logistic regression model for ordinal response. Again, only the 85 most frequent species were considered. P_i , the probability that a species occurred in a plot with an abundance of at least i ($i = +, 1, 2, 3, 4, 5$), was modelled as:

$$P_i \frac{1}{1 + \exp[-(a_i + bx + cx^2)]}, \text{ i.e. } \log\left(\frac{P_i}{1 - P_i}\right) = a_i + bx + cx^2,$$

where x was the difference between $\log(\text{ABP})$ of the relevé and mean $\log(\text{ABP})$ of all 241 relevés. Using this difference instead of the original values made x and x^2 uncorrelated. The parameter b determined whether the species had a general tendency to increase or to decrease with increasing ABP; c determined whether the response curve of the species was monotonous or unimodal. The significance of the parameters b and c was tested using the Wald χ^2 test, an approximation of the likelihood ratio test (Lehman & Sall 1995).

Site conditions. The relation between the abundance of *P. australis* and site conditions was assessed indirectly, based on plant species composition. For each plot we calculated weighted average ecological indicator values after Landolt (1977) for the factors nutrients, soil moisture, soil reaction (pH) and light. These values could range from 1 to 5; high values indicated productive, wet, base-rich, unshaded conditions, respectively.

Calculations were based on all 202 plant species present in the relevés after excluding *P. australis*.

Conservation value. The botanical conservation value of the 241 plots was assessed using four indices rating species diversity, rarity, vulnerability and representativeness (cf. Wheeler 1988; Usher 1994). The calculation of the indices was based on all 202 plant species present in the relevés, except *P. australis*.

Species diversity was measured as species richness (number per 4-m² plot) and as species evenness. Evenness was calculated as H/H_{\max} , where H was the Shannon diversity index, calculated with Braun–Blanquet values transformed to percentage cover, and H_{\max} was the logarithm of species richness (Dierschke 1994).

Rarity and vulnerability were evaluated with the Red List index. This index assessed the number and abundance of Red List species in a plot. To calculate the index each species was given a score, based on the regional Red List (Landolt 1991). The score was 1 for rare species, 2 for endangered species and 3 for strongly endangered species. It was multiplied with the Braun–Blanquet value of the species in the plot. The Red List index was the sum of these weighted scores.

Representativeness was measured with the mire species index. This index assessed whether the species composition of a plot was ‘typical’ for mires, i.e. contained a high proportion of specialized species and few species which are common in other vegetation types. To calculate the index, each species was given a score indicating how frequently it lives in mires compared with other vegetation types (based on Korneck & Sukopp 1988). The score was, for example, 1 for a species living exclusively in mires (e.g. *Carex davalliana*), but only 0.33 for a species living more frequently in another vegetation type (e.g. *Cladium mariscus*). The mire species index of a plot was the weighted average of these scores. Braun–Blanquet values were used as weights.

Relationships between the ecological indicator values or conservation value indices and the ABP were assessed with Spearman rank correlation coefficients (r_s). Differences among alliances were tested with Kruskal–Wallis tests. Calculations were made with the statistical package JMP (SAS Institute Inc., Cary NC, USA).

RESULTS

Abundance of Phragmites australis

The abundance of *P. australis* in the 241 plots of this study ranged from a total absence (six plots) to a density of 139 shoots m⁻² and an aboveground biomass (ABP) of 1274 g m⁻². The maximal mean culm length was 228 cm, and the maximal mean shoot dry weight was 21.2 g.

Three main vegetation types occurred at our study sites. Based on the cluster analysis, 72 relevés were attributed to the alliance *Caricion davallianae*, 64 relevés to the alliance *Molinion* and 105 relevés to the alliance *Filipendulion*. The group *C. davallianae* included several relevés of the association *Caricetum elatae buxbaumietosum* (alliance *Magnocaricion*) from site P1. These relevés were too similar to other *Caricion* relevés to form a distinct group. The high abundances of *P. australis* indicated above were only found in the *Filipendulion* (Fig. 1a). Shoot density did not exceed 59 m⁻² in *Caricion* plots, and 48 m⁻² in *Molinion* plots. The main difference among the alliances, however, was their shoot size (Fig. 1b): almost all *Filipendulion* plots had a mean shoot

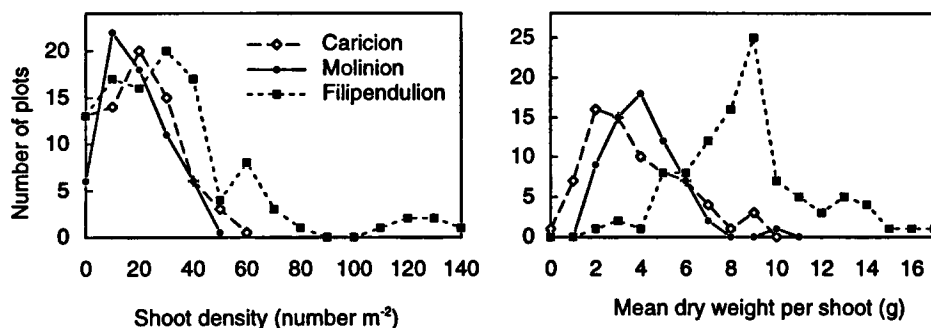


Fig. 1. Distribution of shoot density (a) and shoot dry weight (b) of *P. australis* in the 241 plots. Symbols indicate the number of plots of each alliance belonging to each class of density or of size. Class width was 10 shoots m^{-2} for shoot density and 1 g for shoot dry weight.

dry weight of 6 g or more, whereas this weight was hardly ever exceeded in *Caricion* or *Molinion* plots.

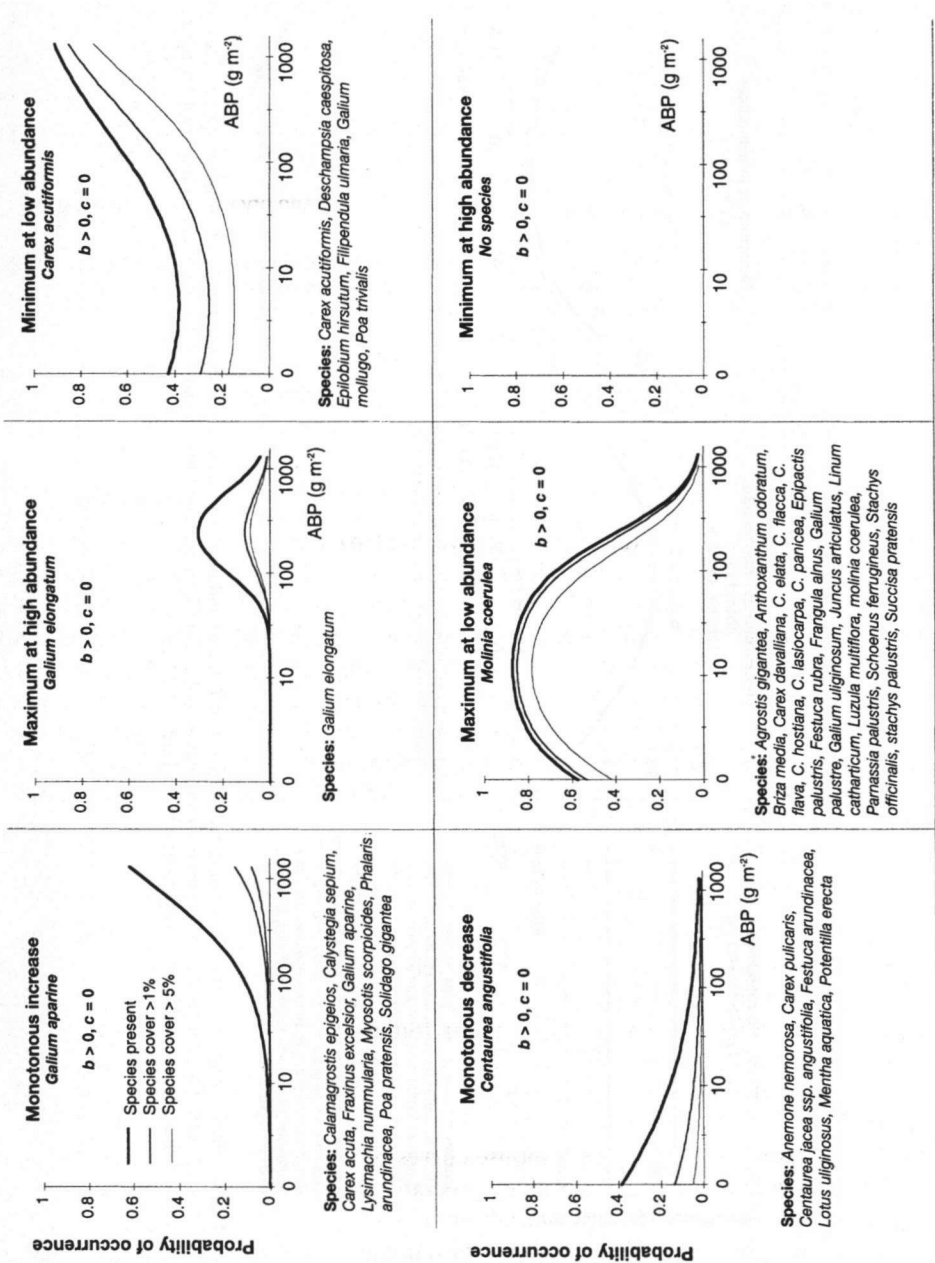
Species responses

A majority of plant species (55 of the 85 investigated) was related significantly to the abundance of *P. australis* (ABP). The response curves could be classified into eight types, according to the values of the two slope parameters of the logistic model (Fig. 2). One-third of the species (31) were less abundant at high ABP ($b < 0$). Only one-fifth of the species (17) increased along the gradient ($b > 0$), and seven species were most abundant at intermediate ABP ($b = 0$, $c \neq 0$). The abundance of the remaining 30 species did not change significantly along the gradient ($b = 0$, $c = 0$). Most response curves were unimodal, i.e. the species composition of plots without *P. australis* was similar to the species composition of plots in which it was relatively abundant. Plots without *P. australis* were dense stands of *Juncus subnodulosus* or tall *Carex* species, and *P. australis* was most probably excluded by competition.

Ecological indicator values

Within most of the study sites, ABP was positively correlated with the nutrient indicator value and negatively correlated with the light indicator value. A negative correlation with the indicator value for soil reaction was found at four sites. A relation between ABP and soil moisture was only indicated by the vegetation at three sites; it was negative in two of them, suggesting that *P. australis* was more abundant under drier conditions.

When all sites were pooled, the response curves of the indicator values for nutrients and light were unimodal. Nutrient values generally increased along the ABP gradient, and light values decreased, but plots without *P. australis* had relatively high nutrient values and low light values (Fig. 3). No relation was apparent between ABP and the indicator values for soil reaction or soil moisture. The soil reaction indicator values only varied between 2.7 and 3.4, indicating that no strongly acidic or strongly basic conditions occurred. Moisture values were more variable (3.3–4.6), but both high and low values could be found at any abundance of *P. australis*.



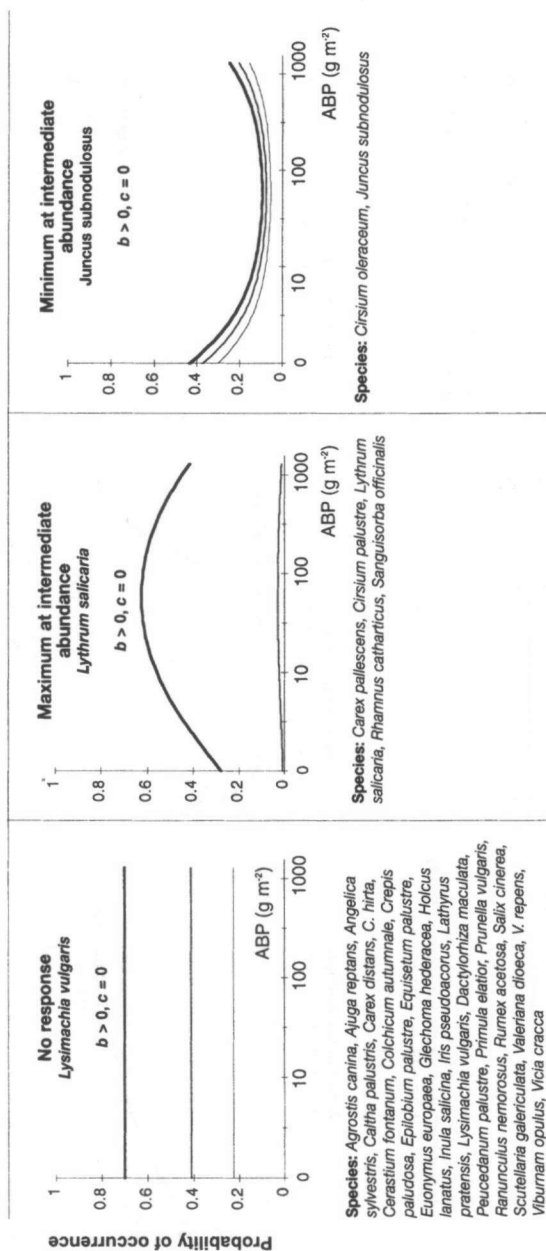


Fig. 2. Species response curves describing relations between the abundance of *P. australis* and the abundance of other species. Heavy lines represent the probability for species to be present in a plot, light lines represent the probability to be present with at least 1% cover, and hairlines, the probability to be present with at least 5% cover.

Table 2. Ecological indicator values of the vegetation of 241 plots belonging to three phytosociological alliances. (a) Mean indicator values and significance of differences among alliances (Kruskal–Wallis). (b) Spearman rank correlations between the indicator values and the aboveground biomass of *P. australis* (ABP); only significant correlations ($P<0.05$) are indicated

| Site | Nutrients | Soil moisture | Soil reaction | Light |
|---|-----------|---------------|---------------|--------|
| (a) Mean indicator values | | | | |
| <i>Caricion</i> | 2.4 | 4.1 | 3.1 | 3.7 |
| <i>Molinion</i> | 2.6 | 3.7 | 3.1 | 3.5 |
| <i>Filipendulion</i> | 3.4 | 3.9 | 3.2 | 3.2 |
| <i>P</i> | <0.001 | <0.001 | NS | <0.001 |
| (b) Correlations between indicator values and ABP | | | | |
| <i>Caricion</i> | 0.30 | — | — | — |
| <i>Molinion</i> | 0.30 | — | — | −0.31 |
| <i>Filipendulion</i> | 0.59 | — | — | −0.54 |

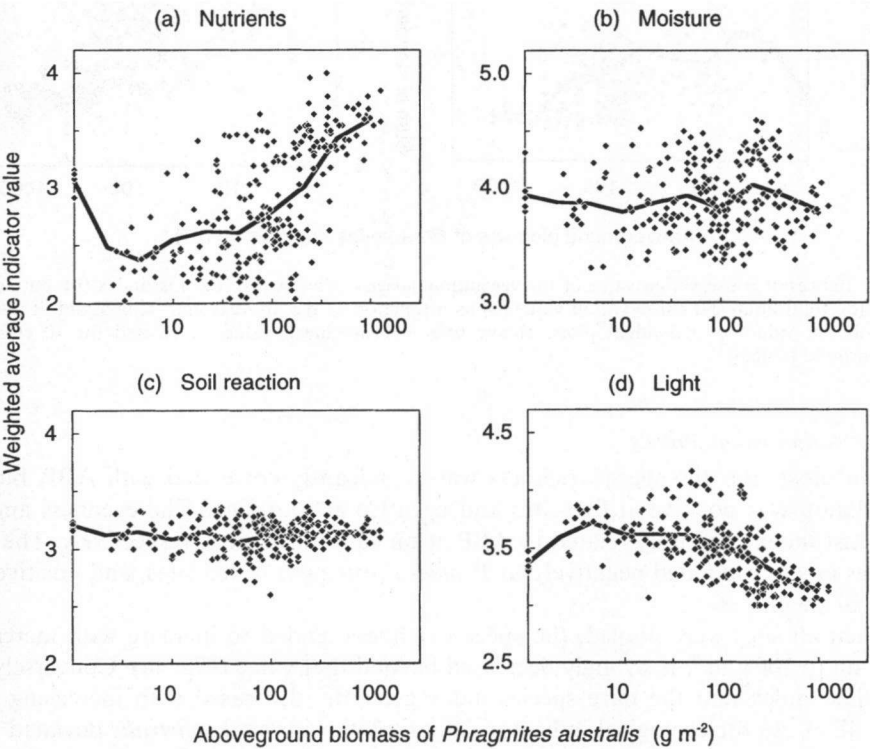


Fig. 3. Ecological indicator values of the vegetation for nutrients (a), soil moisture (b), soil reaction (c) and light conditions (d) as a function of the aboveground biomass of *P. australis*. Symbols are values of individual plots. Heavy lines indicate mean values calculated for 10 classes of aboveground biomass.

The mean indicator values of the three alliances differed strongly, except values for soil reaction (Table 2a). Additionally, nutrient and light indicator values varied within alliances. Their correlations with ABP within each of the three alliances were similar to those in the whole dataset (Table 2b).

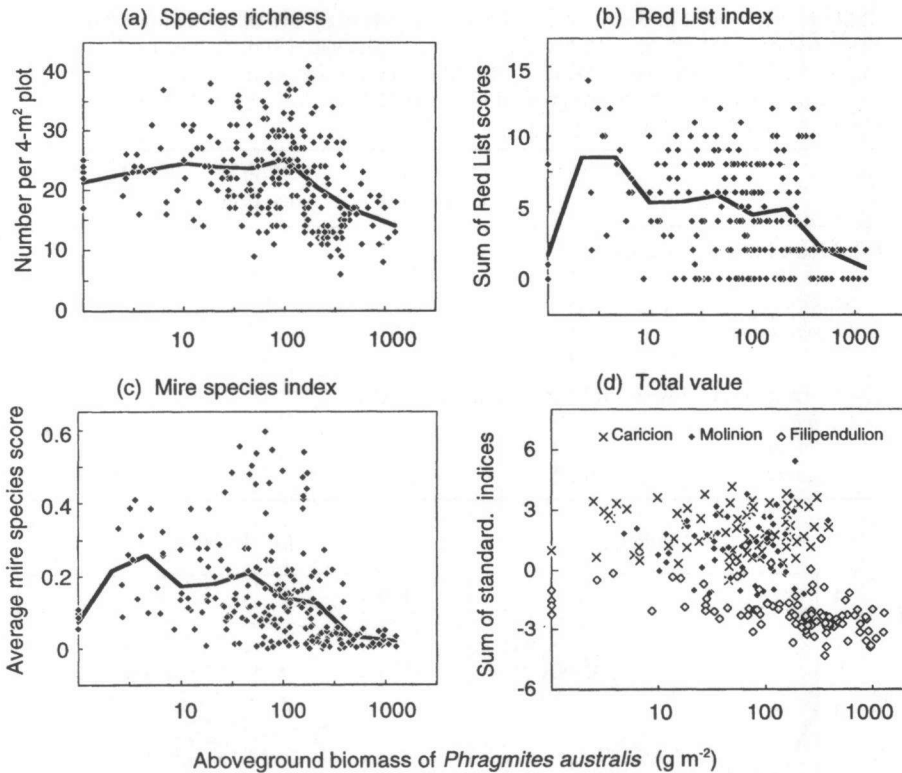


Fig. 4. Indices of conservation value of the vegetation: species richness (a), Red List index (b), mire species index (c), total botanical conservation value (d) as a function of the aboveground biomass of *P. australis*. Symbols are values of individual plots. Heavy lines indicate mean values calculated for 10 classes of aboveground biomass.

Conservation value indices

Within most sites the species richness was significantly correlated with ABP, but the correlation was positive at five sites and negative at four sites. The evenness and the Red List index were only related to ABP at one and three sites, respectively. The mire species index responded negatively to *P. australis* in eight of ten sites, and positively in none of them.

When all sites were pooled, the species richness tended to increase with increasing ABP up to 100 g m⁻²; it strongly decreased beyond that value (Fig. 4a). Conversely, the Red List index and the mire species index generally decreased with increasing ABP (Fig. 4b,c). As for ecological indicator values, plots without *P. australis* deviated from the general pattern, and the curves representing the average responses were unimodal. The evenness hardly changed along the ABP gradient (no figure).

Differences among the alliances accounted for most of the variation in the conservation indices (Table 3a). Within alliances the species number and the mire species index were negatively correlated with the ABP in the *Filipendulion* (Table 3b), whereas the species number increased with increasing ABP in the *Caricion*. As a result, *Caricion* and *Filipendulion* plots did not differ in species richness at a low ABP, but the *Caricion* was more species-rich when the ABP exceeded 100 g m⁻². To summarize the results we

Table 3. Botanical conservation value of the vegetation in 241 plots belonging to three phytosociological alliances. (a) Mean indices and significance of differences among alliances (Kruskal–Wallis). (b) Spearman rank correlations between the indices and the aboveground biomass of *Phragmites australis* (ABP); only significant correlations ($P < 0.05$) are indicated

| | Species number | Evenness | Red List index | Mire species index |
|--|----------------|----------|----------------|--------------------|
| (a) Mean indices | | | | |
| <i>Caricion</i> | 22 | 0.65 | 5.5 | 13 |
| <i>Molinion</i> | 29 | 0.69 | 7.8 | 31 |
| <i>Filipendulion</i> | 18 | 0.67 | 1.8 | 3.2 |
| <i>P</i> | <0.001 | NS | <0.001 | <0.001 |
| (b) Correlations between indices and ABP | | | | |
| <i>Caricion</i> | 0.25 | 0.41 | — | — |
| <i>Molinion</i> | — | — | — | — |
| <i>Filipendulion</i> | −0.49 | — | — | −0.43 |

standardized the indices and used their sum (omitting the evenness) as total index of botanical conservation value (Fig. 4d). The conservation value of *Filipendulion* plots decreased with increasing ABP, but not the conservation value of *Molinion* or *Caricion* plots. All plots with more than 500 g m^{−2} ABP were *Filipendulion* plots and had low conservation value.

DISCUSSION

Abundance of P. australis in fen meadows

P. australis is one of the most productive herbaceous species in the world. Under favourable climatic and edaphic conditions it may attain an aboveground biomass of more than 9000 g m^{−2} (Hocking 1989). Such high values are not reached in central Europe, but a shoot density of 300–400 m^{−2} and a maximal biomass of 2000–3000 g m^{−2} may be found in managed reed-beds (Mook & van der Toorn 1982). In all our plots the aboveground biomass of *P. australis* was much lower, and its contribution to the total biomass was generally less than 40% (Güsewell, unpublished data). Thus, conditions in our fen meadows differed clearly from those in monospecific terrestrial reed beds. Our data are comparable to those of Mochnacka-Lavácz (1975), who found 8–15 shoots m^{−2}, 50–250 g m^{−2} and a relative biomass of 28–29% in Polish fen meadows, or to those of Hirose & Werger (1995), who found 142 g m^{−2} and a relative biomass of 35% in a Dutch floating fen. Thus, the abundance of *P. australis* at our sites seemed, on average, 'normal' for fen meadows.

Is there any evidence that *P. australis* has been spreading at our sites? Various studies indicate that the species was also present formerly in most lakeside fen meadows of the Northern Swiss Plateau (Zobrist 1935; Hürlimann 1951; Heim 1963; Klötzli 1969; Oberdorfer 1993). There are, however, indications that *P. australis* became more abundant within its range. Mapping 25 fens, Marti & Müller (1993) found that 33% of the subsites had higher shoot density in 1991 than in 1976, whereas only 5% of the subsites had a lower density. Similar results were obtained at Lake Pfäffikersee by Lanfranchi & Zimmerli (unpublished, in Klötzli 1997). Wildi & Klötzli (1978) indicated

1–20 shoots m^{-2} as a normal density for *Caricion* communities, 1–3 shoots m^{-2} for the *Molinion* and 0–20 shoots m^{-2} for the *Filipendulion*. These values are much lower than those found in our study. Finally, an increase in abundance has directly been observed by the landowners or by the managers of several of our sites (personal communications).

Relation to site conditions

The abundance of *P. australis* varied considerably among sites and among plots in our study, even though all were managed in the same way. Unfortunately, no reliable information was available on former management. The ecological indicator values of the vegetation suggested that differences in nutrient availability were mainly responsible for differences in the abundance of *P. australis*, whereas water level and soil pH were apparently unimportant. The use of ecological indicator values has limitations, particularly in vegetation influenced by man (Kowarik & Seidling 1989), but the indications of this study were supported by direct measurements at four sites by Brülisauer (1996).

Nutrient indicator value. The unimodal response curve of the mean nutrient indicator value was caused by the six plots in which *P. australis* was missing, probably because it was excluded by other tall species. If we omit these few plots, the nutrient indicator value clearly increased and suggested an increase in nutrient availability along the ABP gradient. This was expected, since *P. australis* strongly responds to the addition of nutrients, especially nitrogen (Hürlimann 1951; Klötzli & Züst 1973a; Bornkamm & Raghi-Atri 1978; Ulrich & Burton 1985; Krumscheid-Plankert 1991; Zelesny 1994). Higher availability of nitrogen seems likely to increase its competitive ability in *Molinion* or *Caricion* communities. Indeed, the productivity of these vegetation types is low and most often limited by phosphorus (Grootjans *et al.* 1986; Egloff 1986; Verhoeven *et al.* 1996). Therefore, nitrogen input might enhance the growth of *P. australis* more than the growth of the other species, and this would give *P. australis* an advantage. Such a process has been shown in chalk grasslands: *Brachypodium pinnatum* increased after nitrogen fertilization, whereas the biomass production of the other species did not change due to phosphorus limitation (Bobbink *et al.* 1988).

Soil moisture. The apparent lack of response to soil moisture is, at first, surprising. As a wetland plant, *P. australis* would be expected to spread mainly into wet sites or parts of sites (Marti & Müller 1993). Since *P. australis* is able to follow the groundwater table with its roots down to 1.5 m or more (Hürlimann 1951; Haslam 1973), it may grow fairly well at sites that completely dry out superficially (Hürlimann 1951). Direct measurements by Brülisauer (1996) even suggested that *P. australis* responded positively to the depth of the groundwater table at our sites. One possible reason is that nitrogen mineralization is generally negatively related to the water level in wet soils (Grootjans *et al.* 1985; Koerselman *et al.* 1993). As seen above, this might be beneficial to *P. australis*. Indeed, there was a weak, but significant, negative correlation at our sites between the nutrient indicator value and the moisture indicator value ($r_s = -0.15$, $P < 0.05$).

Soil reaction. *P. australis* can grow on strongly acidic as well as on calcareous soils (Hürlimann 1951; Haslam 1973; Marks *et al.* 1994). Since the pH conditions were

intermediate at all our sites, the absence of correlation between ABP and the soil reaction indicator value was expected. The correlations found within five of our sites were due to correlations between reaction indicator values and nutrient indicator values. Given the small range of pH indicator values within sites, these correlations had probably no ecological significance.

Light. The decrease of the indicator value for light along the ABP gradient suggested that shading by *P. australis* increasingly displaced light-demanding species (Haslam 1971b; Wheeler & Giller 1982; Klötzli 1986). However, this is not necessarily true, because high ABP was most frequently associated with the presence of other tall and fast-growing species (e.g. *Carex acutiformis*, *Filipendula ulmaria*, cf. Fig. 2). These species formed a dense canopy already in spring or early summer. Their presence was likely to suppress light-demanding species as much, or even more, than the presence of *P. australis* (Buttery & Lambert 1965; Gryseels 1989).

Relation to conservation value

In our assessment of botanical conservation value, plots belonging to the alliances *Caricion* and *Molinion* were generally rated higher than *Filipendulion* plots. This result was, to a certain extent, trivial: to give a plot a high mire species index, or to attribute it to the alliance *Caricion davallianae*, was basically doing the same twice. The main difference was that the mire species index was numeric and, therefore, it could be used to assess gradual changes within each alliance. Thus, the relationship between the abundance of *P. australis* and the average conservation value of a plot could be decomposed into two effects: on one hand, the relative frequency of the three alliances changed along the ABP gradient: the proportion of *Filipendulion* plots increased and was 100% when the ABP was higher than 400 g m⁻². The change in the relative frequency of the three alliances was the main reason for the decrease of conservation value along the ABP gradient. On the other hand, the average conservation value of the plots belonging to the alliance *Filipendulion* decreased along the ABP gradient. Such a decrease was not found for plots belonging to the alliances *Molinion* or *Caricion*.

This last result was surprising. Apparently, shading by *P. australis* had not affected the mire species in those vegetation types generally considered most sensitive to shading. Did this indicate that the current spread of *P. australis* would have no impact on *Molinion* and *Caricion* communities? This conclusion would certainly be premature. It regards the attribution of plots to alliances as fixed, whereas this attribution merely describes the current species composition and may change gradually, e.g. Grootjans *et al.* (1996). Most plots attributed to the *Filipendulion* in our survey supported *Molinion* or *Caricion* vegetation formerly (Gigon & Bocherens 1985; Klötzli 1986; Marti & Möller 1993). Similarly, plots attributed to the alliances *Molinion* or *Caricion* in this study may shift towards the *Filipendulion* in the future. The discussion of a possible impact of *P. australis* on the conservation value of fen meadows must consider the possibility of such shifts.

Thus, the evolution of a *Molinion* or *Caricion* plot that has recently been invaded by *P. australis* might be related to the spread of *P. australis* in different ways (Fig. 5). Five possible scenarios are:

1. *No relation.* The abundance of *P. australis* fluctuates within a certain range, without impact on the species composition. *P. australis* might even decrease to a low level

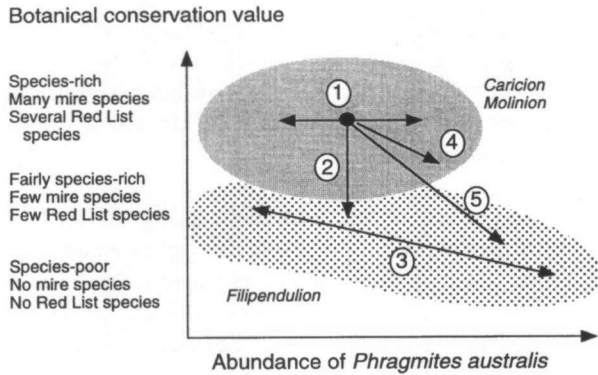


Fig. 5. Model illustrating possible future changes in conservation value of a *Molinion* or *Caricion* meadow in which the abundance of *P. australis* has recently increased. (1) no change, (2) decrease due to a concomitant spread of tall herbs, (3) further decrease due to a further spread of *P. australis* after the spread of tall herbs, (4) decrease due to direct competition (shading) and (5) decrease due to indirect competition (nutrient enrichment leading to the spread of tall herbs).

of abundance again. In that case its present increase would prove to be merely a long-term fluctuation without major ecological significance (example in Krüsi *et al.* 1995).

2. *Early indication.* Tall herbs and sedges increasingly invade the plot and displace mire species. Both the spread of tall herbs and the spread of *P. australis* are probably due to nutrient enrichment (Boller-Elmer 1977; Zelesny 1994; Graf 1996; Brülisauer 1996). *P. australis* spreads particularly fast, and therefore its increase warns that a loss of conservation value is imminent. It is not, however, responsible for that loss.
3. *Additional impact.* After the spread of tall herbs (2), *P. australis* still becomes more abundant. According to Fig. 4d, the spread of *P. australis* results in an additional loss of conservation value, so that the total loss is greater than if tall herbs had spread alone. *P. australis* might, however, also be itself displaced by the tall herbs.
4. *Direct competition.* Light-demanding mire species disappear progressively due to the increased shading by *P. australis*. As a result, the conservation value of the plot is reduced. Nevertheless, the plot still belongs to the same alliance. Such a delayed effect is plausible, because the species composition often responds slowly to changes in site conditions (Grootjans *et al.* 1996).
5. *Indirect competition.* The presence of *P. australis* increases nutrient availability, so that tall herbs and sedges can invade the site and displace other mire species. Thus, *P. australis* is indirectly responsible for the loss of conservation value. Various mechanisms have been suggested for this process, e.g. the transport of nutrients through the rhizomes from zones with high availability, such as ditches, to zones with low availability (Haslam 1971b); the uptake of nutrients from deeper soil layers and their release to the soil surface through leaching and leaf shedding (Krumscheid-Plankert 1991); an enhanced nitrification around the roots of *P. australis* due to exudation of oxygen or losses of carbohydrates (Armstrong 1990); and nitrogen fixation by symbiotic bacteria (M. Aragno, University Neuchâtel, personal communication). However, it is questionable whether these processes may have any significance in fen meadows (cf. Van der Linden 1980; Brix 1989).

These scenarios are only hypotheses, but they illustrate that the conservation value of fen meadows in which *P. australis* has been spreading may decrease in the future, and that the spread of *P. australis* may cause the degradation directly or indirectly. In any case, a spread of tall herbs and a general increase in productivity are other important factors of change. Our study suggested that all these processes are strongly related to each other. Therefore, they must be considered together. Only a long-term monitoring of the abundance of *P. australis* of the species composition and of the biomass production of sites currently invaded by *P. australis* will show whether and how this species can reduce the botanical conservation value of *Molinion* or *Caricion* fen meadows.

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