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Effects of winter mowing on vegetation succession in a lakeshore fen

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Abstract. To assess whether winter mowing in wetlands fulfils the aim of preventing succession towards drier communities, 34 permanent quadrats (15 m^2) were surveyed annually from 1984-1985 to 2000 within large mown and unmown (control) areas (several ha) in a calcareous lake shore fen (W Switzerland). Three trends were noticed: decrease of aquatic species, spread of *Cladium mariscus* and establishment of woody species (especially *Alnus glutinosa* and *Frangula alnus*). None of these trends was prevented by mowing, but mowing did prevent the accumulation of *C. mariscus* litter and kept woody saplings small. Succession was generally slow and often occurred in the form of sudden, discrete changes. Plant species richness increased with mowing and remained constant without mowing. Soil disturbance by the mowing machine contributed more to the effects of management on species composition than the periodic removal of biomass. It is concluded that mowing every three years in winter is insufficient to preserve semi-aquatic communities against succession but sufficient to maintain the plant species richness of a low productive, regularly flooded fen.

Keywords: CCA; *Cladium mariscus*; Hydrosere; Mechanical disturbance; Nature conservation; Permanent quadrat; Vegetation dynamics; Wetland management.

Nomenclature: Lauber & Wagner (1996).

Introduction

Most herbaceous wetlands in central European lowlands are currently managed for nature conservation in order to prevent succession after abandonment which leads to the loss of plant species and communities and their associated fauna (Burgess et al. 1990; Fojt & Harding 1995; Prach 1996; Jensen & Schrautzer 1999; Diemer et al. 2001). Efforts have been made by governmental and private agencies to maintain or restore appropriate forms of management in wetlands (Vermeer & Joosten 1992; Pfadenhauer & Klötzli 1996). From a botanical point of view, management should aim to (1) maintain wet vegetation by preventing succession towards drier communities and forest (van Wirdum et al. 1992; Bakker et al. 1997) and (2) maintain species richness by reducing biomass production, litter accumulation and the dominance of competitive plant species (Wheeler & Giller 1982; Prach 1996; Diemer et al. 2001).

Conservation management in wetlands mostly consists of mowing, burning or grazing (Bakker 1989). The frequency of these measures ranges from once every few years to several times per year (Güsewell et al. 2000). Given the costs and possible detrimental effects on animals and soils, it is generally desirable to manage wetlands as little as possible. On the other hand, the management intensity must be sufficient to prevent undesirable changes in vegetation; what 'sufficient' means depends on the water level and productivity of the site as well as on the local conservation aims (Dierssen & Schrautzer 1997; Pfadenhauer & Grootjans 1999). Long-term management experiments in various wetland types provide the information needed to establish appropriate management regimes (Bakker et al. 1996; Vinther & Hald 2000). Under current conditions, most wetlands in central Europe require mowing at least once a year during, or at the end of, the growing season to maintain their botanical richness (van Diggelen et al. 1996; Verhoeven et al. 1996). However, a lower management intensity may be possible, and even preferable, at flooded or nutrient-poor sites (Buttler 1987).

This paper investigates how mowing every three years in winter influences the vegetation dynamics in a calcareous lake shore fen in western Switzerland (Buttler et al. 1985). The fen has been unmanaged for a long time and is subject to an autogenic succession from aquatic communities towards sedge meadows, followed by the encroachment of woody species (especially *Alnus glutinosa* and *Frangula alnus)* or stands of *Cladium mariscus* (Buttler & Gallandat 1990). The driving factor of this succession was assumed to be the accumulation of plant litter (Buttler & Gallandat 1990); therefore periodic winter mowing (removal of litter) was implemented in 1984 to preserve the present diversity of plant communities. The effects of this management were monitored for 17 yr to test whether vegetation succession (a decrease of aquatic species, increase of terrestrial species (particularly woody), the spread of *C. mariscus* and a decrease in species richness) would indeed proceed more slowly in mown plots than in unmown ones.

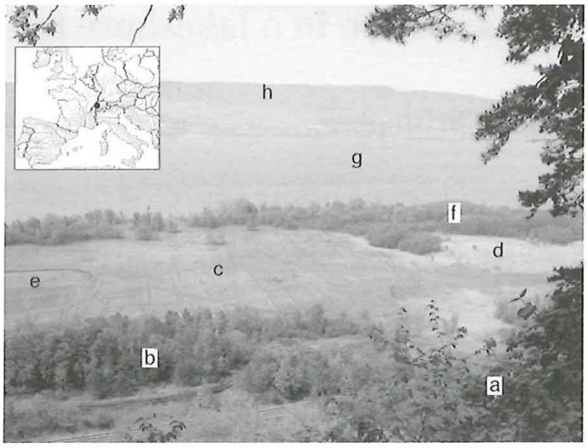

Plate 1. View on the Grande Cariçaie near Châbles, taken in May 2002 from the hills bordering the wetland on the southern side, showing (**a**) the forested slope, (**b**) the alluvial forest that protects the fens from nutrient inflow, (**c**) a mown area, (**d**) an unmown area, (**e**) a shallow pond created to re-establish early stages of succession with aquatic and semi-aquatic vegetation, (**f**) forest on the sand wall that borders the fen lakewards along large parts of the shoreline and prevents direct flooding by lake water, (**g**) Lake Neuchâtel and (**h**) the Jura range. The inset indicates the position of the site within central Europe.

Plate 2. Caterpillar machine used for mowing. The plant material is immediately formed into balls which are loaded on the machine so as to complete the whole management in a single run and thus limit soil damage.

Methods

Study sites, experimental design and field methods

The study took place on the southern shore of Lake Neuchâtel, a meso-eutrophic, alkaline lake in the western part of the Swiss Plateau (46°47' - 47°00' N; 6°38' - 7°04' E, Plate 1). A large wetland (ca. 600 ha), 'Grande Cariçaie' developed after the lake level had been lowered by ca. 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. Soils are neutral to alkaline (pH 7-8.5), gleysols over sandy or clayey lake sediments (Buttler 1987). Peat formation occurs only in some spots with relatively stable, permanently high water level, e.g. shallow ponds. Across most of the wetland the water level fluctuates considerably, being at, or above, soil surface in winter but 20-100 cm below the surface in summer (Buttler 1987). Hydrological differences largely determine the diversity of plant communities encountered across the wetland. The latter range from wet grasslands (*Molinion*) and sedge or rush dominated fen communities (*Caricion davallianae*, *Magnocaricion*) to reed stands (*Phragmition*) and open water (*Nymphaeion*) (Buttler et al. 1985; Buttler 1987).

Since 1984, large parts of the 'Grande Cariçaie' have been mown in a large-scale rotational scheme. The managed area (ca. 400 ha) is subdivided into lots of 2-3 ha, and one third of which are mown each year in winter (October-March) with a special caterpillar machine, which also immediately removes the cuttings (Plate 2). Two control areas including various plant communities have been left unmown since 1984 at Cheyres (3.2 ha) and Chevroux (44.9 ha). Pairs of permanent quadrats (3 m × 5 m) with comparable species composition and representative of the main plant communities present in each area were deliberately placed in unmown controls and adjacent mown areas.

Permanent quadrats were also placed in the flooded parts of the mown zone of Cheyres, even though the corresponding vegetation types were not represented in the control area. Three additional permanent quadrats were placed in more eutrophic reed vegetation within a mown area at Chables; such vegetation was not present at Cheyres nor at Chevroux. There was no unmown control area at Chables. Permanent quadrats in the mown areas were marked with ground-level metal plates so that they could be mown normally with the caterpillar machine. In this way they received exactly the same level of soil pressure and disturbance as the surrounding area. Mowing was discontinued in the aquatic parts of Chevroux in 1992 because obvious soil damage led to the conclusion that the treatment was too detrimental to this part of the nature reserve to justify its continuation for the sake of research. In the analysis, we therefore distinguished three treatments: unmown (13 permanent quadrats), mown (15 quadrats) and mown/unmown (6 quadrats).

Vascular plant species composition of all permanent quadrats was recorded yearly in September from 1984 (or 1985 at Chevroux) to 2000 by estimating the cover-abundance of all species on the Braun-Blanquet scale (cf. van der Maarel 1979). This resulted in a data set of 562 vegetation relevés, in which 68 vascular plant species were recorded (see http://www.grande-caricaie.ch for original relevés and data on vegetation structure).

Data analysis

For data analysis, the Braun-Blanquet codes 'r' and '+' were replaced by the values 0.1 and 0.5, respectively, and the other codes were treated as numbers from 1 to 5. These values were square-root transformed to give more weight to species with low cover. Where rare species might have unduly influenced the results (see below), species occurring less than three times were excluded from analyses involving up to 50 relevés, and those occurring less than five times from analyses involving more than 50 relevés.

The initial species composition of the quadrats was analysed using the mean cover of species in 1985-1987; means were used to reduce the effect of short-term fluctuations. A resemblance matrix was constructed by calculating similarity ratios for all pairwise comparisons of the 34 quadrats (rare species excluded); this resemblance measure ranges from 0 to 1 and takes into account both species presence and abundance (van der Maarel 1979). A cluster analysis was then performed to classify the 34 quadrats into vegetation groups ('minimum variance clustering'; Wildi & Orloci 1996).

Floristic change was analysed in three ways. (1) The difference between 'initial' (1985-1987) and 'final' (1998-2000) relevés of each quadrat was quantified with similarity ratios. A low similarity ratio indicates strong floristic change. (2) Principal co-ordinates analysis of 'initial' and final' relevés (based on a matrix of similarity ratios) revealed for each quadrat whether its species composition changed along the main floristic gradients. (3) Detailed temporal changes were analysed for each quadrat with canonical correspondence analysis (CCA; ter Braak 1986), using years as a numeric explanatory variable, so that the first CCA axis represents the directional temporal change in species composition (successional trend). In the resulting ordination biplots, relevés shift towards the right when their species composition changes according to the overall successional trend of the quadrat; shifts to the left or along higher axes indicate fluctuations. The fraction of the variance explained by the first CCA axis indicates the importance of directional change compared to fluctuations.

Three indicators were used to determine whether floristic change was influenced by mowing. 1. Similarity ratios between 'initial' and 'final' relevés. 2. The fraction of variance explained by the first CCA axis. 3. The mean 'initial' and 'final' species richness of these quadrats. In (1-3), comparisons between mown and unmown plots were only qualitative; statistical testing was prevented by the lack of true replication (permanent quadrats were observation units but not experimental units). Finally, CCAs were performed separately for each year of the study with management (mown or unmown) as nominal explanatory variable and site (Cheyres or Chevroux) as covariable, the aquatic sites from Chevroux being analysed separately. If management caused the species composition to diverge between mown and unmown plots over time, the fraction of variance explained by management in these CCAs should increase with time since 1984 (cf. Güsewell et al. 1998).

Results

The vegetation of the permanent quadrats at the beginning of the monitoring period (1985-1987), was classified into five groups by cluster analysis (Table 1). Two groups represented aquatic or semi-aquatic vegetation found in the permanently flooded parts of the study sites. The '*Lemna*' group was characterised by the regular occurrence of *Lemna minor* and *L. trisulca* and the absence of species characteristic of the *Magnocaricion*. The '*Potamogeton*' group included slightly drier sites in which *Magnocaricion* species occurred regularly. The three other vegetation types were rich fens (*Magnocaricion*). They were all co-dominated by *Carex elata* and *Phragmites australis*, but in one type *C. panicea* was also co-dominant, in the second type *Cladium mariscus* was abundant, and in the third type these two species were sparse (*C. elata* group).

Between the initial (1985-1987) and final (1998-2000) phase of the experiment, the floristic composition of some quadrats changed considerably, while others changed little. Two main directions of change are apparent (Fig. 1): (1) decrease of aquatic species and increase of terrestrial species (shift to the right in Fig. 1); (2) increase of *C. mariscus* (shift downwards in Fig. 1). There was no obvious difference between the shifts of mown quadrats (Fig. 1a) and control quadrats (Fig. 1b).

Similarity ratios between initial and final relevés indicate that the amount of floristic change did not differ between mown and control quadrats but tended to be stronger in the quadrats where mowing was interrupted after 1992 (Table 2). These quadrats all supported aquatic vegetation, whose species composition often changed dramatically before mowing was discontinued. The effect of mowing on floristic change was analysed further by comparing mown and control quadrats separately for aquatic and terrestrial sites. Within aquatic sites, the mean similarity of initial and final relevés (± SD) was 0.60 ± 0.17 in mown quadrats and 0.80 ± 0.05 in control quadrats. Within terrestrial sites, similarities were 0.77 ± 0.07 (mown) and 0.79 ± 0.04 (unmown). Thus, floristic change was stronger in mown than in unmown aquatic quadrats but

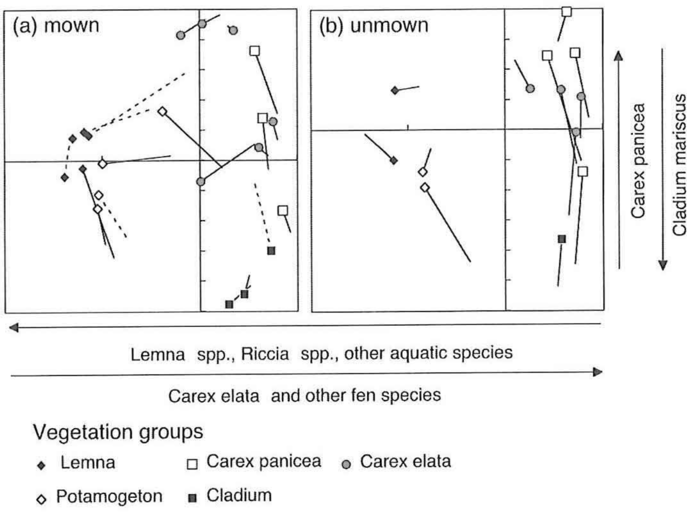

Fig. 1. Ordination biplots based on a joint principal co-ordinates analysis of 'initial' (1985-1987) and 'final' (1998-2000) vegetation relevés to show the overall shifts in species composition of (a) mown and (b) unmown permanent quadrats. Dashed lines in (a) indicate quadrats where mowing was discontinued after 1992. Symbols indicate the position of initial relevés as well as their affinity to five vegetation types identified by cluster analysis (cf. Table 1); lines (end points = final position of relevés) visualize the change in species composition along two main vegetation gradients: from aquatic to terrestrial sites (PCoA axis 1, horizontal, accounting for 22.4% of total variation) and from *C. mariscus* dominated to *C. panicea*-dominated fens (PCoA axis 2, vertical, 9.6% of total variation).

did not differ between mown and unmown terrestrial quadrats.

Four types of vegetation dynamics could be distinguished in the CCA triplots of individual permanent quadrats (Fig. 2). Directional, more or less linear change in species composition occurred when some species increased and others decreased progressively (Fig. 2a). Typically, more than 30% of total variation was explained by CCA axis 1 in these quadrats. Undirected fluctuations (Fig. 2b) mean that species abundances did not shift greatly on the whole. Less than 25% of total variation was explained by CCA axis 1. Many quadrats were intermediate between 3a and 3b (App. 1). In some mown quadrats, a sudden change in species composition followed a disturbance clearly related to mowing, such as the lifting of the root mat from the soil or the

Table 1. Species composition of the 34 permanent quadrats at the beginning of the monitoring period (average for 1985-1987). Quadrats were classified into five groups by cluster analysis. Species were arranged and grouped manually; abbreviations are given with reference to Fig. 2 and App. 1. Codes of quadrats indicate localities: A = Châbles; E = Cheyres; X = Chevroux; management: C = control; M = mown, and the matching of C and M quadrats within localities (numbers). The species cover in each quadrat is indicated using the Braun-Blanquet scale.

Species name	Abbre-viation	X_M_07	X_M_01	X_M_09	X_M_08	X_C_03	X_M_03	E_M_11	E_M_10	E_M_07	X_M_02	X_C_02	X_C_01	E_M_05	X_C_05	X_M_05	E_M_08	E_M_06	A_M_14	A_M_13	X_C_04	X_M_04	E_C_08	E_C_04	E_M_03	E_C_03	E_M_09	A_M_12	E_C_07	E_M_02	X_C_06	X_M_06	E_C_06	E_M_01	E_C_01
Riccia sp.	Riccia	.	.	+	1	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lemna minor	Lem min	+	+	.	+	+	+	.	.	+	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lemna trisulca	Lem tri	+	+	3	1	1	1	+	+	+	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chara sp.	Chara	.	.	.	+	.	.	.	+	.	1	+	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Schoenoplectus lacustris	Sch lac	.	.	3	.	.	.	.	1	2	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potamogeton plantagineus	Pot pla	.	.	.	.	.	.	.	5	1	+	+	.	2	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Typha latifolia	Typ lat	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Hydrocharis morsus-ranae	Hyd mor	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Berula erecta	Ber ere	.	.	.	.	.	.	.	.	+	.	.	.	2	.	.	+	.	1	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Eleocharis palustris	Ele pal	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.
Utricularia minor	Utr min	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Utricularia intermedia	Utr int	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Typha angustifolia	Typ ang	3	5	.	.	.	.	.	.	.	.	1	4	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Utricularia vulgaris	Utr vul	2	3	4	4	+	2	+	2	1	1	+	+	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Nymphaea alba	Nym alb	.	.	3	5	+	1	2	2	3	3	2	2	+	.	.	.	.	.	.	+	1	+	+	1	.	.	.	.	.	.	.	.	.	.
Phragmites australis	Phr aus	2	2	.	2	5	5	2	2	4	2	2	1	2	2	1	1	1	5	5	2	2	2	3	2	2	1	3	2	1	2	2	2	2	1
Cladium mariscus	Cla mar	.	.	.	.	.	.	.	+	+	.	+	+	.	4	5	4	5	.	.	+	+	1	1	1	3	1	.	3	4	+	1	.	.	+
Carex elata	Car ela	.	.	.	.	.	+	.	.	.	1	2	1	1	2	2	2	1	1	.	5	5	4	4	5	3	5	3	2	2	2	2	3	2	3
Calystegia sepium	Cal sep	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	+	1	.	.	.	.	.	.	+	.	.
Symphytum officinale	Sym off	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1
Calamagrostis epigeios	Cal epi	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	+	.	.	.	+	+	.	+	+	.	.	1	+	.	.
Thalictrum flavum	Tha flav	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	.	+	.
Carex lasiocarpa	Car las	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	+	1	.	.	.
Mentha aquatica	Men aqu	.	.	.	.	.	.	.	.	1	.	.	.	2	.	+	.	+	1	1	.	.	1	1	1	1	1	1	.	.	+	+	1	1	+
Eupatorium cannabinum	Eup can	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	+	+	.	+	+	1	+	.	.	.	+	+	+
Peucedanum palustre	Peu pal	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	+	1	+	+	.	+	.	.	.	.	1	.	.
Epipactis palustris	Epi pal	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	2	1	+	+	1	+	+	1	2	+	.	.	.	.	.	+
Epilobium parviflorum	Epi par	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Hypericum tetrapterum	Hyp tet	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	+
Schoenus nigricans	Sch nig	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.	.	.	.
Hydrocotyle vulgaris	Hyd vul	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	1	2	1	1	.	.	2	2	1	2	2	1	2
Carex panicea	Car pan	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	2	2	4	4	3	4	4
Senecio paludosus	Sen pal	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	+	+	+	.
Cirsium palustre	Cir pal	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	+	.
Galium palustre	Gal pal	.	.	.	.	.	.	.	+	+	.	.	.	+	+	+	.	+	1	1	1	1	1	+	+	+	1	1	+	1	+	+	+	+	+
Scutellaria galericulata	Scu gal	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	1	+	1	+	+	+	+	+	+	+	+	+	.	+	+	1	1
Lysimachia vulgaris	Lys vul	.	.	.	.	.	.	.	+	.	.	.	.	.	1	2	.	.	+	.	1	+	1	+	+	1	+	1	+	+	+	2	1	1	+
Lythrum salicaria	Lyt sal	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	+	+	.	+	.	.	+	+	+	+	1	1	.	+	+	+	+	+	+

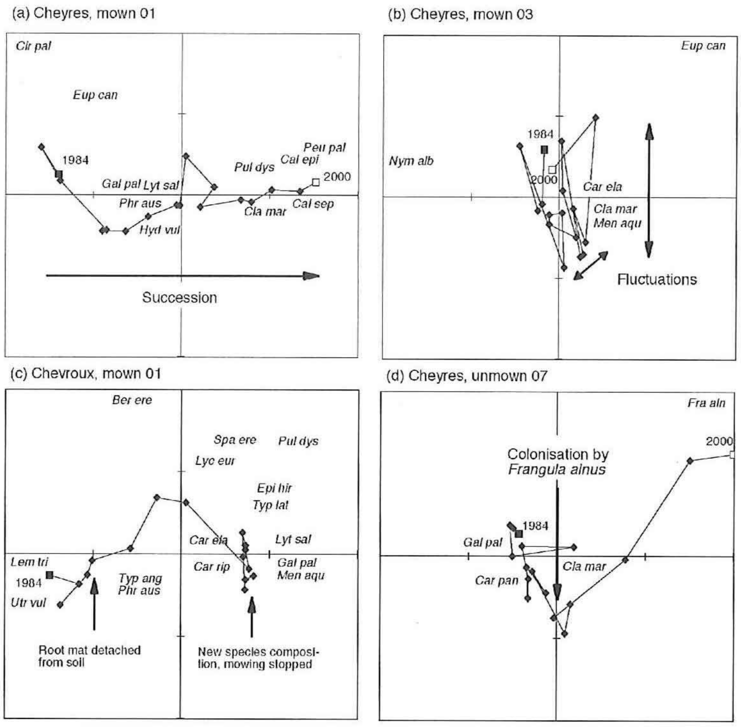

Fig. 2. Changes in the species composition of individual permanent quadrats analysed with CCA, using years as numeric explanatory variable. The horizontal axis (first CCA axis) represents the directional temporal change in species composition (successional trend). Symbols linked by lines represent relevés from consecutive years; ■ = 1984 or 1985; o = 2000; ✦ = 1986-1999. Species scores (see Table 1 for abbreviations) are shown if at least 50% of a species' variance is fitted by the first two ordination axes (or 40% by either ordination axis alone). The four graphs are examples of quadrats **(a)** with clear, nearly linear successional trend, **(b)** without clear successional trend (fluctuations), **(c)** suddenly disturbed by mowing, **(d)** with sudden floristic change unrelated to mowing. CCA triplots from all quadrats are shown in App. 1.

creation of temporary water pools colonized by aquatic pioneers (Fig. 2c). In other quadrats, sudden change in species composition occurred without direct effect of mowing; this was mainly the colonization and subsequent expansion of a new species, e.g. *Frangula alnus* or *Berula erecta* (Fig. 2d).

The four types of vegetation dynamics, and therefore the fraction of variance explained by the first CCA axis, were unrelated to management (Table 2). Therefore, despite considerable changes in individual quadrats, the floristic composition of mown quadrats did not diverge from that of controls: the fraction of variance in species composition explained by treatments was always low (5-20%) and did not increase with time (details not shown).

Table 2. Changes in plant species composition between permanent quadrats from the first three (1985-1987) and last three years (1998-2000) of the monitoring period in relation to management. Means ± *SE* are given for the similarity between the initial and final species composition of a quadrat; the fraction of variance in species composition explained by a linear temporal trend (CCA with years as explanatory variables); the total number of species found in each permanent quadrat in each of the two three-year periods.

	Similarity ratio	Variance explained	Species number initial	Species number final
Mown	0.72 ± 0.03	0.30 ± 0.10	12.1 ±1.0	16.5 ± 0.9
Mown until 1992	0.66 ± 0.08	0.29 ± 0.10	7.7 ± 0.7	10.7 ± 2.1
Unmown	0.77 ± 0.02	0.29 ± 0.07	12.6 ± 1.2	12.2 ± 1.4

The mean species richness per quadrat increased during the study period in the mown quadrats but did not change in the unmown ones (Table 2, Fig. 3). Similarly, the total number of species found in all mown quadrats increased from 42 (1985) to 54 (2000) but only from 38 to 40 in unmown ones. In the quadrats mown until 1992, a strong initial increase in mean species richness was followed by a decrease after 1992 (Table 2, Fig. 3).

The number of woody species increased in 12 of the 18 quadrats where woody species occurred. This concerned most unmown quadrats (six out of eight) and half of the mown quadrats (four out of seven). An increasing cover of woody species (*Alnus glutinosa* or *Salix cinerea)* is also indicated by positive scores for these species on the x-axis in several of the CCA triplots (App. 1).

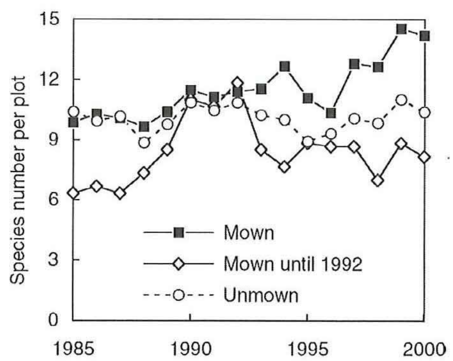

Fig. 3. Changes in mean species richness of the permanent quadrats in relation to their management from 1985 - 2000.

Discussion

Successional trends

The plant species composition of our 34 permanent quadrats changed between 1984 and 2000, showing three main successional trends

1. In aquatic vegetation, submerged species became less abundant, while fen species increased. In some quadrats the vegetation was even no longer classified as aquatic in 1998-2000. This succession was probably driven by the accumulation of organic matter, which would increase the height of the soil surface relative to the water table (Buttler & Gallandat 1990). The role of organic matter accumulation for vegetation succession in wetlands is well known (Olff et al. 1993; Sival 1996; Bakker et al. 1997; Lammerts et al. 1999).

2. The cover of *C. mariscus* increased in quadrats where *C. mariscus* already occurred in 1984 (or occurred nearby). The high competitive ability of *C. mariscus* in the Grande Cariçaie is exceptional for Switzerland and must be due to the particular combination of a mild, suboceanic climate, an alkaline, relatively nutrient-poor soil and strong fluctuations in water level with flooding until late spring (Meredith 1985; Moe 1994; Alvarez-Cobelas et al. 2001). The spread of *C. mariscus* was not generally associated with a decrease in species richness, nor was species richness negatively related to the cover of *C. mariscus* (unlike Meredith 1985; Güsewell et al. 1998). This was because aquatic sites, which are generally species-poor, were less invaded by *C. mariscus* than the more species-rich terrestrial sites.

3. Shrubs and tree cover increased in terrestrial quadrats, particularly in the unmown quadrats of Cheyres. Together, the observed changes confirm the models of autogenic succession proposed by Buttler & Gallandat (1990) and Buttler (1987) based on the vegetation patterns observed by those authors around 1982.

Despite changes in species composition, most permanent quadrats supported the same vegetation type throughout the study. The five vegetation types identified in 1985-1987 were still relatively well separated in 1998-2000 (see also Fig. 1). For most of the permanent quadrats, the similarity between initial (1985-1987) and final (1998-2000) species composition was higher than 0.6, indicating that the type of plant community did not change (Wildi 1988). This relative stability of plant communities contrasts with other studies where successional change was faster (Fojt & Harding 1995; Bakker et al. 1997), presumably due to the undisturbed hydrology and lower nutrient availability of the Grande Cariçaie.

Effects of mowing on vegetation succession

The main purpose of mowing was to preserve the diversity of vegetation types by preventing organic matter accumulation and shrub encroachment. However, the succession towards drier vegetation types was equally or even more rapid in mown quadrats than in unmown ones, suggesting little or no effect of mowing on organic matter accumulation. This could have three reasons: 1. Below-ground production, which is hardly influenced by winter mowing, accounts for a large part of organic matter accumulation in fens (Saarinen 1996); for this reason, even yearly mowing in summer does not prevent vegetation succession (Bakker et al. 1997). 2. Only part of the above-ground biomass production is removed by mowing every three years; the rest reaches the soil as litter. 3. Winter mowing may enhance biomass production by improving light conditions for new shoots in spring (Granéli 1989; Gryseels 1989; Buttler 1992).

The expansion of *C. mariscus* was not prevented by mowing: Ten of the 18 quadrats in which the cover of *C. mariscus* increased were mown. In these quadrats, however, *C. mariscus* covered < 25%, whereas > 75% cover was reached in some unmown quadrats. In addition, morphological measurements showed that culm and leaf length decreased by ca. 15-25% in mown quadrats between 1984 and 2000, whereas they did not change in unmown quadrats (C. Le Nédic unpubl.). Thus, *C. mariscus* was able to expand but did not become dominant in mown quadrats. That *C. mariscus* was hardly reduced in plots where it dominated initially (in contrast to Meredith 1985; Güsewell et al. 1998) must be attributed to favourable site conditions for this species and to the extensive mowing regime (every three years).

Shrub or tree encroachment affected unmown quadrats more than mown quadrats, as six of the nine quadrats that were colonized by new woody species were unmown. However, the effects of mowing were confounded with those of propagule availability. Woody species were most abundant and clearly increased with time in the unmown area of Cheyres, located close to the forest border. In Chevroux, the two quadrats in which woody species increased markedly were both located within the mown area. One was close to the forest border and the other was disturbed by woody debris from where new shoots resprouted. Thus, the availability of propagules was the main factor driving the colonization by woody species. Mowing did limit the size reached after colonization. While tall shrubs developed in some unmown quadrats (up to 5 m high), saplings did not exceed 1 m height in mown quadrats.

Effects of mowing on vegetation diversity

Periodical mowing increased species richness in our quadrats (cf. Prach 1996; Linusson et al. 1998; Vinther & Hald 2000). This is consistent with the results of a small-scale mowing experiment in the same area (Buttler 1992; Güsewell et al. 1998). In more productive fens with a rapid succession after abandonment, mowing must occur every year or even more frequently to prevent a decrease in species richness (Rosenthal 1992b; Schütz & Ochse 1997; Smith et al. 2000). In low-productive montane fens reduction in diversity after abandonment was moderate and was rapidly reverted by mowing in autumn (Billeter 2001; Diemer et al. 2001).

The effect of mowing on species richness partly resulted from the mechanical effect of the caterpillar machine: soil damage transformed the vegetation of some aquatic quadrats into floating fen vegetation (inherently more species-rich than initial communities), and in some terrestrial quadrats, the machine created small water bodies colonized subsequently by pioneer species that would not otherwise occur. The role of mechanical disturbance for species richness was underlined by the quadrats where mowing stopped in 1992 because of soil damage: until 1992, species richness increased more in these quadrats than elsewhere, but it rapidly decreased again when disturbance stopped. Hence there may be a trade-off between the enhancement of species richness and the avoidance of soil damage.

By allowing the occurrence of fen species in aquatic sites and of aquatic pioneer species in terrestrial sites, mechanical disturbance blurred the distinction between aquatic and terrestrial vegetation types. Indeed, when relevés from 1998-2000 were analysed with cluster analysis (similar to Table 1), the distinction of the two groups was less clear than in 1985-1987. The β-diversity of the vegetation therefore decreased.

Implications for management and monitoring

In this experiment treatments were applied at the same spatial scale and with the same caterpillar machine as in the management scheme whose effects we wanted to assess. We found that the effects of management on vegetation dynamics and species diversity were to a large extent mediated by the influence of management on the frequency and intensity of mechanical disturbance. These effects would, therefore, not have been detected in classical small-scale experiments with manual mowing (e.g. Rosenthal 1992a; Güsewell et al. 1998; Billeter 2001; Güsewell in press).

Inevitable drawbacks of the large spatial scale were the lack of adequate replication, the heterogeneity of the permanent quadrats and the use of a fast, relatively imprecise survey method. We believe that none of these drawbacks seriously reduced the confidence in our results and that they were compensated by the advantages of using a realistic spatial scale with a long observation period (cf. Wildi & Krüsi 1992; Güsewell et al. 1998).

In conclusion, autogenic succession in the studied fen vegetation was not prevented by mowing. In particular, semi-aquatic communities still developed towards terrestrial ones; at the same time, considerable soil damage was caused by the mowing machine. In the terrestrial communities, mowing every three years in winter proved sufficient to maintain or enhance the plant species richness by preventing the accumulation of litter, by limiting the size of woody saplings and of herbaceous evergreens, and by causing local disturbance that allowed the temporary establishment of aquatic species. However, by promoting the co-existence of species from different community types, mowing might reduce the vegetation diversity at landscape level.

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