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Vegetation changes in two Swiss fens affected by eutrophication and desiccation

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Abstract

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Wetland vegetation is often affected by eutrophication or desiccation. The aim of this study was to examine how these factors had affected the vegetation in two wetlands of the Zürich region (Sackriet, 3.8 ha, and Wollwisli, 0.8 ha). We compared the present distribution of plant communities within both wetlands with the distribution mapped 20 years earlier and surveyed site conditions within the different vegetation units in order to determine which changes in site conditions might have caused past vegetation changes. Between 1978 and 1997 the vegetation of Sackriet changed considerably: 80% of the former *Caricion davallianae* area changed to *Filipendulion*, *Magnocaricion* or *Molinion*, and 50% of the former *Magnocaricion* area became *Molinion* or *Filipendulion*. In addition, the structure of *Magnocaricion* changed, with the disappearance of tussocks. In contrast, little vegetation change occurred in Wollwisli. Vegetation types differed in biomass production, nutrient content of the vegetation and water level, but not consistently in soil nutrients. These differences suggested that the observed vegetation shifts were due to both eutrophication and desiccation, with the effect of eutrophication depending on water level and the effect of desiccation depending on nutrient supply. Vegetation change has apparently not reduced species diversity up to now, but further desiccation and eutrophication must be prevented to preserve the present species richness which depends on small remnants of endangered vegetation types.

Key words: Wetland conservation, soil chemistry, biomass production, hydrology, succession, space-for-time substitution.

Introduction

Dramatic changes in vegetation have occurred in European wetlands during the last decades, causing the loss of slow-growing and light-demanding species (Landolt

1991). The most relevant causes are nutrient enrichment (eutrophication; Moore and Keddy 1989, Morris 1991), altered hydrology (Fojt and Harding 1995) and cessation of regular management (Müller et al. 1992, Abt and Ege 1993, Prach 1996).

Eutrophication mostly results from agricultural run-off (Boller-Elmer 1977, Sharp-ley and Smith 1990, Stamm et al. 1995, Ruthsatz 1998), inflow of nutrient-rich ground or surface water (Wassen et al. 1996, Spink et al. 1998) or atmospheric deposition (Morris 1991, Bobbink 1998). Different nutrient sources therefore act at different places within wetlands: run-off affects the border zones; nutrient-rich water influences ditch borders or flooded areas; atmospheric deposition occurs everywhere.

Wetlands are characterised by a high water level during much of the year, and therefore only species that are able to tolerate lasting periods of anoxia can survive (Armstrong et al. 1994). Any impacts leading to lower mean water levels or shorter periods of flooding will allow species without special adaptations, such as common grassland species, to invade and eventually to outcompete species adapted to wet conditions (Braak and Wiertz 1994). The effects of hydrological change on wetland vegetation have been reported in numerous studies (Grootjans and Van Diggelen 1995). Changes in hydrology are often associated with changes in trophic status: Drainage tends to drastically enhance the availability of nitrogen to plants (Grootjans et al. 1986), and a lower water table has also been reported to enhance the supply of phosphorus (Broek 1998, Boeye et al. 1999).

Nutrient enrichment and desiccation can both affect the species composition of wetlands and often occur concomitantly. In addition, the two factors interact: effects of eutrophication may depend on whether or not the hydrology has been altered (Vermeer 1986, Verhoeven et al. 1996), and water levels required for the maintenance of particular wetland communities depend on nutrient conditions (Wheeler and Shaw, pers. comm.).

Wetland conservation policy often tends to consider the various factors individually, which may sometimes make conservation efforts inefficient or even contra-productive (Grootjans and Van Diggelen 1995). In Switzerland, wetland conservation has focused on extensive management and on the reduction of nutrient inputs by improvement of surface water quality and establishment of unfertilised buffer strips around nature reserves (Grünig 1992).

In this paper we report on vegetation shifts in two small Swiss fens during the last decades. The purpose of our study was to describe these shifts in terms of changes in the area occupied by different plant communities and to determine which of them had been caused by eutrophication or by a reduction in water level. To this end we (1) compared vegetation maps established in 1978 and in 1997, (2) surveyed current site conditions in both fens and (3) used differences in current site conditions to explain past shifts in plant communities ("space-for-time substitution"). Based on the results, we discuss the relative importance of eutrophication and desiccation as factors threatening wetland vegetation.

Methods

Study sites

Study sites were two small fens in the Zürich region, Swiss Midlands: "Sackriet" (commune of Aathal-Seegräben; 3.8 ha) and "Wollwisli" (commune of Wangen-Brütisellen; 0.8 ha). Both sites are surrounded by agricultural land; buffer zones with no or

restricted fertiliser use were established during the nineties as a protection against eutrophication. Both fens are mown yearly after the 1st of September, and the hay is removed, except in exceptionally wet autumns.

Vegetation shifts

Vegetation maps of Sackriet and Wollwisli had been drawn by J. Burnand and S. Züst (unpublished) in 1976–1978. The two fens were mapped again in June 1997 using the same floristic key. Only major vegetation units, roughly corresponding to alliances of the phytosociological classification (Ellenberg 1996) were distinguished. All maps were digitised with a GIS (ArcView/ArcInfo) in order to compare areas occupied by the different vegetation types between old and new maps.

Survey of current site conditions

A grid of about 50 m mesh width was laid out at both sites, defining 21 points of observation in Sackriet and 10 in Wollwisli. All main vegetation types defined on the maps were represented by several grid points.

Water level was measured weekly between the end of April and mid-October at 24 of the grid points. Perforated plastic tubes (1 m in length and 5 cm in diameter) were pushed into the soil and water level was measured by inserting a scale down to the bottom of the tube, taking it out again and recording up to which depth the scale had remained dry. These values were subsequently corrected for the volume of water displaced by the inserted scale and for the distance from soil surface to the top of the tube. Water levels deeper than 1 m were recorded as –100 cm. The mean of all sampling dates as well as the amount of fluctuation (difference between maximal and minimal level) were used for data analysis.

Soil samples were taken at the end of May, August and October at each grid point. Three PVC tubes per grid point were pushed into the soil to a depth of 20 cm, removed, closed with caps and taken back to the laboratory in cooling boxes. Within 12 hours after collection the three samples were pooled, sieved (4 mm) and analysed for extractable nutrients. A subsample of fresh soil was dried at 105 °C to determine the water content.

NO₃-N and NH₄-N were extracted from 10 g fresh soil shaken in 40 ml 0.01 M CaCl₂ for 1 hour, and PO₄-P from 5 g fresh soil shaken in 50 ml ammonia acetate + EDTA solution for 1 hour. Nutrient concentrations in the extracts were analysed colorimetrically on a FIA autoanalyzer (Tecator, Höganäs, SE), partly after storage at –20 °C. Averages of the three sampling dates were used for data analysis. Results were expressed per unit soil dry weight.

Total soil N and P contents were determined in May samples by Kjeldahl digestion of 0.5 g air-dried soil followed by colorimetric analysis (FIA, Tecator). Soil pH was determined from a suspension of air-dried soil and 0.01 M CaCl₂ (1:2.5).

Site productivity was assessed by harvesting the aboveground biomass above the moss layer in 3 subplots (0.16 m²) at each grid point. The samples were pooled, and their dry weight (70 °C) determined. Total N and P contents were measured colorimetrically (FIA, Tecator) after Kjeldahl digestion of 1 g ground material.

Vegetation types and their relation to site conditions

For a precise attribution of the grid points to vegetation types, their species composition (vascular plants) was recorded in June 1997 in squares of 4 m² according to the Braun-Blanquet method. Nomenclature followed Hess et al. (1991). The relevés

were grouped by cluster analysis (complete linkage based on Euclidean distances between relevés) with the statistical package MULVA 5 (Wildi and Orlóci 1990).

To investigate relationships between vegetation and site conditions, mean values of the surveyed site variables were compared among vegetation types with one-way ANOVA, after log-transformation when required by data distribution. Differences among the vegetation types were then used to explain the shifts in plant communities derived from vegetation maps according to the approach of “space for time substitution” (Pickett and Ostfeld 1994, Maarel 1996).

Results

Vegetation shifts

The vegetation of Sackriet changed considerably between 1978 and 1997 (Fig. 1, Table 1). A large Caricion davallianae stand decreased by 80%, with 20% turning into Filipendulion and Magnocaricion vegetation, and the rest into Molinion meadows. In addition, half of the area bearing Magnocaricion vegetation in 1978 turned into Molinion meadows or Filipendulion stands. These shifts in plant communities primarily affected the fen borders. Important changes in the centre of the fen were mainly associated with open water, i.e. Filipendulion stands established along a small rivulet running into the fen and close to the main ditch. Areas of Caricion davallianae or Magnocaricion vegetation still found in 1997 were mostly located around deep rectangular holes dug for peat exploitation.

Contrary to Sackriet, the vegetation in Wollwisli experienced little change over the past 20 years and mostly remained tussock-forming Magnocaricion or Sphagnum-rich Caricion lasiocarpae (poor fen) vegetation (Fig. 1, Table 1). Filipendulion vegetation only developed in a narrow border zone (not visible in Fig. 1 because it had not been mapped in 1978). A pond was created for conservation purposes, but this had no effect on the surrounding vegetation.

Current site conditions

Soil and plant nutrient contents as well as water levels of all grid points are listed in App. 1. Average water levels during the investigated growing season ranged from 1 to more than 61 cm below soil surface but after a period of heavy rainfall in June, both sites were mostly flooded (Sackriet during one week, Wollwisli during five to seven weeks). Water level fluctuations were negatively correlated with mean water level ($r = -0.7$, $p = 0.0005$), i.e. fluctuations were stronger at the drier sites.

Extractable soil nutrients differed by a factor of 4 (N) or 20 (P) between the poorest and the richest grid points. Total nutrients differed by a factor of 10 (N) or 6 (P). Some spatial patterns in soil chemistry were apparent: total and extractable N tended to increase with distance from fen border; total soil phosphorus did not change with distance from the border, and extractable P decreased.

Peak aboveground biomass at Sackriet ranged from 190 to 990 g m⁻² dry mass, and at Wollwisli from 145 g m⁻² to 640 g m⁻². Soil nutrient contents did mostly not correlate with the aboveground biomass, except for water-extracted NO₃ per unit fresh soil ($r = 0.37$, $p = 0.05$), but plant P concentration did ($r = 0.54$, $p = 0.003$). The average nutrient indicator value (Landolt 1977) was correlated with the aboveground biomass better than any other measure of nutrient availability ($r = 0.69$, $p = 0.0001$).

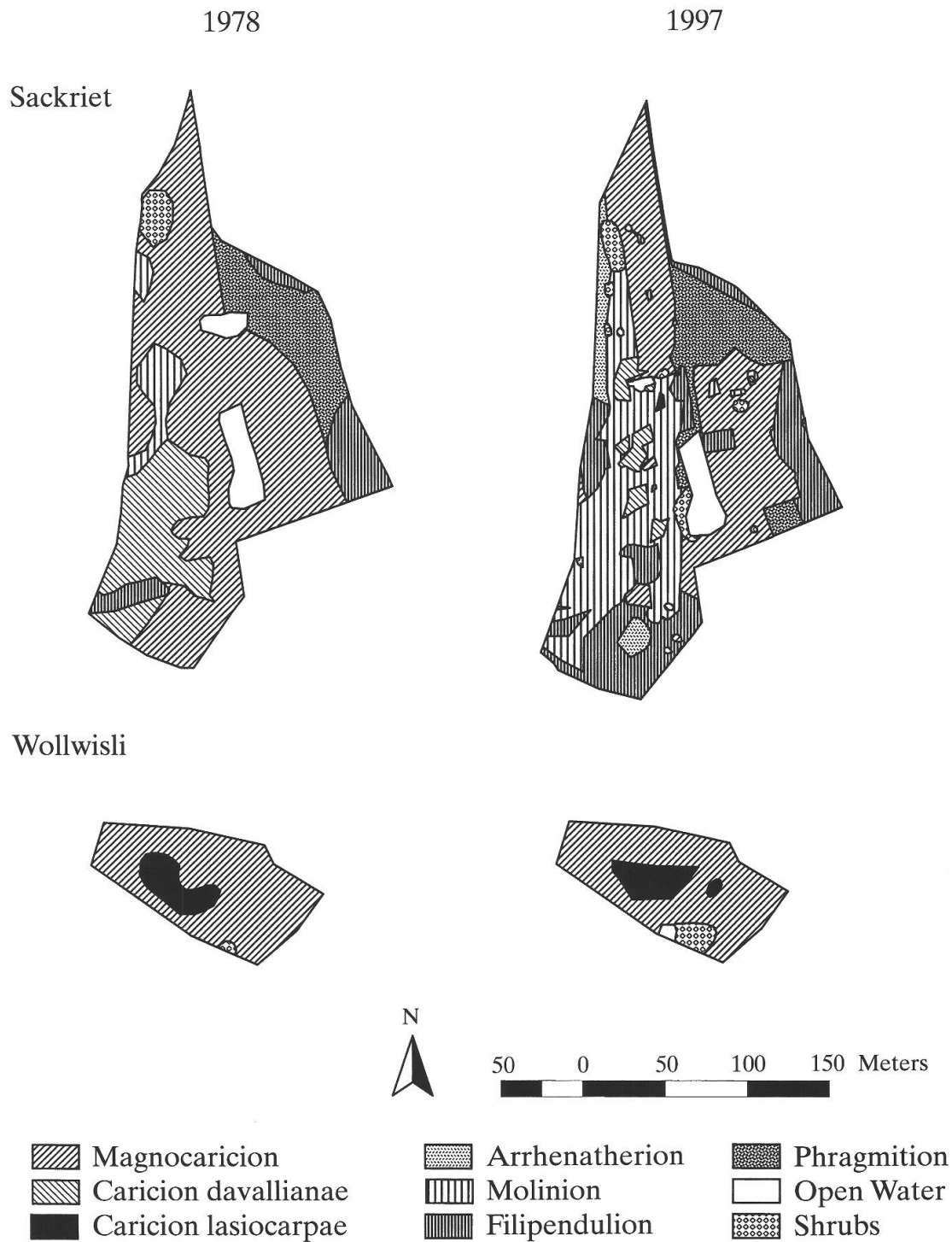


Fig. 1. Vegetation shifts in two Swiss fens (Sackriet and Wollwisli) between 1978 (Burnand and Züst, unpublished) and 1997 (this study). The nomenclature of vegetation units (alliances) follows Ellenberg (1996). "Magnocaricion" includes both the tussock-forming and the tussock-free types (see text). In the case of Wollwisli, only ca. 80% of the current wetland area (area under conservation) are represented because the remaining 20% had not been mapped in 1978.

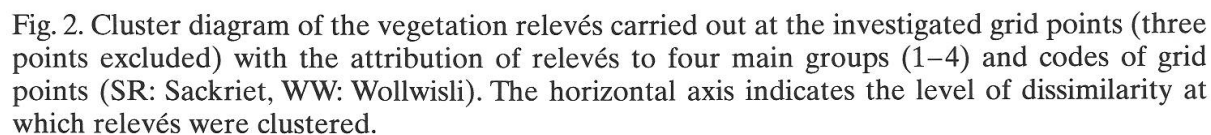
Table 1. Vegetation changes in two Swiss fens (Sackriet and Wollwisli): Area of mapped vegetation units and their percentage of the total area.

	1978		1997		change	
	[m ²]	%	[m ²]	%	[m ²]	1997 in % of 1978
Sackriet						
Magnocaricion	16'367	54%	8'757	29%	-7'610	54%
Caricion davallianae	4'618	15%	945	3%	-3'673	20%
Molinion	1'396	5%	7'840	26%	6'444	561%
Filipendulion	2'265	7%	6'158	20%	3'893	272%
Rhynchosporion	–	0%	54	0.2%	54	–
Phragmitetum	3'651	12%	3'578	12%	-73	98%
Arrhenatherion		0%	1'094	4%	1'094	
Shrubs	550	2%	707	2%	157	129%
Open water	1'381	5%	1'096	4%	-285	79%
Total	30'228	100%	30'228	100%		
Wollwisli						
Magnocaricion	5'999	86%	5'656	81%	-343	94%
Caricion lasiocarpae	942	13%	905	13%	-37	96%
Shrubs	59	1%	348	5%	289	590%
Open water	–	0%	91	1%	91	–
Total	7'000	100%	7'000	100%		

Vegetation types and their relation to site conditions

Vegetation relevés are given in App. 2. A first analysis showed that three relevés were clear outliers, i.e. strongly differed in species composition from all others. One of them was dominated by *Carex acutiformis* (in the border zone of Wollwisli), and two by *Phragmites australis* (in an unmanaged area of Sackriet). Cluster analysis of the remaining relevés revealed 4 well-separated vegetation groups (Fig. 2). Group 1 is tussock-forming Magnocaricion vegetation (dominated by *Carex elata*). Group 2 consists in tussock-free Magnocaricion vegetation with a high cover of *Phragmites* and *Poa palustris*. Group 3 is rather heterogeneous, including grid points within areas mapped as Caricion davallianae, Magnocaricion and Molinion. In the following, this group will be called Molinion since all relevés except one included *Molinia coerulea*. Group 4 consists of all points with Filipendulion vegetation.

Several site variables differed significantly among the four groups (Fig. 3): Biomass production was significantly higher in Filipendulion and tussock-free Magnocaricion than in Molinion (Fig. 3a). Nitrogen concentration in plant biomass was higher in tussock-forming Magnocaricion than in the other groups (Fig. 3c). Phosphorus concentration in plant biomass was higher in Filipendulion than in Molinion vegetation (Fig. 3d). The four groups did not differ significantly in extractable soil nitrogen (Fig. 3e) or phosphorus (Fig. 3f) nor in total soil nitrogen (Fig. 3g). By contrast, total soil phosphorus content was significantly higher in tussock-free Magnocaricion than in Molinion and Filipendulion (Fig. 3h). Mean water level was lowest in Filipendulion (plots were never flooded during the investigation) and highest in tussock-forming Magnocaricion (Fig. 3i). Differences in water level fluctuations and soil pH were not significant, but Filipendulion tended to have the highest soil pH (Fig. 3j, 3b).



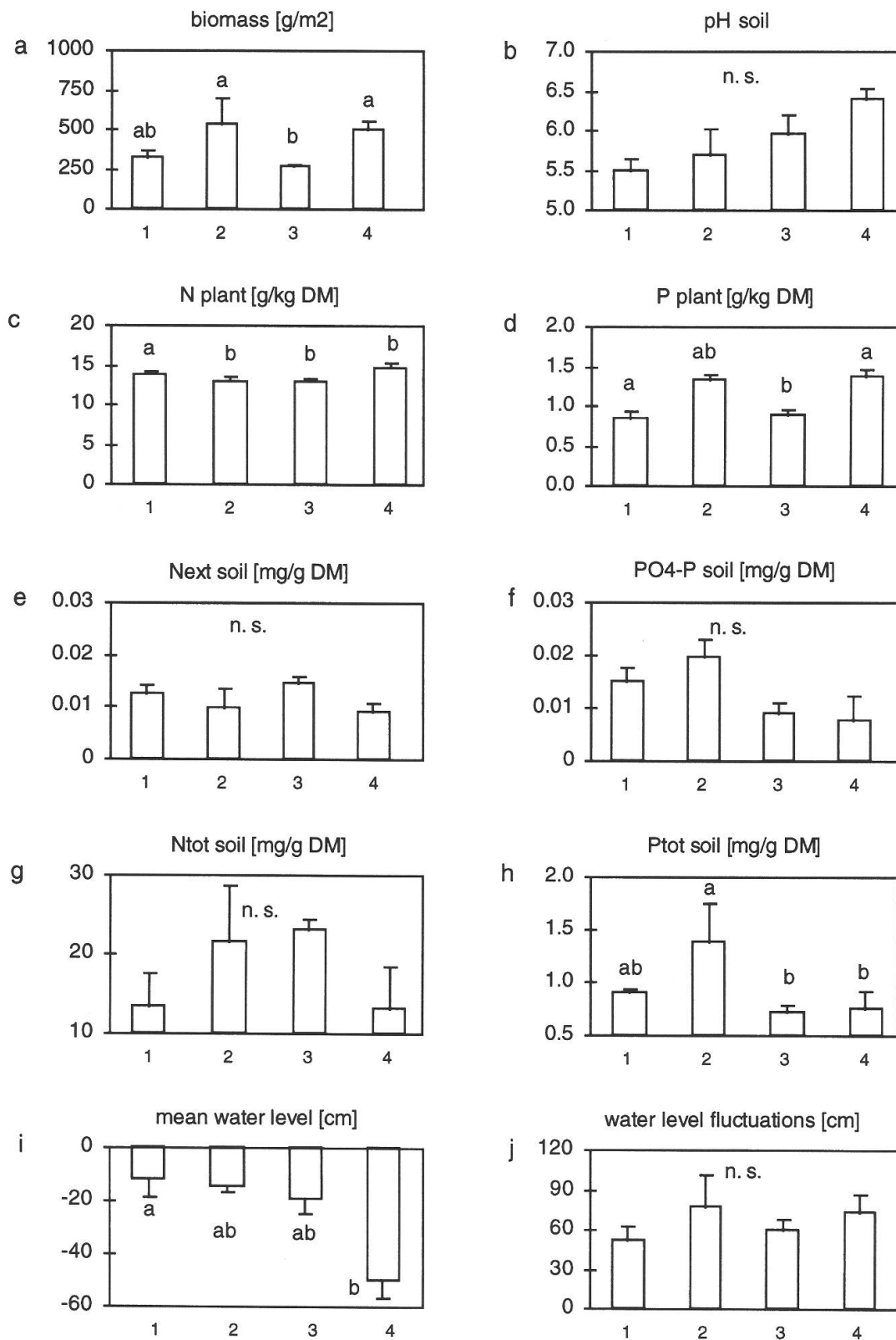


Fig. 3. Biomass, plant nutrient concentrations, soil chemistry and water regime (mean+SE) for the four vegetation types distinguished by cluster analysis (1: Tussock-forming Magnocaricion, 2: Tussock-free Magnocaricion, 3: Molinion, 4: Filipendulion). Means which do not share the same letter differ significantly (Tukey-Kramer test, $p < 0.05$).

The main differences among the four vegetation groups can therefore be summarised as follows: Tussock-forming Magnocaricion occurs at high mean water level and rather strong water level fluctuations. Tussock-free Magnocaricion has high biomass production and high P content in soil. Molinion (and likewise Caricion davallianae, since the group was actually mixed) is characterised by low biomass production. Filipendulion has high biomass production and low water level.

Discussion

Methodological issues

Vegetation change in the two fens was assessed in this study by comparing vegetation maps from 1978 with maps of 1997. To a certain degree, differences between the two maps must be considered with caution, since vegetation mapping tends to differ between authors even when the same key is used (Burnand et al. 1986, Frey 1995). Moreover, vegetation fluctuates considerably over years even in the absence of long-term shift (Egloff 1983, Klötzli and Zielinska 1995, Güsewell et al. 1998, Ruthsatz 1998). However, differences between authors as well as year-to-year fluctuations are likely to concern primarily the lower levels of the phytosociological classification. Since we only discussed vegetation change at the level of alliances (main vegetation units in the key), the risk of overinterpreting results was small.

The approach used in this study to explain vegetation change assumes that the measured variables reflect the nutrient availability and water regime of the vegetation types. While this is most likely to be the case for the measurements of water level, nutrient analyses need a more critical consideration since the relationship between measured soil nutrients and aboveground biomass production was weak (further details see Bollens 2000). This finding, which is consistent with many other studies (Wheeler et al. 1992), may have different reasons. Nutrient contents in soil are always subject to considerable variation in both space and time (Federer et al. 1989), and they do often not represent properly the rates of nutrient supply: total soil nutrient contents are to a large extent unavailable to the vegetation, and extractable nutrients only represent the fraction of available nutrients that was not incorporated by the vegetation. Even mineralisation rates determined *in situ* may not reflect the actual nutrient supply to the vegetation, e.g. because microbial immobilisation is enhanced in the absence of plant uptake (Jonasson et al. 1999). Thus, our finding that three of the four variables measuring soil nutrients did not differ among vegetation types is not surprising and does not contradict the clear differences found in above-ground biomass and plant nutrients.

Causes of vegetation change

Three vegetation types expanded in the two fens between 1978 and 1997. Our comparison of the site conditions among present vegetation types as well as observations by other authors suggest that the causes of spread differed.

1. Filipendulion

Filipendulion typically occurs at base- and nutrient-rich sites (Ellenberg 1996). In Sackriet, Filipendulion developed around ditches and a pond which had been polluted by agricultural waste water for a long time (Escher 1972), as well as in border zones which most probably received nutrient inputs from the adjacent heavily fertilised farmland (Neyer 1999, Cavelti et al. 1999). Since *Filipendula ulmaria* and tall forbs in gen-

eral are favoured by fertiliser addition (Egloff 1986, Duren et al. 1997), peripheral nutrient enrichment, presumably through surface runoff (Sharpley and Smith 1990), is a plausible explanation for the development of tall forb borders between 1978 and 1997. Our finding that extractable soil phosphorus, but not soil nitrogen, was enhanced in border zones suggests that the development of Filipendulion at our sites was primarily due to phosphorus enrichment, as already suggested by other authors for Swiss fens (Boller-Elmer 1977, Egloff 1983, Zelesny 1994). This is also consistent with the high P concentration in the biomass of Filipendulion vegetation.

In our survey aboveground biomass and soil or plant nutrients did not differ between Filipendulion and tussock-free Magnocaricion, suggesting that eutrophication alone was not sufficient for Filipendulion species to establish. Hydrology obviously also played an important role in the development of tall forb stands. Compared to tussock-free Magnocaricion, Filipendulion had higher soil pH and lower mean water level, and it was never flooded during the investigation. This suggests that low pH and high water levels prevented tall forbs from spreading in those areas where tussock-free Magnocaricion developed instead of Filipendulion (part of Wollwisli). Likewise, Fojt and Harding (1995) described tall sedge mires altering into tall forb fens only after drainage.

2. Tussock-free Magnocaricion

Tussock-forming Magnocaricion is characterised by high water levels and flooding periods of several weeks (Marti 1994). In the study of Warnke-Grüttner (1990) *Carex elata*-dominated tussock-forming Magnocaricion occurred where the highest seasonal water level exceeded 20 cm above soil surface, and *Carex lasiocarpa*-dominated tussock-free Magnocaricion occurred where this was not the case. These two types of Magnocaricion did not differ in soil nitrogen, phosphorus or potassium. In contrast, in our study tussock-free Magnocaricion was dominated by *Carex elata* and was not only drier than the original tussock-forming vegetation; it also had a better nutrient (especially P) supply, which suggests that at our sites, both a moderate reduction in water level and nutrient enrichment were responsible for the change in species composition and vegetation structure.

3. Molinion

Stands with *Molinia coerulea* often developed from Magnocaricion vegetation. They had lower mean water level and lower biomass than current Magnocaricion in spite of higher levels of extractable nitrogen. Apparently they experienced phosphorus deficiency. This suggests drainage as the main cause of vegetation shift. A comparable development was observed in a Dutch Molinion after drainage: high nitrate concentrations were measured in the soil, whereas phosphorus availability was reduced, and the biomass production remained low (Grootjans et al. 1986).

Shifts from Caricion davallianae towards Molinion also occurred at our sites. Since the two vegetation types had not been separated by the cluster analysis, we could not analyse causes of this shift with the approach followed in this study. However, previous surveys of fens meadows in the same region had indicated that the alliances Caricion davallianae and Molinion differ in water level more than in nutrient supply, Caricion davallianae being wetter (Klötzli 1969, Güsewell and Klötzli 1998). Grootjans et al. (1986) also document that drainage can induce a shift from small sedges towards *Molinia*-dominated vegetation.

All together these results suggest that at our sites, water level determined whether eutrophication caused a vegetation shift from tussock-forming Magnocaricion towards

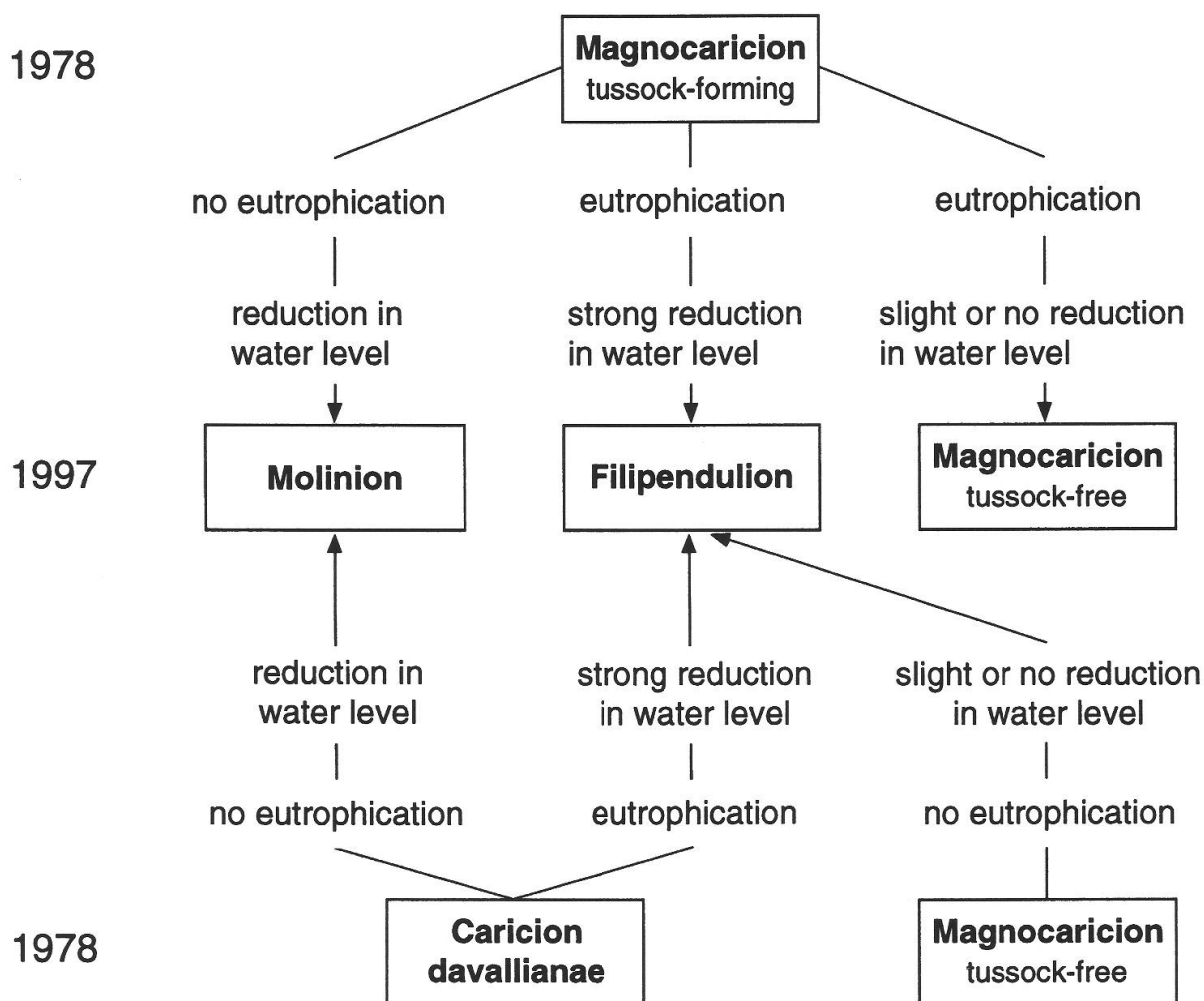


Fig. 4. Qualitative model of vegetation shifts between 1978 and 1997 in the two investigated fens under the influence of eutrophication and/or reduction in water level.

Filipendulion (at dry sites) or towards tussock-free Magnocaricion (at wetter sites). On the other hand, the nutrient supply determined whether desiccation caused a shift from tussock-forming Magnocaricion towards tussock-free Magnocaricion (at enhanced supply, especially of P) or towards Molinion (in the absence of eutrophication). The nutrient supply and the amount of reduction in water level together determined whether Caricion davallianae turned into Molinion or Filipendulion (Fig. 4).

Relevance of vegetation change for conservation

Vegetation shifts in the two investigated wetlands seemed dramatic when changes in the area of the different vegetation types was considered. In contrast, the diversity of vegetation types did not decrease, and probably even increased since several sub-units found in 1997 had not been mapped in 1978.

The main vegetation type in both fens in 1978 was Magnocaricion, which generally has low species diversity (less than 10 species per 4 m² in 1997 in Wollwisli; see also

Kunzmann et al. 1985, Marti 1994). In Sackriet this species-poor vegetation was partly replaced by species-rich Molinion stands containing small sedges (up to 30 species per 4 m²). It can therefore be assumed that Sackriet did not suffer dramatic species loss due to desiccation, although some rare Caricion davallianae species may have disappeared from the study sites due to the strong reduction in area of this vegetation type.

Red list species (Landolt 1991) were found at grid points belonging to all vegetation types except reed stands, but their number was higher in the vegetation types which had decreased between 1978 and 1997 than in the types which had expanded: in Sackriet eight red list species occurred in small sedge stands, nine species in Magnocaricion, eight in Molinion, and five in Filipendulion. Of the twenty endangered species found in our vegetation survey, only seven occurred in more than one vegetation type. There were additional endangered species outside the surveyed plots. In Wollwisli two of the four endangered species grew in Magnocaricion, one in both Magnocaricion and tall forb border, and one in Caricion davallianae. These numbers indicate that a total replacement of the original Magnocaricion and Caricion davallianae vegetation by the expanding vegetation types would result in the loss of several red list species.

Both study sites are important habitats for birds and amphibians (Escher 1972) due to their rich variety of habitat structures and because the present vegetation types are rather rare. The occurrence of new vegetation types, such as the tall forb border in Wollwisli, has increased habitat diversity of the sites and which may have resulted in higher animal species diversity. Therefore, the re-establishment of the status of the seventies should not be a conservation target, but the transformation process needs to be stopped before the remaining vegetation patterns are lost. Especially the desiccation of the last wet holes with Caricion davallianae and floating fens must be prevented.

Relative importance of eutrophication and desiccation and consequences for management

Both eutrophication and desiccation were responsible for the vegetation shifts observed in Sackriet. Desiccation affected a larger area, but eutrophication changed the species composition more strongly and reduced species richness. Thus, the relative importance of the two factors depends on the point of view and cannot be assessed generally. The strongest shifts resulted from the combination of eutrophication and desiccation.

A major limitation of our study is that we only investigated two fens, which was insufficient to evaluate the generality of the model of vegetation change suggested in Fig. 4. However, our two study sites can be considered representative of a large proportion of the fens in the Swiss Midlands with respect to size, topography, management and surrounding land use, so that our results may have some general validity. Two practical implications are suggested by our study:

First, the interaction between effects of eutrophication and those of desiccation means that these effects and their consequences for conservation may be underestimated if they are only evaluated at sites which are undisturbed with respect to the other factor. Thus, considering only Wollwisli, one might perhaps come to the conclusion that eutrophication has no drastic effects, and considering only the non-eutrophicated parts of Sackriet, one might be tempted to conclude that desiccation does not severely threaten species diversity. A more realistic evaluation of the effects would also take into account situations where both factors have been modified.

Second, the prevention or reversion of eutrophication seems most urgent at sites with disturbed hydrology, because it is at these sites that eutrophication will cause the most drastic change. Likewise, the maintenance of a high water table is particularly important for sites which have received considerable nutrient inputs, since desiccation will affect these sites in a much more undesirable way than sites with mesotrophic vegetation. The best policy would always be to prevent both eutrophication and desiccation, since any disturbance in one factor makes a site more vulnerable to change in the other factor.

Thus, taking into account the interacting effects of nutrients and water level, as shown in this study, may help to increase the effectiveness of wetland conservation measures.

Zusammenfassung

Bollens U., Güsewell S. und Klötzli F. 2001. Vegetationsveränderungen in zwei Schweizer Flachmooren unter dem Einfluss von Eutrophierung und Entwässerung. Bot. Helv. 111: 121–137.

Feuchtgebiete sind häufig beeinträchtigt durch Nährstoffeinträge oder Entwässerung. Das Ziel dieser Arbeit war es, die Effekte dieser Faktoren auf die Vegetation in zwei Feuchtgebieten im Kanton Zürich (Sackriet, 3.8 ha und Wollwisli, 0.8 ha) zu untersuchen. Wir verglichen die aktuelle Verteilung von Pflanzengesellschaften in beiden Feuchtgebieten mit der Verteilung, wie sie vor 20 Jahren kartiert worden war. Wir untersuchten die Standortbedingungen innerhalb der verschiedenen Vegetationseinheiten um zu bestimmen, welche Änderungen in den Standortbedingungen als Ursache für Vegetationsveränderungen in Frage kommen. Zwischen 1978 und 1997 hat sich die Vegetation im Sackriet bedeutend verändert: 80% des einstigen Kleinseggenrieds ging über in Hochstaudenried, Großseggenried oder Pfeifengraswiese und 50% der ehemaligen Großseggenried-Fläche ist heute Pfeifengraswiese oder Hochstaudenried. Bultiges Großseggenried wandelte sich in Großseggenried ohne Bulten um. Die Gesamtfläche des Hochstaudenrieds hat sich verdreifacht, während sich Kleinseggenried und bultiges Großseggenried nur in nassen Torfstichlöchern halten konnte. Im Gegensatz dazu hat sich die Vegetation im Wollwisli kaum verändert. Die Vegetationseinheiten unterschieden sich in der Biomasseproduktion, der Nährstoffkonzentration der Biomasse und bezüglich des Wasserstandes am Standort, nicht jedoch in den Bodennährstoffgehalten. Diese Unterschiede lassen vermuten, dass das Hochstaudenried hauptsächlich durch Nährstoffanreicherung gefördert wurde, meist in Kombination mit verringertem Wasserstand. Das Verschwinden von bultigem Großseggenried und vom Kleinseggenried hingegen scheint hauptsächlich auf eine Wasserstandssenkung zurückzuführen zu sein. Die führte unter erhöhter Nährstoffverfügbarkeit zu Großseggenried ohne Bulten oder zu Hochstaudenried und unter knapper Nährstoffverfügbarkeit (vor allem P) zu Pfeifengraswiesen. So hing die Wirkung der Eutrophierung vom Wasserstand ab und die Wirkung der Entwässerung vom Nährstoffangebot. Die Vegetationsveränderung hat den Artenreichtum bis heute vermutlich nicht verändert, aber der fortschreitenden Abtrocknung und Eutrophierung muss Einhalt geboten werden, damit die Artenvielfalt, die auf Grund von kleinen Resten von gefährdeten Vegetationseinheiten hoch geblieben ist, erhalten werden kann.

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Vegetation group	Tussock-forming Magnocaricion								Tussock-free Magnocaricion					Molinion				
Grid point	WWA1	WWA2	WWA3	WWB1	WWB2	WWB3	WWC1	WWC2	SRB7	SRB8	SRC2	SRC3	SRA2	SRA5	SRA6	SRab4		
Biomass [g/m2]	410	410	500	400	140	270	330	250	600	990	260	520	330	260	250	220		
N content of biomass [mg/g]	17	14	14	13	12	15	13	12	12	13	12	15	15	14	15	12		
P content of biomass [mg/g]	1.4	0.84	1	0.93	0.5	1	0.72	0.56	1.3	1.2	1.3	1.5	1.2	1.0	0.95	1.0		
PO4-P [mg/kg]	42.0	12.0	12.0	18.0	17.0	7.9	16.0	10.0	14.0	18.0	19.0	31.0	1.9	6.9	4.7	7.3		
NO3-N [mg/kg]	8.4	2.0	2.6	2.7	2.2	1.7	1.8	2.8	2.7	3.9	3.0	3.1	10.0	5.8	5.1	4.2		
NH4-N [mg/kg]	3.3	4.6	12.0	21.0	17.0	9.2	5.3	14.0	3.2	1.7	13.0	15.0	1.5	6.0	5.2	9.8		
Next [mg/kg]	12.0	6.5	11.0	21.0	15.0	12.0	10.0	17.0	5.9	5.6	16.0	18.0	11.0	12.0	10.0	14.0		
P total soil [mg/g]	1.1	0.83	0.92		0.89	0.94		0.78	2.4	0.75	1.3	1.5	0.62	0.82	0.6	0.84		
N total soil [mg/g]	3.8	11	18		29	14		19	25	9.1	30	31	22	26	23	28		
pH	6	5.8	5.3	5.8	4.6	5.4	5.4	5.6	6.2	6.3	5.1	5.2	7.1	5.6	5.7	6.5		
Mean water level [cm]	-51		-8.7	-1.3	-2.6	-16	-2.5	-1.3		-16	-13		-53		-19	-15		
Max. water level [cm]	6		22	25	5	9	22	15		50	28		-4		18	7.5		
Min. water level [cm]	-100		-36	-21	-14	-45	-23	-19		-51	-24		-100		-38	-33		
Water level max-min [cm]	110		58	46	19	54	45	34		100	52		96		56	41		

Vegetation group	Molinion (cont.)								Filipendulion					Not classified				
Grid point	SRB1	SRB2	SRB3	SRB4	SRB5	SRB6	SRC4	SRA1	SRA3	SRA4	SRD3	WWC3	SRC5	SRC6	WWD1			
Biomass [g/m2]	280	330	190	230	270	280	300	430	450	700	410	570	960	810	640			
N content of biomass [mg/g]	13	12	12	12	12	12	13	17	13	13	14	17	14	17	16			
P content of biomass [mg/g]	1.0	0.53	0.7	0.8	1.1	1.0	0.83	1.2	1.4	1.3	1.3	1.7	1.0	1.5	1.8			
PO4-P [mg/kg]	12.0	10.0	11.0	19.0	14.0	15.0	12.0	6.8	3.3	2.2	33.0	15.0	97.0	41.0	80.0			
NO3-N [mg/kg]	13.0	1.9	3.9	2.8	3.3	3.7	3.8	14.0	6.4	6.3	6.0	3.8	5.0	9.7	6.3			
NH4-N [mg/kg]	3.7	8.7	11.0	15.0	13.0	12.0	22.0	2.8	1.3	2.3	3.2	2.4	9.9	1.6	1.3			
Next [mg/kg]	16.0	11.0	15.0	18.0	16.0	16.0	26.0	16.0	7.7	8.6	9.2	6.4	15.0	11.0	7.6			
P total soil [mg/g]	1.3	0.42	0.67	0.6	0.81	0.83	0.74	1.4	0.62	0.4	0.87	0.76	0.91	1.1	0.85			
N total soil [mg/g]	27	15	21	22	26	20	29	23	15	11	27	3.8	27	18	2.7			
pH	6.5	7.2	5.2	5	6	5.8	5.1	6.9	6.4	6.4	6.2	6.1	6.8	6.8	6			
Mean water level [cm]	-22	-11		-14		-12	-10	-57			-38	-56	-8.4	-51	-61			
Max. water level [cm]	1	5		18		37	38	-2			1	-22	50	13	-6			
Min. water level [cm]	-74	-28		-29		-34	-24	-100			-69	-74	-24	-77	-78			
Water level max-min [cm]	75	33		47		71	62	98			70	52	74	90	72			

Appendix 1. Above-ground biomass, nutrient contents in the vegetation and in the soil, and water levels at each of the 31 investigated grid points. Codes of grid points are WW: Wollwisli, SR: Sackriet.

Group	1	1	1	1	1	1	1	1	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	-	-	-
Grid point	WWA1	WWA2	WWA3	WWB1	WWB2	WWB3	WWC1	WWC2	SRB7	SRB8	SRC2	SRC3	SRA2	SRA5	SRA6	SRAb4	SRB1	SRB2	SRB3	SRB4	SRB5	SRB6	SRC4	SRA1	SRA3	SRA4	SRD3	WWC3	SRC5	SRC6	WWD1					
<i>Agrostis canina</i>														1	+		r																			
<i>Anthoxanthum odoratum</i>														1	+					+					2		+									
<i>Briza media</i>													+			r			r																	
<i>Cardamine palustris</i>									1	1	1	1										1														
<i>Carex acutiformis</i>														1			+									2	1	2	2					5		
<i>Carex elata</i>	3	3	4	3	+	4	3	3	1	1	2	2		2	2	+		+	2	2	2	3	4	1		+										
<i>Carex flava</i>													1	1		1	1																			
<i>Carex hirta</i>	+																r								1			1								
<i>Carex hostiana</i>															2	1	1			2																
<i>Carex lasiocarpa</i>				2										1		+	+			1	r															
<i>Carex panicea</i>													1	2						1			2													
<i>Cerastium holosteoides</i>																								1	+		1									
<i>Epilobium palustre</i>										1	1											1														
<i>Equisetum palustre</i>													1											1	r											
<i>Festuca rubra</i>													1							+			1	2	2	1	1									
<i>Filipendula ulmaria</i>										r	r	r	+									+	1		4	4	2	4	1							
<i>Frangula alnus</i>													1			r		r	r																	
<i>Galium album</i>														+										2		1										
<i>Galium palustre</i>		+							r	+	+	1	1								r	+	+						+							
<i>Galium uliginosum</i>																+			1	1					2	1	2									
<i>Geum rivale</i>										r	r													1												
<i>Holcus lanatus</i>	+													1	+		+			+				1	1	r	1									
<i>Hypericum tetrapterum</i>				r	r												1				1	r														
<i>Iris pseudacorus</i>		+	+																												2					
<i>Linum catharticum</i>													+			+		1	+																	
<i>Lotus uliginosus</i>		+									2	2		1			1	+		+				2	1	+	1	2								
<i>Lysimachia vulgaris</i>		+	+	1	+	1	1	1					1				r			1	1	1	2		+	+										
<i>Lythrum salicaria</i>	r	+									1	1		1	+		1		1	1	+			2	r	1	1									
<i>Mentha aquatica</i>				r										1	1	1	1	1	1	1	r	+	1	1	2											
<i>Molinia coerulea</i>				2									4	2	1	2	3	2	2	2	1		+			2										
<i>Parnassia palustris</i>																1	1		1	r	1															
<i>Phalaris arundinacea</i>	2								1	1																								2		
<i>Phragmites australis</i>									3	3	3	3							1	1						1	1	2			4	3				
<i>Plantago lanceolata</i>																	r		r					1												
<i>Poa palustris</i>									3	3	3	3										1														
<i>Poa pratensis</i>																										+	r									
<i>Potentilla erecta</i>													1		+	+	1	1	2	2	+	+	+			1										
<i>Potentilla palustris</i>		1		1	+	2	1	2																												
<i>Ranunculus nemorosus</i>													+				1							1			+									
<i>Salix cinerea</i>																				r	r	r														
<i>Scutellaria galericulata</i>			+								1	1																								
<i>Selinum carvifolia</i>							r												1	1	+	+	r													
<i>Succisa pratensis</i>													1			r		+		1		r														
<i>Valeriana dioica</i>																+		+	r								1									
<i>Vicia cracca</i>															+	r							+				1									

Species which occur in less than 3 plots are not listed.

Appendix 2. Species composition (vascular plants) at each of the 31 investigated grid points. Data are cover values according to the Braun-Blanquet scale in relevés of 4 m². Vegetation groups are coded as in Fig. 2 and 3.

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