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Evaluation and management of fen meadows invaded by common reed *(Phragmites australis)*

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Summary

Common reed (*Phragmites australis* Trin.) has been frequent since long in fen meadows of the Swiss Plateau. In the last thirty years, however, it became more abundant at many sites. This spread raised the question whether *Phragmites* would affect the conservation value of fen meadows and how a further spread could be prevented. This thesis investigated relations among *Phragmites*, plant species composition and site conditions. Moreover, the effect of mowing at different dates on the biomass and on the nitrogen and phosphorus economy of *Phragmites* and the other species was assessed.

The plant species composition of 241 plots (4 m^2) was surveyed using the Braun-Blanquet method. The aboveground biomass of *Phragmites* (ABP) in August was estimated based on shoot density and mean shoot length. The aboveground biomass of the other phanerogams was determined for 72 of the plots.

The ABP ranged from 0 to 1270 g dry weight per m^2 (0–85% of the total aboveground biomass). Plots dominated by tall herbs (alliance *Filipendulion*) had on an average higher ABP than plots dominated by heath grass or small sedges (alliances *Molinion* and *Caricion davallianae*). Alliances differed more in average shoot size than in shoot density. In each alliance the contribution of *Phragmites* to total aboveground biomass was positively correlated with this biomass, i.e. with site productivity. ABP was not related to the ground water level.

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 characteristic fen species. Strong differences were, however, found among the three alliances. The conservation value of *Filipendulion* plots was generally low and decreased significantly with increasing ABP. The conservation value of *Molinion* and *Caricion* plots was generally high and not related to ABP, i.e. a displacement of mire species through shading by *Phragmites* was not observed in these two alliances. Consequently, the abundance of tall herbs appeared to determine the conservation value of fen meadows more than the abundance of *Phragmites*. Since in the alliances *Molinion* and *Caricion* increasing abundance of *Phragmites* was associated with an increasing proportion of *Filipendulion* species, a future loss of conservation value of reed-invaded fen meadows appeared probable.

The late seasonal development of *Phragmites* probably contributed to the above results. The shading impact of *Phragmites* was low until mid June at most sites. Therefore, species completing most of their seasonal growth early in the vegetation period were likely to be less affected by this shading than species developing later in summer. The earlier and faster development of *Carex*

acutiformis (abundant at high ABP) compared with *Carex panicea* (abundant at low ABP) was consistent with this assumption. Results suggest that a spread of *Phragmites* might indirectly affect the conservation value of fen meadows by promoting tall herbs which, in turn, would displace the mire species.

Two mowing experiments were carried out to evaluate the impact of mowing in summer on the abundance of *Phragmites* in fen meadows.

One experiment had been established in 1982 by A. Buttler (University of Neuchâtel); treatments were (a) mowing in August, (b) mowing in January-February and (c) no mowing. Treatments were applied every year from 1982 to 1987, and every other year since then. The abundance of *Phragmites* (shoot size, shoot number, ABP), which had been investigated in 1983–1986 by A. Buttler, was reinvestigated in 1995–1997. It decreased between the two periods in the mown plots, but did not change in the unmown plots. There was no difference between mowing in August and mowing in winter, making it unlikely that mowing in August would suffice to reduce *Phragmites* in invaded fen meadows.

The other experiment was started in 1995; the two treatments compared were (a) mowing in early September (S) and (b) mowing in late June and early September (JS). During the three years of the study, additional mowing in June reduced neither the shoot density nor the shoot size of *Phragmites.* In the third year of the experiment, the biomass of *Phragmites* was still the same in JS-plots as in S-plots. Conversely, the biomass of the other species was, on an average, 21% lower in JS-plots than in S-plots. Mowing twice removed 90% more nitrogen and 181% more phosphorus from *Phragmites* than mowing once. Only 30% more nitrogen and 64% more phosphorus were removed from the other species. Thus, the impact of additional mowing in June was ambiguous: on the one hand, the biomass of *Phragmites* had been increased in comparison to the biomass of the other species, suggesting that *Phragmites* had been promoted on the short term. On the other hand, the impact of mowing in June on nutrient budgets appeared stronger for *Phragmites* than for the other species. Whether *Phragmites* would be reduced on a longer term, or whether it would retain its advantage over the other species could not yet be predicted.

Nevertheless, mowing twice had favourable effects. It removed more nutrients than mowing once, reduced total aboveground biomass and created a more open vegetation structure. These effects appeared to be more decisive for the conservation value of the fen meadows than a complete eradication of *Phragmites*. There is probably no optimal mowing regime, and a more flexible management with some spatial and temporal variation seems to be the best strategy.

Zusammenfassung

Bewertung und Bewirtschaftung von verschilfenden Streuwiesen

Schilf (*Phragmites australis* Trin.) ist eine verbreitete Pflanzenart in den Streuwiesen des Schweizer Mittellandes. In den letzten dreissig Jahren wurde eine Zunahme seiner Häufigkeit in diesen Wiesen beobachtet. Diese Ausbreitung warf die Frage auf, ob und wie eine zunehmende Verschilfung den Naturschutzwert der Streuwiesen beeinflussen würde und wie sie verhindert werden könnte. In dieser Dissertation wurden daher einerseits Beziehungen zwischen Schilf, Artenzusammensetzung und Standortsbedingungen untersucht, andererseits wurde die Wirkung unterschiedlicher Schnittzeitpunkte auf die Biomasse und den Nährstoffhaushalt des Schilf und der anderen Pflanzenarten beurteilt.

Zur Beurteilung der Artenzusammensetzung verschilfender Streuwiesen wurden auf 241 Flächen (4 m^2) Vegetationsaufnahmen nach Braun-Blanquet durchgeführt. Die oberirdische Biomasse von *Phragmites* (OBP) wurde aufgrund der Halmdichte und mittleren Halmlänge geschätzt. Die oberirdische Biomasse der anderen Arten wurde auf 72 der Flächen durch Abernten von Teilflächen bestimmt.

Die OBP lag zwischen 0 und 1270 g Trockensubstanz pro m^2 (0–85% der gesamten oberirdischen Biomasse). Von Hochstauden und Hochgräsern beherrschte Flächen (Verband *Filipendulion*) hatten im Durchschnitt eine höhere OBP als Pfeifengraswiesen oder Kleinseggenrieder (Verbände *Molinion* und *Caricion davallianae*). Die Verbände unterschieden sich vor allem in der mittleren Grösse der Schilfhalme und weniger in ihrer Dichte. Innerhalb jedes Verbandes war der Schilfanteil an der oberirdischen Biomasse positiv mit dieser Biomasse, d.h. mit der Standortsproduktivität korreliert. Ein Zusammenhang zwischen OBP und Grundwasserstand wurde nicht festgestellt.

Flächen mit hoher OBP hatten im Durchschnitt einen geringeren Naturschutzwert als solche mit niedriger OBP, d.h. ihre Artenzahl, die Anzahl seltener oder bedrohter Arten, und der Anteil charakteristischer Moorarten waren geringer. Hierbei unterschieden sich die drei Verbände deutlich: Aufnahmeflächen des Verbandes *Filipendulion* hatten einen vergleichsweise niedrigen Naturschutzwert und dieser war negativ mit der OBP korreliert. Aufnahmeflächen aus den Verbänden *Molinion* und *Caricion* hatten einen vergleichsweise hohen Naturschutzwert und dieser war unabhängig von der OBP. Eine Verdrängung von Flachmoorarten wegen zunehmender Beschattung durch Schilf wurde in den zwei letzteren Verbänden also nicht nachgewiesen. Deshalb schien die Dominanz von Hochstauden für den Naturschutzwert der Streuwiesen entscheidender zu sein als die Dominanz des Schilfs. Mit zunehmender OBP nahm allerdings auch innerhalb der Verbände *Molinion* und *Caricion* der Anteil Hochstauden in der Vegetation zu, so dass der Naturschutzwert von verschilften Streuwiesen mit der Zeit eher abnehmen dürfte.

Für die Ergebnisse dürfte die späte Entwicklung des Schilfs im Jahresverlauf mitverantwortlich sein. Die beschattende Wirkung des Schilfs war bis Mitte Juni meist unerheblich. Frühentwickelnde Arten dürften von der Beschattung daher weniger betroffen sein als spätentwickelnde Arten. Die frühere und raschere Entwicklung von Carex *acutiformis* (bei hoher OBP häufig) im Vergleich zu *Carex*

panicea (bei niedriger OBP häufig) entsprachen dieser Annahme. Die Ergebnisse liessen vermuten, dass eine Ausbreitung des Schilfs den Naturschutzwert der betroffenen Streuwiesen indirekt beeinträchtigen könnte, indem Arten der Hochstaudenrieder gefördert werden, die ihrerseits die selteneren Flachmoorarten verdrängen können.

Um die Auswirkungen einer Sommermahd auf die Häufigkeit des Schilfs in Streuwiesen zu beurteilen, wurden zwei Mahdexperimente durchgeführt.

Ein erster Versuch war 1982 von der Universität Neuchâtel eingerichtet worden; die Schnittvarianten waren (a) Mahd im August, (b) Mahd im Januar-Februar und (c) Brache. Die Mahd wurde von 1982 bis 1987 jährlich durchgeführt, später nur noch alle zwei Jahre. Die Häufigkeit des Schilfs (Halmlänge, Halmgrösse, OBP) wurde in den ersten vier Versuchsjahren von der Universität Neuchâtel und 1995-1997 im Rahmen dieser Arbeit erhoben. Sie nahm in den gemähten Flächen ab, nicht aber in den Brachflächen. Es bestand allerdings kein Unterschied zwischen Augustmahd und Wintermahd, so dass eine Zurückdrängung des Schilfs aus verschilften Streuwiesen durch Augustmahd eher unwahrscheinlich schien.

Ein zweiter Versuch wurde 1995 begonnen. Verglichen wurden die zwei Behandlungen (a) Mahd Anfang September (S) sowie (b) Mahd Ende Juni und Anfang September (JS). In den drei Untersuchungsjahren verringerte der zusätzliche Junischnitt weder die Halmdichte, noch die Halmgrösse. Im dritten Jahr war die OBP in den JS-Flächen immer noch ebenso hoch wie in den S-Flächen. Im Gegensatz hierzu war die Biomasse der anderen Arten in den JS-Flächen gegenüber den S-Flächen durchschnittlich um 21% reduziert. Zweifache Mahd entzog den Schilfpflanzen durchschnittlich 90% mehr Stickstoff und 181% mehr Phosphor als einfache Mahd. Den anderen Arten wurden durch zweifache Mahd nur 30% mehr Stickstoff und 64% mehr Phosphor entzogen.

So war die Wirkung eines zusätzlichen Junischnittes zweideutig: Der Schilfanteil an der oberirdischen Biomasse war in den JS-Flächen gegenüber den S-Flächen erhöht. Dies deutete auf eine kurzfristige Förderung des Schilfs durch Junischnitt hin. Andererseits wirkte sich der Junischnitt auf den Nährstoffhaushalt des Schilfs stärker aus als auf denjenigen der anderen Arten. Ob das Schilf hierdurch längerfristig zurückgedrängt würde oder ob es seinen anfänglichen Vorteil gegenüber den anderen Arten behalten würde konnte aufgrund der vorliegenden Ergebnisse noch nicht bestimmt werden. Der erhöhte Nährstoffentzug und die verringerte Gesamtbiomasse bei zweifacher Mahd waren aus Naturschutzsicht jedoch positiv zu beurteilen und für die Erhaltung der Streuwiesenvegetation sicherlich entscheidender als eine vollständige Zurückdrängung des Schilfs. Sehr wahrscheinlich gibt es keinen optimalen Schnittzeitpunkt. Daher dürfte eine flexible Bewirtschaftung mit einem gewissen räumlichen und zeitlichen Wechsel die beste Lösung sein.

1. Introduction

1.1. Vegetation dynamics and its significance for nature conservation

The mobility of plants...

Vegetation is more dynamic and less predictable than was assumed by the classic concepts of vegetation science (Klötzli 1995a,b; van der Maarel 1996a,b). Vegetation dynamics is based on the ability of plants to move, either as individuals, through vegetative propagation, or as populations, through dispersal of propagules (Urbanska 1992). The type of dynamics resulting from plant mobility is determined by attributes of the plants, by environmental factors (including the action of animals and man), and by interactions of plant populations among each other and with their environment (e.g. Connell & Slayter 1977; Noble & Slayter 1980; van der Valk 1981; Pickett & McDonnell 1989; van der Maarel & Sykes 1993; Gigon & Leutert 1996). Vegetation dynamics occurs at various spatial and temporal scales, and different types of dynamics may be found at different scales: the same system may appear to shift, to fluctuate or to remain constant, depending on the scale considered (Zobel & Masing 1987; van der Maarel & Sykes 1993; Pärtel & Zobel 1995; Gigon & Grimm 1997).

On a small scale, the mobility of plants becomes apparent as stochastic or 'chaotic' spatio-temporal fluctuations within relatively stable communities (Glenn & Collins 1993; van der Maarel & Sykes 1993; Herben *et al.* 1993a). Such fluctuations have been described in various ways, e.g. as 'patch dynamics' (Pickett & White 1985), as 'species carousel' (van der Maarel & Sykes 1993), or as 'species clouds' (Klötzli 1995a). Small-scale dynamics may be essential to the diversity and to the large-scale stability of communities (Chesson & Huntly 1989; Wissel 1991; Herben *et al.* 1993b; Tilman 1997).

Vegetation change at the site level, i.e. "a progressive alteration in the structure and species composition of the vegetation" (Grime 1979), is usually referred to as 'succession'. Various forms of succession have been distinguished, depending on the initial conditions, the patterns of species replacement and the temporal course of change (Miles 1987; van der Maarel 1996b). Succession was thought to be "orderly, directional and predictable" by early vegetation scientists (Pickett & McDonnell 1989). Yet, modern research revealed that succession often follows multiple, unpredictable pathways (Glenn-Lewin 1980). The 'mosaic cycle concept' (Remmert 1991) suggests that there is no clear-cut limit between within-community fluctuations and 'cyclic succession' among several distinct communities.

A third type of dynamics occurs when individual plant species colonize areas in which they never occurred before. If they become established and penetrate into the existing communities, their spread is called a 'biological invasion' (Mack 1985). Successful plant invaders tend to present certain traits, e.g. many prominent invaders are tall hemicryptophytes from moist and

nutrient-rich sites (Pysek *et al.* 1995), and likewise certain vegetation types are particularly susceptible to invasion, such as wetlands or oceanic islands (Cronk & Fuller 1995). Nevertheless, biological invasion, like fluctuation and succession, is to a large extent unpredictable (Crawley 1987; Kowarik 1995; Williamson 1996).

... and consequences for nature conservation

Efforts of nature conservation are often directed towards the maintenance or restoration of certain (rare) plant species and of vegetation types with high 'conservation interest'. This aim is liable to be affected by the dynamic nature of vegetation. The possibility of both predictable and unpredictable changes in species composition must be acknowledged when conservation objectives are defined for a particular site (Pickett & Parker 1994; Scherzinger 1996; Parker & Pickett 1997). Whether such changes are wanted or unwanted must be decided in each particular case with reference to explicit general conservation aims (Schwartz 1994; Plachter 1992; Randall 1997). Special management may be necessary if unwanted changes occur.

Small-scale dynamics are of minor importance in the definition of conservation objectives. But they may interact with effects of management and thereby prevent an exact prediction of whether and how these objectives will be reached (Klötzli 1997; Parker & Pickett 1997). The assessment of conservation success may be difficult for the same reason, and long-term studies are often necessary because fluctuations overlay short-term trends and management effects (Klötzli 1995a; Bakker *et al.* 1996a). In some cases, small-scale dynamics may be directly relevant to management. A certain level of disturbance may, for example, be essential for the survival of some plant species. To maintain these species, disturbance must be deliberately caused at sites in which it does not occur automatically any more, e.g. because of modified management (e.g. Krenová & Leps 1996).

Successional change and biological invasions can affect many vegetation types that are considered very valuable in nature conservation. Particularly concerned in Central Europe are semi-natural ecosystems that owe their existence to (former) human use. The conservation of most of these vegetation types requires appropriate measures to prevent natural succession or invasion, or to revert these processes where they have already occurred (e.g. Briemle *et al.* 1991). Thus, nature conservation must act 'against nature', a situation that prevents the definition of 'objective' conservation aims and the development of generally valid management strategies.

Invasive plants...

> "One of the main threats to biodiversity in the world is the direct destruction of habitats by people (through inappropriate resource use or pollution). Another serious, but underestimated problem is the threat to natural and semi-natural habitats by invasion of alien organisms, which potentially is a lasting and pervasive threat. It is a lasting threat because when exploitation or pollution stops, ecosystems often begin to recover. However, when the introduction of alien organisms stops, the existing aliens do not disappear; in contrast they sometimes continue to spread and consolidate, and so may be called a more pervasive threat." (Cronk & Fuller 1995. S. 1).

There is no agreement among plant ecologists on the exact definition of 'plant invasion' (Pysek 1995). Although the term has sometimes been used in a rather general sense, meaning any increase in abundance (e.g. Gryseels 1989a), it is generally restricted to the colonization of *new* areas:

> "I will use the term invader in reference to any taxon entering a territory in which it has never before occurred, regardless of the circumstances" (Mack 1985).

However, 'new areas' may be understood in a geographical or in an ecological sense, so that native species may be excluded or included (Pysek 1995). Restricting the concept of 'invasion' to the spread of alien species is necessary in the context of biogeographical or demographical studies, in which the process of colonization or its spatio-temporal pattern is investigated (Mack 1985; Hengeveld 1988; Herben 1995; Kowarik 1995). In the context of nature conservation, on the other hand, an invasive species is more adequately defined as

> "a plant that has moved into a habitat and reproduced so aggressively that it has displaced some of the original components of the vegetative community" (White *et al.* 1993; in Randall 1997).

This definition implies a negative value judgement that is explicitly excluded from the biogeographical concept of invasion (Mack 1985; Rejmanek 1995). Such a valuation is necessary in conservation because the decision whether to control spreading species must depend on whether these species threaten protected or otherwise valuable sites and their populations (Usher 1988). A consequence of defining plant invaders by their impact on established communities is that

> "there is a blurred distinction between invasion by a native species, as part of a succession, and invasion by an alien species. In some nature reserves, the conservation objective is to protect a species assemblage that may be invaded by native species, as part of the natural succession" (Cronk & Fuller 1995, p. 3).

Clearly, alien species are more likely to negatively affect ecosystems than native ones (Randall 1997). For example, *Lythrum salicaria*, a frequent but benign tall herb in Central European wetlands, is considered a particularly troublesome invader in North America (Edwards *et al.* 1995; Piper 1996). The reason is that aliens tend to grow taller, to be less affected by herbivores and

diseases, and to have a higher reproductive success in the invaded area than in the region of origin (e.g. Edwards *et al.* 1995; Williamson 1996).

Nevertheless, the increase of certain native species may also strongly affect the conservation value of sensitive ecosystems in Europe (Bobbink & Willems 1987; Rosenthal 1992; Müller *et al.* 1992; Marks *et al.* 1994; Hansson & Persson 1994; Eberle 1995 etc.). These 'problem plants'[1] differ from alien 'plant invaders' in that they have generally been present since long at the site or close to it as subordinate members of the established plant community. After a change in management (e.g. abandonment), in site conditions (e.g. eutrophication), or, possibly, in climatic conditions, these species may become dominant and start spreading (e.g. Egler 1954; Wolf 1979; Egloff 1986; Rosenthal 1992). This 'time lag', however, is also observed with many plant invaders, which may be present at a low abundance in new areas for a long time before they actually begin to spread (Hengeveld 1988; Kowarik 1995). Likewise, the spread of alien plants is often, though not always, facilitated by human action (e.g. propagation of seeds or disturbance of established vegetation; Usher 1988; Cronk & Fuller 1995).

Thus, from a conservational point of view there is no fundamental difference between native 'problem plants' and alien 'plant invaders', and one might consider 'invaders' all species the spread of which critically affects nature conservation objectives[2]. There are various reasons why the spread of a plant species – alien or native – into nature reserves or other semi-natural habitats should be a problem and need to be controlled. As pointed out by Cronk & Fuller (1995),

> "Change is a feature of all ecosystems and what is at issue is not the change itself but the rate and direction of change, both of which may be dramatically altered by invasion"

Invasive plants may, in particular, reduce the species diversity of invaded sites, often building up monospecific or monodominant stands (e.g. Voser-Huber 1992). They are able to displace rare plant or animal species (Cronk & Fuller 1995; Williamson 1996), to modify the genetic constitution of established populations (Fenster & Dudash 1994; Rhymer & Simberloff 1996), and to alter abiotic site factors, e.g. hydrology, soil chemistry or fire regime (Hellings & Gallagher 1992; Marks *et al.* 1994; Walker & Smith 1997). Their spread may reduce the visual amenity of a landscape (Hellings & Gallagher 1992; Walther 1994), and it may impair management or human use of sites, e.g. by obstruction (Khattab & El-Gharably 1990) or by toxic components (Pakeman & Marrs 1992).

Since all these changes may also occur in relation to fluctuations or succession, the distinction between 'invasions' and 'normal' vegetation dynamics

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[1] Randall (1997) suggested the alternative designation 'natural area weeds'

[2] The conservation objective may, in certain instances, be the exclusion of all non-native species. This particularly applied to areas with high degree of endemism, like many tropical or subtropical oceanic islands. 'Invader' would then be synonymous with 'expanding alien', but only with reference to that specific conservation aim.

involves some arbitrariness (Schwartz 1997). Nevertheless, the distinction needs to be made in order to decide whether measures have to be taken against the spread of a species in nature reserves (Randall 1997). Before measures are implemented, a careful assessment should be done of (1) the general conservation aims, e.g. enhancing diversity or maintaining historical features of a landscape, (2) the dynamics of the species, i.e. the importance and speed of its increase, (3) the impact of the species on the specific ecosystem, (4) the implications of this impact for the conservation aims, (5) the availability of effective measures to control the species, and (6) the consequences of the application of such measures (including ecological, economic and aesthetical aspects).

... and the spread of Phragmites australis in fen meadows

> "Im Verbreitungsgebiet von *Phragmites communis*[3] setzt in Feuchtwiesen wie in Seggenriedern eine Verschilfung ein, die zur Entstehung artenarmer Schilfröhrichte führt. (...) Die Stabilität der Röhrichte scheint von der Wuchskraft von *Phragmites* gesteuert zu werden, die standortabhängig stark variieren kann. Die geschilderte Entwicklung verdeutlicht die potentielle Bedrohung der gefährdeten Pflanzenarten, von denen nur wenige auch in Röhrichten und Gehölzen vorkommen können." (Biewer 1994)

Common reed (*Phragmites australis* Trin.) is a tall grass almost world-wide distributed. Its main habitat is shallow water, but it is also part of most terrestrial wetland plant communities (Hürlimann 1951). Thus, *Phragmites* has been frequent since long in fen meadows (alliances *Molinion* and *Caricion davallianae*) of lakeside wetlands and swampy basins of the Swiss Plateau (Zobrist 1935; Heim 1963; Klötzli 1969). It was generally subordinate in these communities, and the traditional management – mowing in late summer or autumn – appeared sufficient to prevent it from becoming more dominant (Wildi & Klötzli 1978).

In the last thirty years, however, *Phragmites* has been spreading at many sites (Klötzli 1986; Marti & Müller 1993). This spread raised the question whether – and to what degree – *Phragmites* would influence the species composition of fen meadows by competition. It was expected that increased shading would displace specialized, rare and endangered plant species, reducing local and regional species diversity (Biewer *et al.* 1994). Such effects have been observed in other regions (Marks *et al.* 1994; Onimaru & Yabe 1996). Concern about the spread of *Phragmites* in fen meadows was the incentive for the research presented in this thesis.

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[3] The correct species name is *Phragmites australis* (Clayton 1968), but the former name – *Phragmites communis* – is still frequently used

1.2. Research questions

The first aim of the present thesis was to determine whether *Phragmites australis* has to be considered an 'invasive' species and whether it should be controlled by special measures in fen meadows of the Swiss Plateau. It was assumed that this would be the case if *Phragmites* is becoming significantly more abundant in a large number of sites, if this spread is spontaneous, but promoted by human influence, and if high abundance of *Phragmites* is likely to affect the conservation value of fen meadows. Thus, it was investigated whether these conditions are fulfilled.

The second aim was to evaluate measures to control the abundance of *Phragmites* and to restore invaded sites. Control could be attempted using chemical (herbicides) and physical methods (mowing, grazing, burning, flooding, shading etc.)[4]. However, the ecological impacts and costs associated with most of these measures restricted available options. Methods known to be most effective are too destructive or too expensive to be applied on a large scale in nature reserves. Only one type of measures was considered in this thesis, namely changing the time and frequency of mowing (mowing earlier in summer or twice a year). This management has most frequently been recommended and applied in practice. Thus, it was investigated whether it would, indeed, be sufficient to control *Phragmites* in fen meadows.

In the course of the work it appeared that the way of assessing the abundance of *Phragmites* and the species composition – i.e. the variables measured, the sample size and the scale of investigation – could critically affect the reliability of the results. Investigating such methodological questions and giving some indications on a suitable sampling strategy constituted a third aim of the thesis.

1.3. Outline of the thesis

For the management of invasive plants Schwartz & Randall (1995) suggested an 'adaptive management strategy' combining the definition of conservation objectives, the assessment of (potential) problems, the implementation of measures and the evaluation of their effect. It was attempted to follow such a strategy in this thesis (Fig. 1).

The concern about the spread of *Phragmites* in fen meadows may, at first, seem 'contradictory': why should the same species spread in some parts of wetlands and regress in others? Why should the same factor – nitrogen – be involved in both processes? Why, finally, should the same management – mowing – be able to promote *Phragmites* in some cases and to reduce it in others? A brief literature review (Chapter 2) suggests that these

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[4] No examples of successful biological control are known so far (Marks *et al.* 1994)

'contradictions' are, in fact, an 'inevitable' consequence of the particular physiological and ecological features of the species.

Possible problems related to the spread of *Phragmites* are investigated in the following part. Chapters 3 and 4 present results of a vegetation survey conducted in several fen meadows of the Northeast Swiss Plateau. Using a comparative approach, the relation between the abundance of *Phragmites* and plant species richness, species composition and the botanical conservation value of fen meadows is assessed. Moreover, the relation between the abundance of *Phragmites* and site conditions, particularly site productivity,

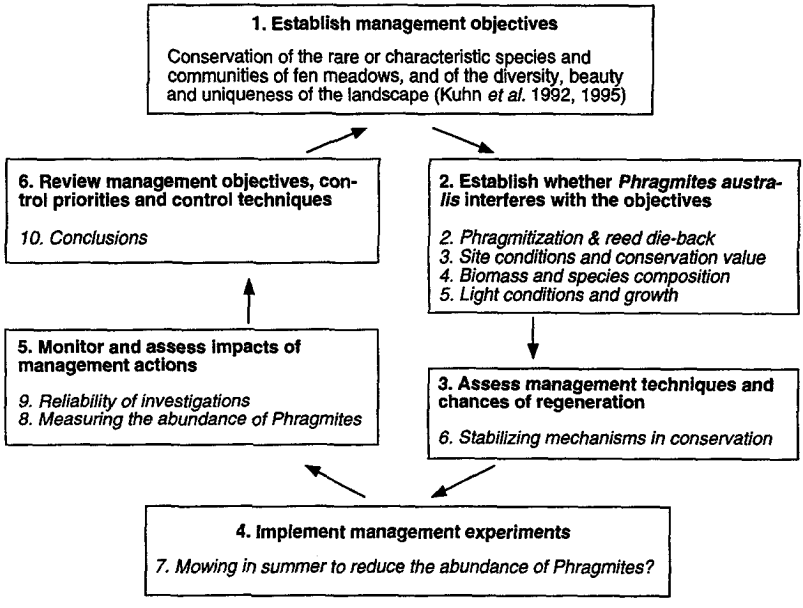

Fig. 1. Flowchart of an adaptive management strategy for fen meadows invaded by common reed (*Phragmites australis* Trin.) with chapters of the thesis (italic) related to each of the steps (boldface). After Schwartz & Randall (1995), modified.

is discussed. It appears that the spread of *Phragmites* must be considered together with the spread of other tall herbs and grasses to be properly evaluated. Based on these investigations, a model for possible impacts of *Phragmites* on the botanical conservation value of fen meadows is developed.

The weakness of a correlative approach is its low predictive power, mainly due to the uncertainty about the mechanisms underlying the correlations. In Chapter 5, a more experimental approach is followed, aiming to assess the importance of shading by *Phragmites*. The investigations reported in this chapter include a removal experiment, light measurements and the growth analysis of two *Carex* species responding differently to increasing abundance of *Phragmites*.

Chapter 6, a literature review, discusses some problems associated with the restoration of degraded fen meadows. The conclusion is that priority should in general be given to the maintenance of valuable fen meadows, rather than attempting to restore strongly degraded ones. This means that a further spread of *Phragmites*, should it be a problem for conservation, ought to be prevented by adequate management long before the species becomes dominant.

Results of two mowing experiments are presented in Chapter 7. One experiment compared the effect of mowing in August with the effect of mowing in winter or not mowing at all. The second experiment investigated the effect of mowing in June in addition to mowing in September. Further, the impact of management on *Phragmites* is discussed in more general terms.

To take measures 'in time', i.e. before restoration becomes necessary, it is important to detect a spread of *Phragmites* or detrimental effects of management as early as possible. However, the variability and unpredictability of vegetation sets limitations to early assessments. Chapter 8 examines how and how accurately the abundance of *Phragmites* can be assessed in fen meadows. Investigations include the choice of variables to measure sample size, accuracy of estimations and spatio-temporal variation.

Chapter 9 investigates how vegetation dynamics in fen meadows influences the assessment of treatment effects in management experiments. Short-term and long-term changes in species composition are compared in one of the mowing experiments of Chapter 7. The influence of plot size and of the context of an experiment on (apparent) treatment effects is discussed.

The final discussion (Chapter 10) attempts to draw some general conclusions of the research presented in this thesis for conservation management and to outline needs for further research.

2. 'Phragmitization' and 'Reed die-back': a contradiction?

2.1 Reed: "a common species in decline"[1]?

"Nearly 40 years ago Hürlimann (1951) reported a frequent retreat of reed belts around many Swiss lakes. But in the following two decades the phenomenon of 'reed die-back' escaped notice. However, in the 1970s changes in littoral vegetation became obvious (...). In some lakes, reed retreat was so serious that the yields of professional fishing were at risk. Shoreside sediment instability increased, the disturbance of the deposition-erosion equilibria provoked mud banks and consequently led to hygiene problems. (...) Authorities spent millions of DM to protect the remaining reed stands. However, the success was small. On the contrary, the retreat of the reed belts proceeded on a European scale." (Ostendorp 1989)

"The pest plant Phragmites (*Phragmites australis*) has spread dramatically throughout Delaware's coastal marshes and impoundments during the last 40 years, greatly reducing the value of these areas as waterfowl, waterbird and fur bearer habitat... *Phragmites'* aggressive growth pattern has enabled it to outcompete traditionally dominant plants and to form a monotype in many Atlantic coastal wetlands." (Jones & Lehman 1987)

Reed 'die-back' has raised much concern among conservationists and has, therefore, been an important research field for wetlands ecologists in Europe during the last thirty years. The notion of reed belts as an endangered ecosystem needing protection has become common even among lay people. Interviews of the author with visitors of a wetland nature reserve (unpublished) showed that most of them regarded *Phragmites* as a plant species with high conservation value, even if part of them admitted to find the open landscape of fen meadows visually more attractive than closed reed stands. Respondents generally associated reed with water and typically explained high or low abundance of *Phragmites* at a particular site with high or low water level. Whereas most of them knew about the tendency of *Phragmites* to colonize shallow water bodies, they did generally not conceive that *Phragmites* might be considered a pest plant spreading in terrestrial habitats. Yet, it is. While much effort is devoted to the protection, enhancement or restoration of reed belts in European lakes, attempts to control or even to eradicate this species are made at other places (Marks *et al.* 1994). This apparent 'contradiction' raises several questions: why should the same species spread in some parts of wetlands and regress in others? Why should the same factor – nitrogen – be involved in both processes? Why, finally, should management be used to promote *Phragmites* in some cases and to reduce it in others?

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[1] Den Hartog *et al.* (1989)

The following chapter briefly discusses these questions. It is not tried to give a comprehensive account of the ecology of the species, since several monographs and reviews are available from other authors, e.g. Hürlimann (1951); Björk (1967); Haslam (1972, 1973a); Rodewald-Rudescu (1974); Binz (1989); Krumscheid-Plankert (1991); Ostendorp (1989, 1993b).

2.2. Aquatic sites: high production at the edge of existence

Limnic reed stands are among the most productive vegetation types. Annual aboveground biomass production can be as high as 9–10 kg m^{-2} under subtropical conditions (Hocking 1989a), and still reaches 3–5 kg m^{-2} in temperate regions (Dykyjová & Hradecká 1976). Thus, reed stands are more productive than most fertilized grasslands. This high biomass production might suggest that the aquatic habitat offers optimal growth conditions and that no environmental stress is experienced by the plants living in it, since stress should "limit the rate of dry-matter production" (Grime 1977). Yet, this impression might be misleading.

As pointed out by Guthruf *et al.* (1993), the high biomass production of reed stands not only reflects favourable conditions for growth. It is a prerequisite for the subsistence of plants under extreme conditions related to their aquatic habitat. An extensive photosynthetic apparatus is necessary to synthesize a large amount of carbohydrates over a short time period. These carbohydrates, in turn, are indispensable for survival in winter and for regeneration in the following growing season. The amount of carbohydrates needed for survival and regeneration is high because many site factors related to the aquatic conditions are harmful to the plant, such as the mechanical action of waves (Klötzli 1974; Binz 1989), grazing by aquatic birds and mammals (Klötzli 1971; Klötzli & Züst 1973b; Krauss 1990), a long period of heterotrophic growth before shoots reach water surface (Guthruf *et al.* 1993), the formation of organic and inorganic phytotoxins in the sediment (Armstrong *et al.* 1996), etc. Like other helophytes, *Phragmites australis* can tolerate these stresses through morphological and physiological adaptations, but these adaptations are associated with an additional demand for carbohydrates. Under undisturbed conditions, this demand can be met, and there is a balance between gains and losses. However, this balance is easily disturbed (Cízková-Konkalová *et al.* 1992).

The problems related to aquatic conditions do not affect *Phragmites* at terrestrial wetland sites, such as fen meadows. It might be expected that these sites are too dry for the species, because its water demand is high owing to its strong transpiration (Krolikovská 1971). Indeed, *Phragmites* can only grow where its roots are able to reach the groundwater (Hürlimann 1951). However, roots may in some cases extend up to a depth of six meters, and a depth of one or two meters is easily reached (Haslam 1973a). Given the groundwater regime of fen meadows (Klötzli 1969), dryness alone should not prevent *Phragmites* from becoming abundant in these communities. The effect of a low

water table is indirect, i.e. it allows other species to reduce *Phragmites* or even to displace it through competition. On the one hand, many potential competitors can grow at terrestrial sites, whereas most of them are excluded at higher water levels (cf. Haslam 1973a; van der Valk 1994). This is why flooding in summer is used in artificial reed beds to maintain monospecific stands (Haslam 1973b). On the other hand, *Phragmites* forms deep roots at terrestrial sites, both in order to reach the groundwater table and because of the root competition by other species (Hürlimann 1951). Deep roots are morphologically different from the shallow roots predominantly formed at aquatic sites. They are coarser and therefore less efficient at water and nutrient uptake (Hürlimann 1951). Inadequate nutrition, in turn, delays the emergence and growth of shoots (Haslam 1970c). This gives *Phragmites* a competitive disadvantage compared with the dominant species of fen meadows (Hürlimann 1951; Mochnacka-Lavácz 1975).

2.3. Nitrogen: key factor, but potential danger

"... dass grosse zusammenhängende und produktive Schilfrohrbestände nur in Gebieten vorkommen, deren Böden verhältnismässig reich an Mineralsalzen, speziell an Nitraten, sind". (Hürlimann 1951)

"*Phragmites* usually grows well in eutrophic habitats. Effective competitors are usually few in nutrient-poor places, but more numerous and luxuriant in eutrophic ones. Consequently, *Phragmites* is frequently limited by competition in the latter. Available nutrients in peat often increase on drier ground, so *Phragmites* in dry places is often denser in nutrient-medium than in nutrient-rich places, competitors growing better in the latter." (Haslam 1973a)

Phragmites australis is known as a fast-growing and nutrient-demanding species. Fertilization experiments have shown its strong growth response to nutrient addition (Szczepanska & Szczepanski 1976; Ulrich & Burton 1985; Krumscheid-Plankert 1991). Nitrogen was normally found to increase production more than phosphorus (Granéli 1985) and phosphorus fertilization sometimes even resulted in lower yields (Bornkamm & Raghi-Atri 1978). A reason for the particularly strong dependence of the plant on nitrogen might be that internal cycling is less efficient for this element than for phosphorus and potassium (Granéli 1990). In the eastern part of the United States, "increases in nutrient concentrations, especially nitrates, have been suggested as a primary cause for increases in *P. australis* populations" (Marks *et al.* 1994).

However, nitrogen seems not always to be the main limiting factor. (Ksenofontova 1988; Haslam 1973a). In any case, the fact that adding a nutrient increases biomass production in fertilizing experiments does not necessarily imply that an increased availability of this nutrient also enhances the robustness or the competitive ability of the species under field conditions.

Even if concentrations of nitrogen much higher than those found in natural water bodies are necessary to produce any toxic effects in *Phragmites* plants (Ostendorp 1990), nitrogen enrichment may be indirectly detrimental to them by affecting their carbohydrates economy. Various processes have been suggested for such effects, e.g. (1) the ratio of aboveground to below ground biomass is increased (Fiala 1976; Ulrich & Burton 1985; Cízková-Konkalová *et al.* 1996), so that the risk for rhizomes to become depleted of carbohydrates is higher. (2) The plant tissue structure is modified. In particular, less sclerenchymatic tissue is formed, and consequently, the mechanical resistance is reduced (Klötzli & Züst 1973b; Klötzli 1974; Bornkamm *et al.* 1980; Binz 1989). (3) In the presence of high concentrations of ammonium (due to limited nitrification under anaerobic conditions) storage of carbohydrates is reduced (Cízková *et al.* 1996). Moreover, sugars are stored rather than starch (Kubín & Melzner 1996). Sugars are more mobile than starch, and therefore, sugar reserves are likely to be depleted faster under conditions of stress (Kubín & Melzner 1996). (4) The growth of filamentous algae may be promoted. These algae may harm *Phragmites* both mechanically and chemically (Klötzli 1971; Binz 1989; Ipsen, *pers. comm.*). However, the role of these processes has been strongly questioned (Ostendorp 1990) and it is likely that none of them can be considered the only, nor even the principal cause of reed die-back.

Under terrestrial conditions high nitrogen availability has no negative consequences for the plant, but it increases the competitive ability of other potential dominants as well (Haslam 1973a). *Phragmites* can take up and use nutrients very efficiently if it has the possibility to form a dense root mat close to soil surface (e.g. Wattenhofer 1980). However, if a low water table or competition by other plants forces it to form deep roots, it may not be able to take advantage of a high nutrient availability and may be outcompeted (Hürlimann 1951; Buttery & Lambert 1965; Haslam 1971b). Nutrient input can be expected to give it a advantage over its competitors (a) if these competitors have a lower inherent growth rate, (b) if the growth of competitors is currently limited by an other nutrient than the growth of *Phragmites*, (c) if nutrients are in a deep soil layer, so that only the roots of *Phragmites* reach them, or (d) if *Phragmites* has the possibility to make nutrients unavailable to competitors by storing them in its rhizomes. Each of these situations can be encountered in fen meadows.

2.4. Management: to promote or to control?

"... dass das Schilf eine wirtschaftlich nicht zu unterschätzende Bedeutung hat und dass sein Fortbestehen an unseren Seeufern und in den Sumpfwiesen in verschiedener Beziehung sehr wünschbar ist. In neuerer Zeit sind dazu noch ästhetische Gesichtspunkte stärker in den Vordergrund getreten, und es wird den Phragmiteten auch aus diesem Grunde erhöhtes Interesse zugewendet." (Hürlimann 1951)

"Large, unbroken stands of *Phragmites* militate against waterfowl, waterbird, and furbearer populations by causing decreases in desirable food plant abundance, habitat heterogeneity, and open water space. *Phragmites* presents other problems by being a serious fire hazard, impeding water flow, penetrating and clogging underground pipelines, restricting access to marshes, and providing roosts for destructive blackbirds" (Jones & Lehman 1987)

Many efforts have been made to regulate the abundance and vigour of *Phragmites australis* (Trin.) through management. Depending on circumstances, aims differed strongly. In Europe, the aim of management was mostly "maintaining or obtaining *Phragmites* dominance and improving its production" (Haslam 1973a). Managed reed stands were used for thatching (Haslam 1973b, 1995; George 1992), for fuel production (Granéli 1984), as a source of cellulose for industry (Rodewald-Rudescu 1974), to purify waste water (e.g. Brix 1990; Mitsch 1992; Weisner *et al.* 1994; Markantonatos *et al.* 1996), to dry out contamined sewage sludge (Bittmann & Seidel 1967) or to stabilize ditches (Bittmann 1953, in Rodewald-Rudescu 1974). Artificial reed stands were established for several of these purposes (Haslam 1973b, Rodewald-Rudescu 1974). Lakeshore reedbelts have been managed in an attempt to remedy the 'die-back' of *Phragmites* (Klötzli & Züst 1973a,b; Schröder 1987; Ostendorp 1987, 1995a,b).

On the other hand, numerous attempts to control or even to eradicate *Phragmites* have been reported. Control is, for example, necessary in fishponds, because *Phragmites* reduces the surface of open water (Husak 1978); in ditches, because it can impair the flow of water (Caffrey 1996); in salt marshes where it alters the vegetation structure and thus the habitat function for a specialized fauna (Hellings & Gallagher 1992); near airports because it attracts birds that can cause accidents (Hellings & Gallagher 1992); in various cultures (rice, cane etc.) where it may be a troublesome crop weed (Izatt 1979).

Since there are both reasons to promote *Phragmites* and to reduce it, depending on the situation, it is necessary to examine more closely the situation in wetland nature reserves.

"The value of littoral or riverine reeds is higher than that of terrestrial reeds; this is especially valid for the species conservation function, whereas for the pollution control function details are unknown. Reeds with open water places can be valued higher than large closed reeds. Reedbeds flooded to a depth of some decimetres for at least some months in the season are ranked higher than unflooded beds. Abundant dead stalks from the previous year's generation are beneficial for the bank protection function." (Ostendorp 1993a)

"One further approach to resolving conflicting restoration options is to assess the scarcity of opportunity for achieving a particular end point. (...) Species-rich fen vegetation is particularly associated with *incommon low-productive habitats*, irrigated by nutrient-poor water. In such conditions, restoration to reedbeds could be seen as a wasted opportunity, because these can be created readily in a wide variety of situations, including wholly artificial ones." (Wheeler 1995)

The quotations suggest that there is no particular reason to promote Phragmites in fen meadows from a conservational point of view. Contrary to aquatic reed stands, terrestrial populations do not (or only to a small extent) fulfil essential functions in landscape ecology. This is due to the different stand structure, to the absence of open water and to the annual mowing regime which makes the dead stalks unavailable as habitats for overwintering birds and insects (Bibby & Lunn 1982, Tschantke 1992). Moreover, terrestrial reed stands can be created e.g. by flooding former fens that have been drained and fertilized for agricultural use for several decades (Pfadenhauer & Klötzli 1996). The characteristic plant communities of fen meadows are more difficult to restore (cf. Chapter 6). But the absence of a need for conservation does not necessarily imply that there is a need for control. This question will be investigated in more detail in the following two chapters (3 and 4).

2.5. Discussion

Phragmites australis is one of the most widespread species, both geographically (Rodewald-Rudescu 1974) and with respect to the range of habitats (Hürlimann 1951). This broad repartition is probably both the cause and the consequence of its high morphological and physiological plasticity, as well as of its genetic variability (e.g. Waisel & Rechav 1971; Dykyjová & Pazourková 1979; Kühl & Neuhaus 1993). It appears almost inevitable that the ecology of *Phragmites* varies and seems 'contradictory' when considered across such a broad range of conditions.

To a certain extent, however, the survival strategy of *Phragmites* seems 'contradictory' in itself. The tall size of this species, its high maximal growth rate, its rhizomatous growth form as well as its abundant litter production are all traits indicating that *Phragmites* should be a strong competitor (Grime 1973; Grime *et al.* 1988). This is certainly true at terrestrial, unmanaged sites, where *Phragmites* can permanently occupy the space with a dense rhizome mat and with its litter, and store enough nutrients for its initial growth in the next spring (Haslam 1973b). However, *Phragmites* often seems to escape

competition by colonizing sites from which most other species are excluded due to adverse abiotic factors, such as salinity, acidity or anoxia (Haslam 1973a; Marks *et al.* 1994). Its partly stunted growth under such conditions (e.g. Dykyjová & Pazourková 1979) suggests that *Phragmites* should rather be considered a stress-tolerant at these sites.

On the other hand, the main habitat of *Phragmites*, shallow water bodies, might be described as sites presenting permanent post-disturbance conditions, i.e. a high availability of resources associated with low interspecific competition. This in turn means that *Phragmites* might be regarded as a ruderal plant, rather than as a competitor, at these sites (cf. Grime 1974). This view would be consistent with several field observations. For example, the start of reed 'die-back' several decades after lake regulation suggested that periodic droughts (i.e. disturbance) are necessary for the rejuvenation of clones (Rea 1996) and for the elimination of toxic substances formed under reducing conditions (Armstrong *et al.* 1996). Periodic floods, on the other hand, may be necessary to remove the accumulated litter, known to be inhibit growth (Granéli 1990; van der Putten 1993). The impossibility to assign one single survival strategy to *Phragmites* remembers that these categories actually constitute a continuum in which all intermediate strategies can be found (cf. Grime 1979; Grime *et al.* 1988). It also supports the recommendation of Hills & Murphy (1996) to assign strategies at the population level rather than at the species level.

Almost all previous field research on *Phragmites* investigated either aquatic stands or artificial reedbeds. The 'contradictions' outlined in this chapter indicate that the ecology of *Phragmites* in fen meadows – i.e. its relation to groundwater table, nutrient availability, competition and management – can not be reliably derived from the available data, since these were gained under strongly different site conditions. In spite of the bulk of research already devoted to this species, further investigations are needed to evaluate and to tackle the problem of 'phragmitization'.

3. Abundance of Common Reed (*Phragmites australis*), site conditions and conservation value of fen meadows in Switzerland[1]

3.1. 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, mainly due to the increase of intensive agricultural use (Hampicke *et al.* 1991; Oomes & Van der Werf 1996). Despite legal protection the remaining sites have mostly 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 practised (Klötzli 1986; Marti & Müller 1993).

Referring to a spread of *Phragmites* as a threat for nature conservation may surprise after the concern that was caused by reed 'die-back' on Central European lakeshores (e.g. Ostendorp 1989; van der Putten 1994). This apparent contradiction is explained by the different ecological character of lakeshore reed belts and wet meadows. In reed belts the presence of Phragmites is limited by various abiotic site factors like water depth (Hürlimann 1951), wind and waves (Klötzli 1974), or the presence of toxic substances in the sediment (Armstrong *et al.* 1996), whereas its density and size are mainly limited by intraspecific competition (Haslam 1971a; Granéli 1987). Reed is weakened and finally dies if changes of site conditions deplete or damage its shoots or rhizomes (Klötzli & Züst 1973b; Cizková-Koncalová *et al.* 1992). This 'die-back' is rated negatively because it results in shoreline erosion and in a loss of habitat for waterfowl (Ostendorp 1993a,b). Conversely, site conditions in fen meadows and other wet terrestrial ecosystems are generally relatively favourable to *Phragmites* (Hürlimann 1951). Its productivity is lower than in aquatic stands, but it is more resistent to stress factors (Guthruf *et al.* 1993). The presence of *Phragmites* in fen meadows and, where it is present, its density and size are mainly limited by interspecific competition for light and nutrients (Haslam 1971b). *Phragmites* tends to spread if changes in site conditions give it a competitive advantage (Marks *et al.* 1994). This spread in fen meadows is considered a threat to nature conservation because *Phragmites* is expected to displace specialized, rare and endangered plant species, i.e. to reduce biodiversity, through increased shading (Biewer *et al.*

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[1] Accepted for publication in Acta Botanica Neerlandica 47/1 (1998, in press)

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 *Phragmites* which would allow to determine where and how much this species is spreading are scarce. The factors that cause *Phragmites* to spread and the patterns of its abundance are not well understood (Leupi 1987; Marti & Müller 1993). Also, it has not been established yet whether *Phragmites* 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 *Phragmites*. We surveyed the current abundance of *Phragmites* 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 *Phragmites* was likely to affect the conservation value of fen meadows.

3.2. Materials and Methods

3.2.1. Study sites

The abundance of *Phragmites australis* (Trin.) and the species composition of the vegetation were investigated in 11 wet meadows in nature reserves near Zürich (altitude 400–540 m; Table 1). Long-term average annual temperature ranges from 7° to 9° C, and average annual rainfall from 1000 to 1400 mm. All sites were part of lakeside wetlands, except K1 and K2, located in a swampy basin. Soils were mostly base-rich peat ; 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 2x2-m^2 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 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 *Phragmites* occurred locally. The sites K1 and K2 were very similar; therefore, they were treated as one site in data analysis.

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-m^2 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

3.2.2. *Measurements and estimations*

The species composition of the vegetation in each of the 241 2x2-m^2 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 *Phragmites* was recorded in mid August of the same year by counting the number of shoots taller than 20 cm per 2x2-m^2 plot, and by measuring the culm length and the basal diameter of all shoots in the front left quarter (1 m^2) 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. Basal diameter was taken in the middle of the second internode.

Part of the plots were originally surveyed with different aims in the context of two other studies. In the study of Brülisauer (1996; one transect at sites P, Z1 and Z2, respectively), only the ten longest shoots had been measured. We estimated plot means using the equations:

log (m.length plots) = log (m.length 10 shoots) + 0.264 - 0.286 log (N shoots) ; r^2=0.87
log (m.diam. plots) = log (m.diam. 10 shoots) + 0.186 - 0.206 log (N shoots) ; r^2=0.81,

where m.length was the mean length, m.diam. the mean diameter, and N shoots the total number of shoots in the plots; regressions were based on 72 plots within sites P, Z1, Z2 in which all shoots had been measured.

Sites G2 and G4 were partly used for mowing experiments (Chapter 7). Vegetation relevés and measurements on *Phragmites* were carried out before

the first experiemental treatment (i.e. in June 1995 at site G4 and in June 1996 at site G2). Based on these measurements we estimated the values that would have been found in the experimental plots in August if these plots had not been mown, using the equations:

density (August) = 2.015 + 0.864 density (June); r^2= 0.965
m. length (August) = 11.47 + 1.126 m. length (June); r^2= 0.961
m.diam. (August)) = 0.979 + 0.753 m.diam. (June); r^2= 0.568

where m.length was the mean length and m.diam. the mean diameter of plots; regressions were based on 18 plots in G4 which were not mown in June 1995 and where measurements had been done both in June and in August 1995.

Aboveground biomass of *Phragmites* (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 the equation (cf. Chapter 8):

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

3.2.3. 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 those 85 species (out 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' (Van der Maarel 1978) 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 Phragmites. The 241 plots surveyed represented a gradient from low to high abundance of *Phragmites australis.* The abundance was expressed as the aboveground biomass of *Phragmites* (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

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

In this model x was the difference between the log-transformed ABP of the relevé and the mean log-transformed 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 chi-square test, an approximation of the Likelihood ratio test (Lehman & Sall 1995).

Site conditions. The relation between the abundance of *Phragmites* 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 *Phragmites.*

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 *Phragmites.*

Species diversity was measured as species richness (number per 4-m^2 plot) and as species evenness. The 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 occurs in mires compared with other vegetation types (based on Korneck & Sukopp 1988). The score was, for example, 1 for a species occurring exclusively in mires (e.g. *Carex davalliana*), but only 0.33 for a species more frequently found in another vegetation type (e.g. *Cladium mariscus*). The 'mire species index' of a plot was the weighted average of the scores of all species in the plot. The Braun-Blanquet values of the species 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).

3.3. Results

Abundance of Phragmites australis

The abundance of *Phragmites* in the 241 plots of this study ranged from 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 *'Caricion 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 *Phragmites* 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. Alliances differed even more with respect to the shoot size (Fig. 1b): Almost all *Filipendulion* plots had a mean shoot dry weight of *Phragmites* of 6 g or more, whereas this weight was hardly ever exceeded in *Caricion* or *Molinion* plots.

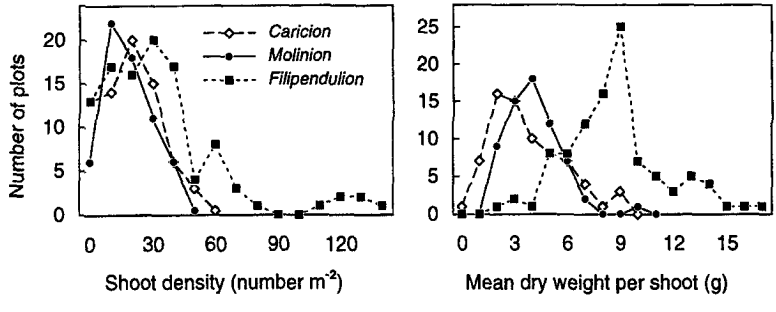
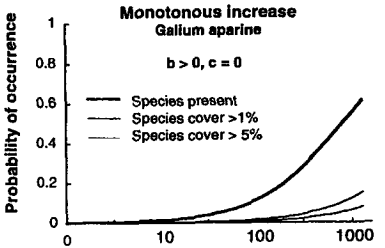
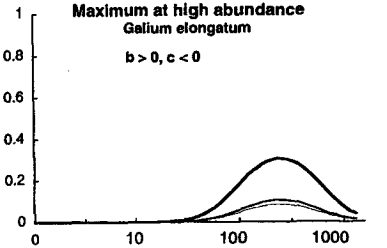


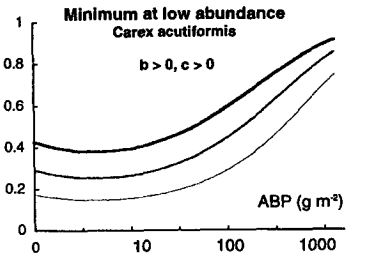
Fig. 1. Distribution of shoot density (a) and shoot dry weight (b) of *Phragmites* in the 241 plots. Symbols indicate the number of plots of each alliance belonging to each class of density or of size. Class width was 10 shoots m^{-2} for shoot density and 1g for shoot dry weight.



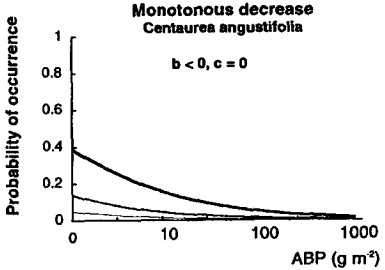
Species: Calamagrostis epigeios, Calystegia sepium, Carex acuta, Fraxinus excelsior, Galium aparine, Lysi-machia nummularia, Myosotis scorpioides, Phalaris arundinacea, Poa pratensis, Solidago gigantea



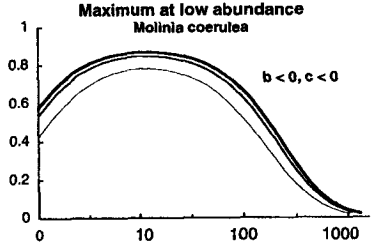
Species: Galium elongatum



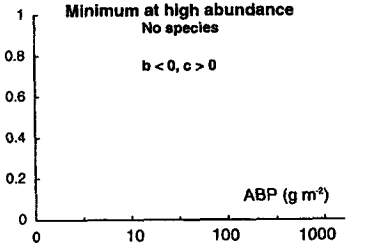
Species: Carex acutiformis, Deschampsia caespitosa, Epilobium hirsutum, Filipendula ulmaria, Galium mollugo, Poa trivialis

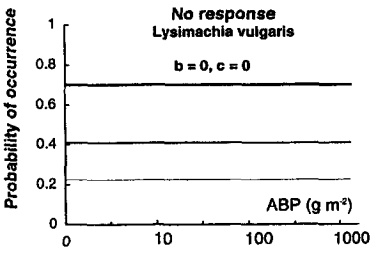


Species: Anemone nemorosa, Carex pulicaris, Centaurea jacea ssp. angustifolia, Festuca arundinacea, Lotus uliginosus, Mentha aquatica, Potentilla erecta

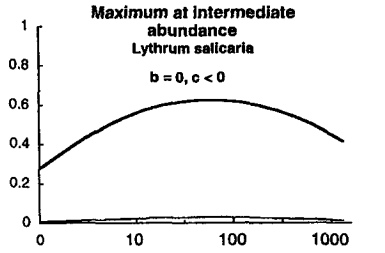


Species: Agrostis gigantea, Anthoxanthum odoratum, Briza media, Carex davalliana, C. elata, C. flacca, C. flava, C. hostiana, C. lasiocarpa, C. panicea, Epipactis palustris, Festuca rubra, Frangula alnus, Galium palustre, Galium uliginosum, Juncus articulatus, Linum catharticum, Luzula multiflora, Molinia coerulea, Parnassia palustris, Schoenus ferrugineus, Stachys officinalis, Stachys palustris, Succisa pratensis

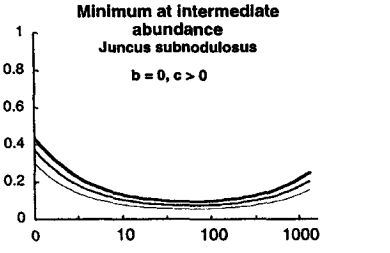




Species: Agrostis canina, Ajuga reptans, Angelica sylvestris, Caltha palustris, Carex distans, C. hirta, Cerastium fontanum, Colchicum autumnale, Crepis paludosa, Epilobium palustre, Equisetum palustre, Euonymus europaea, Glechoma hederacea, Holcus lanatus, Inula salicina, Iris pseudoacorus, Lathyrus pratensis, Lysimachia vulgaris, Dactylorhiza maculata, Peucedanum palustre, Primula elatior, Prunella vulgaris, Ranunculus nemorosus, Rumex acetosa, Salix cinerea, Scutellaria galericulata, Valeriana dioeca, V. repens, Viburnum opulus, Vicia cracca



Species: Carex pallescens, Cirsium palustre, Lythrum salicaria, Rhamnus catharticus, Sanguisorba officinalis



Species: Cirsium oleraceum, Juncus subnodulosus

Fig. 2. Species response curves describing relations between the abundance of *Phragmites* 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.

Species responses

A majority of plant species (55 out of the 85 investigated) was significantly related to the abundance of *Phragmites* (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 ($b=0$, $c\neq0$). 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 *Phragmites* was similar to the species composition of plots in which it was relatively abundant. Plots without *Phragmites* were dense stands of *Juncus subnodulosus* or of tall *Carex* species, and *Phragmites* 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 at three sites; it was negative in two of them, suggesting that *Phragmites* was more abundant under drier conditions.

If 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 *Phragmites* 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 *Phragmites*.

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 data set (Table 2b).

Indices of conservation value

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 *Phragmites* in eight out of ten sites, and positively in none of them.

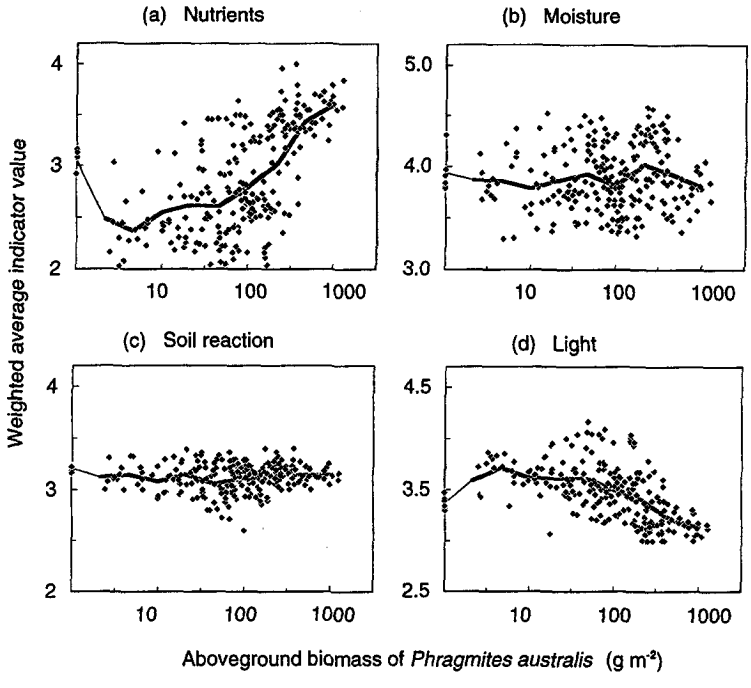


Fig. 3. Ecological indicator values of the vegetation for (a) nutrients, (b) soil moisture, (c), soil reaction and (d) light conditions as a function of the aboveground biomass of *Phragmites* (ABP). Diamonds represent individual plots, lines indicate mean values for ten classes of ABP.

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 *Phragmites* (ABP); only significant correlations ($p < 0.05$) are indicated

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

If 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 *Phragmites* deviated from the general pattern, and the curves representing the average reponses 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}.

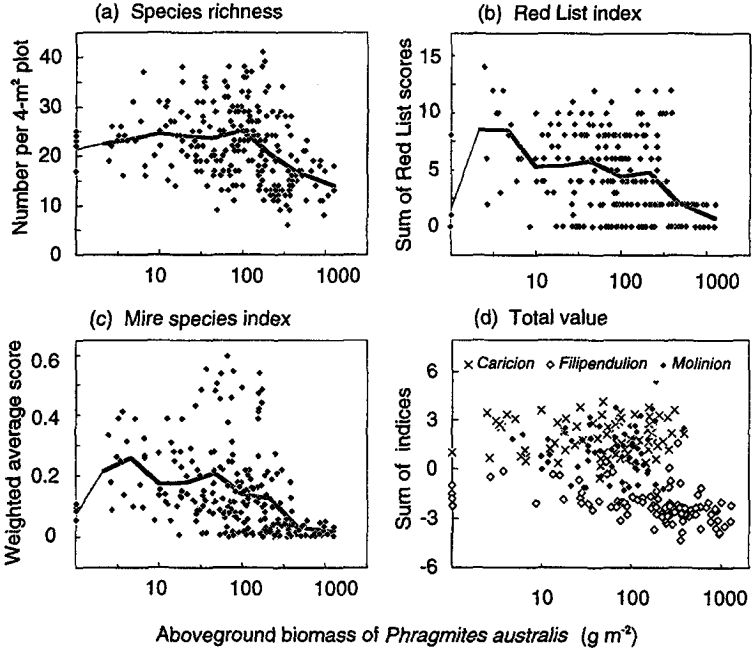


Fig. 4. Indices of conservation value of the vegetation: (a) species richness, (b) 'Red List index', (c) 'mire species index' and (d) 'total botanical conservation value' as a function of the aboveground biomass of *Phragmites*. Symbols are values of individual plots. Heavy lines indicate mean values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

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	Even-ness	Red List index	Mire species index
(a) Mean indices				
Caricion	22	0.65	5.5	31
Molinion	29	0.69	7.8	13
Filipendulion	18	0.67	1.8	3.2
P	< 0.001	ns	< 0.001	< 0.001
(b) Correlations between indices and ABP				
Caricion	0.25	0.41	-	-
Molinion	-	-	-	-
Filipendulion	-0.49	-	-	-0.43

To summarize the results we 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.

3.4. Discussion

Abundance of Phragmites australis in fen meadows

Phragmites 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 1989a). 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 *Phragmites* was much lower, and its contribution to the total biomass was generally less than 40% (Chapter 4). Thus, conditions in our fen meadows differed clearly from those in monospecific terrestrial reed beds. Our data were 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 *Phragmites* at our sites seemed, on an average, 'normal' for fen meadows.

Is there any evidence that *Phragmites* 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 *Phragmites* 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 (pers. communications).

Relation to site conditions

The abundance of *Phragmites australis* varied considerably among sites and among plots in our study, even though they were managed in the same way. Unfortunately, no reliable informations were available on former management. The ecological indicator values of the vegetation suggested that differences in nutrient availability were mostly responsible for differences in the abundance of *Phragmites*, whereas water level and soil pH were apparently unimportant. The use of ecological indicator values has limitations, particularly in vegetation influenced by men (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 *Phragmites* 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 *Phragmites* 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 *Phragmites,* but not the growth of the other species, and this would give *Phragmites* 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, *Phragmites* would be expected to spread mainly into wet sites or parts of sites (Marti & Müller 1993; Walther 1994). However, *Phragmites* is able to follow the groundwater table with its roots down to 1.5 m or more (Hürlimann 1951; Haslam 1973a). It may, therefore, grow well at sites that completely dry out superficially (Hürlimann 1951). Direct measurements by Brülisauer (1996) even suggested that *Phragmites* 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 (Myers *et al.* 1982; Grootjans *et al.* 1985; Koerselman *et al.* 1993). As seen above, this might be beneficial to *Phragmites*. 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. Phragmites can grow on strongly acidic as well as on calcareous soils (Hürlimann 1951; Haslam 1973a; Marks *et al.* 1994). As 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 *Phragmites* increasingly displaced light-demanding species (Haslam 1971b; Wheeler & Giller 1982; Klötzli 1986). Yet, this is not sure, 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 *Phragmites* (Buttery & Lambert 1965; Gryseels 1989a).

Relation to the 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 twice the same. 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 *Phragmites* and the average conservation value of a plot could be decomposed into two effects: On the 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 *Phragmites* had not affected the mire species in the vegetation types generally considered most sensitive to shading. Did this indicate that the current spread of *Phragmites* had no impact on *Molinion* and *Caricion* communities? This conclusion would certainly be prematurate. It regards alliances as fixed categories, whereas the attribution of plots to alliances merely reflects their current species composition, which may change gradually until plots are attributed to a new alliance (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 & Müller 1993). Likewise, 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 *Phragmites* on the conservation value must, therefore, consider the possibility of such shifts.

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

(1) No relation. The abundance of *Phragmites* fluctuates within a certain range, without impact on the species composition. *Phragmites* might even decrease to a low level of abundance again. In that case its present increase would merely be a long-term fluctuation without major ecological significance.

(2) Early indication. Tall herbs and tall sedges increasingly invade the plot and displace mire species. Both the spread of tall herbs and the spread of *Phragmites* are probably due to nutrient enrichment (Boller-Elmer 1977; Zelesny 1994; Graf 1996; Brülisauer 1996). *Phragmites* 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), *Phragmites* still becomes more abundant. According to Fig. 4d, the spread of *Phragmites* results in an additional loss of conservation value, so that the total loss is greater than if tall herbs had spread alone. *Phragmites* might, however, also be itself displaced by the tall herbs *(6)*.

(4) Direct competition. Light-demanding mire species disappear progressively due to the increased shading by *Phragmites*. As a result, the conservation value of the plot is reduced. Nevertheless, the plot still belongs to the alliance *Molinion*. 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 *Phragmites* increases the nutrient availability, so that tall herbs and tall sedges can invade the site and displace mire species. Thus, *Phragmites* is indirectly responsible for the loss of conser-

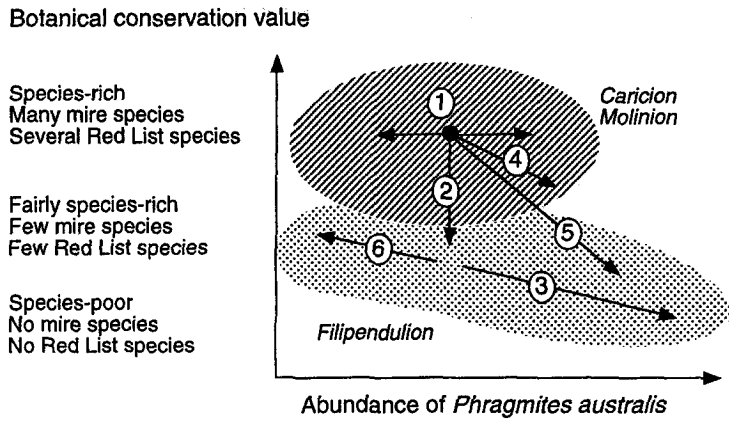


Fig. 5. Model illustrating possible future changes in conservation value of a *Molinion* or *Caricion* meadow in which the abundance of *Phragmites* has increased recently. (1) no change, (2) decrease due to a concomitant spread of tall herbs, (3) further decrease due to a further spread of *Phragmites* 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). *Phragmites* might also be displaced by tall herbs (6).

vation 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 *Phragmites* due to exudation of oxygen or losses of carbohydrates (Armstrong 1990); and nitrogen fixation by symbiontic 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, 1990).

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

4. Species richness and species composition of fen meadows in relation to the abundance of *Phragmites australis*

4.1. Introduction

Species richness and aboveground biomass

Factors determining species richness of plant communities have received particular attention in ecological research and gave rise to innumerable hypotheses (Palmer 1994). According to Grime (1973, 1979), two factors limit species richness in herbaceous communities, namely stress (e.g. acidity, strong nutrient deficiency, toxicity) and competition (interactions between plants, particularly mutual shading). This model was frequently used to explain the unimodal ('hump-backed') relationship between species richness and aboveground biomass found by various authors (Al-Mufti *et al.* 1977; Vermeer & Berendse 1983; Moore & Keddy 1989; Wisheu & Keddy 1989; Wheeler & Shaw 1991). Species richness was assumed to be limited by stress at sites with low productivity (only few species tolerating the stress factor) and by competition at sites with high productivity (strong competitors displacing weak competitors). Maximal species richness was expected to occur at a biomass (dry weight) of 400–600 g m^{-2}.

This model has been challenged from different sides. Oksanen (1996) noted that an unimodal relationship could simply result from the number of organisms present in a plot, "without assuming environmental or biological stress factors". Various alternative interpretations of the humped relation were also provided by Abrams (1995) who, moreover, suggested mechanisms that would produce a monotonous (increasing) relation between biomass and species richness despite (or even because of) competition. Gough *et al.* (1994) argued that a strong stress factor (e.g. flooding) can exclude most species from a site without necessarily reducing the biomass of the species adapted to it.

Also, numerous field data showed that both the biomass at which species richness is maximal and the corresponding maximal value of species richness differ regionally and among vegetation types (Kunzmann *et al.* 1985; Willems & Van Nieuwstadt 1996). It became obvious that biomass – as an indicator for the availability of resources and the intensity of competition – can only be related to species richness within the limits of the 'actual species pool' of the site, i.e. the totality of species potentially occurring in it. This species pool is determined by evolutionary, historical and ecological factors (Zobel 1992; Eriksson 1993; Gough *et al.* 1994; Pärtel *et al.* 1996).

The vegetation structure was also found to influence the species richness-biomass relation. In their survey of the Broadland fen vegetation, Wheeler & Giller (1982) found lower species richness in managed reedbeds than in managed sedge beds with same biomass. They explained the low species richness in reedbeds with strong shading and concluded that "a simple rela-

tionship between total crop and light penetration cannot be assumed". One important factor was probably plant height: tall plants intercept more light than small plants with same biomass (Hirose & Werger 1995), and are, therefore, likely to be stronger competitors (Gaudet & Keddy 1988). As a result, an increase in vegetation height is expected to result in more severe competition for light, and, according to Grime's (1973, 1979) model, to lower species richness even if other site factors and biomass production remain more or less unchanged. This appeared to be the case in Dutch chalk grasslands, where higher dominance of the tall grass *Brachypodium pinnatum* was associated with lower species richness, even though total aboveground biomass hardly differed (Bobbink & Willems 1987).

This theoretical background suggests that a loss of species richness should have occured in fen meadows of the Swiss Plateau in which *Phragmites australis,* a tall grass, has become more abundant during the last thirty years (Klötzli 1986; Marti & Müller 1993; Biewer *et al.* 1994). Since *Phragmites* is taller than all other species of fen meadows, a higher proportion of *Phragmites* in total biomass means a greater average plant height and more unfavourable light conditions for the smaller plants. As discussed above, this should reduce species richness. It might, therefore, be expected that the proportion of *Phragmites* in total biomass and species richness are negatively correlated for a given (fixed) value of total biomass.

Decreasing species richness with increasing abundance (aboveground biomass) of *Phragmites* was, indeed, found in the vegetation survey reported in Chapter 3. However, the correlation was weak. Moreover, only the biomass of *Phragmites* (ABP) had been recorded in that survey, and not the total aboveground biomass. The positive correlation of ABP with the 'nutrient indicator value' of the vegetation (Landolt 1977) suggested that the abundance of *Phragmites* was positively correlated with site productivity. Therefore, the negative relation between ABP and species richness could have been determined either by the proportion of *Phragmites* in aboveground biomass or by site productivity. The first part of this chapter investigates which of the two possibilities applies.

Limitations of species richness in the evaluation of fen meadows

Species richness is the most widely used criterium in nature conservation evaluation (Usher 1994). One reason is that preserving global and regional biodiversity is considered the main objective of nature conservation (Spellerberg 1992; Kunin & Lawton 1996). Another reason is that species richness is often correlated with other objectives of nature conservation, such as the presence of rare species or of unfragmented habitats, and may, therefore, be considered an indicator for conservation value in a broader sense (Wheeler 1988). Furthermore, species richness offers practical advantages, because it yields 'objective', quantitative data which can be compared among regions, being independent of regional Red Lists or species

inventories. Nevertheless, species richness may be an unsuitable criterium for evaluation at the local scale, where the conservation objective often consists in preserving or rehabilitating certain endangered species, rare communities or specific vegetation types associated with former land use.

This situation applies to wetland communities. Their species richness decreases both with increasing wetness and with increasing acidity (Wheeler 1993). Reedbelts, bogs or wet heaths are species-poor vegetation types; nevertheless, they also have a high conservation value, e.g. because of characteristic rare species or because of their ecological functions (Haslam 1973b; Wheeler & Giller 1982; Kunzmann *et al.* 1985; Ostendorp 1993). At the other end of the scale, small-sedge fens and litter meadows are generally species-rich and their degradation reduces species richness (Klötzli 1986; Fojt & Harding 1995). However, species loss does often not take place immediately. In an early stage of degradation (e.g. first years after abandonment, slight drainage or beginning eutrophication), fens may even become more species-rich (Boller-Elmer 1977; Zelesny 1994). The reason hereof is that species from other vegetation types establish. They increase species richness for a certain period, but eventually displace the original species (Kapfer & Pfadenhauer 1986). This species replacement may leave species richness at the plot level unaffected (Regimbeau & Clément 1996). Yet, species richness at the landscape level decreases since species that occurred uniquely in fens are replaced by species also found in other vegetation types.

To assess such changes Wheeler (1988) proposed a 'principal fen species score' that was the number of 'characteristic fen species' in 4-m^2 plots. A 'mire species index' similar to this 'principal fen species score' was introduced in Chapter 3. One difference is that Wheeler's (1988) score assesses the *number* of fen species, whereas the 'mire species index' assesses the *proportion* of fen species. Both methods have advantages and disadvantages, depending on the situation[1]. Another difference is that in Wheeler's (1988) index species are classified in two clear-cut groups, namely fen species and accompanying species, whereas in the 'mire species index' species are considered to be 'to a certain degree' fen species, depending on their relative frequency in fens compared with other vegetation types. This seemed appropriate, since

> "while the botanical importance of fens may reside particularly in their characteristic species, their importance as a reservoir of more widespread species is also considerable. For example, *Listera ovata* occupies a wide range of habitats but is frequent in various types of fen. In some regions, destruction of some of the drier habitats favoured by this species may mean that remnant fen sites now have a proportionately greater importance in maintaining populations of this species than they once did. It is clear that, by providing an unimproved semi-natural habitat, fens can form important repositories for a wide range of plant species in addition to their more characteristic taxa" (Wheeler 1993)

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[1] The establishment of new species at an early stage of degradation (see introduction) would be detected by the 'mire species index', but not by the 'fen species score'. In contrast, the loss of three fen species associated with the disappearance of three widespread species would be reflected in the 'fen species score' but not necessarily in the 'mire species index'.

Whereas *Listera ovata* would not have been included in Wheeler's (1988) 'principal fen species score', it would have contributed to the 'mire species index'. There is, however, a change that could not be assessed with that index either: the index would not change if *Listera ovata* is replaced by a species occurring in fens and in fertilized meadows (e.g. *Ajuga reptans*). Yet, *Listera* should contribute more to the botanical conservation value of the plot than *Ajuga*, because its second habitat type, dry unfertilized meadows, is as rare as fens in the Swiss Plateau (Landolt 1991; Kuhn *et al.* 1992), contrary to the other habitats of *Ajuga*. A second index would be necessary to assess this difference.

The example of *Listera ovata* shows that any index of conservation value is likely to reveal certain types of change and to be insensitive to others. Consequently, indices of conservation value are not suitable to assess differences in species composition *per se*, i.e. their quantitative importance and their relation to presumed causes. However, such an assessment may be important: if differences in species composition are small, or if only a minor part of the variation in species composition is related to the presumed cause, care should be taken not to overinterpret differences in conservation indices, even if they appear statistically significant.

Limitations to the use of species richness and of the 'mire species index' became apparent in Chapter 3 (Fig. 1). It was found that both species richness and the 'mire species index' decreased with increasing abundance of *Phragmites* (aboveground biomass, ABP). However, species richness did not decrease over the whole range of ABP. It even increased slightly up to an ABP of 100 g m^{-2}. Moreover, the relation of these indices to ABP differed among the three alliances *Caricion, Molinion* and *Filipendulion*. A significant decrease in species richness and in the 'mire species index' along the ABP gradient was found in plots belonging to the alliance *Filipendulion*, but not in those of the alliances *Molinion* and *Caricion*. As one possible interpretation it was suggested that *Phragmites* had only spread recently into *Molinion* or *Caricion* plots and that there was a certain time lag before an impact of *Phragmites* would become apparent. An alternative interpretation would be that the indices used in Chapter 3 were suitable to assess a strong degradation of fen meadows, but not suitable to evaluate relatively slight changes in species composition caused by an increase of ABP in the alliances *Molinion* and *Caricion*. The conclusion of this interpretation would be that a more detailed assessment is required.

In the second part of this chapter, the relationship between the abundance of *Phragmites* and species composition will be reassessed using two different approaches: (a) a quantitative approach, where canonical correspondence analysis is used to assess how strongly ABP is related to species composition; (b) a qualitative approach to assess how the proportion of species belonging to various vegetation types (not only mires) changes along the ABP gradient.

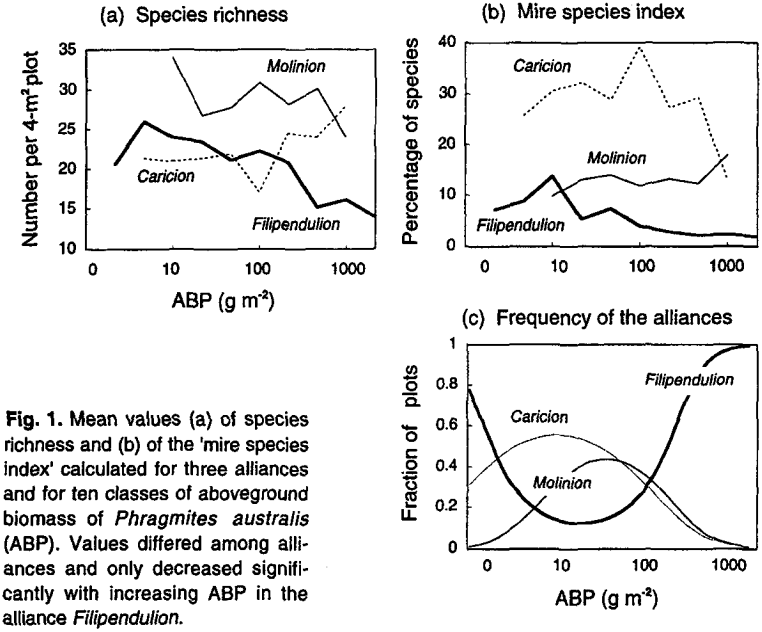

Fig. 1. Mean values (a) of species richness and (b) of the 'mire species index' calculated for three alliances and for ten classes of aboveground biomass of *Phragmites australis* (ABP). Values differed among alliances and only decreased significantly with increasing ABP in the alliance *Filipendulion*.

In (c) the relative frequency of plots belonging to the three alliances has been modelled as a function of ABP with quadratic logistic regression. Plots without *Phragmites* or plots with ABP higher than 200 g m^{-2} mostly belonged to the alliance *Filipendulion*. This frequency distribution is mainly responsible for the relation between ABP and the conservation value of fen meadows. Figures are based on results from Chapter 3.

4.2. Methods

Field methods

The abundance of *Phragmites australis* (Trin.) and the species composition of the vegetation were investigated in 11 wet meadows in nature reserves near Zürich. A series of 2x2-m^2 plots were arranged along parallel transects at each site; the total number of plots was 241. The species composition of the vegetation in each plot was recorded between late May and early July (five sites in 1995, six sites in 1996) using the Braun-Blanquet scale (Dierschke 1994). The abundance of *Phragmites* was recorded in mid August of the same year by counting the number of shoots taller than 20 cm per 2x2-m^2 plot, and by measuring culm length and basal diameter of all shoots in the front left quarter (1 m^2) of the plots. See Chapter 3 for more details on field sites and measurements.

The aboveground biomass of all other plant species was determined on only one transect per site; sites K1, G3, G5 (cf. Table 1, Chapter 3) could not be sampled due to a lack of time. All vascular plants except *Phragmites* were clipped within three 0.16-m^2 quadrats per 2x2-m^2 plot in late July 1995 or 1996. The dry weight (70° C) of the sampled material was determined. Additional biomass data (both *Phragmites* and other species) were available from Brülisauer (1996) for 23 plots in two other fen meadows close to our sites (K3 and P2 [2]). They had been sampled in the same way, except that the vegetation was harvested in two 0.25-m^2 quadrats per 2x2-m^2 plot. Thus, data for a total of 72 plots could be analysed.

Biomass of Phragmites and of other species

The aboveground biomass of *Phragmites* (ABP, dry weight in g m^{-2}) was estimated from field measurements as indicated in Chapter 3. Total aboveground biomass of plots was estimated by adding the aboveground biomass of *Phragmites* to the mean aboveground biomass of all other species in the 0.16-m^2 quadrats. The fraction of *Phragmites* in the biomass was slightly overestimated by this procedure because *Phragmites* had been sampled a few weeks later than the other species. However, measurements in permanent plots indicated that the error was less than 10% and no correction was made.

Correlations between aboveground biomass (*Phragmites,* others and total), species richness and the 'mire species index' were calculated as in Chapter 3.

Quantitative assessment of species composition

The strength of the relations between species composition and abundance of *Phragmites* (explained variance) was analysed with canonical correspondence analysis (CCA). This multivariate technique combines (a) the calculation of ordination axes through iterative weighted averaging with (b) the regression of the axes on one or several external variables at each iteration step. Thus, axes are 'constrained' on external variables (Ter Braak 1986). CCA yields the percentage of variance in species composition 'explained' by the external variable(s). 'Explained variance' must be understood in a statistical sense: it is the dispersion of the species optima[3] along the gradient defined by the external variables, divided by the dispersion of the plot centroids along this gradient (Ter Braak 1988). A causal relation is not necessarily implied.

In our study, the only external variable was the logarithm of the aboveground biomass of *Phragmites australis* (ABP). CCA was done (a) for each

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2 Coordinates: K3: 679'400 / 254'500 and P2: 701'075 / 244'125

3 CCA assumes unimodal species responses to one or several environmental gradient(s), which are defined as linear combinations of the external variables in the analysis. The linear combinations yielding the strongest gradients are calculated and response curves are modelled for each species on each gradient. The variance of the optima of these response curves measures the dispersion of the species optima along the gradient.

site, (b) for each alliance and (c) pooling all plots. The fraction of variance in species composition explained by ABP was given by the eigenvalue of the first CCA axis. For its interpretation it was compared with the eigenvalue of the first axis of a correspondence analysis (CA). CA uses the same weighted averaging procedure as CCA, but without constraint on ABP. Therefore, the eigenvalue of the first CA axis is the maximal fraction of variance that can be 'explained' by a single axis calculated with this method in the data set. This fraction is often rather low, because a considerable loss of information is inevitable when high-dimensional data are represented on a single axis (Ter Braak 1990). In the present study, it corresponds to the fraction of explained variance that would be obtained in a CCA if ABP were perfectly correlated with the main gradient in species composition. Therefore, comparison of CCA and CA eigenvalues indicated whether the abundance of *Phragmites* was related to a major vegetation gradient.

Monte Carlo permutation tests (500 random permutations) were used to test the null hypothesis that ABP would have explained the same fraction of variance if the abundance of *Phragmites* had been distributed randomly among plots, without relation to species composition. Calculations were made with the programme CANOCO, Version 3.1 (Ter Braak 1987-1992).

Qualitative assessment of species composition

To interpret changes in species composition along the ABP gradient in terms of changes at the community level, the proportion of species belonging to various vegetation types was calculated for each plot. Calculations were based on the 'fuzzy set theory' (Roberts 1986) to take into account the fact that most species do not 'belong' to just one vegetation type: they occur in several vegetation types and therefore have a certain 'degree of belonging' to each of them. 'Degrees of belonging' indicate how frequently a species occurs in a certain vegetation type compared with its frequency in other vegetation types.

In this study, twelve vegetation types were considered (Table 1). Eight types were based on the 23 formations defined by Korneck & Sukopp (1988) for Germany[4]. One of these types, the formation 'wet meadows' (class *Molinietalia*), was subdivided again because it was the main vegetation type at the study sites, and because it included four phytosociological alliances (Klötzli 1969) the conservation value of which had to be rated differently in the context of this study: the alliances *Molinion* and *Juncion* are typical for nutrient-poor, yearly mown wet meadows. The alliance *Calthion* is characteristic of more nutrient-rich sites, generally mown twice a year; *Calthion* meadows are still rated highly because of their species richness, of certain rare species and of their visual amenity (Grootjans *et al.* 1996; Pfadenhauer & Klötzli 1996). The alliance *Filipendulion* is characteristic of nutrient-rich or unmown wet mea-

[4] It was assumed that this classification is also sufficiently valid for the northern Swiss Plateau

dows; its presence in fens is generally regarded as a sign of degradation (Boller-Elmer 1977; Egloff 1986; Klötzli 1986).

The degree of belonging of species i to formation f (t_{if}) was given by

$$t_{if} = \frac{\text{frequency in formation}_{if}}{\sum_{f=1}^{23} (\text{frequency in formation}_{if})}$$

where 'frequency in formation $_{if}$' was a score indicating how frequently species i occurs in formation f according to the classification of Korneck & Sukopp (1988); this score was (arbitrarily) chosen to be 4 if the species occurs mainly in that formation, 2 if it occurs frequently and 1 if it occurs occasionally in it. For vegetation types including several formations (cf. Table 1), t_{if}-values were the sum of the t_{if}-values of the individual formations.

The degree of belonging of species i to alliance a (t_{ia}) was given by

$$t_{ia} = \frac{\text{frequency in alliance}_{ia}}{\sum_{a=1}^{4} (\text{frequency in alliance}_{ia})}$$

where 'frequency in alliance $_{ia}$' was a score indicating how frequently species i occurs in alliance a according to the phytosociological table in Oberdorfer (1993, pp. 405–409). A species was (arbitrarily) given the score 4 for an alliance if it was present in 80% of the relevés of at least one association of that alliance. It was given the score 3 if it reached a frequency of 50–79% in one association, the score 2 if it reached 20–49%, and the score 1 if it reached 1–19%.

The proportion of species belonging to a certain vegetation type was calculated for each plot as the weighted average of the 'degrees of belonging' to that vegetation type of all species occurring in the plot. Braun-Blanquet values of species in the plot were used as weights, replacing '+' by 1, '1' by 2, '2' by 3, etc.

Table 1. Vegetation types used in the qualitative assessment. Numbers in parantheses indicate which formations (according to Korneck & Sukopp 1988) were included in each combination. Alliances (italics) were defined according to Oberdorfer (1993)

Uncommon vegetation types	Common vegetation types
Mires (10)	Pioneer and ruderal vegetation (5, 6, 8, 9, 12)
Dry meadows and heaths (17, 18, 19)	Forest (21, 22, 23, 24)
Wet meadows (15)	Nitrophilous herbs (7, 20)
Molinion	Reeds and tall sedge fens (13)
Juncion	Intermediate fertilized meadows and pastures (16)
Calthion	*Filipendulion*

4.3. Results

Biomass of Phragmites and of other species

Total aboveground biomass in the 72 plots harvested ranged from 200 to 1000 g m^{-2}. The aboveground biomass of *Phragmites australis* (ABP) ranged from 0 to 650 g m^{-2}, and represented up to 83% of total biomass (Fig. 2). Both the biomass of *Phragmites* and its contribution to total biomass were positively correlated with total aboveground biomass (Spearman rank correlation r_S = 0.65 and 0.52, respectively). However, ABP was not correlated to the biomass of all other species (r_S = 0.08). The correlation between the biomass of all other species and total aboveground biomass was stronger than the correlation between ABP and total aboveground biomass (r_S = 0.76 versus 0.65). The correlation between total biomass and the proportion of *Phragmites* was significant not only for the whole data set, but also for each of the three alliances (r_S = 0.52–0.59).

Correlations between aboveground biomass, species richness and the 'mire species index' are given in Table 2. If all plots were considered, species number was negatively related to total aboveground biomass and to the biomass of other species (Fig. 3a), but not to ABP nor to the proportion of *Phragmites* (Fig. 3b). The 'mire species index', on the other hand, was negatively correlated with total biomass and with both fractions (*Phragmites* and other species).

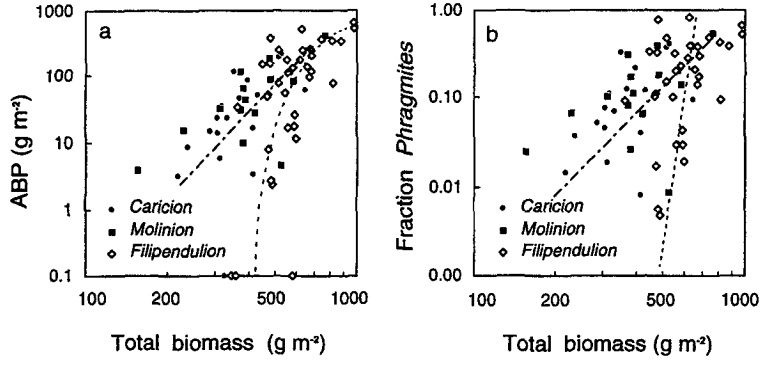

Fig. 2. Relation between total aboveground biomass and (a) aboveground biomass of *Phragmites australis* or (b) the biomass fraction of *Phragmites* in 72 plots in fen meadows. Dashed and dotted lines were drawn manually to visualize the different relations suggested by the data for the *Filipendulion* and for the two other alliances. Note the logarithmic scale of the axes.

Table 2. Spearman rank correlation coefficients between aboveground biomass (g m^{-2}) and two indices of conservation value, calculated for 72 4-m^2 plots (all plots) and separately for each alliance. S.N = Species number in plots; Mire s.i. = 'Mire species index' = proportion of mire species in the vegetation; Fraction *Phragmites* = ABP / total aboveground biomass.

	All plots		*Caricion*		*Molinion*		*Filipendulion*	
	S.N	Mire s.i.	S.N	Mire s.i.	S.N	Mire s.i.	S.N	Mire s.i.
Total aboveground biomass	-0.29	-0.77	(0.44)[1]	-0.59	-	-	-	-0.47
Biomass of other species	-0.30	-0.62	0.63	-0.70	-0.58	-	-	-
Biomass of *Phragmites* (ABP)	-	-0.59	-	-	-	-	-0.53	-
Fraction *Phragmites*	-	-0.49	-	-	-	-	-0.49	-

[1] p = 0.053

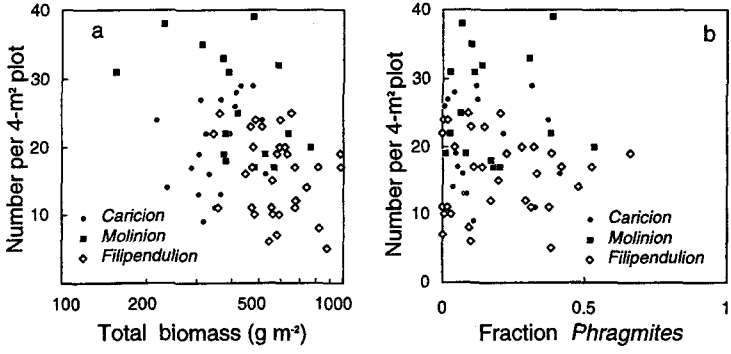

Fig. 3. Species richness of 4-m^2 plots as a function of (a) total aboveground biomass in July and (b) the contribution of *Phragmites australis* to aboveground biomass (fraction *Phragmites*)

As in the more extensive survey (Chapter 3), the three alliances differed from each other: the species number was correlated with the biomass of *Phragmites* in the *Filipendulion*, but with the biomass of other species in the *Caricion* (positively) and in the *Molinion* (negatively). The 'mire species index' was correlated with total biomass in the *Caricion* and in the *Filipendulion*, but not in the *Molinion*; it was not related to ABP in any one of the three alliances.

Quantitative relation between ABP and species composition

The relation between the abundance of *Phragmites australis* (ABP) and species composition, as determined with CCA, was significant ($p < 0.05$) for all sites except G2. Between 6.1% and 27.4% of the variance in species composition were explained by ABP (Fig. 4a). The first axis of CA explained between 12.8% and 33.5% of the variance in species composition. Eigenvalues of CCA and CA were similar for seven of eleven sites. Apparently, an ABP gradient often corresponds to a major gradient in species composition, but not always: at four sites, large differences between results of CCA and those of CA suggested a poor relation between ABP and the main vegetation gradient. If relevés from all sites were analysed together, ABP was hardly related to the species composition (Fig. 4b): only 3.4% of the variance in the whole data set were explained by ABP, compared to 8.2% explained by the first axis of a CA. The explained variance was only slightly higher if the three alliances were considered separately: the explained variance was 4–6% with CCA, which represented 35–40% of the variance explained by CA.

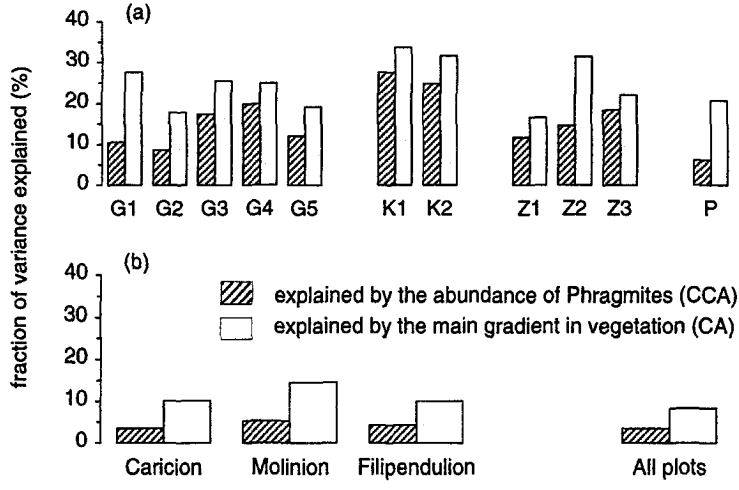

Fig. 4. Fraction of variance in the species composition of 4-m^2 plots explained by the abundance of *Phragmites australis* (a) in each of the study sites and (b) for all sites together, determined with canonical correspondence analysis (CCA). The fraction of variance explained by the main vegetation gradient, determined with correspondence analysis (CA), is also shown for comparison.

Qualitative relation between ABP and species composition

The relative abundance of species belonging to the different vegetation types clearly changed along the ABP gradient. The proportion of species belonging to four vegetation types indicating nutrient-rich or shady conditions increased significantly (Fig. 5). Conversely, the proportion of species belonging to four vegetation types indicating nutrient-poor conditions decreased along the gradient. The mean values for these proportions as well as their change along the ABP gradient differed among the three alliances (Table 3). All *Caricion* plots had a high proportion of mire species, but the proportion of species from nutrient-rich, shady sites was higher in plots with high ABP. *Molinion* plots had the highest proportion of species that also grow in dry meadows; the proportion of forest species and of *Filipendulion* species increased along the ABP gradient. *Filipendulion* plots had a high proportion of species from nutrient-rich, shady sites. With increasing ABP the proportion of nitrophilous herbs increased and the proportion of species from oligotrophic grasslands decreased.

Table 3. Average proportion of species belonging to different vegetation types in the vegetation of 241 4-m^2 plots (mean), and Spearman rank correlation coefficients (r_S) between these proprtions and aboveground biomass of *Phragmites australis* (g m^{-2}) and these indices. Calculations were made separately for plots of each alliance. Only significant correlations ($p < 0.05$) are indicated. 'Grassland of high conservation interest' included the vegetation types 'dry meadows', 'mires', *Molinion, Calthion* and *Juncion*.

	Caricion		*Molinion*		*Filipendulion*	
Species group	mean	r_S	mean	r_S	mean	r_S
(a) Formations						
Pioneer vegetation	3.1		4.1	-0.41	4.9	
Nitrophilous herbs	3.9	0.23	7.7		13.9	0.33
Forest	15.9	0.30	20.5	0.35	23.2	
Fertilized meadows	2.7		7.6		8.5	
Dry meadows	7.8		12.2	-0.42	2.8	-0.47
Wet meadows	24.0		27.7		28.6	
Mires	30.6		12.8		3.2	-0.43
Reeds and tall sedges	11.5		6.5		14.1	
(b) Alliances						
Molinion	7.8	-0.24	8.1		6.1	-0.28
Calthion	7.0		8.1		9.5	
Juncion	5.7		7.0		4.7	-0.31
Filipendulion	3.5	0.28	4.5	0.40	8.3	
c) Combined index for grassland of high conservation interest						
	58.9	(-0.22)[1]	48.3	-0.33	26.3	-0.42

[1] $p = 0.058$

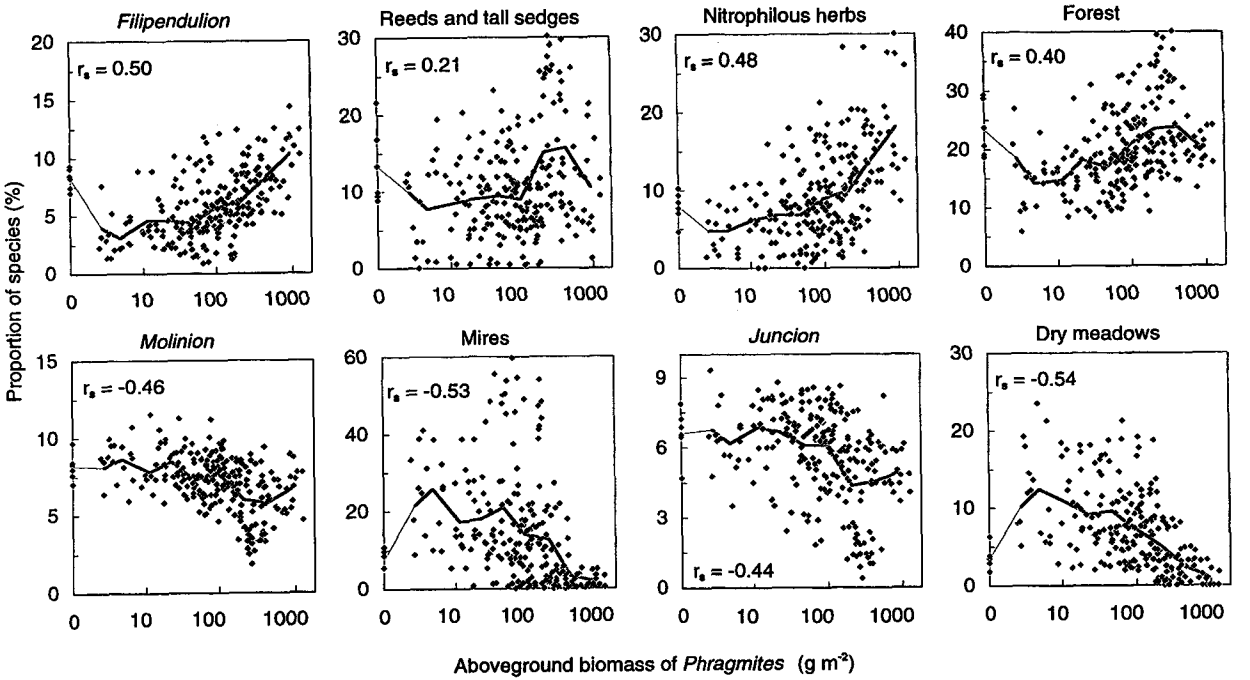

Fig. 5. Proportion of species belonging to eight vegetation types (formations or alliances) in relation to the aboveground biomass of *Phragmites australis* (ABP). Heavy lines indicate mean values, calculated after grouping plots in ten classes of ABP. Rank correlations are indicated in the graphs. Only vegetation types for which the correlation was significant are represented.

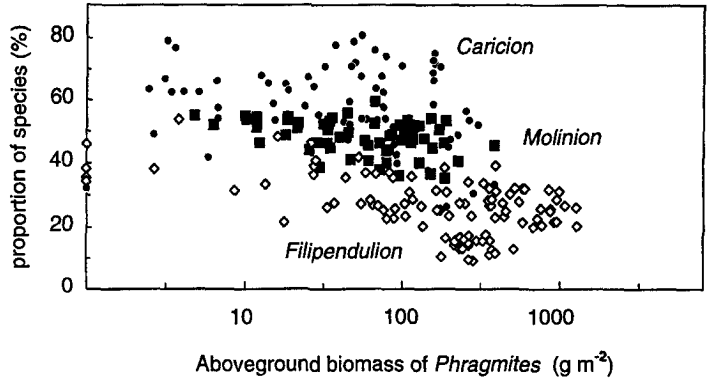

Fig. 6. Relation between the aboveground biomass of *Phragmites australis* and a combined index of conservation value representing the proportion of species belonging to the vegetation types 'dry meadows', 'mires', *Molinion*, *Juncion* and *Calthion*. All these vegetation types are unfertilized or slightly fertilized, species-rich grasslands, and have become rare in the Swiss Plateau.

A combined index, consisting in the sum of indices for grassland types of high 'conservation interest' ('dry meadows', 'mires', *Molinion, Calthion* and *Juncion*), decreased significantly along the ABP gradient for the alliances *Molinion* and *Filipendulion*; in the alliance *Caricion* the correlation just failed to be significant, but also indicated a decreasing tendency (cf. Fig. 6).

4.5. Discussion

The species composition of the fen meadows investigated was significantly related to the abundance of *Phragmites australis* (ABP), not only in the whole data set, but also within each of the three alliances. Conversely, species richness showed no relation to ABP, except in the alliance *Filipendulion*. Thus the results of this chapter were partly at variance with those of Chapter 3. The 'contradictions' suggest that (a) the indices used for this evaluation, (b) the relation among aboveground biomass, plant height and competition in general, and (c) the relation between *Phragmites* and the other plant species in particular should be considered critically.

Indices of conservation value

Significant correlations between ABP and species composition were not only found for the alliance *Filipendulion*, but also for the alliances *Molinion* and *Caricion.* Thus, differences in species composition that could not be detected with the indices of conservation value used in Chapter 3 became apparent in the degrees of belonging of plots to various vegetation types. The vegetation types for which significant correlations with ABP were found differed among the three alliances, but in each alliance light-demanding species from nutrient-poor sites appeared to be increasingly replaced by more shade-tolerant and more nutrient-demanding species. Thus, the indices based on 'degrees of belonging' to vegetation types revealed a beginning degradation of fen meadows invaded by *Phragmites* which had not yet significantly affected species richness or the number of rare species. The method can be used as well to analyse spatial gradients, as in Graf (1996). One problem is that any index or any combination of them can be selected for an evaluation, possibly leading to quite different conclusions. Yet, this possibility is inherent to any evaluation and not particular to the indices used here. Therefore, the explicit statement and justification of choices made in defining indices of conservation value is primordial (Plachter 1992; Jessel 1996). It is also important to assess the quantitative importance of differences that are being evaluated. For example, the ecological significance of the (statistically significant) negative correlation between ABP and the combined index for uncommon vegetation types in the alliances *Molinion* and *Caricion* appears somewhat questionable when the scatter of points for these alliances is considered in Fig. 6.

One more technical problem arises if the 'degrees of belonging' are calculated at different levels of the syntaxonomical classification. In this study, some vegetation types were 'formations' after Korneck & Sukopp (1988), some types included several formations and some types were alliances, i.e. subdivisions of one formation (cf. Table 1). Alliances belonging to the same formation share far more species than different formations or groups of formations. Since degrees of belonging indicate the relative frequency of species in each vegetation type[5], degrees of belonging to alliances are in general lower than degrees of belonging to formations. The consequence of considering both formations and alliances in the present study was that the maximal values (and thus the range) of the indices strongly differed among vegetation types. For example, plots of the alliance *Molinion* seemed to contain more species of forests than species of the *Molinion* itself. This is not a serious problem as long as indices are considered separately, but it becomes critical if indices are added together: vegetation types for which the maximal values are high will mostly determine the resulting combined indices. Thus, the combined index for 'grassland of high conservation interest' (Fig. 6) reflected differences in the proportion of mire species much more than

[5] i.e. their sum over all vegetation types is 1 for each species

differences in the proportion of species of other vegetation types. It might, therefore, be preferable to use standardized indices (as was done in Chapter 3, Fig. 4d), or to give indices different weights, or to apply multivariate techniques. Again, such choices inevitably involve a certain degree of arbitrariness (cf. Plachter 1992).

Aboveground biomass, plant height and their relation to species richness

Species richness in the 72 plots sampled for biomass decreased with increasing total aboveground biomass. Thus, the relation between species richness and biomass was monotonous and not unimodal. The results of this study were nevertheless consistent with the model of an unimodal relation because the lowest values of biomass were still within the range of 'optimal values' found in wetlands by other authors. Moore & Keddy (1989), for example, found high species numbers at biomass ranging from 60 to 400 g m^{-2} and only at very low biomass (less than 25 g m^{-2}) was the species richness significantly reduced. Wheeler & Giller (1982), on the other hand, obtained a monotonous relation, and their plots with lowest biomass were comparable to those of this study.

Species richness in the 72 plots was not correlated with the aboveground biomass of *Phragmites*, which contrasted with the weak, but significant correlation found with the 241 plots in Chapter 3. The differing results were probably simply due to the smaller sample. Likewise, species richness was not correlated with the proportional contribution of *Phragmites* to total biomass. Therefore, the hypothesis that increased average plant height would lead to lower species richness (due to increased shading) was not supported. According to this hypothesis, the proportion of *Phragmites* should have been negatively correlated with species richness for a fixed value of total biomass. In our case, the proportion of *Phragmites* was positively correlated with total biomass, and therefore a negative correlation with species richness would have been expected even more.

One reason for this absence of correlation is probably that the contribution of *Phragmites* to total biomass was higher in the alliances *Molinion* and *Caricion* than in the alliance *Filipendulion* at a given level of total biomass (Fig. 2b), and that the two first alliances were, on an average, more species-rich than the latter (Chapter 3). Also, the proportion of *Phragmites* in total biomass was mostly less than 40%. An extensive survey of British fens showed that certain types of *Phragmitetum* communities, in which *Phragmites* is not too dominant, can be as species-rich as small-sedge fens (Wheeler 1988). Moreover, even if in that survey the average species richness decreased slightly when the cover of *Phragmites* exceeded 20%, high species numbers (up to 50 per 100 m^2) were still found in plots with 40–60% cover of *Phragmites* (Wheeler 1988), suggesting that relatively high abundance of *Phragmites* and high species richness are not incompatible.

Abundance of Phragmites in relation to site productivity

A positive correlation was found in Chapter 3 between ABP and the nutrient indicator value of the vegetation, suggesting that ABP was related to site productivity. This hypothesis was confirmed by the analysis of biomass data, since both ABP and the contribution of *Phragmites* to total biomass increased with increasing total aboveground biomass. This supports the assumption that nutrient enrichment contributes to the current spread of *Phragmites* (Klötzli 1986; Brülisauer 1996). However, differences among the three alliances suggest that this might be only true in *Molinion* or *Caricion* communities. In the *Filipendulion* the biomass fraction of *Phragmites* varied from 0 to 83% over a fairly small range of total biomass (Fig. 1b). It seems likely that site productivity only determined the *maximal* ABP that could be found at a site, whereas *actual* ABP could range from zero to this maximal value and was determined by the competition between *Phragmites* and the dominant species of the *Filipendulion*. The suppressive effect of tall grasses or sedges on *Phragmites* was described by Hürlimann (1951), Haslam (1971b), Mochnacka-Lavácz (1974), George (1992), and tested experimentally by Szczepańska (1977). This interpretation was also suggested by the patterns of abundance observed in the field. Very steep gradients (from 0 to 100 *Phragmites* shoots m^{-2} over a few meters) could be found within *Filipendulion* communities, but not within the two other alliances. Such steep gradients were more likely to result from competition than from changes in site conditions.

High abundance of Phragmites – a threat for the conservation value?

The results of Chapter 3 suggested that the conservation value of fen meadows was related to the abundance of *Phragmites* for plots belonging to the alliance *Filipendulion*, but not for plots belonging to the alliances *Molinion* or *Caricion*. Based on these results, five scenarios were proposed for the future change of a *Molinion* or *Caricion* meadow currently invaded by *Phragmites* (cf. 3.4). Three of these scenarios were supported by the results presented in this chapter, namely those called 'early indication', 'additional impact' and 'indirect competition'. These models all postulated that an increase in the abundance of tall herbs would follow the spread of *Phragmites* and eventually cause a decrease in the conservation value. The significant positive correlations found in this study among ABP and the proportion of *Filipendulion* species, of forest species and of nitrophilous herbs suggest that this spread is actually already happening. The model 'no relation' appeared very unlikely. The model 'direct competition' was neither supported nor rejected: direct competition by *Phragmites* and by tall herbs might act simultaneously, and they might be either related or independent from each other. Thus, the results indicate once again that both competitive effects must be investigated together, if they are to be understood.

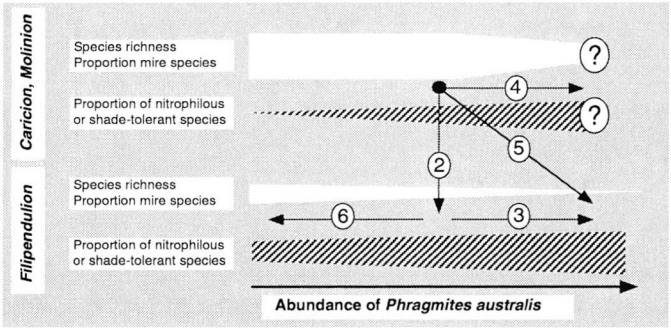

Fig. 7. Model illustrating possible future changes in conservation value of a *Molinion* or *Caricion* meadow in which the abundance of *Phragmites* has increased recently. Numbers refer to the same scenarios as in Fig. 5, Chapter 3, i.e. (2) decreasing value due to a concomitant spread of tall herbs, (3) further decrease due to a further spread of *Phragmites* after the spread of tall herbs, (4) decreasing value due to direct competition (shading) and (5) decreasing value due to indirect competition (nutrient enrichment leading to the spread of tall herbs), (6) displacement of *Phragmites* by tall herbs and slight increase in conservation value.
The thickness of the white bar in this model is equivalent to the y-axis in the model of Chapter 3.

A new model including the main results of this chapter is presented in Fig. 7. The difference to the model in Chapter 3 (Fig. 5) is that indices measuring degradation (presence of nitrophilous or shade-tolerant species) are also taken into account. With this extension, the conservation value is found to decrease along the ABP gradient not only in the alliance *Filipendulion,* but also in the alliances *Molinion* and *Caricion.* However, it remains unclear whether and how *Phragmites* might cause these changes. Of the five possible scenarios from Chapter 3, four are still possible. This ambiguity is a consequence of the correlative approach followed so far: the existence of correlations between high (or increasing) abundance of some species and low (or decreasing) abundance of others does not necessarily mean that competition of the first on the latter is responsible (cf. Bakker *et al.* 1996a). The question whether and how competition can be identified based on the field distribution of organisms is a controversial issue (Hastings 1987; Abrams 1995). More detailed analyses of competition mechanisms are generally necessary, which in turn requires an experimental approach (e.g. Szcepanska 1977; Berendse 1983; Zajicek *et al.* 1986; Aerts *et al.* 1991; Dijk & Olff 1994; Maas 1995; Conolly 1997). Thus, field experiments are needed to evaluate more directly the influence of *Phragmites* on fen species.

5. Light conditions and growth of two *Carex* species in fen meadows invaded by *Phragmites australis*

5.1. Introduction

Light is one of the main factors determining plant primary production and therefore the biomass, structure and species composition of the vegetation (Monsi & Saeki 1953). Whereas the supply of light to ecosystems only depends on their geographic, topographic and climatic situation, light availability to individual plants is additionally limited by intra- and interspecific competition. Competition for light is of minor importance at sites where plant biomass is strongly restricted either by stress (e.g. toxicity, acidity or low nutrient availability) or by disturbance (e.g. frequent mowing or periodic flooding; cf. Grime 1974). Conversely, at sites with moderate or low levels of stress and disturbance, plants can only subsist if they are able (a) to tolerate shade, (b) to compete for light, or (c) to avoid shade by exploiting spatio-temporal niches with high light availability[1]. Different morphological and physiological adaptations are related to each of these strategies (e.g. Monsi & Saeki 1953; Grime 1965; Corré 1983a; Hirose & Werger 1987, 1994; Hirose *et al.* 1988; Dijkstra 1989; Henry & Aarssen 1997). Which of the three strategies is most successful in a given vegetation type depends on the horizontal, vertical and temporal pattern of light availability within the canopy (Grime 1965; Givnish 1982; Hirose & Werger 1995; Henry & Aarssen 1997). Plant species differ not only in the degree to which they are genetically adapted to each of the strategies, but also in their ability to respond phenotypically to changes in light regime (Grime & Jarvis 1974; Givnish 1987; Olff 1992; Kühn 1997). This plasticity may also be limited by ecological constraints, such as the availability of nutrients and water (Givnish 1982; Peace & Grubb 1982; Corré 1983b).

The 'resource ratio hypothesis' of Tilman (1985, 1987a and references therein) postulated a trade-off between the ability of species to compete for light and their ability to compete for limiting soil resources. This hypothesis was based on the argument that there must be a trade-off between the fraction of biomass production allocated to leaves (determining light interception) and the fraction allocated to roots (determining the uptake of nutrients and water). Tilman (1985) suggested that the ratio of the rates at which the growth-limiting factors are supplied at a given site and the relative competitive abilities of species for these factors determine the species composition of the vegetation. The basic argument of the resource ratio hypothesis is questionable because it does not take into account morphological traits such as specific leaf area, specific root length or tissue density, which allow certain species to be strong competitors both above and below ground (Grime 1979; Ryser & Lambers 1995; Ryser *et al.* 1997). Also, species of nutrient-poor sites owe their supe-

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[1] The term 'shade avoidance' has been given a different sense by Grime (1965) and other authors, who used it to denote the strategy that is called 'competition for light' here.

riority at low nutrient availability to low nutrient losses rather than to high nutrient uptake (Berendse & Elberse 1989; Van der Werf *et al.* 1993a,b; Ryser 1996; but see Van der Werf *et al.* 1988). But even if underlying mechanisms may differ from those assumed initially, the resource ratio hypothesis proved fairly successful in explaining or predicting changes in species composition along spatial gradients or during succession (Tilman 1984, 1987b). Among others, it predicts that spatio-temporal patterns in grassland vegetation which are generally related to differences in the availability of nutrients should also be brought about by differences in light availability at constant nutrient availability. This prediction was supported by the results of growth chamber experiments comparing plant development at different resource ratios (Olff 1992) and by field experiments with artificially enhanced light supply (Eek & Zobel 1997).

This implication of the resource ratio hypothesis might be relevant for the conservation value of fen meadows invaded by common reed (*Phragmites australis*). It suggests that a shift from low-productive, species-rich small-sedge and heathgrass fen meadows (*Caricion davallianae, Molinion*) to high-productive, rather species-poor, tall-sedge and tall-herb stands (*Magnocaricion, Filipendulion*) might not only result from an increased nutrient availability (e.g. Boller-Elmer 1977, Egloff 1986; Klötzli 1986), but also from a reduced light availability. Thus, such a shift, which is undesirable from the point of view of nature conservation, might be triggered by an increasing abundance of *Phragmites australis,* since the latter causes increased shading. This might even occur independently of changes in nutrient availability. In the vegetation survey presented in Chapters 3 and 4 it was, indeed, found that the proportion of species of the alliance *Filipendulion* was positively correlated with the aboveground biomass of *Phragmites* (ABP) in the alliances *Caricion* and *Molinion.* However, this correlation might simply be caused by a correlation of ABP with site productivity, and a possible role of shading by *Phragmites* still needs to be investigated.

An other result of this vegetation survey was that plant species richness was only negatively related to ABP in the alliance *Filipendulion*, but not in the alliances *Caricion* and *Molinion.* This second result seemed at first to contradict the resource ratio hypothesis. It could be explained by the fact that both the competitive ability of species and the availability of resources vary in space as well as in time. As a result, the effective availability of resources differs for individual species within one site and this may allow the coexistence of species that would exclude each other in a homogeneous environment (see e.g. Hirose & Werger 1995 for the vertical structure, Berendse 1983 for differences in root depth, Willems *et al.* 1993 for small-scale patterns in growth form, Chesson & Huntly 1989 and Gigon 1997 for stochastic temporal fluctuations, Remmert 1991 and Wissel 1991 for cyclic changes, and Palmer 1994 for a comprehensive review of hypotheses on species coexistence).

Various investigations indicated that spatial and temporal patterns in light availability are probably essential in the competitive relationship between

Phragmites australis and other species of fen meadows (Hürlimann 1951; Buttery & Lambert 1965; Haslam 1971; Gryseels 1989a). In particular, seasonal patterns of growth might be such that the effect of shading by *Phragmites* is stronger for subordinate species of the alliance *Filipendulion* than for those of the alliances *Caricion* and *Molinion*, whereas it is stronger for the dominant species of the alliances *Caricion* and *Molinion* than for those of the alliance *Filipendulion*. The aim of this chapter is to provide empirical evidence supporting these hypotheses and to suggest mechanisms by which light interception by *Phragmites* could influence species composition in fen meadows. Data are presented on (a) short-term effects of changes in light conditions on biomass production, (b) the quantitative importance of shading by *Phragmites* and its seasonal pattern and (c) the leaf morphology and leaf turnover of *Carex acutiformis* and *Carex panicea*. *C. acutiformis* is abundant the alliance *Filipendulion* and *C. panicea*, in the alliances *Caricion* and *Molinion*. The two species were chosen as examples of species the abundance of which increases and decreases, respectively, with increasing abundance of *Phragmites*.

5.2. Materials and methods

5.2.1. Study sites

All field investigations were carried out in fen meadows (alliances *Molinion*, *Caricion davallianae* and *Filipendulion*) located within wetland reserves of the northern Swiss Plateau and mown yearly in autumn for nature conservation. Sites were mostly the same as described in Chapters 3 and 7. The shading-removal experiment took place in 1996 at site P1, the removal experiment in 1997 at sites K1, K2, G1 and Z2; leaf turnover was investigated from May to August 1997 at sites P1, G4, 'Katz' (outside the experimental plots) and additionally in a *Filipendulion* stand along the rivulet 'Chämtnerbach' (coordinates 702'800 / 244'200); Leaf morphology was investigated in July 1997 at sites K1, K3, G1, G2, G4, 'Katz', and additionally in a low-productive *Caricion davallianae* fen near site G2 (coordinates 692'400 / 247'700) .

5.2.2. Shading-removal experiment

To investigate the effect of shading on the biomass production of dominant and subordinate species, part of site P1 was divided into 18 experimental plots (4×4 m^2). Plots were grouped in four blocks, based on vegetation relevés carried out in the central part (1 m^2) of each plot. Block 1 was dominated by *Molinia coerulea* and *Carex elata*, block 2 was a transition, blocks 3 and 4 were dominated by *Schoenus ferrugineus, Carex elata, C. panicea* and *C. buxbaumii*.

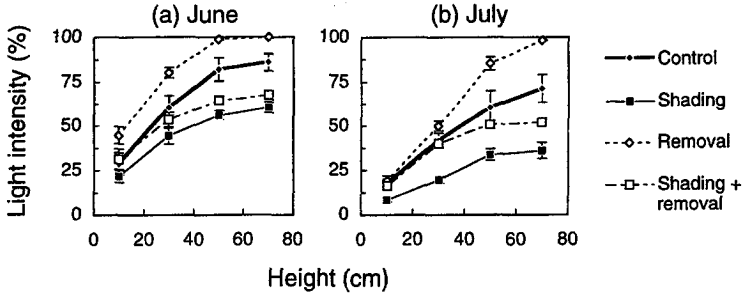

Fig. 1. Light conditions associated with the four treatment combinations in the shading-removal experiment, (a) in June (shading with 13 strips) and (b) in July (shading with 25 strips). Profiles are the mean light intensity (fraction of PAR above canopy) in the four or five plots per treatment.

The two experimental treatments were (a) removal of all *Phragmites* shoots by selective clipping every month and (b) shading with strips of green shading fabric (Hortima, ST30, 75% light interception). The four treatment combinations (cf. Fig. 1) were randomly allocated to plots within each block. Strips used for shading were about 5 cm large and 2 m long. They were attached on a wooden frame (1.5 x 1.5 x 1.2 m^3). Shading started on 5 June 1996 with 13 strips per frame. Twelve further strips were added on 10 July to simulate the growth of *Phragmites* shoots. As shown in Fig. 1, strips created a vertical pattern of light intensity that was reasonably similar to the effect of shading by *Phragmites* at this site.

On 27 August a quadrat of 50x50 cm^2 was harvested in the middle of each experimental plot. All plants within the quadrat were clipped at soil surface. Samples were sorted to species or species groups[2], and dry weight (70°C) of the fractions was determined. Effects of treatments were tested with an analysis of variance, using log-transformed data and applying the model

*Biomass = Constant + Shade + Removal + Shade*Removal + Block + Error.*

All interactions of treatments with blocks were pooled and used as error term.

5.2.3. Selective removal experiment

Nine experimental blocks were selected at sites K1 (one block), K2 (two blocks), G1 (three blocks) and Z2 (three blocks), so as to include different vegetation types (alliances *Molinion* and *Filipendulion*) and different degrees of abundance on *Phragmites*. Each block consisted of three adjacent plots (2x2 m^2 in *Molinion* blocks, 4x4 m^2 in *Filipendulion* blocks). Treatments were

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[2] Groups were: (1) *Schoenus ferrugineus + Carex davalliana*, (2) *Carex elata + C. panicea + C. buxbaumii*, and (3) all small forbs

(a) selective removal of all *Phragmites* shoots, (b) selective removal of all other species and (c) no removal (control). The removal was limited to the central part of the plots (1.5x1.5 – 2x2 m^2), but tall shoots of *Phragmites* were cut or broken at about 50 cm height on a larger area to prevent them from shading the central part.

Treatments were applied three times during the growing season 1997, i.e. late May or early June, late June or early July and mid August. At each date the culm length (from soil surface to the base of the uppermost leaf) and leaf number of all *Phragmites* shoots within a 1-m^2 quadrat in the central part of the (b) and (c) plots were measured.

Light profiles were measured for each plot at each of the three dates (after removing plants in plots with treatment a or b). Photosynthetically active radiation (PAR, wavelength 400-700 nm) was measured with a Decagon Sunfleck Ceptometer (Delta-T Devices LTD). This instrument had 40 light sensors placed at 1-cm intervals along a probe. The mean light intensity (µmol m^{-2} s^{-1}) reaching these 40 sensors was displayed at each reading. Measurements were done above the canopy, at a height of 90, 70, 50, 30 and 10 cm above soil, and again above the canopy. Ten readings were taken at each level, introducing the probe ten times into the canopy at intervals of about 10 cm. Thus, the average PAR reaching 400 points regularly distributed within an area of 40x100 cm^2 was determined. If possible, measurements were done on bright days. In June it was necessary to work under cloudy conditions. This should not have significantly influenced the results, since light profiles based on diffuse light and those based on on direct light are almost identical (Monsi & Saeki 1953). On these cloudy days reference measurements above the canopy were taken between each level within the canopy to allow for the changing light attenuation by clouds. All measurements used for data analysis were done between 11^{00} and 15^{00} (summer time). Control measurements done in the morning (7^{00}–8^{00}) yielded similar results: light attenuation by the canopy was stronger in the morning (or evening), but it was increased by a relatively constant factor at all levels and treatments.

The fraction of PAR reaching each level (light intensity in percentage of the PAR above canopy) was calculated by dividing the mean PAR at this level by the PAR above canopy. The latter was estimated as the mean of the reference measurements done before and after the measurements within the canopy.

At the last date (mid August) the *Phragmites* shoots within the central 1-m^2 quadrat of all plots with treatments (b) and (c) were not only measured, but also harvested. Furthermore, all other species were harvested within the central 60x60 cm^2 of plots with treatments (a) and (c). Dry weight (70°C) of *Phragmites* and of the other species (aboveground biomass) was determined. Differences between treatments (a) and (c) in the biomass of other species were tested with a two-way analysis of variance with factors treatments and blocks, using log-transformed data.

5.2.4. Leaf morphology of different *Carex* species

To investigate how the leaf morphology of *Carex acutiformis* and *C. panicea* responds to differences in light conditions, shoots of these species were sampled in July 1997 at ten sites differing in vegetation structure, and therefore in light attenuation by the canopy. If *C. flacca* or *C. flava* were present at a site, they were also sampled. Four groups of three shoots each were sampled arbitrarily within an area of 2x2 m^2 at each of the sites for each of the species occurring there. Damaged or badly developed shoots were discarded. Shoots were wrapped in wet paper and transported to the laboratory in plastic bags to prevent any water loss.

The two longest leaves were taken from each shoot and their length was measured. A piece of 10 cm was cut out of the middle of each leaf. Only these pieces were used in order to make measurements more comparable. The six pieces from each shoot group were pooled and their fresh weight, leaf area and dry weight (24h, 70°C) was determined. Leaf area (cm^2) was measured twice for each group with a LI-3100 area meter (Li-Cor Inc., Lincoln Nebraska, USA). Readings were considered to be correct if they differed by less than 2% and the mean of the two values was used for data analysis. Based on the measurements, the following morphological parameters were calculated: mean leaf length, mean leaf width, fresh-weight/dry-weight ratio (inversely related to tissue density), leaf-area/fresh-weight ratio (inversely related to leaf thickness) and leaf-area/dry-weight ratio (specific leaf area, SLA).

To characterize light conditions under which shoots had grown light intensity at a height of 20 cm (percentage of PAR transmitted, see above) was measured at each of the sampling sites. Linear regressions were calculated for each species and each morphological parameter to describe its dependence on light intensity. Analyses of covariance were used to test whether the regression coefficients differed among species, i.e. whether the four *Carex* species differed in plasticity.

5.2.5. Leaf turnover of two *Carex* species

To study the leaf turnover of *Carex panicea* and *Carex acutiformis* under field conditions, ten shoots of each species were tagged in mid May at each of four sites (two *Filipendulion* and two *Molinion* stands). The two youngest well-developed leaves of each plant were marked with a small incision near their tip. The length of all living leaves was measured. Leaves were considered 'living' if at least a small part of them was still green. Green or yellow (senescent) and dead parts were measured separately. Measurements were repeated in mid June, mid July and mid August. In June, a third leaf was marked with an incision (again the youngest well-developed leaf).

Based on the measurements, the number and total length of leaves formed or lost by each shoot between mid May and each sampling date could be

established[3]. Moreover, for each pair of consecutive sampling dates, the changes in length of the green parts of all leaves (providing were present at both dates) were calculated. Leaf growth was estimated as the sum of all increases. Leaf senescence was estimated as the sum of all decreases. These data underestimated the true values for growth and senescence because some leaves would grow and senesce at the same time.

Additionally, the leaf number, average leaf length, total leaf length per shoot and total green leaf length per shoot (sum of the length of green leaf parts) were calculated for each sampling date (month). Mean values per species, site and month were used for data analysis. Differences between species, among months, and the species-by-month interaction were tested with an univariate repeated measures analysis of variance. Data could be analysed without transformation. To characterize light conditions at each site, profiles of PAR transmission were established in August as described for the selective removal experiment.

To study the leaf turnover of *Carex panicea* and *Carex acutiformis* in full light, ten shoots of each species were transplanted in mid May from site 'Katz' to the garden of the Geobotanical Institute ETH. Shoots were planted in plots filled with peat-based garden compost. Pots were placed in the garden with distances of about 20 cm between them, alternating rows with each species. Shoots were watered with plenty of tap water daily if there was no rain. After two weeks, the two youngest well-developed leaves of eight plants per species were marked either with small incisions, as in the field, or with pieces of plastic foil[4]. The length of these marked leaves, the number of younger leaves and the number of older leaves were determined every ten days until early September. The leaf turnover and the length increase of the marked leaves were calculated from these measurements.

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[3] The number of leaves formed was the number of leaves younger than the marked ones. The number of leaves lost was the number of 'old' living leaves (either marked or older) present in May minus the number of remaining 'old' living leaves at each of the following dates.

[4] The relative length increase of leaves marked with incisions and of leaves marked with pieces of foil was compared with a three-way analysis of variance (factors treatment, species and leaf number), to test for a possible effect of the incisions on leaf growth. The length of leaves with an incision increased slightly less than the length of leaves with plastic foils ($p = 0.07$), but this effect did not differ between the two species ($p = 0.45$) and should, therefore, not have influenced the interspecific comparisons. There was no indication that incisions increased leaf mortality.

5.3. Results

5.3.1. Biomass production (shading-removal experiment and selective removal experiment)

Shading or removing the shoots of *Phragmites* from June to August did not affect the aboveground biomass production of the other species, i.e. the biomass of the other species at the end of August did not differ between the treated and the control plots (Table 1). In the shading-removal experiment, this was true for the total biomass production (all species) as well as for the biomass of the separate fractions (data not shown in detail here).

5.3.2. Light conditions (selective removal experiment)

Light interception by *Phragmites* was negligible until early June (Fig. 2). It strongly increased in the *Filipendulion* plots between early June and mid August, but remained relatively weak in the *Molinion* plots. These differences were due to differences in shoot density and size among dates of sampling and between alliances.

Light interception by *Phragmites* (measured in plots with treatment b, where all other species had been removed) followed the law of Beer-Lambert , i.e.

$$\frac{PAR(level\ h)}{PAR(above\ canopy)} = 10^{-k \times D \times L^2} \text{ or } log(light\ intensity\ in\ \%) = 2 - k \times D \times L^2$$

where D (density) was the number of shoots per m^2, L the mean shoot length (cm), and k a parameter depending on the level h considered, but not on the month or on the vegetation type. The product D x L^2 was approximately proportional to the leaf area index (cf. Chapter 8). The relation has been represented for a height of 50 cm in Fig. 3.

Table 1. Aboveground biomass of all species except *Phragmites* at the end of August (a) in the shading-removal experiment and (b) in the selective removal experiment. Data are mean values for treated and corresponding control plots, as well as F-ratios and the significance of treatment effects determined with a two- or three-way ANOVA based on log-transformed data.

	Aboveground biomass (g m^{-2})		Treatment effects	
	treated	control	*F*	*p*
(a) Shading-removal experiment				
shaded versus unshaded	345.3	358.9	0.03	ns
Phragmites removed versus left	349.8	354.3	0.03	ns
(b) Selective removal experiment				
in *Molinion* plots	337.5	365.0	0.66	ns
in *Filipendulion* plots	362.5	354.4	0.20	ns

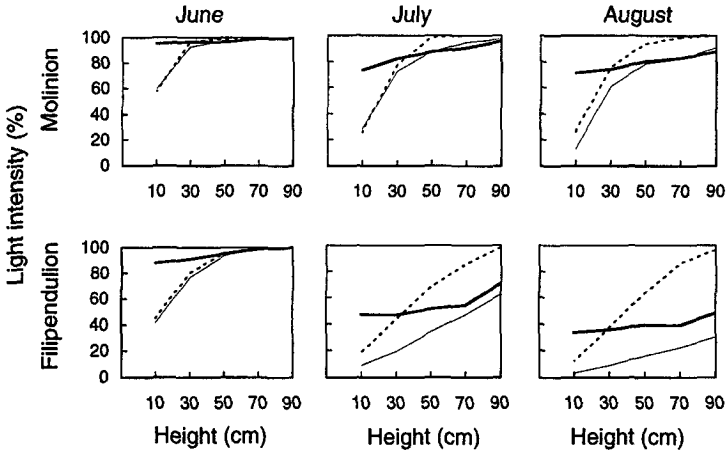


Fig. 2. Light conditions in plots of the selective removal experiment in early June, early July and mid August. Profiles are the mean light intensity (fraction of PAR above canopy) in the three *Molinion* plots and in the six *Filipendulion* plots per treatment. Dotted line: treatment a (*Phragmites* removed), heavy lines: treatment b (all other species removed) and light lines: treatment c (control, all species present).

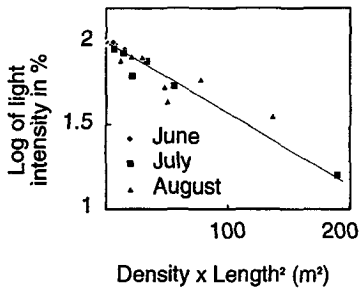


Fig. 3. Light intensity at a height of 50 cm in pure *Phragmites* stands (plots in which all other species were removed), as a function of the product of shoot density and squared culm length, based on light measurements taken in nine plots and at three dates. The value of k (see text) was 0.00456, the coefficient of determination of the regression (r^2) was 0.946.

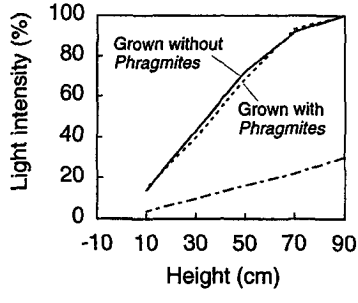


Fig. 4. Light conditions in plots of the selective removal experiment in mid August. Profiles are the mean light intensity (fraction of PAR above canopy) in five *Filipendulion* plots (without site G1). Full line: treatment a (*Phragmites* removed since June), dotted line: treatment c (control, all species present), dashed line: treatment c after removing *Phragmites*.

Light interception by the other species was stronger in *Filipendulion* than in *Molinion* plots, in spite of the very similar biomass (Fig. 2). After removing *Phragmites* from the control plots (treatment c) in August, light interception by the other species was, on an average, the same as in plots with treatment a, where *Phragmites* had been removed since June (Fig. 4). Thus, shading by *Phragmites* appeared not to influence the canopy structure of the other species in the same year.

5.3.3. Leaf morphology of four *Carex* species

All morphological traits investigated were negatively related to light intensity 20 cm above soil (Fig. 5; $p < 0.001$ for the fresh-weight/dry-weight ratio and for the leaf-area/dry-weight ratio, $p < 0.01$ for leaf width, leaf length and for the leaf-area/fresh-weight ratio). The dependence of leaf morphology on light intensity was the same for the four *Carex* species investigated: the slopes of linear regressions did not differ among species for any of the parameters (Table 2). Intercepts, however, differed among species, except for the fresh-weight/dry-weight ratio. *Carex flava* had particularly thin leaves (high SLA) and *Carex acutiformis* had particularly long and wide leaves.

Table 2. *Coefficients of linear regressions describing the dependence of leaf morphology on light intensity 20 cm above soil for four* ***Carex*** *species, and results of an analysis of covariance testing the significance of interspecific differences in regression coefficients.*

		Regression coefficients				Interspecific differences	
		C.panicea	*C.acutiformis*	*C.flacca*	*C.flava*	F-ratio	p
fresh weight / dry weight	slope	-0.01	-0.01	-0.01	-0.00	1.407	ns
	intercept	3.50	3.31	3.33	3.32	0.364	ns
Leaf area / dry weight	slope	-0.89	-0.61	-0.83	-1.00	0.370	ns
	intercept	224.05	179.97	203.28	267.72	6.69	<0.01
Leaf area / fresh weight	slope	-0.15	-0.02	-0.18	-0.24	1.301	ns
	intercept	64.37	54.47	60.43	80.96	6.73	<0.01
Leaf width	slope	-0.00	-0.01	-0.01	-0.02	1.11	ns
	intercept	3.71	7.05	3.61	5.09	30.56	<0.001
Leaf length	slope	-0.19	-0.40	-0.27	-0.21	1.00	ns
	intercept	39.8	62.02	41.30	37.66	5.89	<0.01

5.3.4. Leaf turnover of *Carex panicea* and *Carex acutiformis*

A considerable leaf turnover was found for both species between late May and late August. Leaf mortality was higher under field conditions than in full light: at the field sites almost all leaves present in May were lost until August, whereas only 30% of the leaves had been lost in full light.

In full light both *Carex* species formed and lost on an average the same number of leaves between each pair of sampling dates (Fig. 6). In the field *C. panicea* formed significantly more leaves than *C. acutiformis* during the observation period, whereas both species lost the same number of leaves (Fig. 7a,b). For both species average as well as total leaf length increased between May and August (Fig. 7c,d). The average leaf length of both species increased by the same amount, whereas total leaf length increased more for *C. panicea* than for *C. acutiformis*, due to the greater number of new leaves formed by the first species (Table 3).

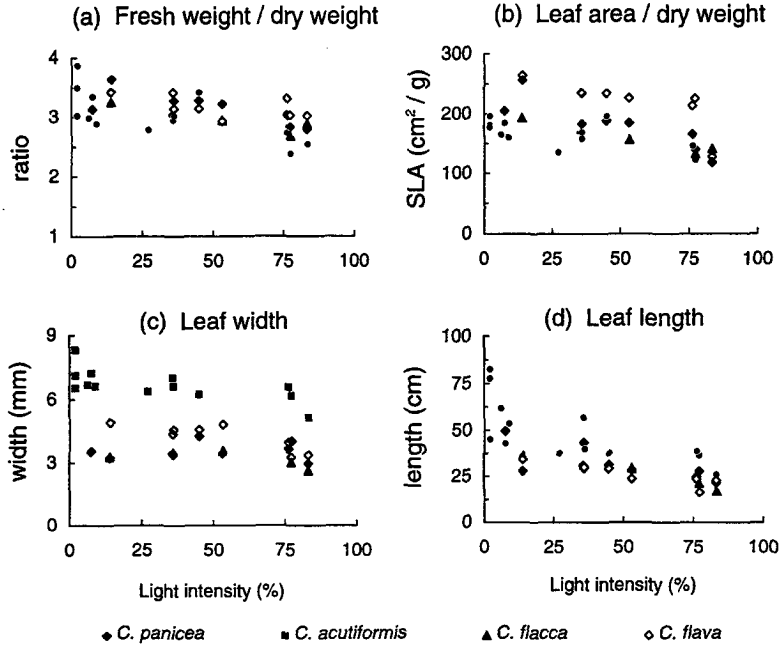
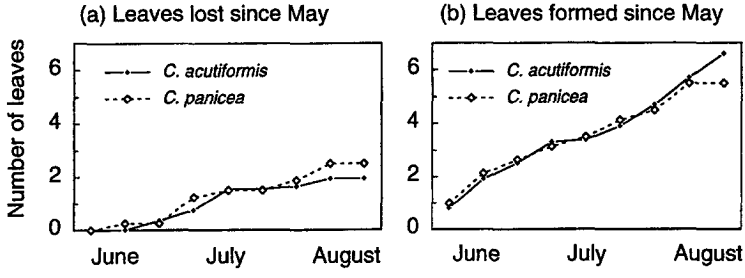


Fig. 5. Relation between the leaf morphology of four *Carex* species and light intensity 20 cm above soil (fraction of PAR above canopy).



Fig, 6. Leaf turnover and leaf length of *Carex acutiformis* (full line) and *Carex panicea* (dashed line) grown in full light. Symbols are mean values for eight shoots.

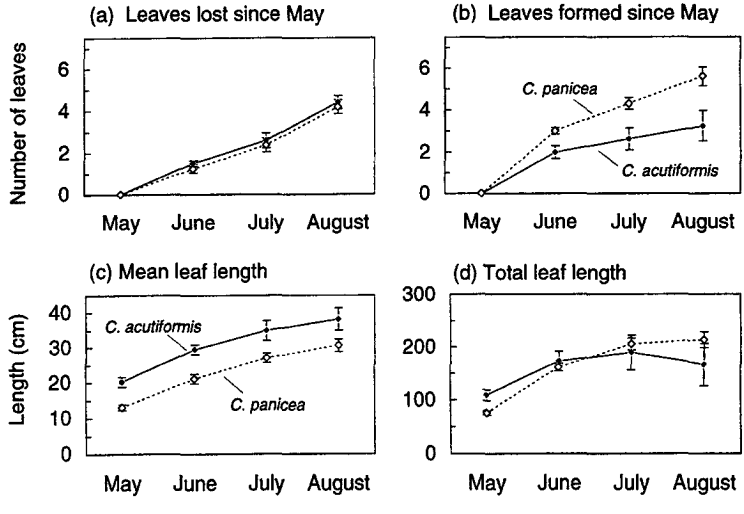


Fig. 7. Leaf turnover and changes in leaf length of *Carex acutiformis* (full line) and *Carex panicea* (dashed line) between May and August at four field sites. Symbols are mean values for 40 shoots and error bars are standard errors based on differences among sites.

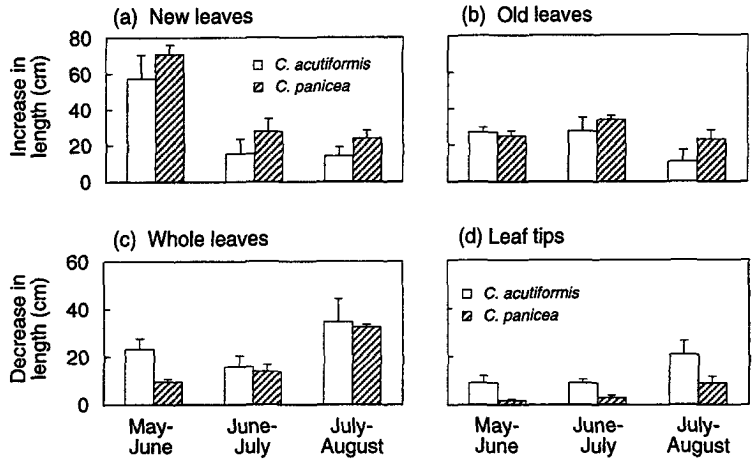


Fig. 8. Changes in the total leaf length of *Carex acutiformis* (open) and *Carex panicea* (dashed) between May and August at four field sites. (a) Length increase due to the formation of new leaves, (b) length increase due to the growth of existing leaves, (c) length decrease due to the loss of whole leaves, and (d) length decrease due to the senescence of leaf tips. All values were estimated from differences in the length of green leaf parts between each pair of consecutive sampling dates. Bars are mean values for 40 shoots and error bars are standard errors based on differences among sites.

Table 3. Leaf turnover of *C. panicea* and *C. acutiformis* in the field. Data are F-ratios and the significance of differences between species, sampling dates and of the species-by-date interaction. Significant interactions mean that species differed in their seasonal pattern of growth.

	Species		Sampling date		Species * date	
	F	*p*	*F*	*p*	*F*	*p*
New leaves	12.80	<0.05	63.29	<0.001	16.04	<0.001
Lost leaves	0.28	ns	303.14	<0.001	0.16	ns
Leaf number	16.43	<0.05	5.29	<0.05	7.95	<0.01
Length total	0.49	ns	15.30	<0.001	6.79	<0.05
Length green	0.40	ns	14.89	<0.001	9.46	<0.01
Length average	29.26	<0.05	62.37	<0.001	0.16	ns

The more detailed analysis of changes in leaf length (Fig. 8) showed that species differed in the total length of new leaves formed and in the senescence of old leaves throughout the investigation period, but not in the two other components.

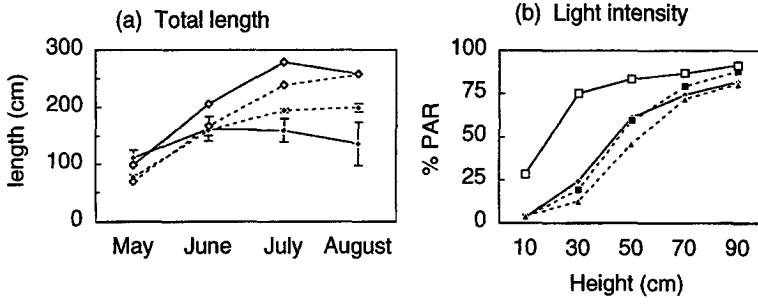


Fig. 9. (A) Total leaf length of *Carex acutiformis* (full lines) and *Carex panicea* (dashed lines) at site P1 (open symbols) and at the three other field sites (closed symbols); error bars are standard errors based on differences among sites. (B) Light conditions at the four field sites (open symbols: site P1).

The two *Carex* species differed less from each other at site P1 than at the three other sites (Fig. 9 a). At the same time, light attenuation by the canopy was lower at site P1 than at the three other sites (Fig. 9 b). Thus, the absence of interspecific differences in full light was paralleled by smaller interspecific differences at a site with more favourable light conditions.

5.4. Discussion

Absence of immediate effects of shading or removing Phragmites on biomass production and canopy structure

One implication of the resource ratio hypothesis (Tilman 1985) is that biomass production of the vegetation is always limited both by nutrients and by light availability, regardless of the supply rate of the two factors at a given site. Increased shading without concomitant increase in nutrient availability (as in the shading experiment) should result in decreased biomass production. Likewise, reduced shading without reduction in nutrient availability (e.g. after removing *Phragmites*), should enhance biomass production. These effects, however, were not observed in the experiments.

As one possible explanation, the resource ratio hypothesis is probably only valid within a certain range of resource supply, so that outside this range only one of the factors, nutrients or light, will limit biomass production. Thus, in low-productive fen meadows light is most probably not limiting because plant growth is strongly restricted by the low availability of nutrients. In this case a moderate decrease of light availability would not be expected to decrease

*biomass production. This explanation appeared plausible in the shading-*removal experiment (at least blocks 3 and 4) and in the three *Molinion* plots of the selective removal experiment. In the latter light interception by *Phragmites* and light interception by other species were almost additive, suggesting that light availability to the other species was hardly affected by the presence of *Phragmites.* If the biomass production of *Phragmites* actually added to the biomass production of the other species without reducing it, this means that total biomass production, and thus total nutrient uptake by the vegetation were increased by the presence of *Phragmites.* This seems indeed possible, even under nutrient-limited conditions, due to the difference in rooting depth between *Phragmites* and most fen species (Hürlimann 1951). According to Berendse (1983), the total yield of two competing species may be higher than the yield of each species alone (at same nutrient supply) if one of the species responds to belowground competition by forming deeper roots.

The above explanation could not account for the absence of treatment effects in the *Filipendulion* plots of the selective removal experiment. In these plots light interception by all species (treatment c) was lower than the sum of light interception by *Phragmites* (treatment b) and light interception by the other species (treatment a). This means that the light absorption and, consequently, the assimilation of the other species were reduced by *Phragmites.* The absence of treatment effects on current year's aboveground biomass indicates that the latter was mostly determined by carbohydrates (and nutrients) stored during the previous summer as well as by photosynthesis in spring, so that shading from June to August or removing *Phragmites* would only affect aboveground biomass production in the next year. Indeed, stored carbohydrates are known to be essential for the growth of dominant species in permanent grasslands (e.g. Bernard *et al.* 1988). It was originally planned to reinvestigate the shading-removal experiment in 1997. Unfortunately, this was not possible because the experimental plots were not mown in winter 1996–1997.

Temporal patterns of light conditions and strategies in competition for light

Light interception by *Phragmites* followed a strong seasonal pattern and was negligible until June. Therefore, the shading impact of *Phragmites* on subordinate species adapted to avoid shade through a fast development in spring (many small *Carex* species or small forbs, such as *Cardamine palustris*) was likely to be small. Light conditions might even be improved for early developing species if the biomass (and leaf area) of dominants in spring is reduced at sites with high ABP. However, light conditions in the lower vegetation layers deteriorated fast in *Filipendulion* vegetation. They were liable to be even worse in *Filipendulion* stands with relatively low ABP than in the experimental plots from which *Phragmites* had been removed, because the experimental plots had a lower biomass of other species than 'normal' *Filipendulion* stands (cf. Chapter 4). Therefore, except for species with a very

short annual cycle, avoiding the shade of *Phragmites* through an early development appeared to be less successful a strategy in the *Filipendulion* than in the *Molinion* or *Caricion*.

On the other hand, species adapted to compete for light by placing their leaves above those of other species are expected to be affected by a high abundance of *Phragmites*, since their attempt to reach light by growing taller must remain unsuccessful and may result in a net loss of resources. Such typical light competitors are rather found in nutrient-rich than in nutrient-poor vegetation types (e.g. Fliervoet 1984; Olff 1992).

'Light parasites' may take advantage of the presence of *Phragmites* because climbing on *Phragmites* shoots enables them to escape the shade of both *Phragmites* and lower species (Monsi & Saeki 1953). Some of them may even become so dominant that they suppress *Phragmites*, e.g. *Convolvulus sepium* (Gryseels 1989a and pers. observations). However, a strong dominance of climbers did not occur in the meadows investigated, probably because of the annual mowing, which severely affects this group of species (Gryseels 1989a).

Growth and leaf morphology of Carex *species*

As a species from nutrient-rich, but partly shady sites (tall-herb stands, swamp forests) *C. acutiformis* was likely to be more shade-tolerant than *C. panicea*. The plasticity of specific leaf area in response to shade was used as an indicator of shade tolerance in this study, because SLA tends to be more plastic in shade plants than in sun plants (Dijkstra 1989; Olff 1992). For example, comparing *Carex thunbergii* and *Carex lasiocarpa*, Onimaru & Yabe (1996) found that the first species had a more plastic specific leaf area than the latter and concluded that this was one of the reasons why *C. thunbergii* was able to subsist in dense *Phragmites* stands, but not *C. lasiocarpa*. Similar adaptations might allow *C. acutiformis* to be less sensitive to shading by *Phragmites* than *C. panicea* and therefore to be promoted by a spread of *Phragmites* in fen meadows.

Contrary to expectation, the response of leaf morphology to differing light conditions was closely similar for *C. panicea* and *C. acutiformis* (as well as for *C. flacca* and *C. flava*). Both species had the same tissue density. Their leaf thickness decreased and their leaf length increased in the same way with decreasing light intensity. This absence of interspecific differences in the plasticity of SLA differed from the results of the aforementioned studies, but it was consistent with results of Corré (1983a), who found no systematic difference between sun and shade plants in their morphological response to differing light conditions. Other ecological constraints might have been involved. It is possible that the SLA of *C. acutiformis* would have been more plastic at higher nutrient availability (Dijkstra 1989). However, SLA and its response to light conditions were often found to be hardly influenced by nutrients (Peace & Grubb 1982; Olff 1992).

Another possible reason for the absence of interspecific differences was that SLA was only measured for pieces of 10 cm taken in the central part of the leaves. Since SLA decreases from the base towards the tip of the leaf (unpublished data; Hirose *et al.* 1989), measurements on these pieces would not reflect interspecific differences in SLA of the whole leaf caused by differences in the distribution of SLA along the leaves. Since the distribution of nitrogen along the leaves of *C. acutiformis* depends on light conditions (Schieving *et al.* 1992), a similar effect on SLA could not be excluded.

The number of leaves newly formed or lost between May and August was the same for *Carex panicea* and *C. acutiformis* in full light. At the field sites both species still lost the same number of leaves, but they differed in the number of leaves newly formed. Moreover, in spite of the similar number of dying leaves the loss of leaf length was greater for *C. acutiformis* than for *C. panicea* because *C. acutiformis* lost leaf length in form of senescing leaf tips in addition to the dying of whole leaves (Fig. 9d). This senescence was probably due to a translocation of nitrogen from leaf tips to the base of the leaves, i.e. to the growing parts (Hirose *et al.* 1989; Schieving *et al.* 1992). Only few leaves of *C. panicea* presented dead tips, suggesting that the internal translocation of nitrogen was less important in this species.

Results suggest that the greater shade tolerance of *C. acutiformis* compared with *C. panicea* is not primarily due to a greater plasticity in leaf morphology (e.g. length and SLA), but rather to a faster growth in early spring, a more variable distribution of nitrogen along leaves and a greater plasticity in leaf turnover. Under unfavourable light conditions, investment in the formation of new leaves is decreased, whereas *C. panicea* still forms the same number of new leaves. A comparable difference in the seasonal pattern of growth was found between the shoot production of *C. acutiformis* and that of *C. diandra* (Verhoeven *et al.* 1988). The strategy of *C. acutiformis* differs from the typical strategy of light-competing herbs, that tend to have a higher leaf turnover in shade (Fliervoet 1984). The adaptive significance of the difference is obvious: Whereas new leaves of herbs would be inserted high in the canopy and thus experience good light conditions, new leaves of *Carex* species must grow from the base of the shoot, i.e. under particularly unfavourable light conditions (Hirose *et al.* 1989). The strategy of *C. acutiformis* allows the species both to compete efficiently for light in the first part of the summer, when light conditions are still good, and to use its assimilates more economically in the second part of the summer, compared with *C. panicea,* if light conditions are unsuitable then.

Conclusions

To summarise this discussion, the impact of shading by *Phragmites* on subordinate species in the alliances *Caricion davallianae* or *Molinion* might be reduced by the fact that this shading is only strong in late summer. Indeed, late shading will hardly affect plants with an early and short annual cycle,

which is a suitable and therefore frequent life strategy in relatively low-productive fen meadows. On the other hand, shading in late summer is expected to be detrimental to species the strategy of which is to grow until they reach good light conditions. Such a strategy is frequently found in nutrient-rich herbaceous communities, such as the *Filipendulion*, and this might explain why the abundance of *Phragmites* appeared to affect the species richness of *Filipendulion* stands more than the species richness of *Caricion* or *Molinion* stands. Finally, shading in late summer might favour those dominant species that are able to adapt their life strategy to the seasonal pattern of light availability produced by *Phragmites* and to the year-to-year fluctuations in its abundance. Such species should be able to reduce their investment in leaf production under low light conditions (years with high abundance of *Phragmites*), but continue to grow and to compete for light if light conditions are favourable (years with low abundance of *Phragmites*). This study suggested that *Carex acutiformis* has this plasticity, contrary to *Carex panicea*, and that *C. acutiformis* might, therefore, be promoted in comparison to *C. panicea* by a spread of *Phragmites*.

However, the spread of *Phragmites* is most probably also associated with changes in nutrient conditions and the effects discussed here may also, or even principally, be related to nutrient availability (Klötzli 1986; Olff 1992). Moreover, parameters such as species richness or the proportion of fen species are probably more related to the aboveground biomass of *Phragmites* in the preceding year(s) than to its biomass in the current year, because species composition, biomass production and canopy structure do not respond immediately to fluctuations in the abundance of *Phragmites*, as was shown by the removal experiments. This means that an assessment of the impact of *Phragmites* on the conservation value of fen meadows based on only one year of observation (Chapter 3) may be misleading if the abundance of *Phragmites* is particularly high or low in that year. The same applies if the abundance of *Phragmites* has been increasing recently: there may be a time lag between this increase and the response of species composition to it. This means that the results of Chapters 3 and 4 should be verified by more long-term investigations and that the effects of shading on interspecific competition suggested in this chapter should be tested under more controlled experimental conditions.

6. Stabilizing mechanisms in the restoration of wet grasslands

6.1. Introduction

The maintenance and restoration of semi-natural grasslands is one of the major tasks of nature conservation in Central Europe (Hampicke *et al.* 1991; Kuhn *et al.* 1995). In this chapter, 'maintenance' will stand for all measures aiming to maintain the current 'conservation interest' of grassland ecosystems, e.g. species richness, presence of rare species or rare communities, ecological functions, or visual amenity (Plachter 1992; Usher 1994). This frequently involves maintaining or resuming traditional management, such as mowing or extensive grazing. Additional measures may be necessary to prevent external impacts (e.g. 'buffer zones', Marti & Müller 1994) or to promote certain species (Krenová & Leps 1996). The term of 'restoration', on the other hand, will be used in a broad sense and include all measures to enhance the conservation interest of (grassland) ecosystems, ranging from modified management practices to *de novo* regeneration (Wheeler 1995) and from modest improvements to complete restitution (Bradshaw 1997a). Grassland restoration is attempted (a) on disrupted, more or less unvegetated sites, such as landslides, open-cast mines or old fields, (b) on forested sites after clearing and (c) in current grasslands whose species composition or structure is considered undesirable. Incentives for the restoration of semi-natural grasslands are either the conservation value of these ecosystems (Hutter *et al.* 1993) or economical and ecological problems related to the current state, such as agricultural overproduction, pollution of ground and surface water, soil erosion, or loss of amenity in touristic areas (Presler & Gysi 1989; Hampicke *et al.* 1991; Zimka & Stachurski 1996).

Various criteria can be applied to measure the success of restoration, depending on the objective of a project. In the restoration of machine-graded ski runs, for example, the structure of the topsoil, vegetation cover, biomass production and herbage quality, the reproductive success of native species, species diversity, or visual amenity might all be used as evaluation criteria. However, only the first two items in this list would be suitable if the restoration aim is simply to prevent erosion: a species-poor lawn may fulfill this function as well as a species-rich one. In practice, no grassland restoration project is ever 'successful' according to all potential criteria (Table 1). Different aims may even conflict with each other, e.g. 'naturalness' and 'rarity' in semi-natural grasslands, because many of their rare species depend on management for their persistence (Kollmann & Staub 1995; Dierßen & Schrautzer 1997). In some cases choices have to be made that are to a certain extent arbitrary (Wheeler 1995). More frequently, there is a 'hierarchy' of aims: some of them are easily reached, whereas others would require more time, cause higher costs, or affect other ecosystems. It is then preferable to choose the first aims.

Table 1 - Examples of restoration experiments that were successful with respect to certain criteria and failed with respect to others.

Original state	Restoration measures	Success	Failures	Author
Poor fen to be destructed by the construction of an airstrip	Transplantation of the fen to a nearby wet meadow	Typical poor fen species maintained No substantial change in soil and water chemistry Scientific interest	Disappearance of rare species, e.g. several orchids. Encroachment of ruderal species Loss of the recreational / aesthetical value.	Klötzli 1987
Heavily fertilized grassland	Removing the topsoil Raising the groundwater level Haymaking without fertilization	Low-productive, open sward during several years Increase in species richness	Same production as without topsoil removal after few years	Oomes & Van der Werf 1996
Machine-graded ski run	Transplantation of ramets of autochthonous species Creation of safe sites with geotextiles	Establishment and reproduction of the tranplants. Increase in species richness.	Low cover of vegetation Low biomass production Low visual amenity	Urbanska 1994, 1997
Former chalk grassland invaded by shrubs	Clearing shrubs	Typical chalk grassland vegetation reappeared	Presence of weeds No establishment of rare species	Kollmann & Staub 1995

Various factors may impair or even prevent successful restoration. External factors are often responsible, like unsuitable hydrological conditions (Grootjans & Van Diggelen 1995) or air pollution (Morris 1991). In addition, the ecosystem itself may 'resist' human attempts to modify it. The present contribution aims to explain this internal resistance of grassland systems to human manipulation. We will first define the main mechanisms responsible for it, then illustrate them with examples from experiments attempting to restore fen meadows. Finally, we present a simple model of management options comparing 'maintenance' and 'restoration', and discuss implications for decision-making in grassland conservation.

6.2. Stabilizing mechanisms in grassland ecosystems

Natural or semi-natural ecosystems are characterized by a number of stabilizing mechanisms that enable them to persist even if natural of anthropogenic disturbances may cause some fluctuation (Gigon 1981; Klötzli 1993). The same or similar mechanisms are also effective in sites to be restored and prevent their deliberate modification through restoration measures. Although many stabilizing mechanisms exist, most of them can be attributed to one of the following principles.

Irreversible changes

Soils of many grassland ecosystems and even more, the genetic pool of their plant and animal populations have developed over long time periods. This development mostly took place under past environmental conditions that no longer hold. If soils are destroyed, or if the genetic pool is altered, restoration to the previous state is often not possible. Irreversible damages to soils include perturbations of the soil profile, loss of topsoil (e.g. erosion or deflation), structural changes in the topsoil, and chemical or radioactive contamination (Kuntze *et al.* 1992). The genetic pool may not only be impoverished by the extinction of species, but also by the disappearance of local populations (Daily & Ehrlich 1994), and by losses of genes as a consequence of inbreeding or outbreeding (Rhymer & Simberloff 1996).

Large pools, small fluxes, cycles

Processes in ecosystems can be described as fluxes of matter, energy and information between various pools (Odum 1971). Thus, plant growth involves the transfer of nutrients from the soil solution into the plant body, and pollination involves the transfer of information from one plant to another, mediated by a pollinator. The size of the pools, among others, determines the rate of the fluxes and thereby the functioning of the ecosystem. Conversely, the relative rate of the fluxes (rate/pool size) determines the impact of associated processes on the size of the pools.

The development of ecosystems from pioneer to late-successional systems[1] generally involves an increase in the size of pools and hence a decrease in the relative rates of fluxes. Moreover, internal fluxes (cycling of nutrients among various compartments of the system) become more important than exchanges with the environment (inputs and outputs). The succession of a mire from open water to a bog illustrates this development (Koerselman & Verhoeven 1995). During the aquatic phase, nutrients for biomass production are mostly supplied by the water and leached again to the water body from the decaying litter. Therefore, fluxes are high and pools are small (Ostendorp 1988). During the fen phase, nutrients are increasingly stored in the accumulating peat, whereas the groundwater flow, i.e. the supply of new nutrients, decreases due to the increasing hydraulic resistance of the peat (Verhoeven & Schmitz 1991). In a bog, finally, large quantities of nutrients are stored in the peat body; their supply to plants comes almost completely from internal sources, since inputs are reduced to the small amount provided by rainwater (Burmeister *et al.* 1990).

A consequence from the decreasing relative rate of fluxes is that it becomes more difficult to influence the state and functioning of the ecosystem by influencing the associated processes. Thus, mowing a bog would have virtually no effect on the amount of nutrients stored in the peat body.

Interrelationship of processes (side effects, feedback)

The many components of an ecosystem are related to each other by a potentially infinite number of processes (Odum 1971). If management changes the rate of one process, the rates of other processes must be expected to change, too. The (often unintended) secondary effects of management may influence either the same or other components than the (intended) primary effects. If other components are influenced, the management has *side effects* that may be favourable or detrimental and that may or may not be relevant to restoration. If the same components are influenced, a *positive* or *negative feedback* occurs (Gigon 1981). The net effect of management on the system is then either enhanced or reduced. Again, each of these two possibilities may be either favourable or detrimental

Side effects and feedback may, of course, occur simultaneously. For example, if nitrogen fertilizer is applied in the restoration of skeletal soils (e.g. colliery spoil sites, machine-graded ski runs; Bloomfield *et al.* 1982), part of it is leached due to coarse soil structure (Bradshaw 1997b). This constitutes a negative feedback, since the amount of nitrogen remaining in the soil is reduced. As an unfavourable side effect, the groundwater quality may be deteriorated, which may, for example, affect nearby nature reserves (Klötzli 1986).

High species diversity has often been assumed to stabilize ecosystems (e.g. McNaughton 1977), and indeed, experimental evidence indicated a

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[1] Where these concepts apply (cf. Pickett & McDonnell 1989)

correlation between diversity and stability (Frank & McNaughton 1991; Tilman & Downing 1994; Tilman 1997). However, high diversity does not necessarily beget stability (May 1973; Pimm 1984; Givnish 1994). This only holds if diversity allows negative feedback mechanisms to operate. For example, if some disturbance reduces the abundance of species S, the abundance of other species may increase. These species may take over part of the functions of species S, providing they are functionally similar. Such compensation mechanisms can stabilize the functioning of ecosystems (Frost *et al.* 1995).

Hystereses

Relations between the state of ecosystems (e.g. the presence or absence or the abundance of a species) and environmental factors such as groundwater level, or human impacts are often complex (e.g. May 1977): at a given value of an environmental factor (x) a system may be in two or more different states because it shifts from state A to state B at different value(s) of x than from state B to state A. Pathways of shift, i.e. intermediate states between A and B, may also depend on the direction of change. To take a simple hypothetical example, a rare plant species S only occurring in low-productive grasslands is likely to need a lower level of productivity to colonize a site than to remain in it (Fig. 1). If a site with productivity x_1 and supporting species S is fertilized up to productivity x_2, S will most probably (though not certainly) disappear. Stopping fertilization and reducing site productivity back to level x_1 will hardly restore S. Productivity must be reduced to x_3, or additional measures may be necessary for successful restoration.

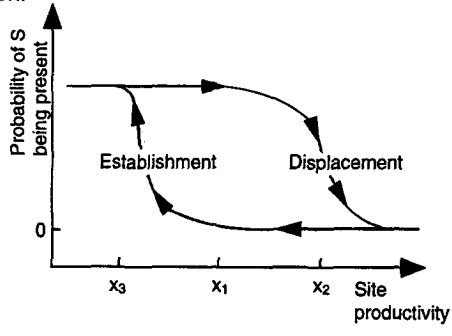


Fig. 1. Probability of occurrence of a hypothetical slow-growing species S as a function of site productivity (x). Values of x at which S can be expected to establish at a new site are generally lower than the values at which other species displace S from sites where it is established. Labels (x_1-x_3) refer to the text.

6.3. Impediments to the restoration of degraded fen meadows

Fen meadows are semi-natural grasslands on organic or mineral soils that are waterlogged in winter, but relatively dry in summer (Klötzli 1969; Wheeler 1995). They require appropriate management to prevent succession towards eutrophic tall herb communities or forest (Klötzli 1978). They are traditionally mown once a year, but not fertilized. The traditional date of mowing is July-August in certain regions (Rowell *et al.* 1985), but autumn or winter in others (Wildi & Klötzli 1978). The conservation value of fen meadows is high because

of their species richness, their importance for specialized plant and animal species, their visual amenity and as a cultural heritage (Egloff 1986a). Nevertheless, they have been reduced to a small fraction of their previous area during this century, mainly due to the increase of intensive agricultural use (Hampicke *et al.* 1991; Kuhn *et al.* 1992; Oomes & van der Werf 1996), and most of the remaining fens have been degraded by external impacts or insufficient management (Gigon & Bocherens 1985; Klötzli 1986; Marti & Müller 1993; Fojt & Harding 1995). Therefore, many attempts were made to restore former or degraded fen meadows in the last 20-30 years (reviews in Klötzli 1991; Pfadenhauer & Klötzli 1996), but these attempts had to face problems due to internal stabilizing mechanisms.

Rewetting drained peat soils: facing irreversible changes

If fen meadows on peat soil have been drained for agricultural use, the most important measure in restoration is to re-establish wet conditions during most of the year. Rewetting is essential in order to prevent further peat loss through mineralization (Pfadenhauer & Klötzli 1996). It is a way to reduce nitrogen availability (Koerselman & Verhoeven 1995) and thus biomass production (Berendse *et al.* 1994), as well as leaching of nutrients to the groundwater (Bockholt *et al.* 1992). Wet conditions are also necessary for the occurrence of specialized plant and animal species (e.g. Bölscher 1992; Beckers 1997).

Rewetting is relatively easy if the site was only moderately drained and if the regional hydrology is still favourable, e.g. if discharge of groundwater still occurs. It may then be sufficient to block or to remove the draining system (Okruszko 1995; Pfadenhauer & Klötzli 1996). After severe drainage, however, the structure of the peat is irreversibly altered: the decomposition of the organic material leads to strong compaction and loss of porosity. The density of the upper peat layer may increase by 100–300% (Schmidt 1994) and the resulting subsidence amounts to 6-25 mm per year in Europe (Presler & Gysi 1989). The proportion of mesopores in the peat, which are most important for water storage and water supply to plants, is decreased from over 50% to less than 30% (Okruszko 1995). The decomposition of peat leads from a fibrous to an amorphous, microporous structure with a low permeability and hydrophobic surfaces (Burghardt 1985; Schmidt 1994). These structural changes inhibit both the infiltration of rainwater and the capillary rise of groundwater (Hennings 1994). Once dry, such amorphous peat strongly resists rewetting (Anderson *et al.* 1995). Moreover, the process of shrinking may eventually lead to the formation of deep fissures and of grainy aggregates (Schmidt 1994); such a soil cannot retain rainwater any more and dries out soon after rainfall (Grootjans *et al.* 1985; Okruszko 1995). The extent to which these transformations take place depends on the initial type of peat and on the severity of the drainage (Schmidt 1994; Okruszko 1995). In many cases blocking the drainage system or even raising the water level in the former drainage ditches will not be sufficient to rewet the sites (Hennings 1994; Anderson *et al.* 1995; Pfadenhauer & Klötzli 1996).

Strongly degraded fens may still be rewetted by flooding with surface water (e.g. Hennings 1994). However, both the different hydrology (stagnant water instead of groundwater) and the changes in chemistry (particularly high availability of nitrogen, often associated with acidification and a deficiency in potassium; Grootjans *et al.* 1985; De Mars *et al.* 1996; Zimka & Stachurski 1996) mean that species-poor reeds will develop instead of the initial species-rich fen communities (Van Diggelen *et al.* 1994; Hellberg 1995; Pfadenhauer & Klötzli 1996).

Additionally, rewetting may have unfavourable side effects. If only polluted water is available, the input of water is associated with an input of nutrients. In addition to the direct effect (input of nitrate and phosphate) there are indirect effects of wetting with polluted water. Sulphate-rich water, for example, may increase the availability of phosphate by stimulating its release from peat soil (Koerselman *et al.* 1993). Nutrient loads can be reduced e.g. by filtering the water in a reed bed. An unfavourable side effect of this measure is that base cations are also retained by the reeds. Wetting with such base-poor water can lead to further acidification of the peat at sites where this is already a problem (Grootjans 1997).

Reducing soil fertility through management: large pools and small fluxes

Reduction of soil fertility is a second main aim in the restoration of fen meadows because their species richness and the proportion of rare species tend to decrease with increasing biomass production (Grime 1973; Wheeler & Giller 1982; Moore *et al.* 1989; Bakker & Olff 1995). The occurrence of many fen species is directly dependent on a low productivity of the vegetation, i.e. a low and open canopy (Schopp-Guth 1993; Dijk & Olff 1994). Mowing once or several times a year is the measure most frequently used to remove nutrients from the site (Van Duuren *et al.* 1981; Kapfer 1988; Bakker 1989; Marrs 1993). However, the amounts of nutrients removed with the harvested biomass are generally only a small percentage of the nutrient pool stored in the soil (Table 2). As a result, the soil nutrient pool decreases significantly only after long-term management (Pfadenhauer *et al.* 1987; Marrs 1993; Olff *et al.* 1994; Bakker & Olff 1995).

The amounts of nutrients stored in a soil and, therefore, the time needed to reduce them, depend on both the soil type and the fertilization history. Nitrogen is almost exclusively stored in the organic material and therefore contained in large amounts in all peaty soils, but scarce in humus-poor mineral soils. Potassium is almost exclusively contained in clay minerals. Phosphorus, finally, can be adsorbed to organic compounds as well as to Ca, Fe and Al minerals. A relatively fast nutrient depletion due to management may, therefore, be expected on soils with low content of organic material (N), on permeable sandy soils (N, P or K), or on purely organic soils (K or P). Soils with high clay content store such amounts of nutrients that their fertility may remain high after decades of hay making without fertilization (Marrs 1985; Klötzli 1991; Bakker & Olff 1995).

Table 2. Examples of large pools and small fluxes: total nutrient pools in soil (pool, kg ha^{-1}) and nutrient removal through management (rem, kg $ha^{-1}y^{-1}$)

Vegetation	Topsoil	Depth (cm)	Treat-ment*	Nitrogen pool	Nitrogen rem	Phosphorus pool	Phosphorus rem	Potassium pool	Potassium rem	Author
Intensive pasture	Anmoor	0-30	8	16 000	72					Sach & Schrautzer 1994
Tall herbs	Anmoor	40-20	8	1000	150					Boller-Elmer 1977 (maximum)
Litter meadow	?	40-20	8	1000	30					Boller-Elmer 1977 (maximum)
Intensive pasture	Anmoor		6+8	16 000	123					Sach & Schrautzer 1994
Intensive pasture	Anmoor	0-20	9	4 759	110	2 000	20	5 300	60	Bakker 1989
Intensive pasture	Anmoor	0-20	6+9	4 759	157	2 000	33	5 300	60	Bakker 1989
Moist meadow	Peat+loam	0-20	10			1 590	35	1 590	47	Kapfer 1987
Moist meadow	Peat+clay	0-20	10			480	9	480	6	Kapfer 1987
Moist meadow	Peat+clay	0-20	6+8+10			480	11	480	8	Kapfer 1987
Moist meadow	Peat+sand	0-20	6+8+10			1 590	56	1 590	52	Kapfer 1987
Moist pasture	Fluvisol	0-10	L	4 400	64	820	8.5			Van Oorschot *et al.* 1997
Wet heath	Loam	0-10	L	3 120	30	210	1.4			Van Oorschot *et al.* 1997
Moist pasture	Fluvisol	0-10	G	4 400	102	820	9.5			Van Oorschot *et al.* 1997
Intensive pasture	?	0-30	G	10 460	110	3 020	9	13 610	5	Perkins (1978) in Bakker (1989)
Wet heath	Loam	0-10	G	3 120	18	210	1.4			Van Oorschot *et al.* 1997

* Number = month(s) of mowing. L = litter (date of mowing not indicated). G = grazing

A decrease in yields may nevertheless be obtained in the short term, because only a small fraction (less than 6%) of the total nutrient pool is available for uptake by plant roots (Dickinson 1984; Richardson & Marshall 1986; Olff *et al.* 1994). This fraction actually controls plant growth and is more easily depleted than the total nutrient pool. The rate of mobilization of new nutrients from the 'reservoir pool' to the 'cycling pool' (Odum 1971) is then the key factor limiting biomass production. This rate may be influenced by hydrological measures, but different measures are required to reduce the availability of nitrogen than to reduce the availability of phosphorus (Koerselman & Verhoeven 1995).

Mowing several times a year removes more nutrients than mowing only once. Three or more cuts were necessary in some experiments to obtain a significant reduction in biomass production after a few years (Pfadenhauer *et al.* 1987; Briemle 1994). However, the efficiency of mowing decreases if it is done frequently, because the yield per harvest is reduced. In an experiment started in 1995, mowing twice did not, in most plots, remove more biomass than mowing once, and it removed only slightly more nitrogen (Fig. 2). Moreover, repeated mowing has various unfavourable side effects, like soil disturbance and damages to the epigeious fauna (Ost 1979; Claßen *et al.* 1993; Huemer 1996), or changes in plant species composition: species of intensive grasslands, adapted to frequent mowing, are promoted (Egloff 1986; Kapfer & Pfadenhauer 1986; Briemle & Ellenberg 1994).

Grazing removes even smaller amounts of nutrients because the uptake by animals is partly returned to the soil as dung and urine (cf. Table 2). Since these nutrients are easily available, grazing may increase the rate of nutrient cycling. Moreover, mineralization rates tend to increase in soils that are disturbed by trampling. For both reasons grazing can cause a net increase in site productivity (Bakker 1989; Marrs 1993). Additionally, grazing changes the species composition of sites due to the selective foraging of cattle and to the differing sensitivity of plant species to mechanical damage (e.g. Roze 1993).

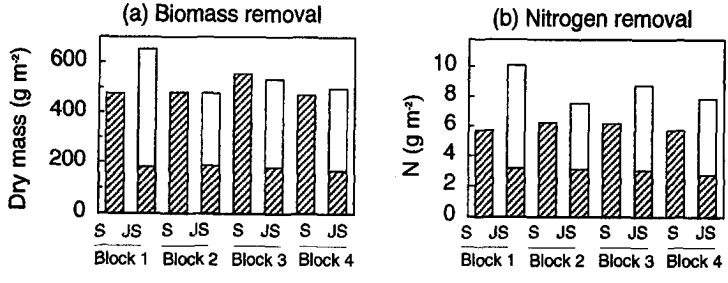


Fig. 2. Removal of (a) biomass and (b) nitrogen through mowing in eight experimental plots mown either in early September (S) or in late June and early September (JS), three years after starting the experiment (1997). In the JS bars, the white part represents the first harvest and the hatched part, the second harvest (Güsewell, unpublished).

Countering acidification by liming: the problem of negative feedback

After deep drainage of peaty soils the low groundwater table and the increased soil permeability lead to leaching of mobile cations and to increased nitrification. Both result in the acidification of the upper peat layers (Grootjans *et al.* 1986; Presler & Gysi 1989; Zimka & Stachurski 1996). This is often unwanted in nature reserves because poor (acidic) fens are generally less species-rich than rich fens (Wheeler 1993). Attempts to raise the peat pH by liming may have relatively little effect, because the humic acids in the decomposed peat have a high cationic exchange capacity (CEC). The added calcium cations are then mostly exchanged against hydrogen cations (de Graaf *et al.* 1996). Moreover, the CEC depends on the soil pH. It is twice as high at pH 5 as at pH 3 (Kuntze *et al.* 1992). As a result, the effect of further liming decreases with increasing pH.

Tospoil removal: favourable and unfavourable side effects

The most effective way to reduce nutrient availability is to remove the topsoil, since most nutrients are concentrated in the upper soil layers (Kuntze & Scheffer 1992; Marrs 1993). Topsoil removal has the positive side effect that it reduces the distance from the groundwater to the soil surface and thereby creates wetter soil conditions (Patzelt *et al.* 1997). As another side effect, the CEC may either increase (Grootjans 1997) or decrease (de Graaf *et al.* 1996), which in turn modifies the response of soil pH to liming (see above). A further side effect is that the bulk of germinable seeds are removed. For example, in a wet heath, 97% of the seeds of *Molinia* and *Agrostis* were found in the uppermost 4 cm (Putwain & Gilham 1990). Depending on the composition of the seed bank, this side effect may be favourable or not. After a long period of intensive agricultural use the favourable effect is likely to be predominant (see below); if necessary, seeds of fen species can be introduced with hay from other sites (Patzelt *et al.* 1997). Important unfavourable 'side effects' are the financial and environmental costs associated with the removal of the peat and its transport to another place. Costs are reduced or may even be completely covered if the removed peat can be used e.g. in horticulture. To minimze environmental effects, this should be done nearby the original site, whenever possible.

Increasing species richness: the problem of hystereses

The re-establishment of suitable site conditions, i.e. rewetting and reduction of biomass production (to approximately 4 t/ha), is the first condition for the restoration of species-rich fen meadows. It must have priority even if short-term effects on the species composition are negative (Pfadenhauer & Klötzli 1996). However, reaching this objective is often not sufficient to rehabilitate species richness and the occurrence of rare species. New (desired) species often fail to replace the (partly undesirable) species present at the site.

A first reason is the relatively low dispersal ability of many grassland species. Their immigration is often only possible from adjacent sites or where particular (e.g. anthropogenic) dispersal mechanisms are effective (Fischer *et al.* 1996; Strykstra *et al.* 1996). The seed bank of most fen species is transient or short-term persistent and therefore unlikely to contribute to restoration after several years of intensive agricultural use (Bernhardt & Poschlod 1993; Schopp-Guth 1993, 1997; Bakker *et al.* 1996).

Second, once seeds of potential new species have reached a (restored) fen meadow, they must germinate and seedlings must become established. However, they will often fail to do so, because germination and early establishment are two particularly sensitive phases in the life cycle of plants (Urbanska 1992). Previous investigations suggest that soil moisture, rather than light conditions, is decisive for germination success in various types of grasslands (Zajicek *et al.* 1986; Ryser 1993; Sliva *et al.* 1997). Light, however, determines the survival and growth after germination (Maas 1988; Kühn 1997). Seed establishment of fen species was investigated on a fen drained 50 years ago and used as an arable field since then (Ramseier & Gabriel, unpublished). Forty species from fens or moist meadows were sown in plots in which the topsoil (0-30 cm) had been either removed or not removed, and where weeds emerging from the seed bank were either eliminated or not eliminated by hand-weeding. Results for the four combinations of treatments are shown in Fig. 3. Successful or fairly successful establishment after the first growing season was obtained for about half of the species if the topsoil was removed, or if weeds were eliminated, or both. The combination of both treatments did not increase the number of fen species that could establish, but rates of establishment (number of individuals) were generally higher. The average size of the individuals was lower in plots without topsoil, indicating less nutrient-rich and wetter soil conditions. Apparently, weeds still present in the soil seed bank were the main factor limiting short-term establishment of the sown species, and not site conditions. For the long-term persistence of most of the species, however, nutrient-poor, wet conditions would still be essential.

A third problem is that undesirable species (alien invaders, tall herbs or reeds) may invade sites as result of soil disturbance, nutrient input or aban

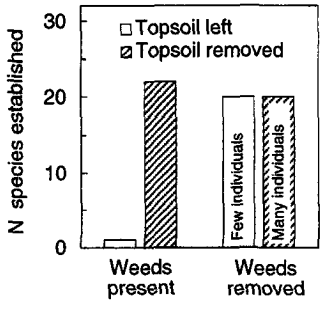


Fig. 3. Short-term success of establishment (number of species with good or fair germination success) for 40 plant species sown in plots with four different treatments on a former arable field (Ramseier & Gabriel, unpublished).

donment. Once established, these species tend to build up a strong rhizome system, which allows them to persist even if disturbance has stopped, or management been resumed. They may form species-poor stands, excluding most fen species. To restore these meadows, special measures must be taken to deplete or destroy the rhizomes of these species (Voser-Huber 1992).

6.4. Consequences for management

Adapting restoration objectives

Various internal stabilizing mechanisms may impede the successful restoration of grasslands. The action of such mechanisms needs to be evaluated before planning restoration measures. There are then basically two options: *either choosing restoration aims that are compatible with the stabilizing* mechanisms or supplementing the planned action by additional measures to overcome the stabilization.

For example, the main objective in the restoration of drained bogs is the reinstatement of peat growth by rewetting (Pfadenhauer & Klötzli 1996). This will, however, often be difficult and expensive, due to modifications in the regional hydrology, changes in peat structure (see above), and irregularities in the surface of the peat, which may prevent the regulation of the water table just at the soil surface, as required for the growth of *Sphagnum* mosses (Okruszko 1995; Sliva *et al.* 1997). Therefore, it may be ecologically and economically more efficient to 'restore' the site to a fen or to open water by deep peat extraction, simulating the former peat cuttings (Wheeler 1995). Under favourable climatic conditions, a new bog may develop, so that the original aim may still be reached. But with a maximum peat accumulation rate of 2 mm per year (Tillotson 1992), a time span of several hundred years must be allowed for such a development (Pfadenhauer & Klötzli 1996). Likewise, several options exist for the restoration of eutrophicated, species-poor fen meadows. The adequate measures depend on the local and regional hydrology, the soil type, the type of nutrient limitation, the current productivity, the current species composition, the surrounding vegetation, the type of seed bank, etc. (Table 3).

In any case, the importance of internal stabilizing mechanisms should not be overestimated. External factors (in particular the regional hydrology) are often decisive for the success or failure of restoration. Moreover, external factors may interact with internal stabilizing mechanisms. For example, the removal of nitrogen through harvest is not only small compared with pools; it is partly or totally compensated by atmospheric nitrogen inputs (Koerselman *et al.* 1990). Acidic conditions in drained peat are not only maintained by buffering processes, but even increased by acidic precipitation (Grootjans 1997). Climate change towards warmer and drier conditions might further accelerate internal eutrophication (Koerselman *et al.* 1993) or prevent peat growth in ombrotrophic mires (Anderson *et al.* 1995). Attempts to rewet a site may have little success if added water is drained away from it due to

Table 3. Management options for reducing the amount of nutrients accumulated in the soil, problems possibly associated with the measures, recommendations for their application and authors who tried or discussed the measures

Measures	Potential problems	Recommendations	Authors
Mowing 1-2 times	Effects often only after long time	Suitable if production <3.5 t/ha or if fen species are still present	Kapfer 1987; Olff et al. 1994
Frequent mowing	Species of fen meadows are excluded	Suitable if production >5 t/ha or if it is 3.5-5 t/ha and no fen species are present	Kapfer 1987; Klötzli 1991
Crop cultivation	Leaching of nitrogen	Only on mineral soils	Marrs 1985
Intensive grazing	No or low net nutrient removal	Controlled, intensive grazing during short periods on highly productive meadows	Marrs 1993
		Extensive grazing on low-productive meadows e.g. by ponies or highland cattle.	Walther 1994
N fertilisation *	N accumulation or leaching	Only if P or K is limiting and if leaching of nitrogen is low	Van der Woude *et al.* 1994; Marrs 1993
Stripping topsoil	High costs and environmental impacts	Only if really necessary and if the stripped soil can be used nearby	Ramseier & Gabriel unpubl.; Marrs 1993
	Native vegetation or seed bank removed	Only if no more fen species present	Oomes & Van der Werf 1996
		Reinoculation with hay from surrounding fens	Patzelt *et al.* 1997
Rewetting	Reduces availability of N, but not of P and K	Only if N is limiting	Koerselman & Verhoeven 1995
Ca/Fe-rich water	Reduces availability of P, but not the nitrification	Only if P is limiting	Koerselman & Verhoeven 1995; Boeye *et al.* 1996
Abandoning		If reduction of fertility too difficult	Van Diggelen *et al.* 1994
		Periodic management to remove scrubs and improve habitat value for animals	Haslam 1973c; Schütz & Ochse 1997

* to increase the removal of other nutrients through harvest

groundwater abstraction in the surrounding area (Van Diggelen *et al.* 1994). Thus, "the realization of particular conservation or restoration objectives may demand control of such 'external' factors as well as 'internal' ones. Where this is not possible, it may be necessary to redefine the objectives to be compatible with the present ecohydrological *status quo*; that is, to accept that 'restoration' *sensu stricto* cannot be achieved" (Wheeler 1995).

Maintenance rather than restoration

Stabilizing mechanisms are not necessarily a problem to nature conservation. They are often essential to the maintenance of sites, and they may assist restoration as well. In particular, hystereses may prevent an undesirable change in species composition during shorter periods of unfavourable conditions or during restoration work. For example, the transplantation of various fen types at the airport of Zurich was followed by an initial 'transplantation shock' which allowed more nutrient-demanding and ruderal species to invade sites. Several particularly sensitive species disappeared (Klötzli 1987). Nonetheless, the fen vegetation mostly retained its characteristic species combination and soil chemistry, even where these features contrasted sharply with the surrounding vegetation (e.g. an acidic *Caricetum diandrae* transplanted in a basic *Molinietum*). Also, the long life span of certain rare plant species gives managers of nature reserves time to modify the management regime if the present vegetation structure is unsuitable for the sexual reproduction of these species (*Liparis loeselii:* 20 years, Willems 1989 in Urbanska 1992; *Gentiana pneumonanthe:* 30 years, Oostermeijer *et al.* 1994).

Distinction between favourable and unfavourable stabilizing mechanisms and the assessment of external impacts are essential to an efficient allocation of financial means to nature conservation. Fig. 4 presents a simple model relating the degree of 'conservation effort' to the 'species conservation value' of fen meadows. In this model 'conservation effort' combines the absence of disrupting impacts such as deep drainage or fertilization with the presence of management, supervision, etc. 'Species conservation value' includes species diversity, the presence of rare or typical fen species, as well as low biomass production, since the latter is an important determinant of the two former (see above). The relationship between the variables is positive, but not continuous. Rather, it consists of discrete states. Each state corresponds to a certain range of efforts and of species conservation value. Within this range, the relation between the variables is positive again, but 'fuzzy' due to natural fluctuations in species richness and species composition (Klötzli 1995a,b; Pärtel & Zobel 1995).

If a species-rich fen meadow is managed irregularly, it generally loses some rare species and thus, part of its species richness, moving from A to A' in Fig. 4. Yet, it still remains basically the same vegetation type as before, due to its natural stability, and resuming original management may bring it back to

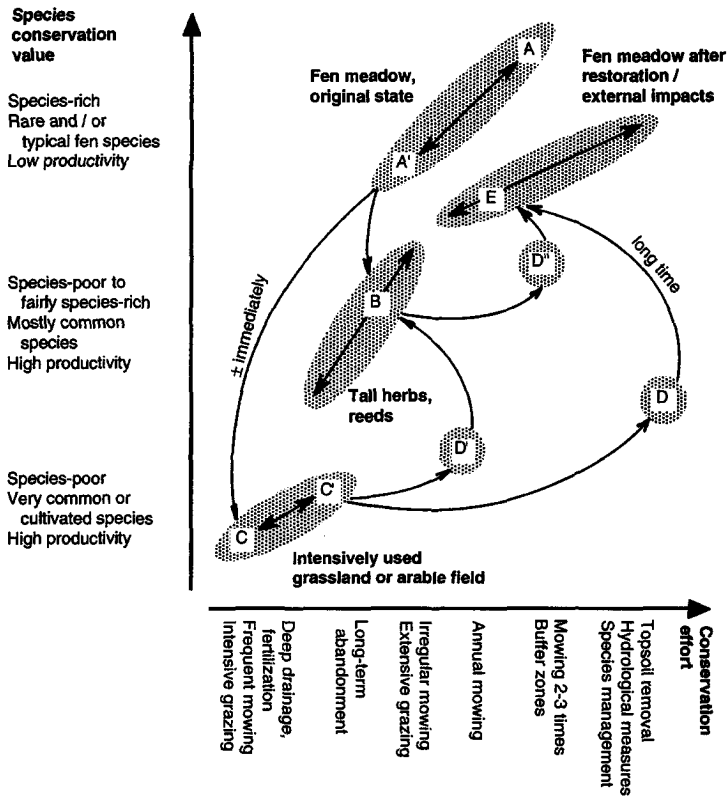


Fig. 4. Model relating the species conservation value of a fen meadow site to the conservation effort (management and restricted use). Each state covers a certain range of effort and of value. This makes reversible changes in management possible. But beyond a given threshold, sites change to a new state. Restoration to other states then requires high conservation efforts and is only partially successful: the original species conservation value can possibly not be reached any more and the 'restored' site needs more efforts than previously for its maintenance. See also text for further explanations.

the original state (from A' to A). Under favourable site conditions (e.g discharge of nutrient-poor water) this may even be the case if management is totally abandoned. Such conditions, however, have become rare in the cultural landscape of Central Europe. More frequently, internal stabilizing mechanisms are not able to prevent a strong degradation of abandoned meadows: succession towards eutrophic tall-herb or reed stands generally takes place (B). If the meadow is deeply drained and fertilized, a species-poor, intensive

grassland is obtained (C). In both cases, direct return to the original vegetation type by resuming traditional management is not possible any more. As before, the ecosystem is stabilized by internal mechanisms, but in a new state.

To restore reclaimed sites (C), a 'loop' with a period of high conservation effort (D) is may be necessary. Alternatively, the site may be 'restored' within the limits of the new stabilizing mechanisms (from C to C'), or brought to an intermediate state (B), requiring only a smaller 'loop' (D'). Thus, attempting to restore mire vegetation (A) in a heavily drained and fertilized fen (C) may require the removal of topsoil and possibly even hydrological measures, as well as the reintroduction of fen species (D). Such measures will be relatively expensive. Also, it will generally not be possible to return to exactly the original state (A). Due to irreversible changes during the disturbed period, e.g. the extinction of local populations, but also due to the changed global environmental conditions, restored meadows (state E) generally have lower conservation value and require higher conservation efforts than the original ones (Klötzli 1987; Wheeler 1995). Whereas occasional mowing in winter is sufficient to maintain small-sedge fens under undisturbed, oligotrophic conditions (Wildi & Klötzli 1978, Buttler 1992), this leads to a productive tall-herb or reed stand under the eutrophic conditions prevailing in most fen meadows today (Gryseels 1989a; Rosenthal 1992; Schütz & Ochse 1997). Alternatively, wetting the reclaimed fen (C) with available surface water and mowing it irregularly (D') will lead to a reed stand (B) that has a low botanical value, but that may present a high ornithological interest. The money saved by choosing the restoration aim B instead of E could be used to restore other fens that are still in state A' to state A, resulting in a greater overall increase of species conservation value. Moreover, species conservation is not the only aim of restoration. If new peat growth is initiated by flooding site C, the site will again act as a sink of carbon and nutrients and as a water reservoir, which are other, equally important, functions of fens in the landscape (Maltby *et al.* 1994).

6.5. Conclusions

The effort needed to restore grasslands, i.e. to increase their conservation value, is often much higher than the effort needed to preserve valuable sites, particularly if restoration is done against external impacts or against internal stabilizing mechanisms. Attempting to restore strongly degraded sites to meadows of high species conservation value is often inefficient because rather high efforts are needed to overcome these mechanisms. For financial and environmental reasons, priority should be given to the maintenance of meadows that are still valuable from the point of view of species conservation, and to the restitution of the abiotic functions where sites have been strongly degraded.

7. Mowing in summer: a measure to reduce the abundance of common reed *(Phragmites australis)* ?

7.1. Introduction

An increase in the abundance of *Phragmites australis* (Trin.) has been observed in fen meadows of Switzerland and southern Germany (Klötzli 1986; Marti & Müller 1993; Biewer *et al.* 1994). *Phragmites* is a natural component of mires and wet grasslands, and at a low or moderate abundance it has no negative impact on other plant species (Hürlimann 1951). However, dense reed stands are species-poor, and rare or endangered fen species are excluded (Wheeler & Giller 1982). Therefore, managers of wetland nature reserves seek to control the abundance of *Phragmites* before it becomes too dominant.

Various management techniques have already been used to regulate the abundance and vigour of *Phragmites.* Management aims and methods vary depending on the circumstances. If management aims at "maintaining or obtaining *Phragmites* dominance and improving its production" (Haslam 1973a), occasional mowing or burning in winter and shallow flooding in early summer are applied (Rodewald-Rudescu 1974; Granéli 1984). Lakeshore reedbelts have also been mown or burnt in an attempt to remedy the 'die-back' of *Phragmites* (Klötzli & Züst 1973b; Schröder 1987). In fishponds, ditches, salt marshes or rice fields, on the other hand, the aim of management is often to control or to eradicate *Phragmites* (Marks *et al.* 1994). Management to reduce the abundance of *Phragmites* usually combines the use of herbicides, mostly Glyphosate and Dalapon, with various physical methods (mowing, grazing, burning, ploughing, deep flooding). Good results have been obtained by spraying herbicides followed by mowing or burning (Izatt 1979; Jones & Lehman 1987), sometimes in turn followed by ploughing and flooding (Ashour Ahmed 1990). Mowing or burning followed by deep flooding (without herbicides) is sufficient to control the species, but not to eradicate it (Husák 1978, Hellings & Gallagher 1992, Demina 1979). Almost complete eradication has been achieved by shading the bottom of a pond with a black screen (Bernatovicz 1966).

The use of 'drastic' measures such as herbicides or deep flooding is mostly restricted to species-poor vegetation types strongly dominated by *Phragmites.* Such measures are ordinarily not suitable in fen meadows, in which the conservation of species richness and of rare plant and animal species is the main aim of management. If need is to control *Phragmites* at such sites, this must be attempted with techniques that cause as little damage as possible to the species to be protected. Measures that resemble the traditional management are the most likely to fulfill this condition.

Lowland fen meadows have traditionally been mown in late summer or autumn in Switzerland (Egloff 1984). Unfortunately, this management is apparently not sufficient to prevent the spread of *Phragmites* or to regenerate areas that are already invaded (e.g. Biewer *et al.* 1994; Schütz & Ochse 1997; but

see Briemle & Ellenberg 1994). It is generally assumed that mowing earlier in summer (June–July) depletes the below ground reserves of *Phragmites* and thus reduces its abundance (Egloff 1984; Bressous *et al.* 1992; Biewer *et al.* 1994). This assumption is supported by the observation that wet meadows that have been regularly mown in summer for a long time support little or no *Phragmites* (e.g. van Diggelen *et al.* 1996). But even though several management experiments in fen meadows included mowing in summer, there is little direct evidence that this treatment reduces the abundance of *Phragmites*. Either *Phragmites* was not present at the experimental sites (Wolf *et al.* 1984; Bakker & de Vries 1985; Kapfer & Pfadenhauer 1986; Oomes & Altena 1987), or it appeared to increase (Rowell *et al.* 1985; Egloff 1986), or it fluctuated without consistent trend (Finckh 1960; Andres *et al.* 1987). A significant reduction of *Phragmites* was only obtained in experiments in which mowing in summer was applied after long-term abandonment (Gryseels 1989b; Briemle & Ellenberg 1994).

Different reasons may account for this poor experimental evidence: First, experiments were often only conducted for short time periods (3-5 years). This duration was probably insufficient to deplete rhizomes if *Phragmites* had previously stored large amounts of nutrients in them. Second, mowing in summer is likely to affect the other dominant species of fen meadows as well (Egloff 1984), and reduced competition by these species might compensate a possible negative impact of mowing in summer on *Phragmites*. Third, percentage cover or shoot density was most often used in the aforementioned experiments to assess the abundance of *Phragmites*. It is known that *Phragmites* responds to mowing, as to many other stress factors, by an increased number of small shoots (Haslam 1970c). This reduction in shoot size can compensate or even overcompensate the increase in shoot density, so that higher shoot density can be associated with lower aboveground biomass (Mook & Van der Toorn 1982). However, the opposite (higher density indicating higher biomass) may also occur. Therefore, density alone is an unreliable indicator of abundance (cf. Chapter 8).

To examine in more detail the effect of mowing in summer on *Phragmites*, mowing experiments have been established in three fen meadows of the region of Zurich. The following hypotheses are tested:

- Mowing in summer increases the number of shoots, but decreases their size even more, so that the aboveground biomass decreases
- The effect of mowing in summer only becomes apparent after several years
- *Phragmites* is reduced by mowing in summer, but not more – possibly even less – than other dominant species of fen meadows.

This chapter presents preliminary results after the first three years of management. Additionally, a mid-term experiment established by Buttler (1987) was reinvestigated to compare short- and mid-term management effects. Together, the results of these experiments make it possible to draw some conclusions for the management of fen meadows invaded by *Phragmites*.

7.2. Methods

7.2.1. Field sites and experimental design

The experiments were located in the Swiss Plateau, at an altitude of 430–440 m (Fig. 1). The long-term average annual temperature of the area is 8–10° C, the average annual rainfall 900–1200 mm. Soils are calcareous dystric or humic gleysols, with an 'Anmoor' top layer (strongly decomposed and humified peat mixed with the mineral soil). Due to fluctuations in the groundwater table, soils are waterlogged in winter, but relatively dry in summer.

Mowing twice versus mowing once

One experiment ('short-term experiment') was started in 1995 in three fen meadows near Zurich, with a total of six experimental blocks (Fig. 1). Site 'Greif' (coordinates 692'550 / 247'750) was a wet meadow near lake Greifensee (Schwerzenbach), dominated by *Molinia coerulea* and various *Carex* species. *Phragmites* was moderately abundant (blocks 2 and 3). A ditch draining nutrient-rich water from the adjacent farmland ran through the site. Along this ditch the vegetation was highly productive, dominated by *Phragmites australis, Carex acutiformis, Holcus lanatus* and various tall forbs (block 1). Site 'Katz' (680'550 /254'100) lay in 'Allmend Katzensee', a flat swampy basin near Zurich. It had been drained and fertilized with sewage sludge between 1970 and 1980, but had since been managed for conservation.

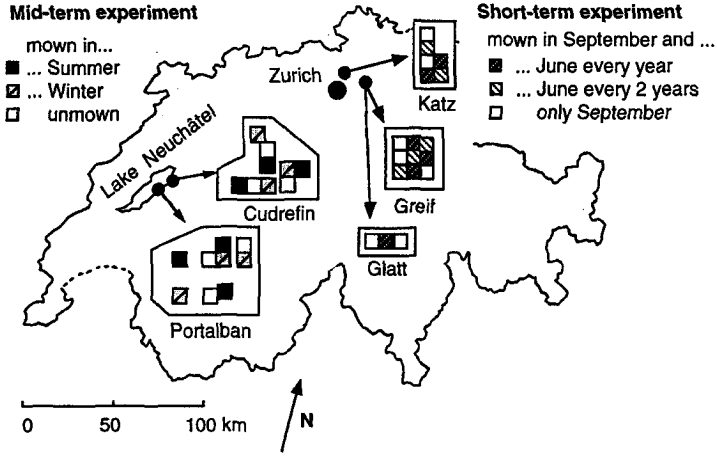


Fig. 1. The five study sites and the experimental design (spatial arrangement of plots)

The vegetation was dominated by *Molinia coerulea*, *Carex acutiformis* and various tall herbs in the drier parts (block 4), by *Carex panicea, C. elata, Juncus subnodulosus* and tall herbs in the wetter parts (block 5). *Phragmites* was fairly abundant in block 4, but sparse in block 5. Site 'Glatt' (691'950 / 247'650) was a tall-sedge fen at the outlet of river Glatt from lake Greifensee (block 6). It had not been mown during several years before 1990 and has since been dominated by *Phragmites australis, Carex acutiformis, Phalaris arundinacea and Solidago serotina.*

Each block consisted of three experimental plots (10x10 m^2). All plots were mown yearly in September, and the litter was removed soon after mowing. The three experimental treatments, randomly attributed to the plots, were: additional mowing in late June every year ('JS treatment'); additional mowing in late June every other year ('jS treatment'); no additional mowing ('S treatment'). In this paper, only the treatments 'JS' and 'S' will be considered for most analyses, because of the short duration of the experiment. For practical reasons, mowing started only in 1996 in blocks 3 and 6; these blocks were not considered in the repeated measures analyses.

Mowing in summer versus mowing in winter

The second experiment ('mid-term experiment') had been started in 1982 in two fen meadows on the south bank of Lake Neuchâtel, with a total of six experimental blocks (Fig. 1). Sites differed from those near Zurich by the absence of direct or indirect fertilization. Site 'Cudrefin' (coordinates 569'900 / 203'000) was dominated by *Carex panicea, C. hostiana* and *C. elata*, and site 'Portalban' (563'400 / 197'100), by *Schoenus nigricans* and *Molinia coerulea*, with dense patches of *Cladium mariscus*. Sites had not been mown for more than 10 years before the beginning of the experiment (Buttler 1987). Each block consisted of three plots (13 x 13 m^2 in Portalban and 11 x 11 m^2 in Cudrefin). Treatments were randomly allocated within blocks: mowing in August ('summer'), mowing in January-February ('winter'), and not mowing ('control'). Mowing was done every year from 1982 to 1987, and every other year since then (see also Chapter 9 and references therein).

7.2.2. Density and size of *Phragmites*

Short-term experiment (mowing twice versus mowing once)

The abundance of *Phragmites* was recorded every year in June and August, at the time of mowing. The number of shoots taller than 20 cm was counted in twelve 1-m^2 quadrats per experimental plot. Quadrats were arranged systematically in three groups of four quadrats (i.e. three 4-m^2 plots) to minimize trampling and edge effects. The culm length and the basal diameter of all shoots were measured in one randomly chosen quadrat of each 4-m^2 plot. The 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. The basal diame-

ter was taken in the middle of the second internode. The mean shoot density (number m^{-2}) as well as the mean culm length and the mean basal diameter were used for data analysis.

To investigate in more detail the effect of mowing on the growth of *Phragmites* and other dominant species, three 0.16-m^2 quadrats were delimited in the JS-plots of blocks 1, 3, 4, 6 and in the jS-plot of block 3 in spring 1996. The height of all plants within each quadrat was measured and the mean height was calculated for the frequent species. Measurements were done in May and in early August 1996, to compare the initial growth with the regrowth after mowing. Furthermore, the vegetation in all quadrats was harvested just before mowing, i.e. in late June and in late August, and sorted according to species. Fractions were dried 24–48 h at 70°C and weighed. The ratios r_i

$$r_i = \frac{height(biomass)\ of\ species\ i}{height(biomass)\ of\ Phragmites}$$

were used to compare the first growth and the regrowth (May versus early August for height, June versus late August for biomass).

Mid-term experiment (mowing in summer versus mowing in winter)

Each experimental plot included one permanent plot of 5 x 5 m^2 for vegetation relevés (Buttler 1992; Chapter 9). Three quadrats (1 x 1 m^2) were randomly distributed within this quadrat. The abundance of *Phragmites* was measured in 1983–86 and in 1995–97 with the same methods as for the short-term experiment, except that the culm length was not measured in 1983-86 and that the diameter was measured at a height of 30 cm (third or fourth internode).

7.2.3. Aboveground biomass of other species and nutrient analyses

Short-term experiment (mowing twice versus mowing once)

In the short-term experiment, aboveground biomass was harvested in late June and late August 1997 in the blocks 1, 3, 4 and 5. Only plots with the treatments JS or S were sampled. The living biomass of all vascular plants, except *Phragmites*, was cut off at ground level in three quadrats of 0.16 m^2 per plot. Shoots of *Phragmites* were harvested in three 1-m^2 quadrats next to the small quadrats. Care was taken in S-plots to sample new quadrats at the second date. The plant material was dried at 70°C, weighed and ground. Total N and P were extracted using a modified Kjeldahl method. Ground plant material (1g) was digested during 1h at 420°C with 15 ml H_2SO_4 98% and a copper sulphate - titane oxide catalyst (MERCK). Concentrations of N and P were determined colorimetrically on a flow injection analyser (TECATOR).

Mid-term experiment (mowing in summer versus mowing in winter)

In the mid-term experiment, the biomass of the other vascular plants was determined in 1983–86 and in 1996–97, as for the short-term experiment, except that larger quadrats were harvested (0.25 m^2 in Cudrefin, 0.50 m^2 in Portalban). Only two blocks per site were sampled in 1983–86. N, P and K concentrations in *Phragmites* were measured in 1995. The K concentration was determined by dry combustion (5h, 450°C), extraction with HCl 20% and analysis on an atomic absorption spectrometer.

7.2.4. Data analysis

Estimating the aboveground biomass of Phragmites

The biomass of *Phragmites* in the permanent quadrats was estimated non-destructively as far as possible. In June and August 1996, respectively, 20–40 shoots were harvested in each experimental plot of the short-term experiment. Likewise, 10 shoots were harvested in each plot of the mid-term experiment in July 1996. Shoots were taken from outside the permanent quadrats, unless plots would be mown just afterwards (in the short-term experiment). Each shoot was measured (length and diameter), dried for 24–48 h at 70°C and weighed. The relationship between shoot length and shoot dry weight was used to estimate the biomass of *Phragmites* in the permanent quadrats in 1996. Regression coefficients and the regression fit are given in Table 1 for the short-term experiment. Fig. 2 shows the strong linear relationship between the two log-transformed variables. It also illustrates that different coefficients had to be used for certain blocks (Fig. 2a), and that plots with different treatment had to be analysed separately in August (Fig. 2b), but not in June (Fig. 2c).

The equations from 1996 could not be used to estimate the biomass of *Phragmites* in 1995 and 1997 because the relationship between culm length and basal diameter (and consequently between culm length and shoot dry weight) differed among years. Instead, the total biomass of each quadrat was estimated from the product of mean shoot density, mean shoot length and mean shoot diameter. This product was a good predictor of biomass across treatments and months in 1996 (Fig. 2d), and regressions were therefore likely to be also valid in the other years. The equations were:

*Greif: Log (Dry weight) = 0.134+ 0.992 Log (Density*length*diameter*0.01), $r^2 = 0.97$, n = 36*

*Katz: Log (Dry weight) = –0.071+ 1.077 Log (Density*length*diameter*0.01), $r^2 = 0.97$, n = 48*

Control harvests performed in 1997 confirmed that fairly precise estimations were obtained in this way. With the mid-term experiments, coefficients were calculated separately for each site and treatment; they are not presented in detail here.

Table 1. Parameters of the regressions used to estimate the biomass of *Phragmites* in the short-term experiment: a= intercept, b = slope, r^2 = coefficient of determination, n = number of shoots

Month	Site	Block(s)	Treatment	a	b	r^2	n
June	Greif	1 + 2	S + JS	-3.40	2.07	0.92	142
June	Greif	3	S + JS	-3.81	2.15	0.89	49
June	Katz	4 + 5	S + JS	-3.62	2.19	0.91	113
August	Greif	1 + 2	JS	-3.08	1.91	0.94	20
August	Greif	1 + 2	S	-3.70	2.15	0.98	20
August	Greif	3	JS	– *	– *	– *	– *
August	Greif	3	S	-4.84	2.63	0.90	31
August	Katz	4 + 5	JS	-2.88	1.86	0.94	48
August	Katz	4 + 5	S	-3.76	2.22	0.94	49

* not determined

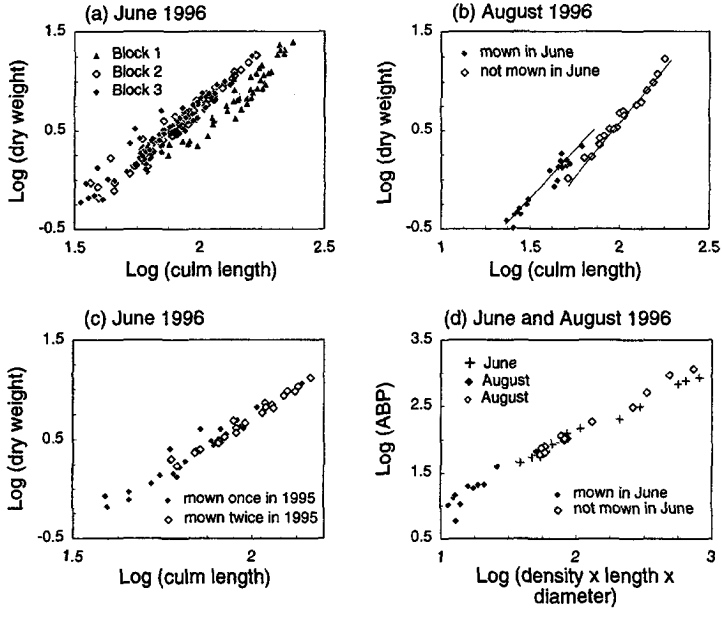


Fig. 2. Relation between shoot size and shoot dry weight of *Phragmites australis* used for the non-destructive estimation of aboveground biomass. The accuracy of regression coefficients was improved if (a) certain blocks and (b) plots mown or unmown in June (for the August estimation) were considered separately. The treatment in the previous year (mown once or twice) had no influence (c). If density, length and diameter were combined (d), the aboveground biomass (ABP in g m^{-2}) could be estimated with the same equation in all experimental plots.

Test of treatment effects

For the statistical analyses shoot densities were square-root transformed, the (estimated) biomass data, nutrient concentrations and ratios were log-transformed. The shoot length and shoot diameter could be analysed without transformation.

Shoot density and size were analysed with an univariate repeated measures analysis of variance (ANOVA). The effects of treatments, years and the 'treatment-by-year' interaction were tested against their interactions with the 'block' factor ('treatment' against 'treatment-by-block' etc.). Separate ANOVAs were computed for the short-term experiment and for each of the two sites in the mid-term experiment. For the latter, the 'year' effect was decomposed into the difference between the two periods (83–86 and 95–97) and the differences among years within each period (orthogonal comparisons, cf. Sokal & Rohlf 1995, pp. 231–236).

Three-way ANOVA was used to analyse the biomass and nutrient data of the short-term experiment. The effects of treatments, the differences among *Phragmites* and the other species and the 'treatment-by-species' interaction were tested against their interactions with the 'block' factor.

Growth data were only examined qualitatively because most species only occurred in one or two plots; moreover, biomass in August had not been recorded in plot JS4 and the height of plants had not been measured in plot jS3. These missing data precluded a complete statistical test. For similar reasons only the biomass data from 1996–97 were tested in the mid-term experiment.

Because of the relatively low number of experimental plots and the intrinsically high spatio-temporal variability of *Phragmites* (Chapter 8), the power of the statistical tests was expected to be low. Therefore, effects with type I error probabilities of 0.05–0.10 were considered to indicate tendencies, not confirmed yet, but still relevant for conservation management.

7.3. Results

Mowing twice versus mowing once

During the three years of the experiment, the density of the shoots in June increased in all plots ($p < 0.01$), whereas their size (culm length and basal diameter) decreased ($p < 0.01$; Fig. 3, Table 2). The density of shoots in August did not change consistently, but their size decreased ($p < 0.01$). Treatment effects on the density of shoots were found neither in June nor in August. Shoots were slightly shorter and thinner in JS-plots than in S-plots ($p < 0.05$). However, this difference was already present in 1995, before the first experimental mowing, and its magnitude did not change significantly over the three years ($p_{interaction} > 0.05$). Consequently, the difference appeared not to result from mowing and was most probably only due to spatial heterogeneity.

Table 2. Analysis of variance of the shoot density and shoot size of *Phragmites* in the short-term experiment. Data are the F values and the significance of the effects of mowing frequency (once versus twice), years (1995–1997) and their interaction, based on a repeated measures ANOVA. The (random) block factor was not tested.

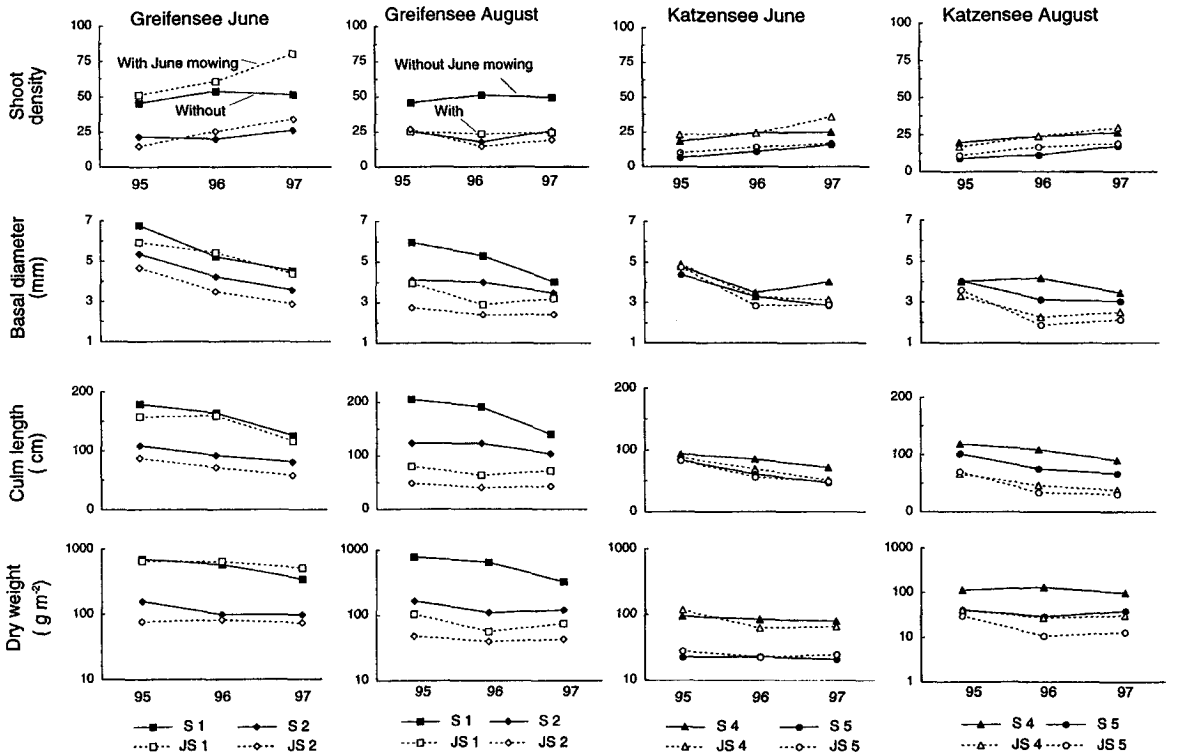
Variable	Month	Mowing		Year		Mowing * Year	
Density	June	10.63	< 0.05	237.64	< 0.01	1.51	*ns*
	Sept	0.77	ns	1.29	ns	0.17	ns
Length	June	7.70	< 0.1	22.30	< 0.01	0.01	ns
	Sept	20.39	< 0.05	17.17	< 0.01	2.62	ns
Diameter	June	5.12	ns	51.68	< 0.01	0.10	ns
	Sept	48.79	< 0.01	12.24	< 0.01	4.84	<0.1
Biomass	June	0.21	ns	7.07	< 0.05	0.29	ns
	Sept	22.95	< 0.05	12.88	< 0.01	3.32	ns

Table 3. *Analysis of variance of the biomass data from the short-term experiment.* Data are the *F* values and the significance (*P*) of the effects of mowing frequency (once versus twice), species (*Phragmites* versus other species) and their interaction, based on a mixed model three-way ANOVA.

Variable	Month	Mowing		Species		Mowing * Species	
		F	*P*	*F*	*P*	*F*	*P*
N conc.	June	0.00	ns	11.07	< 0.05	0.06	ns
	August	248.07	< 0.05	0.13	ns	0.79	ns
P conc.	June	1.39	ns	0.08	ns	0.69	ns
	August	229.52	< 0.01	15.16	< 0.05	7.40	< 0.1
N:P ratio	June	6.94	< 0.1	0.37	ns	0.12	ns
	August	28.05	< 0.05	6.00	< 0.1	7.98	< 0.1
Biomass	June	0.26	ns	7.89	< 0.1	6.92	< 0.1
	August	3859.09	< 0.01	35.54	< 0.01	2.56	ns
	Total [1)]	1.74	ns	14.37	< 0.05	2.30	ns
N removal	June	0.63	ns	7.78	< 0.1	8.90	< 0.1
	August	307.61	< 0.01	57.51	< 0.01	2.78	ns
	Total [1)]	21.58	< 0.05	22.06	< 0.05	2.72	ns
P removal	June	0.00	ns	13.96	< 0.05	12.00	< 0.05
	August	54.00	< 0.01	47.60	< 0.01	0.60	ns
	Total [1)]	198.8	< 0.01	20.29	< 0.05	33.00	< 0.05

[1)] Total biomass (total removal) = biomass (removal) in late August for the plots mown once and sum of the biomass (removal) in late June and late August for the plots mown twice.

Fig. 3 (next page). *Evolution of mean density, size and aboveground biomass of* *Phragmites* shoots in late June and late August, in eight experimental plots (Blocks 1 and 2 at site 'Greif'; blocks 4 and 5 at site 'Katz'). Open symbols: plots mown in June and September. *Closed symbols: plots only mown in September.*


Greifensee June
Greifensee August
Katzensee June
Katzensee August
Shoot density
Basal diameter (mm)
Culm length (cm)
Dry weight (g m-2)
With June mowing
Without
Without June mowing
With
95
96
97
S 1
S 2
JS 1
JS 2
S 4
S 5
JS 4
JS 5

Nutrient concentrations in June were similar for both treatments (Fig. 4, Table 3). Nitrogen concentrations were higher in *Phragmites* than in the other species ($p < 0.05$), whereas phosphorus concentrations did not differ. The N:P ratio tended to be lower in the plots mown twice a year ($p < 0.10$). Nutrient concentrations in August were markedly higher in JS-plots (mown for the second time) than in S-plots (mown for the first time; $p < 0.001$ for N; $p < 0.01$ for P). In the S-plots P (but not N) concentrations were lower in *Phragmites* than in the other species. This difference was not found in the JS-plots. The N:P ratio was again lower in mown than in unmown plots; in unmown plots it was higher for *Phragmites* than for the other species.

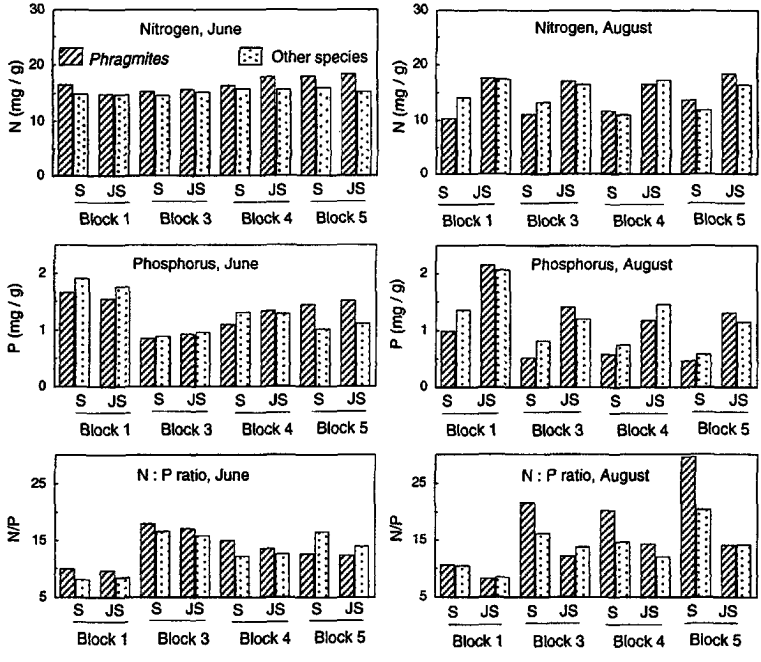


Fig. 4. Nutrient concentrations and N:P ratio in the aboveground biomass of *Phragmites australis* (hatched) and of the other species (dotted), measured in late June and late August in eight experimental plots (Blocks 1 and 3 at site Greifensee, blocks 4 and 5 at site Katzensee). S: plots only mown in September, JS: plots mown in June and September. Whereas all concentrations were similar in June, differences between treatments and between species are apparent in August.

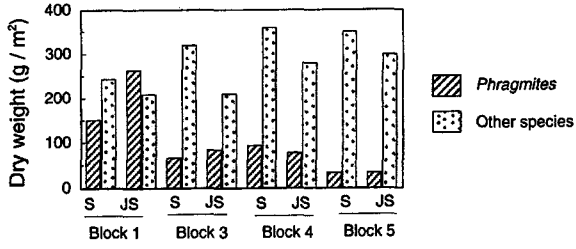


Fig. 5. Biomass of *Phragmites australis* (hatched) and of the other species (dotted), measured in late June in eight experimental plots, after two years of different management. S: plots only mown in September, JS: plots mown in June and September. The biomass of *Phragmites* did not differ among treatments, contrary to the biomass of the other species.

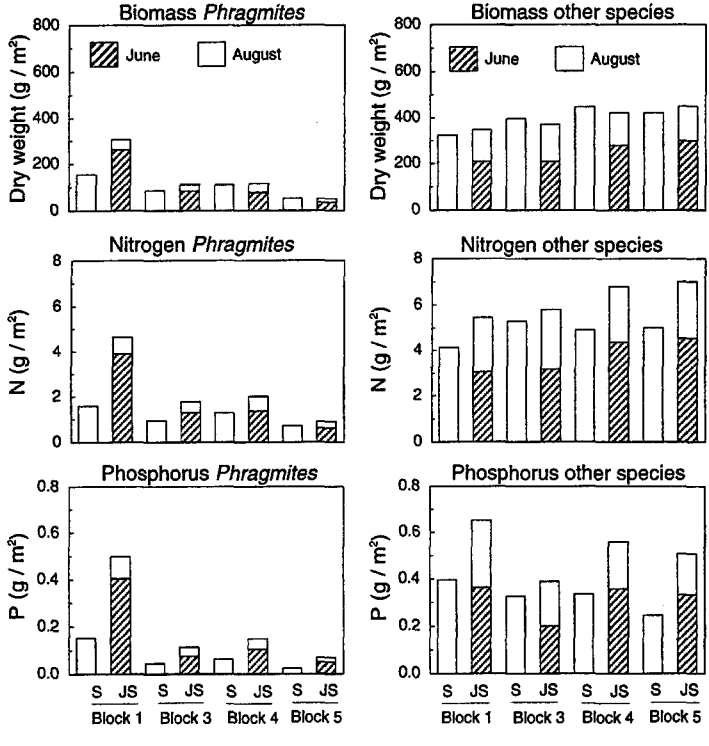


Fig. 6. Removal of biomass and of nutrients through mowing in eight experimental plots, after two years of different management. Removal in late August is given for plots only mown in September (S) and total removal (late June + late August) for plots mown twice. The hatched fraction of the JS bars indicates the contribution of the June harvest to total removal.

In June, the aboveground biomass of the other species was lower in JS-plots than in S-plots. There was no difference for *Phragmites* (Fig. 5; Table 3). The total amount of biomass removed by mowing was the same under both treatments, both for *Phragmites* (except block 1, where it was much higher in the JS-plot) and for the other species (Fig. 6, Table 3). The reason for this equalization was the poor regeneration of *Phragmites* after the first harvest: in the JS-plots the biomass in August (regrowth) was only 17–49% of the biomass in June for *Phragmites*, whereas it was 50–76% of the biomass in June for the other species. In the S-plots, the biomass increased by 26 and 27%, respectively, from June to August.

Table 4. Ratio of biomass or nutrient contents in August to biomass or nutrient contents in June. Data are mean ratios and standard errors (n = 4), calculated separately for *Phragmites* and for the other species, for plots mown in June (Treatment JS) and plots not mown in June (Treatment S).

	Mown in June (JS)		Not mown in June (S)	
	Phragmites	others	*Phragmites*	others
Biomass	0.37 ± 0.08	0.61 ± 0.06	1.27 ± 0.11	1.26 ± 0.03
N concentration	1.05 ± 0.06	1.11 ± 0.02	0.71 ± 0.03	0.82 ± 0.06
P concentration	1.17 ± 0.17	1.15 ± 0.04	0.51 ± 0.07	0.70 ± 0.08
N standing stock	0.38 ± 0.07	0.68 ± 0.08	0.91 ± 0.12	1.01 ± 0.08
P standing stock	0.40 ± 0.06	0.71 ± 0.10	0.63 ± 0.06	0.86 ± 0.11

Differences between *Phragmites* and the other species were also found when nutrient concentrations or nutrient standing stocks (g m^{-2}) in August were compared to nutrient concentrations or nutrient standing stocks in June (Table 4). In JS-plots nutrient concentrations were slightly higher in August than in June, but standing stocks were lower due to the lower biomass; this difference was twice as large for *Phragmites* than for the other species. In S-plots, nutrient concentrations and nutrient standing stocks were lower in August than in June. The difference was greater for *Phragmites* than for the other species, and greater for phosphorus than for nitrogen.

The total removal of nutrients in JS-plots exceeded the nutrient removal in S-plots, due to the differences in nutrient concentrations mentioned above. On an average, mowing twice removed 44% more nitrogen and 85% more phosphorus than mowing once ($p < 0.05$ for N and P). Differences between treatments were stronger for *Phragmites* than for the other species: mowing twice removed 90% more N from *Phragmites*, but only 30% more N from other species. It removed 181% more P from *Phragmites*, but only 64% more P from other species. Differences were particularly large in block 1, where 191% more N and 225% more P were removed from *Phragmites* in JS-plots than in S-plots, compared with 32% and 64% for the other species. In blocks 3–5 only

57% more N, but still 166% more P were removed from *Phragmites* in JS-plots than in S-plots (29% and 64% for the other species). This treatment-by-species interaction was significant ($p < 0.05$) only for P because of the strong difference between block 1 and blocks 3–5 for N.

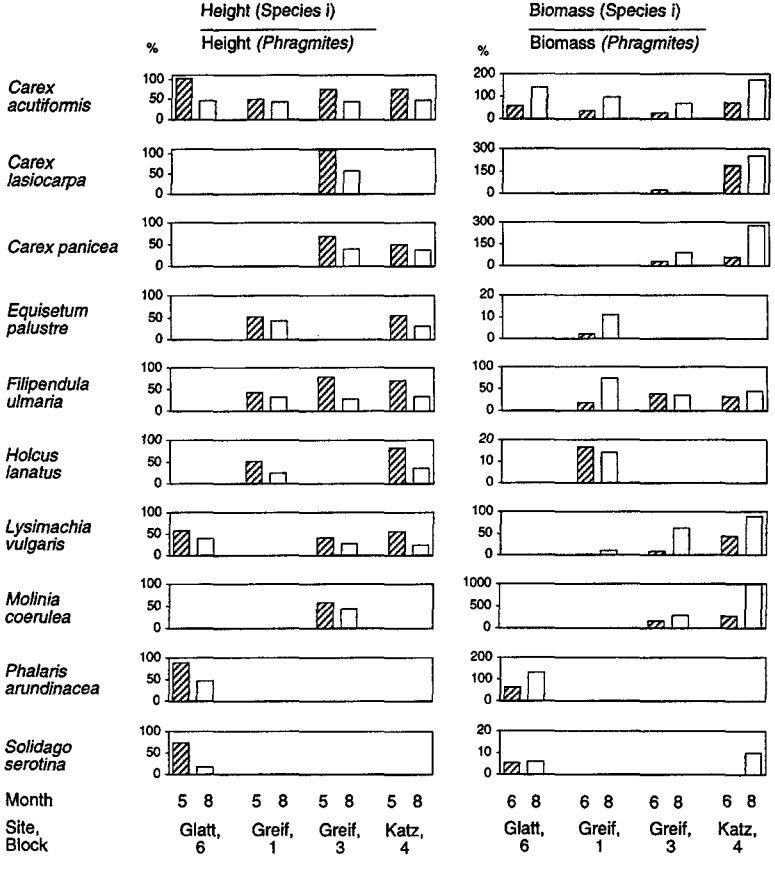


Fig. 7. Size of the ten most frequent species compared to the size of *Phragmites* in four experimental plots, in the first growth (months 5 or 6) and in the regrowth after mowing (month 8). For each species bars indicate the ratio of its mean size (a: height, b: biomass) to the mean size of *Phragmites* in the same plot. Bars are missing for plots in which the species was not present at both sampling dates in at least one quadrat .

The comparison between the first growth (one month after emergence) and the regrowth (one month after mowing) indicated that differences in height between *Phragmites* and the other species were greater in the regrowth, i.e. the other species were relatively shorter (Fig. 7a). This suggests that *Phragmites* dominated the other species faster after mowing than after the emergence in spring. However, the biomass of the other species relative to that of *Phragmites* was higher at the second harvest than at the first harvest (Fig. 7b), suggesting that mowing affected the relation between height and biomass differently for *Phragmites* and for the other species.

Mowing in summer versus mowing in winter

Strong year-to-year changes in shoot density and size occurred in the mid-term experiment (Fig. 8). During the first four years (1983–86), mowing in summer raised shoot density and reduced shoot diameter compared with mowing in winter or not mowing. The treatment-by-time interactions for that period were significant ($p < 0.01$), except for shoot density in Portalban (Table 5).

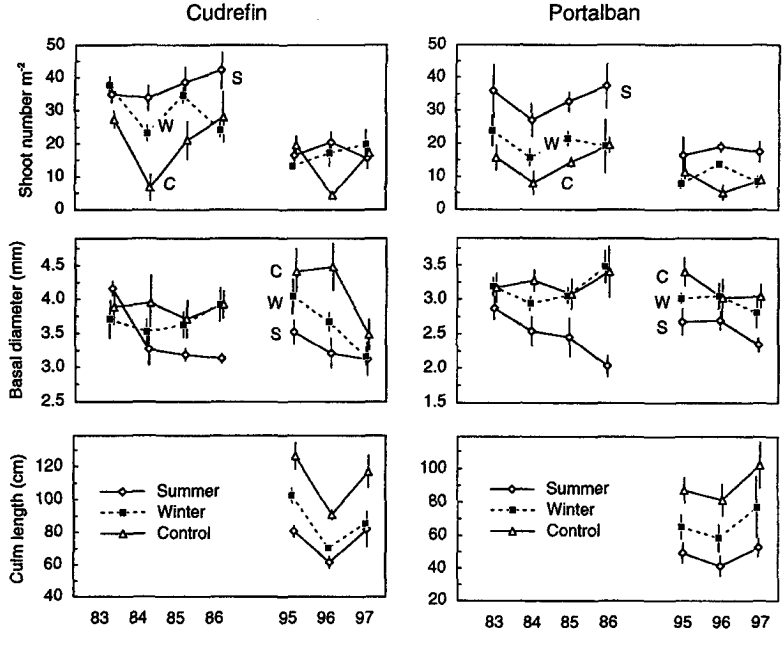


Fig. 8. Evolution of mean density, diameter and length of *Phragmites* shoots in the mid-term experiment. Points are means of the three blocks per site; bars are standard errors calculated with values corrected for differences among blocks. Culm length was not measured in 1983-86.

Table 5. Repeated measures analysis of variance of shoot density, diameter and length of *Phragmites australis* in the mid-term experiment. Indicated are the *F* values and the significance of the effects of treatments, time (years), and their interaction.

Factor	df	Diameter		Density	
		Cudrefin	Portalban	Cudrefin	Portalban
Treatment	2	5.90 < 0.1	10.90 < 0.05	17.83 < 0.05	62.05 < 0.01
Year	6	7.10 < 0.01	6.01 < 0.01	21.66 < 0.01	17.55 < 0.01
Periods	1	0.01 ns	3.08 ns	93.22 < 0.01	85.34 < 0.01
83–86	5	3.56 < 0.05	3.75 < 0.05	10.36 < 0.01	6.62 < 0.01
95–97	2	16.04 < 0.01	10.98 < 0.01	2.80 ns	0.04 ns
Treatment * Year	12	5.82 < 0.01	6.48 < 0.01	10.68 < 0.01	2.05 < 0.1
Periods	2	5.97 < 0.01	4.67 < 0.05	9.24 < 0.01	2.41 ns
83–86	10	6.64 < 0.01	10.06 < 0.01	8.45 < 0.01	0.93 ns
95–97	4	4.35 < 0.01	2.01 ns	14.72 < 0.01	3.55 < 0.05

Table 6. *F* values and significance of treatment effects on nutrient concentrations of *Phragmites australis*, on the biomass of *Phragmites* and other species, and on the contribution of *Phragmites* to total aboveground biomass (fraction) in the mid-term experiment.

Factor	Nutrient concentrations			Biomass		Fraction
	N	P	K	*Phragmites*	Others	*Phragmites*
Cudrefin	1.22 ns	0.88 ns	0.13 ns	16.63 < 0.05	0.31 ns	19.17 < 0.01
Portalban	4.43 < 0.1	2.10 ns	1.04 ns	2.42 ns	3.42 ns	4.14 ns

However, this trend was only partly confirmed in the second period (1995–97). Between the first and the second period, the shoot density decreased in all plots, regardless of the treatment ($p < 0.01$). It remained highest in the summer-mown plots of Portalban ($p < 0.05$), but this was no longer the case in Cudrefin. Even in Portalban, the difference between summer-mown and other plots was smaller in 1995–97 than in 1983–86. Diameters were the same in both periods. A clear treatment effect on shoot length was found in the second period at both sites ($p < 0.01$), but the change since the beginning of the experi-ment could not be evaluated, since no data were available for the first period.

The biomass of *Phragmites* decreased between the first and the second period in the mown plots. It fluctuated in the control plots and no trend was apparent (Fig. 9). The biomass of the other species increased slightly. As a result, the contribution of *Phragmites* to total biomass decreased. Treatment effects on the biomass of *Phragmites* and on its contribution to total biomass were significant in Cudrefin (data from 1996–97), but not in Portalban (data

from 1997; Table 6). Even in Cudrefin, the contribution of *Phragmites* to total biomass did not differ consistently between summer-mown and winter-mown plots: it was higher in summer-mown plots in 1996, but lower in 1997.

No treatment effect was found in the nutrient concentrations of *Phragmites*, except a slightly higher N concentration in the control plots of Portalban (Table 6). Treatments effects on nutrient removal (g m^{-2}) mainly reflected differences in biomass, i.e. more nutrients were removed from *Phragmites* in the control plots in Cudrefin ($p < 0.05$), but not in Portalban.

Evaluation of the hypotheses

The first hypothesis of this study was that mowing in summer would cause an increase in shoot number which would be more than compensated by a concomitant decrease in shoot size. This hypothesis could not be confirmed. A negative relation between shoot density and shoot size was apparent in both experiments, but the variation in these traits was mostly unrelated to the treatments. This was particularly obvious in the short-term experiment, where the shoot size and the shoot density of plots mown once or twice changed almost exactly in the same way during the three years of the study. No difference was found either between short-term and mid-term treatment effects (second hypothesis) in the mid-term experiment. This question still has to be examined for the comparison between mowing twice and mowing once. Results tended to support the third hypothesis, which was that the effect of mowing on *Phragmites* would be balanced by a similar effect on the other species. For example, additional mowing in June twice did not reduce the biomass of *Phragmites* in the short-term experiment, and the reason could have been that this treatment reduced the biomass of the other species, so that the effects of more frequent mowing and of lower competition by other species compensated each other.

7.4. Discussion

The abundance of *Phragmites australis* in fen meadows is generally limited by its ability to compete with other plant species for light and nutrients (Hürlimann 1951; Haslam 1971b). This ability depends on various factors. The amount of carbohydrates and of mineral nutrients stored in the rhizomes during previous growing seasons is likely to be particularly important because these belowground reserves allow a fast growth of roots and shoots in spring (Fiala 1976). Fast growth may be essential for *Phragmites* because this species emerges and develops later than most of its competitors (Hürlimann 1951; Buttery & Lambert 1965) and must compensate this initial disadvantage by a high rate of growth and nutrient acquisition after emergence in spring. In addition, the amount of mineral nutrients supplied by rhizomes to roots and shoots determines the amount of mineral nutrients that must be taken up by the plant for biomass production during the growing season (Van der Linden

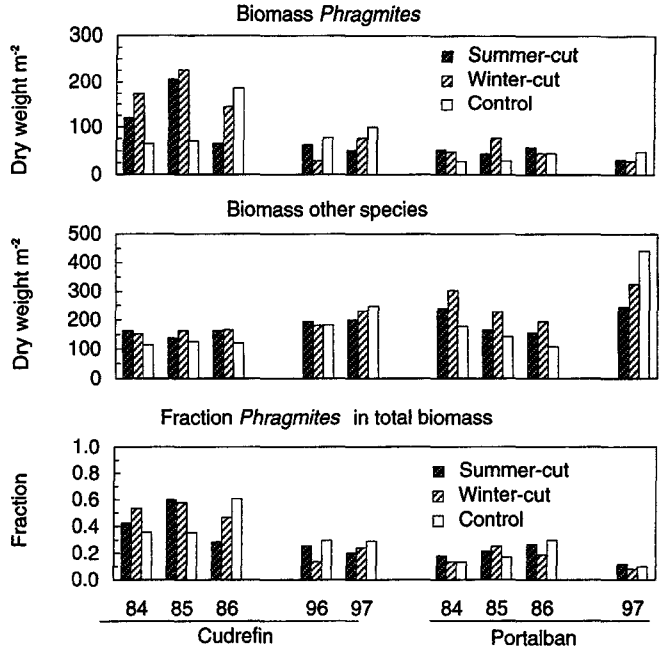


Fig. 9. Evolution of the aboveground biomass of *Phragmites* and other species, as well as of the fraction of *Phragmites* in total biomass, in the long-term experiment. Bars are means of the three blocks per site.

1980, 1986; Hocking 1989a,b). If most of the nutrients needed for annual production can be supplied by below ground parts, the plant is almost independent of current nutrient availability in soil and experiences little below ground competition from other plants.

To understand or to predict how mowing at different dates affects *Phragmites*, it is necessary to consider the importance and the seasonal patterns of (a) shoot production and assimilation, (b) storage of carbohydrates, and (c) storage of mineral nutrients. Furthermore, effects of additional site factors and the role of competing species have to be discussed.

Shoot production and assimilation. Aboveground biomass production of *Phragmites* follows a seasonal pattern that is determined by genetic, climatic and edaphic factors (Haslam 1973; Rodewald-Rudescu 1974; Hocking

1989a). In Central Europe the growing season starts in April and ends in September or October (Haslam 1973; Fiala 1976). At dry sites, shoots tend to emerge later than at flooded sites, and late frosts may further delay the development of the population (Haslam 1969, 1970a,b). Assimilation depends on many factors, such as the area, inclination and vertical distribution of leaves in the canopy (Ondok 1970, 1973; Ondok & Gloser 1978; Hirose & Werger 1995), or the nitrogen content of leaves, which varies both vertically and during the growing season (Hirose & Werger 1987, 1995; Hocking 1989b). According to Ondok & Gloser (1978), the assimilation rate of a *Phragmites* stand decreases exponentially from May to September, but their model was developed for dense stands with intense intraspecific competition and is not necessarily valid for sparse populations in fen meadows. Interspecific competition for light normally plays a role only at the beginning of the growing season in fen meadows since later *Phragmites* places its leaves above those of all other species (Hürlimann 1951; Hirose & Werger 1995).

Storage of carbohydrates. Carbohydrates are the main component of rhizomes, but only part of them, "nonstructural" carbohydrates (starch and sugars), can be translocated to shoots. Their concentration is maximal in autumn, when it reaches 40–50% of total rhizome dry weight in aquatic stands. It decreases slightly during the winter and drops to 25–35% in spring, when shoots emerge (Fiala 1976; Granéli *et al.* 1992; Guthruf *et al.* 1993). This means that typically 30–50% of the reserves are supplied to the shoots. In terrestrial stands, the amount of carbohydrates stored and translocated is lower: Guthruf *et al.* (1993) measured a maximal concentration of 30%, of which about one third was supplied to the shoots in spring. The minimum carbohydrates content is reached in June; concentrations increase again in July, reaching a maximum between late August and late September (Fiala 1976; Granéli *et al.* 1992). According to Guthruf *et al.* (1993), the maximum is reached earlier in terrestrial than in aquatic stands.

Mineral nutrients economy. The internal cycles of the different nutrients are not equally important. Only for nitrogen, phosphorus and potassium do they represent more than half of the demand of the plant. Between 50% and 80% of the maximal shoot content of these nutrients are translocated to below ground parts in late summer (Rodewald-Rudescu 1974; Dykyjová & Hradecká 1976; Granéli 1984; Hocking 1989a; Warnke-Grüttner 1990). Translocation starts between early July and late August.

These indications suggest that mowing in August (mid-term experiment) did not significantly affect the carbohydrates economy of *Phragmites*: Assimilation and translocation of carbohydrates were almost completed at that time. Conversely, nutrients had only partly been translocated to the rhizomes. Apparently, however, sufficient amounts of nutrients could be taken up to compensate losses in this experiment. This result was certainly influenced by the fact that mowing was only done every other year. Nevertheless, if the summer treat-

ment had had a significantly higher impact on *Phragmites* than the winter treatment, this should have become apparent over 14 years, even with a biennial mowing regime. The closely similar effects of mowing in August and mowing in winter in this experiment were consistent with experiments or observations of Hürlimann (1951); Morgan *et al.* 1983; Weisner & Granéli (1989); Schütz & Ochse (1997). In contrast, Rodewald-Rudescu (1974) mentions experiments where mowing reduced shoot size by 30% when done in August, but only by 13% when done in September and by 3% when done in October. Haslam (1969) stated that the effect of mowing in August was intermediate between that of mowing in July and that of mowing in winter. It is possible that flooding played a role in such cases, although flooding did not increase the effect of mowing in August in the experiment of Weisner & Granéli (1989).

Mowing in late June, on the other hand, should have strongly affected the nutrient economy of *Phragmites*. According to the above data, rhizomes were maximally depleted of carbohydrates and of mineral nutrients at the time of mowing. Indeed, more nutrients were removed by mowing in June than by mowing in September, and mowing twice (JS treatment) removed significantly more nutrients than mowing once (S treatment). Nutrient concentrations in the JS plots were as high in late August as in late June, indicating that *Phragmites* was still in full growth at the second cut. This means that most assimilates were probably used for growth and not stored in the rhizomes in August. Moreover, the regrowth after the first cut was so poor that in any case, only small amounts of carbohydrates could be stored in the rhizomes before the second cut. Therefore, an effect of mowing twice on shoot size, aboveground biomass or nutrient contents could be expected. Yet, no effect was observed.

The most obvious explanation for the absence of treatment effects was the limited duration of the experiment. In long-term management experiments, the abundance of some species did not noticeably change during up to ten years and suddenly increased or decreased after that period (Olff & Bakker 1991; Chapter 9). Whether a species' response to management is slow or fast depends on its growth form and life history (Dumortier *et al.* 1996). For several rhizomatous geophytes (the growth form of *Phragmites*), Briemle & Schreiber (1994) found a different response to mowing or burning after four years than after ten years; *Phragmites* might indeed be expected to respond slowly to management because of its longevity and its below ground stores. However, this was not the case in other management experiments, where treatments significantly reduced the abundance of *Phragmites* within one or two years. The reason for this difference has to be seen in various site factors:

Litter. Some experiments were established at unmanaged sites (Gryseels 1989b; Briemle & Ellenberg 1994), where the accumulated litter of *Phragmites* probably excluded other species (Haslam 1971b; George 1992). Litter removal allowed other species to invade and to compete against *Phragmites*.

Anoxia. In waterlogged soils, anoxic conditions may amplify the effect of mowing. Removing the culms reduces the supply of oxygen to the below

ground parts (Brix 1990; Armstrong & Armstrong 1991). The subsequent anoxia in the rhizomes may cause important losses of carbohydrates (inefficient metabolism and increased permeability of roots; Cízková-Koncalová *et al.* 1992). An interaction between management and soil aeration was demonstrated by Weisner & Granéli (1989). In their experiment, mowing reduced *Phragmites* after one year if it was done in June and under strongly reducing conditions in the sediment. Mowing in June at a well-aerated site or mowing in August at both sites had no short-term effect.

Flooding. In aquatic stands, stubbles may become flooded after mowing. The penetration of water into the below ground organs leads to putrefaction of the rhizomes (Husák 1978). Salt water proved particularly detrimental (Hellings & Gallagher 1992). It also seems that *Phragmites* is generally more sensitive to the effects of mowing under aquatic conditions because its growth depends more strongly on stored carbohydrates. If these reserves are insufficient, shoots die before reaching the water surface, and subsequently rhizomes may also die (Guthruf *et al.* 1993).

Strong competitors. In highly productive terrestrial stands, *Phragmites* may be displaced by certain grass species, e.g. *Agrostis stolonifera* or *Glyceria maxima.* Mowing in summer gives these species an advantage because they regenerate better than *Phragmites* (George 1992; Rodwell 1995)

Mechanical damage to rhizomes. In grazing experiments *Phragmites* was not only preferentially eaten by cattle or horses; additionally, continued trampling during the vegetation period prevented the regeneration of shoots from dormant buds and created gaps that could be colonized by other species (Morgan *et al.* 1983; Van Deursen & Rost 1990; Roze 1993; Walther 1994). The damaging effect of heavy machines used to harvest reed has been described e.g. by Björk (1967) and Rodewald-Rudescu (1974).

None of the above situations applied to the short-term mowing experiment reported here. All experimental plots were mown at least once a year, so that no litter could accumulate before or during the experiment. Strongly anoxic soil conditions or deep flooding did not occur at the study sites and no strong competitors were present. The mechanical damage caused by mowing was probably low because heavy machines were only used if the soil was sufficiently dry; otherwise mowing and litter removal were done by hand. This absence of factors likely to cause a rapid decline of *Phragmites* may explain why no short-term treatment effects were observed in the present study in contrast to other experiments.

As it seems plausible that *Phragmites* would strongly decrease once its below ground reserves are depleted, it would be interesting to estimate the time needed for this depletion. Unfortunately, this is hardly possible without field measurements of below ground biomass and of its turnover rate. Indeed, the below ground biomass of *Phragmites* varies between half and ten times

the aboveground biomass (Westlake 1968, in Fiala 1976) and this variance can only partly be explained by site factors (Cízková-Koncalová *et al.* 1996; Weisner & Strand 1996). The life span of rhizomes has been estimated to 3–4 years by Fiala (1976) as well as Granéli *et al.* (1996), but to 5–10 years by Haslam (1973a) and to 20 years by Hocking (1989a). Likewise, root production and decay vary considerably among sites (Fiala 1976). Due to the depth of the rhizomes and roots of *Phragmites* at terrestrial sites and to their spatial variability (Kvet 1973, Ondok 1978), direct measurements of below ground biomass at the experimental sites would have been both unreliable and destructive and were therefore not even attempted.

Besides, it must be remembered that internal nutrient cycling is not particular to *Phragmites*. It is the strategy of all dominant species in fen meadows (Kuhn *et al.* 1982; Ganzert & Pfadenhauer 1986; Bernard *et al.* 1988). Consequently, other species are likely to be affected by nutrient depletion as much as *Phragmites*. In this experiment the amount of additional nutrients removed by mowing twice (compared with mowing once) was greater for *Phragmites* than for the other species, but this was mainly because the biomass of *Phragmites* in June did not differ between treatments, whereas the biomass of other species was lower in the JS-plots. If the June biomass of *Phragmites* had been reduced as much as the biomass of the other species, the additional nutrient removal due to mowing twice would have been lower for *Phragmites* than for the other species because of the lower regrowth of *Phragmites* after the first cut.

It is worth noting that mowing only in early September appeared to promote *Phragmites*, since this species had already translocated a greater fraction of nutrients to rhizomes than the other species in late August (consistent with results of Warnke-Grüttner 1990). The difference was greater for phosphorus than for nitrogen, suggesting that additional nitrogen input might promote *Phragmites* more than the other species (cf. Chapter 3).

The possibility that mowing might benefit *Phragmites* indirectly by reducing the competitive impact of other species has been described e.g. by Gryseels (1989a) for mowing in winter:

> "The cut reedbed is more 'homogeneous', of a greater density, composed of healthy, well-flowering plants of the same height (over 2 m). The beneficial effect on reed growth is striking, especially in the wettest plots. Competition for space and light is also shown in the high presence of *Calystegia sepium* and *Urtica dioica* in the uncut reedbed. Both species grow vigorously and strongly affect the performance of *Phragmites*, which does not even flower; *Calystegia sepium* forms 'blankets' over the reed, tangling the stems."

and by Hürlimann (1951) for mowing in late summer:

> "In unseren Gegenden wird die Streuemahd in den Riedern im Spätsommer, in den Monaten August und September, vorgenommen. Zu dieser Zeit scheint der Eingriff keinen nachteiligen Einfluss mehr auf das Gedeihen des Schilfs auszuüben, obschon eine Verminderung der Reservestoffe eintreten muss. (...) Dennoch ist beispielsweise in gemähten Molinieten keine Schwächung des Wuchses von *Phragmites* gegenüber ungenutzten Parzellen festzustellen, ja, es kann sogar, wie später

noch auszuführen sein wird, das Schilf in jenen – wohl infolge einer Beeinträchtigung seiner Konkurrenten durch den Schnitt und einer Verzögerung des natürlichen Sukzessionsablaufes – besser gedeihen als an nicht gemähten Stellen."

During the first three years of the short-term experiment, mowing twice apparently promoted *Phragmites* compared to the other species, at least if their contributions to aboveground biomass were considered. The future evolution is difficult to predict. *Phragmites* might keep this initial advantage if it is able to take up more nutrients than other species to compensate greater losses. This might be the case, for example, if there is an inflow of nutrient-rich groundwater at a depth reachable for roots of *Phragmites*, but not for roots of smaller species (Boller-Elmer 1977, Klötzli 1986). Otherwise, either a new 'steady state' might establish or *Phragmites* might be displaced in the future. Alternatively, both *Phragmites* and its present competitors might be replaced by species better adapted to frequent mowing (cf. Briemle & Ellenberg 1994).

Various experiments showed that mowing twice different affects the species composition of fen meadows depending on the nutrient supply. In the experiment of Finckh (1960), mowing twice a fen meadow *(Schoenetum ferruginei)* during seven years did not modify the percentage cover of *Molinia*, nor the cover of *Phragmites. Schoenus ferrugineus* was reduced, whereas *Carex panicea* and *C. hostiana* strongly increased. Species from more intensive grasslands, such as *Holcus lanatus, Poa pratensis* or *Festuca pratensis* could establish, but their cover remained low (1–2 %). Addition of nitrogen fertilizer did not modify the results. However, if phosphorus fertilizer was added, *Molinia* was strongly reduced, *Schoenus* disappeared and the cover of the *Carex* species increased only slightly; more nutrient-demanding grass species covered up to 15 % and *Phragmites* remained unaffected. Similarly, long-term treatment effects are likely to depend on the nutrient supply in the present experiment.

Summarizing the results, mowing in August appeared not to affect *Phragmites* more than mowing in winter. Mowing in September seemed to promote it. The effect of additional mowing in June was ambiguous: the contribution of *Phragmites* to total biomass was increased, suggesting a favourable short-term effect. However, the impact of mowing in June on nutrient budgets was stronger for *Phragmites* than for the other species, and *Phragmites* might be reduced in the future. It appeared clearly that the experiment must be monitored over a longer time period to evaluate the effect of additional mowing in June (Chapter 9). Finally, reducing the abundance of *Phragmites* is not necessarily the aim of management (Chapters 3 and 4). Mowing twice removed more nutrients than mowing once, reduced total aboveground biomass, created a more open vegetation structure and slightly increased species richness (data not shown). These effects are probably more important for the conservation value of the fen meadows studied here than a possible future reduction of *Phragmites.*

8. Measuring the abundance of *Phragmites australis* in fen meadows – a methodological investigation[1]

8.1. Introduction

Common reed (*Phragmites australis* Trin.) is a worldwide distributed tall grass with outstanding ecological and economic significance (Rodewald-Rudescu 1974). It has been extensively studied during the last decades, but almost exclusively in more or less monospecific aquatic stands or in artificial reed-beds. More attention is now being paid to the occurrence of *Phragmites* in fens and fen meadows, where it is spreading and possibly displacing rare and endangered plant species (Ellenberg & Klötzli 1967; Klötzli 1986; Marti & Müller 1993; Brülisauer 1996). This spread should be considered in nature conservation management; strongly invaded sites might, for instance, be mown more frequently (Bressous *et al.* 1992). Measuring the abundance of *Phragmites* accurately and efficiently is necessary for taking such decisions.

Abundance measurements should be related to the tendency of *Phragmites* to spread and to suppress other plant species; suitable criteria are aboveground biomass (*ABP*), leaf area index (*LAI*), and nutrient concentrations of shoots. The aboveground biomass in late summer is approximately equal to the aboveground production (error of 5–15% according to Granéli 1984). Biomass production is generally considered the best measure of the overall performance of species. The aboveground biomass is also a good predictor for competitive effects on other plants (Gaudet & Keddy 1988). Measuring belowground biomass is not practicable because it requires extensive and destructive sampling (Ondok & Kvet 1978). The leaf area index indicates the amount of light absorbed by *Phragmites* and thus its shading effect on smaller plants (Dykyjová 1971; Hirose & Werger 1995). Nutrient concentrations in shoots may indicate nutrient availability of the site (Wassen *et al.* 1995). Increased nutrient availability is assumed to give *Phragmites* a competitive advantage over other fen meadow species (Klötzli 1986; Brülisauer 1996).

Whenever direct and destructive measurement of the three above criteria is too time-consuming (especially *LAI*) or problematic (e.g. in permanent plot research), non-destructive estimation methods based on morphological measurements are preferable. Appropriate measurements and sampling design depend on the correlations of morphological traits and on their spatial and temporal variability. Therefore, we investigated these aspects in 14 fen meadows to answer the following questions:

- Can shoot density (shoot number per unit area) be used to monitor changes in the dominance of *Phragmites*?
- If not: which additional variable(s) should be measured ?
- Which sample size and which sampling design are needed in field measurements and in the calibrations to obtain sufficiently accurate estimations?

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8.2. Methods

8.2.1. Study sites

The 14 study sites were fen meadows in the Swiss Plateau, i.e. the region between the Alps and the Jura range, at an altitude of 400–440 meters a.s.l. (except sites P1 and P2: 540 m; Table 1). The long-term average annual temperature of the area is 8–10° C, the average annual rainfall 900–1400 cm. 1995 was a particularly warm year with high precipitation, whereas 1996 was average in temperature but dry.

The soils at the study sites have developed on glacial sediments or on lake gyttia and are mostly rich fen peat soils. The groundwater table is at or above soil surface in winter, and can drop to 1 m or more below surface in summer (Klötzli 1969). The vegetation types are given in Table 1. Most sites were subject to eutrophication, thus original communities (alliances *Molinion* and *Caricion davallianae*) were increasingly replaced by tall species of the alliances *Filipendulion, Magnocaricion* and *Phragmition* (Boller-Elmer 1977; Klötzli 1986).

Fen meadows were traditionally mown by farmers in autumn or winter. In the study sites this management had either been maintained or resumed about ten years ago, except in the sites N1, N2, G4 and K1, which had been subjected to mowing experiments (Buttler 1992). In those four sites measurements were carried out on the established permanent plots. Unless otherwise stated, only the plots mown in autumn or winter were included in the analyses. The other sites were chosen to represent different degrees of invasion by *Phragmites*.

Table 1. Characteristics of the study sites with abbreviations used in the text, coordinates as defined by the Swiss topographic map, and vegetation types after Klötzli (1969)

Lake	Label	Coordinates	Vegetation types (alliances)
Neuenburger-	N1	563.40–197.10	*Caricion davallianae*
See	N2	569.90–203.00	*Magnocaricion*
Katzensee	K1	680.55–254.10	*Molinion - Filipendulion*
	K2	680.55–253.70	*Filipendulion*
	K3	680.45–254.05	*Filipendulion*
Greifensee	G1	692.35–247.90	*Molinion - Filipendulion*
	G2	691.95–247.65	*Magnocaricion - Filipendulion*
	G3	692.50–247.80	*Calthion - Filipendulion*
	G4	692.55–247.75	*Caricion davallianae - Molinion - Filipendulion*
Zürichsee	Z1	702.35–229.05	*Caricion davallianae - Molinion - Filipendulion*
	Z2	702.30–229.20	*Caricion davallianae - Molinion - Filipendulion*
	Z3	709.70–229.60	*Molinion*
Pfäffikersee	P1	702.20–244.60	*Molinion*
	P2	702.30–244.60	Caricion davallianae

Plots for morphological measurements were arranged systematically on two or more parallel transects through each site. Biomass samples were taken either on or close to these plots.

8.2.2. Measurements and data analysis

Relations between morphological traits

Culm length and basal diameter were measured in August 1995 or 1996 for all *Phragmites* shoots within 93 1-m^2 plots in six of the sites. The culm length was measured from the soil surface to the base of the panicle, if present, or to the base of the uppermost leaf. The basal diameter was determined in the middle of the second internode. In addition, shoots within three adjacent 1-m^2 plots were counted. The mean shoot number in these four plots was taken as shoot density and the percentage of shoots with panicle as fecundity. We assessed correlations between pairs of variables with Pearson coefficients (r) and used analyses of covariance to test whether regression lines differed among sites.

All shoots in 51 1-m^2 plots were harvested in June, July or August 1996 at five of the sites. We measured the length and the diameter of culms and counted all well-developed leaves, including dry ones. The length and width of the largest leaf were also measured for some samples. The shoots were dried at 70 °C and weighed individually. We calculated correlations among morphological traits and compared the fit of various regression models for the estimation of shoot biomass. On one hand, we used different independent variables (culm length, culm diameter, leaf number and their combinations), on the other hand we applied three different models for each independent variable: (a) simple regression model, (b) model allowing regression parameters to differ among sites and months, and (c) model allowing regression parameters to differ among plots and months. We also used analyses of covariance to test the significance of parameter differences (a) among sites and (b) among months.

A total of 33 shoots was harvested arbitrarily in July 1996 in six of the sites (5-7 shoots per site). We measured culm length and diameter, determined the length, the width and the area of all leaves, using a LI-3100 area meter (Li-Cor Inc., Lincoln Nebraska, USA), and calculated linear regressions for the estimation of leaf areas.

Temporal variation

In 54 plots of 1m^2, shoot density, mean culm length, and mean basal diameter were measured in two consecutive years (1995 and 1996). Fecundity, as the percentage of flowering shoots, was only measured in 20 plots. We tested differences between years using the Wilcoxon test for each site and each variable.

The relative mean change of each variable in each site was calculated as

$$\Sigma_j (x_{j96} - x_{j95}) / \Sigma_j (x_{j95}),$$

where x_{jk} = value of the variable in plot j in year k.

Spatial variation

Large-scale variation was studied qualitatively by comparing the 93 plots mentioned above. Small-scale variation was studied in four large plots of 9 m^2 to 20 m^2, divided into contiguous squares of 25 x 25 cm^2. We counted the shoots in each square, grouped adjacent quadrats into blocks of 2, 4, 9, 16, 24 and 36, and calculated the total shoot numbers in each block. The coefficient of distribution (*CD*)

$$CD = \frac{\textit{Variance of (total) shoot numbers}}{\textit{Mean (total) shoot number}},$$

calculated for the single quadrats and for each block size, was used to measure the degree of spatial aggregation. *CD* is 1 for a random distribution, and >1 for a contagious distribution (Greig-Smith 1952, 1983). The standard error of *CD* was calculated after Greig-Smith (1952) as $\sqrt{2 / N-1}$, and a *t*-test was applied to test the significance of non-randomness.

Variability of nutrient concentrations

In August 1995, all shoots were harvested within two 1-m^2 plots in the site K1 and two plots in the site G4. One plot per site had already been mown in June. Shoots were sorted according to culm length, grouped into size classes of five shoots, dried, ground and analysed for total N, P and K. Additionally, eight plots were sampled in July or August 1996. Shoots were again grouped according to the culm length, but in order to obtain size classes as homogeneous as possible, the shoot number varied between 3 and 7 per group. Shoots were divided into leaf blades, leaf sheaths and culms, and the fractions were analysed separately. Total N and P were extracted by a modified Kjeldahl method (SKALAR Methods 155-432/503-324) and analysed colorimetrically on a continuous flow analyser; K was extracted with 20% hydrochloric acid after dry digestion and analysed by atomic absorption. Extractions and measurements were carried out at FAL (Reckenholz, Zürich).

We tested with two-way ANOVA (factors 'plant part' and 'shoot group') whether nutrient concentrations differed among plant parts. The dependence of nutrient concentrations on shoot size was tested with the regression model

DConc = Constant + DLength + Plot x DLength,

where *DConc* and *DLength* were differences between the concentration (culm length) in the size class and the mean concentration (culm length) for the plot. If the interaction term was significant, we tested the dependence of *DConc* on *DLength* for each plot separately, using Bonferroni probabilities.

8.3. Results

Correlations between morphological traits

The traits related to the size of individual *Phragmites* shoots were all positively correlated (Table 2a). The correlation was strongest between culm length and diameter (r = 0.87) and between culm length and maximal leaf length (r = 0.81). Either slope or intercept of linear regressions differed among sites and among months for most pairs of variables. Consequently, correlations between traits were stronger when calculated separately for each site. The correlation of culm length and diameter, for instance, reached 0.92.

Traits related to whole plots (shoot density, shoot fertility, and mean shoot size) were also positively correlated (Table 2b), but all correlations with density were weak; again did regression parameters differ among sites.

Estimation of aboveground biomass

Aboveground biomass could be estimated either directly for a whole plot, or as the sum of biomass estimated separately for each shoot in the plot. For the direct estimation a loglinear relation was established between the mean shoot dry weight of a plot and the product of mean culm length and mean basal diameter:

Log (dry weight) = -1.97 + 1.04 x log (length x diameter), $r^2 = 0.94$

ABP = shoot density x mean shoot biomass

Table 2. Correlations and results of analyses of covariance for pairs of morphological traits of *Phragmites communis*: (a) measured on single shoots in June, July or August (n = 486), and (b) determined for 1-m^2 plots in August (n = 93). Given are Pearson correlation coefficients and the significance of differences in regression lines among sites (n = 8 in a, 6 in b) and among months (n = 3 in a); * : significant differences in regression slopes; ° , significant differences in intercept; * / °: $P < 0.05$; ** / °°: $P < 0.01$; *** / °°°: $P < 0.001$; ns, $P > 0.05$

(a) Single shoots	Culm length		Basal diameter		Leaf number		Leaf width	
Basal diameter	0.87	* / ***						
Leaf number	0.62	*** / ***	0.52	*** / ***				
Leaf length	0.81	** / ns	0.74	° / °	0.56	*** / *	0.79	* / *

(b) 1-m^2 plots	Culm length		Basal diameter		Shoot density	
Basal diameter	0.91	**				
Shoot density	0.35	***	0.17	**		
Fecundity	0.86	*	0.80	°°	0.06	***

Using this equation, we estimated *ABP* for the 93 plots in which length and diameter had been measured, and plotted this estimate against the shoot density (Fig. 1). A regression yielded

Log (ABP) = -0.61 + 1.17 x log (shoot density), $r^2 = 0.88$

Thus, if only an approximate ranking of *Phragmites* abundance was needed, the shoot density would have been sufficient. However, a large range of biomass was found at densities of 20–60 shoots m^{-2}, which is typical for reed-invaded fen meadows; at these densities shoot density could hardly be used to estimate *ABP*.

Various models with 1, 2 or 3 independent variables were used to estimate the biomass of individual shoots (cf. Table 3). The best fit was obtained with both length and diameter as predictor variables. This could be done either through a multiple regression or through a simple regression on the product of culm length and diameter. Both models fitted equally well (i.e. similar r^2 and standard error), but the simple regression had more stable coefficients.

Comparing the models with only one independent variable, culm length yielded a better fit than basal diameter and leaf number. Leaf number hardly improved the regression fit when added to culm length; r^2 increased by less than 1%. Regression parameters (either slope or intercept) differed both among sites and among months, and consequently the regression fit (r^2) was improved by up to 0.26 if a grouping factor (sites and months or plots and months) was included in the model. Thus, in practice *ABP* estimations will be more accurate if calibrations are performed separately for each site or for each part of a site and for each time period.

Estimation of leaf area index

The most accurate estimation of *LAI* would consist in measuring length and width of all leaves in a plot, estimating individual area as

leaf area = 0.53 x leaf length x leaf width ($r^2 = 0.99$; $n = 292$),

and adding up leaf areas over all shoots. However, the sampling effort would be prohibitive. Since mean and maximal leaf size were strongly correlated, it appeared possible to measure only the area of the largest leaf of each shoot.

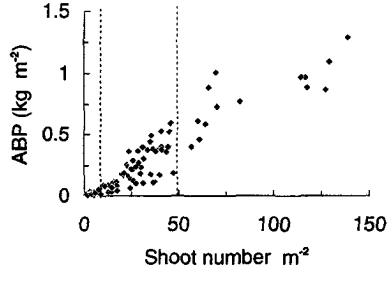

Fig. 1. Relation between shoot density and estimated aboveground biomass (*ABP*) in 93 1-m^2 plots. The dashed lines indicate the limits of shoot density classes according to Marti & Müller (1993). Despite a strong overall correlation between density and *ABP*, a large range of biomass was found within each class.

Table 3. Regression models, fit and analyses of covariance for the estimation of shoot biomass (dry weight) based on shoot morphology; r^2 = multiple squared r (r^2_{all}, for simple models; $r^2_{s/m}$, for models with grouping factor sites and months; $r^2_{p/m}$, for models with grouping factor plots and months); P_{site} or P_{month} = significance of differences in regression parameters among sites or among months; cf. Table 2

Simple regression model	r^2_{all}	$r^2_{s/m}$	$r^2_{p/m}$	P_{site}	P_{month}
log (DW)= -2.4 + 1.2 x log (diameter x length)	0.95	0.97	0.98	***	***
log (DW)= -2.9 + 1.8 x log (length)	0.88	0.92	0.96	***	○○○
log (DW)= -0.89 + 2.5 x log (diameter)	0.80	0.91	0.93	***	***
log (DW)= -1.05 + 1.8 x log (leaf number)	0.39	0.61	0.65	**	○○○

The mean area could then be estimated:

mean leaf area of a shoot = - 2.5 + 0.85 x max. leaf area (r^2 = 0.98; n = 33)

$LAI = \sum_{all\ shoots}$ *(mean leaf area x leaf number)*

A further simplification consisted in estimating the mean per-leaf area from squared culm length:

Mean per-leaf area = 9.4 + 10.2 x (culm length)^2 (r^2 = 0.83; n = 33)

If leaf numbers had not been counted, the total leaf area would have to be estimated directly from culm length or diameter:

Total leaf area = 43 + 120 x (culm length)^2 (r^2 = 0.71), and

Total leaf area = 35 + 10 x (basal diameter)^2 (r^2 = 0.59).

As for shoot biomass, the best fit was obtained with culm length, but there was no advantage in using both length and diameter (r^2 = 0.71). In any case, a considerable loss of precision would result from excluding leaf numbers.

Temporal variation

The differences in shoot density and shoot size between consecutive years were considerable in those plots studied during two consecutive years: shoot density changed up to 236%, culm length up to 42% and basal diameter up to 59% (Fig. 2). Yet, these differences were inconsistent across plots within sites, across sites, and across variables. In each site one or two variables changed significantly among years, but which variables did change depended on the site. For each variable the average relative change was positive in some sites and negative in others, and the same was mostly true for plots within sites. An increase of culm length was usually associated with an increase of basal diameter in all six sites (rank correlation r_S = 0.12–0.93). Conversely, changes in shoot density were either positively or negatively correlated with changes in culm length or diameter (r_S = -0.68 to +0.78). These results suggest large and unpredictable year-to-year fluctuations in shoot density, size and fecundity.

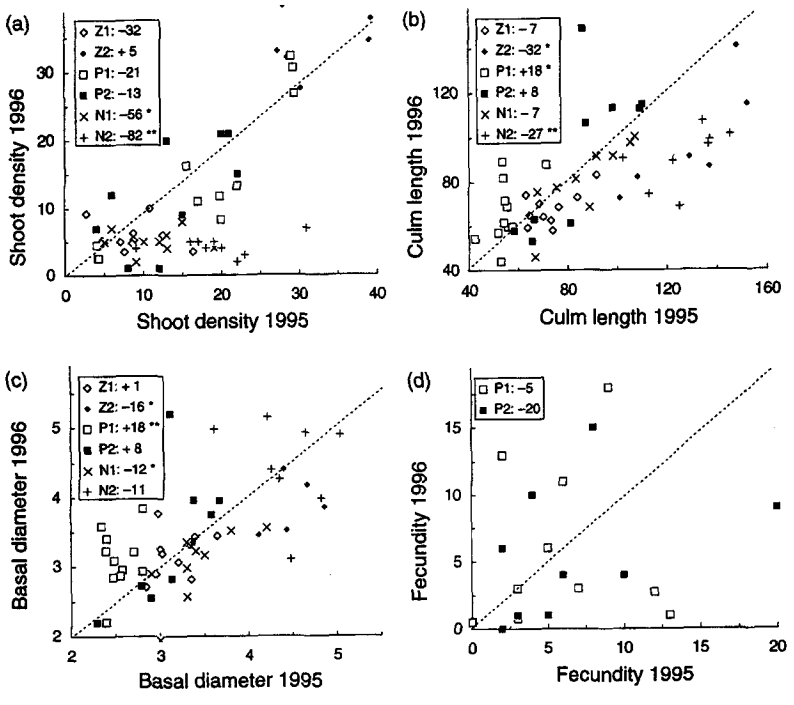

Fig. 2. Fluctuations of (a) shoot density, (b) culm length, (c) basal diameter and (d) fecundity in 54 1-m^2 plots between two consecutive years, illustrating the differences among and within sites in the direction and the amount of change. Dashed lines correspond to unchanged abundance; legends include mean changes of sites in % of the 1995 mean and the significance of changes tested with the Wilcoxon signed rank test (*: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$)

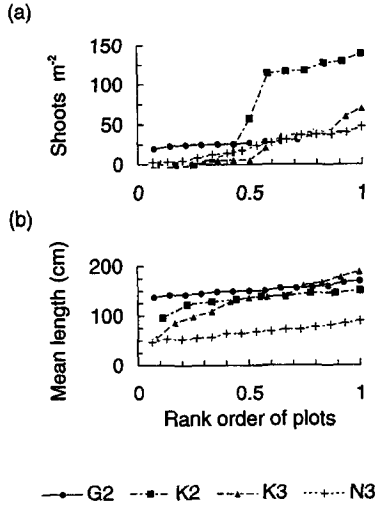

Fig. 3. Distribution of shoot density and culm length among 1-m^2 plots within four of the study sites (cf. Table 1), indicating differences in the range of abundances and in the steepness of gradients in invasive *Phragmites* stands.

Spatial variation

Spatial variation occurred at different scales, i.e. among sites, among plots within sites, and within plots. Sites differed not only in average shoot density and size, but also in the variances among plots and in the shape of the distribution: both progressive gradients and sharp limits occurred (Fig. 3).

Within plots, shoot distribution was contagious. In all four plots investigated by contiguous quadrats the variance of shoot numbers per quadrat was significantly greater than the mean shoot number (CD = 1.6–2.4, P<0.001).The CD hardly changed with block size up to blocks of about 20 shoots (Fig. 4). In larger blocks the CD increased steadily in the sites K2 and G4, whereas it decreased in K1, and reached a maximum at a block size of 49.9 shoots (16 quadrats) in K3. The relatively constant CD found at the smaller block sizes suggested that the accuracy of shoot density estimation depended on the total number of shoots counted, regardless of shoot density and of the number of subplots.

Indeed, from $CD = s^2/\bar{x}$ follows that $s = \sqrt{CD \times \bar{x}}$ and hence $s/\bar{x} = \sqrt{CD}/\sqrt{\bar{x}}$.

If shoots were counted in n subplots with m shoots per plot, shoot density would be estimated with a relative standard error of $\sqrt{CD}/\sqrt{nm}$. According to our data, 200–300 shoots would have to be counted to estimate the density with a relative standard error of 10%. For verification CD was also calculated for the 93 plots in which shoots had been counted on 4 adjacent 1-m² subplots. Most plots had indeed a CD between 1 and 3, but CD values up to 10 also occurred at various shoot densities; therefore, large errors will sometimes be made in determining the shoot density. The size of shoots also varied strongly within plots, with coefficients of variation of 40–100% for shoot dry weight, 15–47% for culm length, 15–40% for basal diameter, and 5–32% for leaf number (data from the 51 plots used for biomass sampling). Thus, the mean of a sample of e.g. 10 shoots would be estimated with an average standard error of 21% for dry weight, 9% for culm length, 8% for basal diameter and 6% for leaf number. Again, these errors would strongly differ from plot to plot.

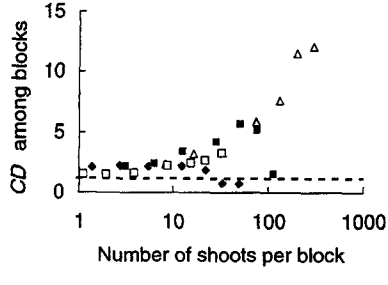

Fig. 4. Spatial variability of shoot densities (CD, coefficient of distribution) in relation to the number of shoots counted. The dashed line (CD =1) corresponds to randomly distributed shoots; higher CD indicate spatial aggregation. Site symbols: ♦: K1; Δ: K2; ■: K3; □: G4.

Nutrient concentrations

The concentrations of nitrogen (N) and phosphorus (P) varied among different plant parts, i.e. leaf blades had higher concentrations than culms and sheaths ($P < 0.001$). Shoots from plots mown in June had higher P and K concentrations than shoots from unmown plots ($P < 0.05$), while no significant difference was found for N. Concentrations of N and P were unrelated to shoot size in whole shoots and in individual plant parts, except N concentration in leaf blades, which appeared to be higher in large shoots ($P < 0.01$). The variance among shoot classes within plots approximated therefore the variance that would have been found among samples of five shoots randomly harvested within each plot. Coefficients of variation among shoot classes, calculated for each plot (Table 4), suggested that 20–30 shoots would normally estimate mean N and P concentrations with a standard error of 10%, whereas K measurements were subject to much larger errors.

Table 4. Coefficients of variation (*CV*) of nutrient concentrations measured in different groups of shoots sampled within the same plots. Data are ranges of *CV* (in %) calculated for 4–8 different plots

Nutrient	Whole shoots	Blades	Sheaths	Culms
N	1.8 – 15.6	4.9 – 8.1	7.7 –19.2	2.3 – 24.0
P	7.8 –23.3	0.0 –19.3	13.3 – 29.6	39.2 – 173.2

8.4. Discussion

A method for assessing the abundance of *Phragmites* in fen meadows must be adapted to the growth form of this plant and to the objective of the study. In the context of nature conservation the mere presence of *Phragmites* is not an assessment criterium in itself, because low or medium abundance of *Phragmites* is common in fen meadows. Therefore, the specific degree of abundance has to be considered, particularly aboveground biomass (*ABP*) and the leaf area index (*LAI*).

Abundance measurement based on shoot density

The relationship between shoot density and *ABP* or *LAI* is variable because the average size of shoots varies strongly among sites, within sites and among years, and because its relation to shoot density may be either positive or negative. A negative relation between shoot density and *ABP* has been found in monospecific *Phragmites* stands under optimal site conditions, where

intraspecific competition limits shoot growth (Graneli 1984). In terrestrial mixed stands, however, interspecific competition and nutrient availability are limiting (Haslam 1971b). As a result, we found the density and the average size of shoots to be positively correlated, and thus shoot density may be used as a measure of abundance, provided the differences are large enough. The four density classes defined by Marti & Müller (1993), viz. <10 shoots m^{-2}, 10–50, >50, or 'monospecific stands' fulfil this requirement since a change towards a higher class is likely to reflect a real increase of biomass (cf. Fig. 1). However, a large range of abundances may be found in the class 10–50. Therefore, this classification does not reflect the more subtle changes in abundance, which would be essential to detect a spread or a management effect. For an exact assessment of the abundance of *Phagmites*, not only shoot counts, but also morphological measurements are necessary.

Selection of morphological variables for abundance estimation

Size proportions of *Phragmites* shoots often vary among different ecotypes (e.g. Dykyjová 1978). However, the morphological variables measured in this study were strongly correlated to each other. This is probably due to the relatively small range of soil conditions at the study sites compared with the ecological amplitude of the species. Moreover, the size proportions of *Phragmites* shoots appear to be relatively insensitive to varying light conditions (Ekstam 1995). The relatively constant proportions found in fen meadows imply that a single morphological variable describes the shoot size fairly well.

We found culm length to be the best predictor for both shoot biomass and leaf area. Basal diameter has often been preferably used as shoot size variable because of its good correlation with other morphological traits (van der Toorn & Mook 1982), its relative independence on short-time environmental fluctuations (Haslam 1970A), its ecological significance (Ostendorp 1993a,b), or simply for practical reasons: in a dense and high reed stand, culm diameter is generally easier to measure than culm length or leaf number. At our sites, however, culm length could be measured more easily and accurately than basal diameter, and was generally better correlated with other morphological traits (cf. Graf 1996; Hills & Murphy 1996). As regards the ecological significance, the diameter is important for stem-boring or gall-making insects or nesting birds (Ostendorp 1993a,b), but the possible suppressive effect of *Phragmites* on endangered plant species is more likely to depend on the height of the plant (Gaudet & Keddy 1988).

Thus, if only one trait is measured, culm length should be preferred to basal diameter. If a second trait is measured, the choice depends on the criterium to be assessed. In our study, measuring basal diameter did improve estimates of biomass, but did not impove estimates of leaf area. Counting leaf number, on the other hand, increased the accuracy of estimates of leaf area, but had no effect on estimates of biomass. Therefore, the variables to measure in a field study are either a combination of culm legth and culm diameter (for *ABP* as-

sessment), or a combination of culm length and leaf number (for *LAI* assessment), or culm length on its own.

Sampling design for field measurements

The abundance of *Phragmites* is often heterogeneous within a site. Both sharp limits and progressive gradients occur, and sites strongly differ in the variability and distribution of shoot densites. These differences may reflect different causes of spreading. Some factors (e.g. atmospheric N deposition) may influence whole sites, others (e.g. local inflow of nutrient- and oxygen-rich water through drainage ditches) affect only parts of the site. It may therefore be important to describe the pattern of spread, rather than only comparing site means. A random distribution of plots within sites is not efficient in revealing such patterns, and a site stratification is arbitrary if gradients are progressive (cf. Greig-Smith 1983). Most suitable is a systematic design with transects perpendicular to the steepest abundance gradient, sampled either by contiguous plots or at fixed intervalls (Ondok & Kvet 1978). Several parallel transects allow to detect two-dimensional gradients.

The plot size should be adapted to the small-scale variation in the size and density of the shoots. Ondok (1971) reported clusters of 20 x 40 cm^2 to 40 x 80 cm^2, but he noted that the cluster size was inversely related to the average shoot density and that aggregation was weaker in sparse stands. This is consistent with our results, which revealed no clear cluster limits. Plots with 20–30 shoots appeared suitable to determine the shoot density in the sites investigated. This number corresponded to 1 m^2 in moderately invaded sites, and to 0.25–0.5 m^2 in severely invaded ones. Ten plots of that size would usually allow an assessment of shoot density with a standard error of 10%.

Sampling design for calibrations and nutrient analyses

Despite the strong correlations between pairs of morphological variables, regression parameters differed among sites and months. Sites with strong gradients of *Phragmites* abundance should therefore be stratified into subsites with similar shoot size; separate calibrations should be calculated for each subsite. If field measurements are carried out in different parts of the growing season (e.g. for a growth analysis), new calibrations are needed approximately monthly. Other authors used 50 (Kauppi *et al.* 1983) or even 100 shoots (Ulrich & Burton 1985) for their calibrations, but in this study 20 shoots provided reliable estimates of regression parameters at the plot level.

Nutrient concentrations were as variable as the shoot size, but mostly unrelated to it. The higher N concentrations in leaves of large shoots compared with those in leaves of small shoots of the same plot may be a strategy that enables the leaves receiving most light to assimilate more efficiently (Hirose *et al.* 1988). In a clonal plant such as *Phragmites*, this may increase the performance of both tall and small shoots, since assimilates can be redistributed from tall to small shoots (Hara *et al.* 1993). A similar effect is attained through

vertical gradients in nutrient concentration within shoots. Hocking (1989b) measured twice as high N concentrations in the top leaves as in basal leaves of *Phragmites.* These results suggest that exact comparisons of nutrient concentrations are only possible for given plant parts (e.g. leaf blades) and for a given position in the shoot (Allen & Pearshall 1963). The failure of previous investigations to establish a relation between the dominance of *Phragmites* and nutrient concentrations (Boller-Elmer 1977; Zelesny 1994; Brülisauer 1996) might partly be due to the fact that only whole shoots were analysed. However, such detailed measurements are probably of small indicative value for nature conservation and certainly too expensive for a routine monitoring.

Sampling design for the assessment of temporal dynamics

It is often difficult to determine whether *Phragmites* is actually spreading at a site because trends in abundance occur slowly and are difficult to differentiate from the strong annual fluctuations which result from differences in climatic or hydrological conditions (Haslam 1972). Moreover, changes are inconsistent within sites, differing even between neighbouring plots. The strong within-site heterogeneity, both spatial and temporal, would make systematically arranged permanent plots more efficient than a random selection of different plots each year (Weber *et al.* 1995). A nested sampling design (e.g. four contiguous 1-m^2 plots) would allow a distinction between divergent evolutions within sites and purely local fluctuations (Wildi & Krüsi 1992).

The marked spatial and temporal patterns found in this study are not particular to *Phragmites*: High mobility and strong fluctuations have been described for many species in a large number of vegetation types (Klötzli 1995a,b; van der Maarel 1996). Whether a trend proves significant or not is often a matter of the scale applied (Zobel *et al.* 1987). This ambiguity does not make it impossible or useless to assess changes in the abundance of *Phragmites* , but it means that (a) any statement about an increase or decrease in abundance must be related to a definite spatial and temporal scale with reliable error estimations, (b) establishing a progressive increase of abundance may require many years of repeated measurements, (c) any rating of changes in abundance as an 'improvement' or 'deterioration' must be based on spatially and temporally explicit aims of nature conservation. Moreover, additional measurements will be necessary, depending on the context of the investigation. Indeed, predictions about future changes of abundance may require measurements of environmental factors (cf. Van Hulst 1980). The assessment of management techniques should include an assessment of the impact of management on other plant and animal species (e.g. Ditlhogo *et al.* 1992; Klieber *et al.* 1995). Finally, the causes of the spread of *Phragmites* cannot be fully understood without addressing the underlying social, economical and political factors (Finlayson 1994). Thus, measuring the abundance of *Phragmites* must be part of a broader monitoring programme in order to help preventing a further degradation of the last Swiss fen meadows.

9. Assessing management effects on vegetation in fen meadows: reliability of short-term, small-scale investigations[1]

9.1. Introduction

Fen meadows are semi-natural wet grasslands with outstanding conservation value because they are species-rich and support rare or endangered plant and animal species (Korneck & Sukopp 1988; Wheeler 1988; Landolt 1991). They require an adequate management to prevent species loss or undesirable changes in species assemblages, notably a succession towards eutrophic reed stands or swamp forest (Briemle *et al.* 1991; Dierßen & Schrautzer 1997). General guidelines for the management of fen meadows are available since long (Wildi & Klötzli 1978; Egloff 1984), but particular measures are often required on account of specific site conditions, conservation aims or human impacts. Possible measures include mowing at various dates, once or several times a year (e.g. Kapfer 1988; Buttler 1992; Dumortier *et al.* 1996), grazing (Grant *et al.* 1996), burning (Bakker 1989), rewetting (Oomes & van der Werf 1996), topsoil removal (Jansen *et al.* 1996) or even fertilization (van der Woude 1994). Field experiments are an important tool to evaluate the impact of conservation techniques. Ideally, experiments should be conducted on relatively large areas, over a long time, and with an accurate, regular monitoring (Bakker *et al.* 1996). However, financial limitations or the risk of damaging sensitive ecosystems usually make a trade-off between the scale and the intensity of investigation necessary in such experiments (e.g. Weber *et al.* 1995). An optimal design and detailed investigations are often possible only in small-scale, short-term experiments (Krüsi 1989; Buttler 1992). Conversely, large-scale, long-term experiments must often be monitored more extensively and their design is frequently affected by external constraints (e.g. heterogeneous initial conditions, Olff & Bakker 1991).

Short-term investigations are unreliable because of the temporal variability of the vegetation with respect to the floristic composition, the species richness, or the biomass production (e.g. Klötzli 1995a,b; Pärtel & Zobel 1995; Oomes & Van der Werf 1996). Evidence from long-term vegetation surveys suggested that "only very long time scales, 20 years or more, can give an idea which species are actually showing successional trends" (Klötzli 1995a). This might also be true for management experiments, where short-term treatment effects can be confounded with fluctuations or may intrinsically differ from long-term effects (Tilman 1987; Magnuson *et al.* 1991; Pickett 1991). For example, three types of species dynamics were observed in two long-term mowing experiments in Dutch wet meadows: the abundance of some species changed immediately and remained stable after several years. For other species a change in abundance occurred only after 5–10 years. For a third group of

[1] Submitted for publication to the Journal of Vegetation Science

species, an initial increase was followed by a decrease to or even below the original abundance (Olff & Bakker 1991; Oomes & van der Werf 1996). The short-term changes in abundance would have predicted the long-term dynamics correctly only for the first group of species.

Small-scale investigations may be unreliable because of the spatial heterogeneity of the vegetation: small plots may not adequately reflect the biomass or species composition of the experimental site. Small-scale spatial patterns vary strongly over time (e.g. Glenn & Collins 1993; Herben *et al.* 1993), and treatment effects may be confounded with these 'patch dynamics' if they are studied in small plots. Moreover, different dynamics or vegetation-environment correlations can be observed at different spatial scales (Magnuson *et al.* 1991; Herben *et al.* 1993; Reed *et al.* 1993; Pärtel & Zobel 1995; Oksanen 1996). Treatment effects observable only at a small scale are possibly not relevant to nature conservation.

The purpose of the present study was to investigate how reliably short-term effects are assessed in small-scale experiments under 'optimal' conditions, i.e. where spatial heterogeneity is controlled through a replicated block design, and where treatment effects are separated from overall temporal trends in data analysis. Such a controlled experiment had been established in 1982 on the southern shore of Lake Neuchâtel (Switzerland) to determine whether mowing was necessary to preserve these fens and whether it should be carried out in summer or in winter (Buttler 1987). After four years of investigation it was concluded that mowing in winter was the best management because it enhanced the vitality of most plant species (Buttler 1992). We reinvestigated this experiment in 1995 and in 1996 to see whether the short-term conclusions were confirmed by the long-term treatment effects[2]. To this end we compared how species composition had been influenced by treatments during the first four years and over the whole observation period (14 years). At the same time we were interested in several methodological questions, namely (a) whether treatment effects could be assessed 'retrospectively', based on differences among plots in a single year, i.e. doing a kind of 'space-for-time substitution' (Pickett 1989); (b) whether vegetation relevés by cover estimation are less reliable, and therefore less suitable in the context of a short-term survey, than the more quantitative method of counting plants or plant parts (Buttler 1992); (c) whether different treatment effects on species richness were apparent at different plot size (Oksanen 1996); and (d) whether results could be expected to be valid for other sites in the Swiss Plateau or whether they strongly depended on particular local site conditions. Treatment effects were assessed at three different levels: impact on species composition at the community level, impact on the abundance of individual species and impact on species richness and species turnover.

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[2] Bakker *et al.* (1996) defined long-term research as research lasting for at least 10 years.

9.2. Methods

Field sites

The two experimental sites (Cudrefin and Portalban) were located on the southern shore of Lake Neuchâtel, a typical meso-eutrophic lake of the Swiss Plateau (Fig. 1). They were part of a large wetland area which developed on the former south bank of the lake after its level had been lowered by about 3 m in 1869 (Buttler *et al.* 1985). The soil was a highly calcareous typic Haplaquoll, with pH 7.6–7.7 in Cudrefin and 7.9–8.8 in Portalban (Buttler 1987). The topsoil layer, 10–15 cm thick, was an Anmoor-Hydromull with 17–23% organic material. The Portalban site was slightly drier than the Cudrefin site (mean water level: -10 cm in Cudrefin, -15 cm in Portalban) and protected against flooding with lake water by a forested ridge.

Both sites were relatively nutrient-poor, with average nutrient indicator values of 2.2–2.5 in Portalban and 2.4–2.6 in Cudrefin (on a scale ranging from 1 to 5, after Landolt 1977). The Portalban site was dominated by *Schoenus nigricans*, with dense patches of *Cladium mariscus*, whereas the Cudrefin site was co-dominated by several *Carex* and grass species. In terms of the phytosociological classification, site Portalban belonged to the association *Orchio-Schoenetum nigricantis* (alliance *Caricion Davallianae*) and site Cudrefin, to the association *Caricetum elatae* (alliance *Magnocaricion*; Buttler & Gallandat 1990). Sites had not been mown for more than 10 years at the beginning of the experiment (Buttler 1987).

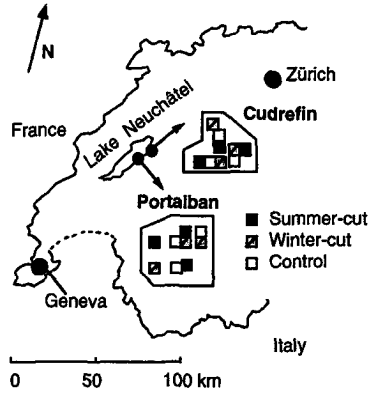

Fig. 1. Location of the experimental sites in western Switzerland and arrangement of the experimental plots within each site

Experimental design and sampling methods

The experiment was established in 1982. Three treatments were compared, i.e. mowing in August ('summer'), mowing in January-February ('winter'), and no mowing ('control'). Mowing was carried out with a portable machine, and the litter was removed manually as soon as possible from the experimental area. Management was annual from 1982 to 1987, and biennial since then. Each treatment was performed on three experimental plots per site, according to a randomized block design (three blocks per site). The blocks were irregularly shaped to take optimally account of the heterogeneity of the site

(Fig. 1). The size of the plots was 13 x 13 m^2 in Portalban and 11 x 11 m^2 in Cudrefin. Each experimental plot included one permanent quadrat of 5 x 5 m^2. Three smaller quadrats (1x1 m^2) were randomly placed along the inner border of the 25-m^2 quadrat. One quarter of each 1-m^2 quadrat was taken as a subplot for plant counts (more details in Buttler 1992)

The experiment had been surveyed from 1982 to 1985, using various methods of investigation (Buttler 1987, 1992). It was reinvestigated in 1995 and 1996. The cover of all species was estimated on a percentage scale in late July in the 1-m^2 quadrats in Cudrefin and in the 25-m^2 quadrats in Portalban. The reason for this choice was the finer vegetation structure in Cudrefin compared with Portalban. Vegetation relevés were also made in the 1-m^2 quadrats in Portalban and in the 25-m^2 quadrats in Cudrefin in 1996. Additionally, shoots, stems or leaves of frequent forbs were counted in the 0.25-m^2 subplots; inflorescences of frequent grasses and sedges were counted in the 1-m^2 quadrats.

Data analysis

Treatment effects on species composition (community level)

The impact of the treatments on species composition was analysed by redundancy analysis (RDA), using the statistical software CANOCO 3.0. (ter Braak 1987-1992). RDA is a 'constrained' ordination method, i.e. both species data and other ('explanatory') variables are used to calculate the ordination axes. As a result axes are linear combinations of the explanatory variables. The sum of their eigenvalues is the fraction of the variance (i.e. of the total sum of squares) in the species' abundances accounted for by the explanatory variables. The use of RDA, which assumes a linear relation between species abundances and environmental factors, seemed appropriate here because the sites were relatively homogeneous (axes of a detrended correspondence analysis shorter than 2 standard deviations; cf. ter Braak 1987). The explanatory variables were 'treatment' (factor with 3 levels), 'block' (factor with 3 levels) and 'time' (treated either as a factor or as a numeric variable). Factors were coded with dummy variables (i.e. each level was represented by a binary variable), to analyse their effects with linear regression models. As species data we used the square root of percentage cover, centred by species, which means that RDA was based on a covariance similarity matrix. Species with less than 5 (Cudrefin) or 3 (Portalban) presences were excluded from the analysis. Thus, analyses were based on 30 species in Cudrefin and on 32 species in Portalban.

To evaluate the relative importance of the various factors, a first RDA was carried out on the whole data set with the model:

$$\textit{Species abundance} = \textit{Constant} + \textit{Block} + \textit{Treatment} + \textit{Time} + \textit{Treatment} * \textit{Time} \qquad (1)$$

In this model, *time* was treated as a factor with 6 levels (= years) in Cudrefin and 5 levels in Portalban (where the 1984 data were missing). The fraction of

variance in the species data explained by each factor was determined through a series of partial RDAs, i.e. some of the explanatory variables were used as covariables to eliminate their effects from the ordination (Borcard *et al.* 1992, Økland & Eilertsen 1994). To determine the variance explained by the 'treatment-by-time' interaction, the dummy variables coding treatments and years were multiplied among each other, yielding a set of 18 (15) product variables ('treatment x time'). A RDA was carried out with these product variables. The variance explained by interaction effects was the difference between the variance explained by the product variables and the variance explained by the original variables:

*Treatment * Time = Treatment x Time – Treatment – Time* (1')

To compare the results that would be obtained for different periods of observation, RDAs were carried out with different data subsets. The model was:

Abundance of species i adjusted for the temporal trend =
*Constant + Treatment + Treatment *Time + Block* (2)

Contrary to model (1), the time variable was numeric (see below). It was not included in the model, but used as a covariable to eliminate the overall temporal trend from the analysis (cf. Fig. 2). The 'abundances of species adjusted for temporal trend' were the residuals of the regression model

Average abundance of species i = Constant + Time (2')

These adjusted abundances represented the differences between the abundances of species in a particular relevé and their expected abundances under the assumption that all plots evolved in the same way and linearly with time.

The data subsets used to simulate three different periods of observation were:

1) The relevés from 1982–1985. The time variable was -3 for 1982, -1 for 1983, 1 for 1984, 3 for 1985. The 'treatment-by-time' interaction modelled a linear increase in treatment effects during the first 4 years of the experiment.
2) The relevés from 1982–1983 and those from 1995–1996. The time variable was -1 for 1982-1983 and +1 for 1995-1996. The 'treatment-by-time' interaction modelled an increase in treatment effects between the first two and the last two years of the experiment.
3) The relevés from each single year. The time variable was 1 and model (2) was therefore equivalent to a simple ANOVA model without interaction:

   Species abundance = Constant + Treatment + Block (3)

   With this last model partial RDAs (see above) were used to decompose the effects of the treatments into two orthogonal contrasts, i.e. 'mown' versus 'unmown' ('control') and 'mown in summer' versus 'mown in winter'.

The significance of the models was tested by means of Monte Carlo permutation tests, i.e. a series of new RDAs were calculated with treatments being 'permuted' (attributed to different vegetation relevés) each time. The effect of

treatments on species composition was considered significant if treatments explained a larger fraction of variance in the original data set than in 95% ($p < 0.05$) or 99% ($p < 0.01$) of the permuted data sets. To take into account the block design of the experiment, treatments were only permuted within each block. Moreover, the three 1–m^2 quadrats per permanent plot (Cudrefin) were permuted together, i.e. always attributed to the same treatment, because they were not independent from each other. Relevés made in the same quadrats, but in different years, were also permuted together for the same reason. This restriction limited the number of possible permutations to 215. In fact, more permutations could have been computed with subsets 1 and 2 by inverting or shifting the order of the years (ter Braak 1990), but the number and type of possible permutations would then have differed between the two sites and among the subsets. As we were mainly interested in the treatment effects, we preferred to permute only the treatments and thus, to use the same permutation design for both sites and for all data subsets.

We did not correct the significance levels for multiple testing. This should have been done to examine whether there had been a significant treatment effect in any of the subsets. Our question was slightly different, namely, for which subset a significant effect would have been found, if only that particular subset had been investigated.

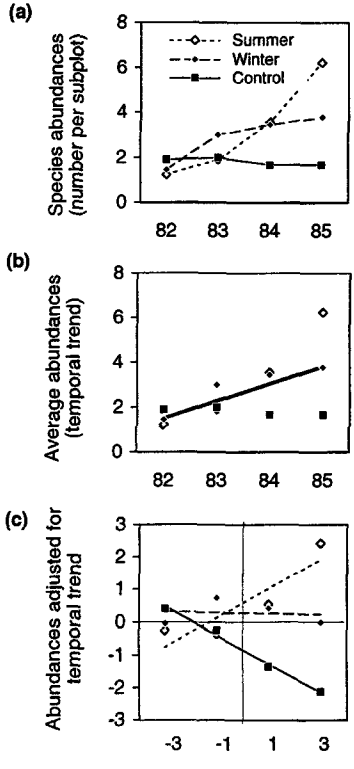

Fig. 2. Example illustrating how the treatment effects on the abundances of individual species were obtained. The abundances of *Mentha aquatica* in Cudrefin (points in a) were decomposed into an overall temporal trend (regression line in b) and residuals. The residuals, or 'adjusted abundances' (points in c) were regressed against the variables 'treatment' and 'treatment-by-time' (regression lines in c). Due to the centring of the time variable the intercept of the regression lines is the average treatment effect and their slope, the 'treatment-by-time' interaction. Each point in a–c is the mean of nine subplots.

Treatment effects on the abundances of individual species

Based on the results of RDA we assessed the responses of each species to each treatment. These responses were given by the correlations between species and treatments or treatment-by-time interactions (ter Braak 1987-1992). If r_{ik}, the correlation coefficient of species i with treatment k was positive, this indicated that treatment k was favourable to species i compared with the two other treatments. R_{ik} was the cosine of the angle between the vector of species i and the vector of treatment k. With model 2 (data subsets 1 and 2), these vectors were defined by their scores (c_{ij} and c_{kj}, $1 \le j \le 4$) on the first four RDA axes[3], and r_{ik} was calculated as

$$r_{ik} = \frac{c_{i1} \times c_{k1} + c_{i2} \times c_{k2} + c_{i3} \times c_{k3} + c_{i4} \times c_{k4}}{\sqrt{c_{i1}^2 + c_{i2}^2 + c_{i3}^2 + c_{i4}^2} \times \sqrt{c_{k1}^2 + c_{k2}^2 + c_{k3}^2 + c_{k4}^2}}$$

With model 3 (data subset 3), only the first two RDA axes had to be considered[3]. The correlations of the species with the treatment-by-time interactions were calculated in the same way. As the correlations of species with treatments and with treatment-by-time interactions were almost identical, only the latter were used to assess the responses of the species.

For the interpretation of the correlations we chose a threshold of 10% explained variance, i.e. a species was only considered to respond to treatments in a given time period if at least 10% of the variation in its abundance was explained. This threshold yielded results that were similar to the use of t-values biplots (ter Braak 1990). The exlplaied variances of all species were included as 'percentage fit per species' in the RDA output provided by CANOCO.

Counts of vegetative units or of inflorescences were analysed after square-root transformation with the same data subsets and models as the vegetation relevés, but calculations were made separately for each species, using the general linear model procedure provided by the statistical package SYSTAT (Systat, Inc. Evanston). The univariate analyses were used because the high proportion of 0 values would have made an ordination unreliable (Wildi, pers. comm.)

Treatment effects on species richness

Species richness was analysed for the full data set and for subset 1 with a repeated measures ANOVA, (factors time, treatment and block), and for the individual years with a mixed model two-way ANOVA (factors treatment and block), followed by orthogonal comparisons (Sokal & Rohlf 1995). Again, no correction for multiple testing was applied (see above).

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[3] In a RDA with n independent explanatory variables, the whole correlation between the species and the variables is expressed by the first n ordination axes ('canonical axes'), whereas all other ordination axes are uncorrelated to the explanatory variables. With model 2, there were four canonical axes (only two of the three dummy variables coding treatments and 'treatment-by-time' interactions were independent from each other). With model 3, there were two canonical axes.

We also determined cumulative species numbers (the number of species present in a given plot in at least one year since 1982). Furthermore, with the 1-m^2 and the 25-m^2 relevés made in 1996, we determined species numbers at five scales, namely 1, 3, 9, 25 and 75 m^2. Plot sizes of 3, 9 and 75 m^2 were simulated by pooling the three 1-m^2 quadrats in the same experimental plot, the nine 1-m^2 quadrats with the same treatment, and the three 25-m^2 quadrats with the same treatment, respectively. Finally, we calculated the rates of species turnover (appearances and disappearances) for each pair of consecutive years, plus for the ten-years interval 1985-1995, as

$$\text{Rate of appearances} = \frac{b}{a+b+c} \quad \text{and} \quad \text{Rate of disappearances} = \frac{a}{a+b+c},$$

where a = number of species present only in the first year; b = number of species present only in the second year; c = number of species present in both years.

9.3. Results

Treatment effects on the whole species composition

The vegetation of the experimental plots was determined to a comparable degree by the factors treatments, blocks, time and by the treatment-by-time interaction, i.e. all these factors explained an important fraction of the total variance in species composition (Fig. 3). The treatment-by-time interaction was mostly due to an increase in treatment effects over the years. Indeed, the fraction of variance explained by treatments was small and non-significant in 1982 (Fig. 4). It increased thereafter, and significant treatment effects ($p < 0.05$) could be found from 1984 for Cudrefin and from 1995 for Portalban. The contrast between mown plots (either in summer or in winter) and controls accounted for most of the increase in the explained variance. Plots mown in summer and plots mown in winter hardly differed throughout the observation period. Treatments and treatment-by-time interactions explained together 10.5 % of the variance during the first four years of the experiment (data subset 1) in Cudrefin, and 18.1 % in Portalban. If the first and the last two years were compared (subset 2), 17.9 % of the variance were explained by treatments and treatment-by-time interactions in Cudrefin, and 24.1% in Portalban. The effect of treatments on species composition, as assessed by these models, was significant in both data subsets and for both sites ($p < 0.01$).

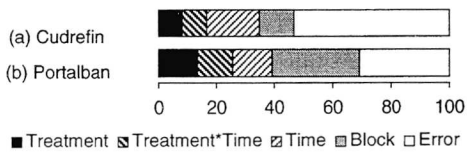

Fig. 3. Decomposition of the variance in the whole data set. Bar sections represent the fraction of the total sum of squares accounted for by each factor.

Table 1. Correlations between the adjusted abundances of the species (percentage cover in the relevés) and the treatment-by-time interactions, based on RDAs calculated for three different time periods. A positive coefficient indicates that the species was favoured by the treatment in the time period considered. Coefficients were only given for a species and time period, if the treatment and treatment-by-time variables explained at least 10% of the variance in the abundances of the species. If more than 20% variance were explained, coefficients are boldface.
(a) = Cudrefin, (b) = Portalban.

(a)	Summer * Time			Winter * Time			Control * Time		
Time period	82–85	82–96	96	82–85	82–96	96	82–85	82–96	96
Agrostis alba		0.65	**0.92**		0.03	**-0.11**		-0.67	**-0.81**
Calamagrostis epigeios	0.89			-0.34			-0.55		
Carex elata	**0.83**	0.85	**0.93**	**0.05**	-0.16	**-0.15**	**-0.88**	-0.68	**-0.78**
Carex flava	-0.59	0.77	**0.98**	0.00	-0.30	**-0.32**	0.59	-0.46	**-0.66**
Carex panicea	0.73		-0.08	0.17		-0.82	-0.90		0.89
Eleocharis palustris		**0.90**	**0.90**		**-0.24**	**-0.07**		**-0.66**	**-0.83**
Equisetum palustre			0.50			0.50			-1.00
Galium palustre			0.94			-0.19			-0.76
Juncus alpinus	**0.16**	**0.52**	**0.49**	**0.71**	**0.48**	**0.37**	**-0.88**	**-1.00**	**-1.00**
Lathyrus paluster	-0.44			0.95			-0.51		
Lysimachia vulgaris			**0.43**			**0.56**			**-1.00**
Lythrum salicaria	0.79			0.10			-0.90		
Mentha aquatica	0.46	0.57	0.49	0.50	0.40	0.38	-0.95	-0.97	-1.00
Molinia coerulea		**0.07**	**0.10**		**0.82**	**0.81**		**-0.90**	**-0.91**
Phragmites communis	**0.38**		**0.70**	**0.56**		**0.27**	**-0.95**		**-0.97**
Salix spec.	-0.50			1.00			-0.50		
Stachys palustris	-0.76			0.88			-0.11		
Taraxacum palustre		**0.89**	**0.91**		**-0.08**	**-0.09**		**-0.81**	**-0.82**

Species with less than 10% variance explained in all time periods
Carex lasiocarpa, Cirsium palustre, Epipactis palustris, Gentiana pneumonanthe, Hydrocotyle vulgaris, Peucedanum palustre, Phalaris arundinacea, Rhamnus cathartica, Sanguisorba officinalis, Scutellaria galericulata, Senecio paludosus, Thalictrum flavum

(b)	Summer * Time			Winter * Time			Control * Time		
Time period	82–85	82–96	96	82–85	82–96	96	82–85	82–96	96
Agrostis alba	0.69	**0.81**	**1.00**	-0.53	**-0.33**	**-0.50**	-0.16	**-0.48**	**-0.50**
Carex panicea		0.90	**1.00**		-0.44	**-0.50**		-0.46	**-0.50**
Cirsium palustre	0.94	**0.95**	**0.87**	-0.27	**-0.22**	**0.00**	-0.67	**-0.73**	**-0.87**
Cladium mariscus		**-0.53**	-0.66		**-0.31**	-0.33		**0.85**	0.98
Epilobium palustre	-0.33		**-0.50**	-0.53		**-0.50**	0.86		**1.00**
Epipactis palustris	**0.97**	**0.95**	**0.94**	**-0.35**	**-0.26**	**-0.19**	**-0.62**	**-0.69**	**-0.76**
Equisetum palustre	**-0.52**	-0.54	**-0.50**	**0.92**	0.88	**1.00**	**-0.40**	-0.34	**-0.50**
Eupatorium cannabinum	**-0.45**	-0.45		**0.91**	-0.45		**-0.45**	0.89	
Euphorbia palustris	**0.91**	**0.89**	**1.00**	**-0.45**	**-0.45**	**-0.50**	**-0.45**	**-0.45**	**-0.50**
Filipendula ulmaria	**0.87**	**0.91**	**1.00**	**-0.43**	**-0.46**	**-0.50**	**-0.43**	**-0.46**	**-0.50**
Frangula alnus	**0.57**	**0.34**	0.50	**-0.82**	**-0.67**	-1.00	**0.25**	**0.33**	0.50
Galium palustre		0.20	**0.50**		-0.62	**-1.00**		0.43	**0.50**
Gentiana pneumonanthe	-0.07	**-0.45**	**-0.50**	0.82	**0.89**	**1.00**	-0.75	**-0.45**	**-0.50**
Hydrocotyle vulgaris	**0.90**	-0.05	0.37	**-0.11**	0.86	0.62	**-0.79**	-0.80	-0.99
Juncus alpinus	**-0.51**	0.95		**0.88**	-0.47		**-0.37**	-0.47	
Lythrum salicaria	**0.82**	0.49	0.50	**-0.08**	0.00	0.50	**-0.74**	-0.49	-1.00
Mentha aquatica	0.07			0.73			-0.81		
Molinia coerulea	**0.26**	**0.45**	**0.25**	**0.65**	**0.48**	**0.72**	**-0.91**	**-0.93**	**-0.96**
Orchis incarnata	**0.70**	0.13	0.50	**0.19**	0.54	0.50	**-0.89**	-0.67	-1.00
Peucedanum palustre	0.85		-0.50	-0.88		1.00	0.04		-0.50
Phragmites communis		0.91	**0.61**		-0.23	**0.38**		-0.67	**-0.99**
Pinus silvestris	0.27	-0.78	-1.00	0.53	0.89	0.50	-0.80	-0.11	0.50
Salix spec.	**0.88**	0.80	**1.00**	**-0.44**	-0.40	**-0.50**	**-0.44**	-0.40	**-0.50**
Schoenus ferrugineus	**-0.50**	-0.39		**0.80**	0.00		**-0.29**	0.39	
Schoenus nigricans	**0.32**	0.75	**0.50**	**0.60**	0.19	**0.50**	**-0.92**	-0.94	**-1.00**
Scutellaria galericulata	0.64		0.50	0.24		0.50	-0.89		-1.00
Senecio paludosus		-0.59	**-0.50**		-0.34	**-0.50**		0.93	**1.00**
Stachys palustris	**0.87**	**0.76**		**-0.43**	**-0.38**		**-0.43**	**-0.38**	
Taraxacum palustre	**0.51**	1.00	**1.00**	**-0.88**	-0.50	**-0.50**	**0.37**	-0.50	**-0.50**

Species with less than 10% variance explained in all time periods:
Carex elata, Lycopus europaeus, Thalictrum flavum

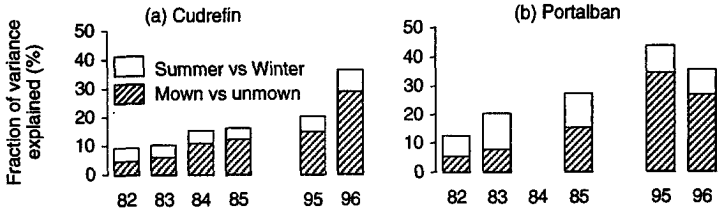

Fig. 4. Fraction of the variance in species composition explained by treatments in each year from 1982 to 1996. Treatment effects began to significant ($p < 0.05$) in 1984 in Cudrefin and in 1995 in Portalban. The explained variance was decomposed into two contrasts, i.e. 'unmown' versus 'mown' (hatched) and 'mown in summer' versus 'mown in winter' (white).

Table 2. Comparison of the effects of treatments on species abundances in different time periods; (a) 'short-term' versus 'long-term' and (b)'retrospective' versus 'long-term'. For each comparison and site it is indicated how many species responded to the treatments (at least 10% variance explained) in both periods (yes / yes), only in one period (yes / no ; no / yes), or in none of the periods (no / no)

		(a) Short-term (82–85)				(b) Retrospective (1996)			
		Cudrefin		Portalban		Cudrefin		Portalban	
	Response	yes	no	yes	no	yes	no	yes	no
Long-term	yes	4	4	20	5	8	0	21	4
(82–96)	no	7	15	4	3	5	17	3	4

Treatment effects on individual species

In each data subset only part of the species responded 'significantly' to the treatments according to our threshold of 10% explained variance (Table 1). In Cudrefin, treatment effects were found for 11 species in the 1982–85 data, for 8 species in the 1982–96 data, and for 13 species in the 1996 data. In Portalban, the numbers were 25, 24 and 27, respectively. Which species responded significantly to the treatments differed among the time periods (Table 2). Only few species showed both short-term and long-term treatment effects in Cudrefin. The total number of species with a significant response in at least one of the three data subsets was 18 (of 30) in Cudrefin and 29 (of 32) in Portalban. Thus, treatment effects on species composition were stronger and more consistent over different time periods in Portalban than in Cudrefin.

If responses could be assessed in two or three time periods (data subsets) for a species, then the ranking of the three treatments was mostly consistent across these periods. In other words, if a treatment favoured a certain species

in one time period, it was unlikely to be detrimental in the other time periods. This was even true if the responses to mowing in summer and to mowing in winter were compared with each other: If mowing in summer was more favourable than mowing in winter in one time period, it was likely to be more favourable in the other time periods, providing responses explained more than 10% variance in the respective data subsets.

Nevertheless, the proportion of species (among those with 'significant' responses) that responded positively to the each of the treatments differed between the 1982–85 and the 1982–96 data subset (Table 3). These differences were mainly due to species fulfilling the '10% explained variance' criterion in only one of the two time periods. A positive response to the winter treatment was found for a higher proportion of species in the 1982-85 data than in the 1982-96 data, i.e. the winter treatment seemed to be more favourable on the short term than on the long term. Conversely, the summer treatment appeared more favourable on the long term than on the short term in Cudrefin, and approximately equivalent in both time periods in Portalban. The retrospective assessment (1996 data subset) yielded results that were partly similar to the short-term assessment, partly similar to the long-term assessment, and intermediate in one case.

If treatment effects were evaluated based on counts of shoots, leaves or inflorescences, results were basically the same: the short-term and the retrospective assessment were not more reliable (i.e. more similar to the long-term assessment) than those based on the percentage cover (data not shown in detail here). Moreover, the number of species that could be evaluated was much lower because most species occurred too rarely in the subplots used for

Table 3. Number of species responding positively or negatively to each of the treatments in the three data subsets (a) in Cudrefin and (b) in Portalban. A response was counted if treatments explained at least 10% variance for that species and that data subset (Table 1) and if the correlation coefficient was higher than 0.10 in absolute value.

	Summer			Winter			Control		
	82–85	82–96	96	82–85	82–96	96	82–85	82–96	96
(a) Cudrefin									
Species with $r_{ik} > 0.10$	7	7	12	8	3	6	1	0	1
Species with $r_{ik} < -0.10$	4	0	0	1	4	5	10	8	12
% positive responses	64	100	100	89	43	55	9	0	8
(b) Portalban									
Species with $r_{ik} > 0.10$	17	17	17	11	7	11	3	6	6
Species with $r_{ik} < -0.10$	5	7	7	12	16	12	20	19	18
% positive responses	77	71	71	48	30	48	13	24	25

counts. Only 14 species in Cudrefin (5 species in Portalban) had been found in more than five of the subplots and could be analysed. For these species, data subsets in which 'significant' treatment effects were found based on counts partly differed from subsets in which percentage cover had revealed significant treatment effects. If 10% variance were explained with both methods for a certain species and a certain data subset, the ranking of the treatments was not necessarily the same, particularly if inflorescences had been counted. Thus, counts were complementary to cover estimates, rather than being superior.

Species richness

Species numbers were similar across treatments at the beginning of the experiment, but after 14 years (1996), they differed among treatments ($p < 0.05$). The mown plots were more species-rich than the controls ($p < 0.05$), whereas differences between the summer and winter treatment were not significant. These results were equally valid for both sites, but the details of species dynamics strongly differed between them.

In Cudrefin, treatment-by-time and block-by-time interactions were significant in the whole data set, but none of the main effects (Table 4a). Block effects strongly increased during the first years of the experiment, but decreased afterwards. Treatment effects increased steadily (Fig. 5a). Therefore, a significant block effect would have been found in 1985, but no treatment effect, and just the opposite in 1996 (Table 5a). As the increase in treatment effects was small until 1985, neither this effect not the treatment-by-time interaction was significant if only data from 1982-1985 were considered (data not shown).

In Portalban, species numbers already varied strongly in 1982, but almost exclusively due to high block effects (Fig. 5b). Treatment effects increased until 1985 and did not change any more after that year. All main effects and interactions were significant in the whole data set (Table 4b). Both treatment and block effects were found in 1996 (Table 5b). In 1985, the contrast between mown and unmown plots, accounting for most of the variance among treatments, appeared to be significant, even though the overall treatment effect was just not ($p=0.06$; Table 5b). With only data from 1982-1985, the treatment effect was not significant, but the treatment-by-time interaction was ($p < 0.05$; data not shown).

Differences in species richness between mown and unmown plots depended on plot size in Cudrefin (cf. Fig. 6): in 1996, at the 1-m^2 scale, mown plots had on an average 1.69 times the species number of unmown plots. This ratio decreased to 1.55 at the 3-m^2 scale, 1.58 on 9 m^2, 1.25 on 25 m^2 and 1.20 on 75 m^2, and no treatment effects would have been detected if only the 25-m^2 plots had been investigated (ANOVA, $p > 0.05$). In Portalban, the ratio of species richness was 1.23–1.31 at all spatial scales, but the variability in species numbers was larger on small plots and no treatment effects would have been detected if only the 1-m^2 plots had been investigated ($p > 0.05$).

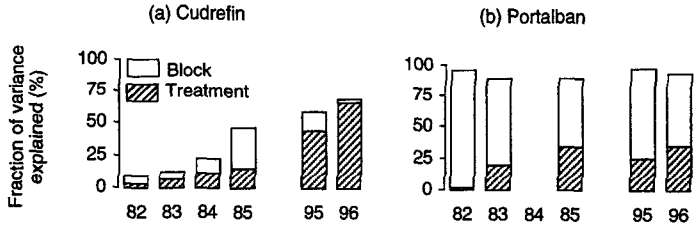

Fig. 5. Fraction of the total variance in the species richness explained by treatments and blocks (a) in Cudrefin, in 1-m^2 quadrats, and (b) in Portalban, in 25-m^2 quadrats.

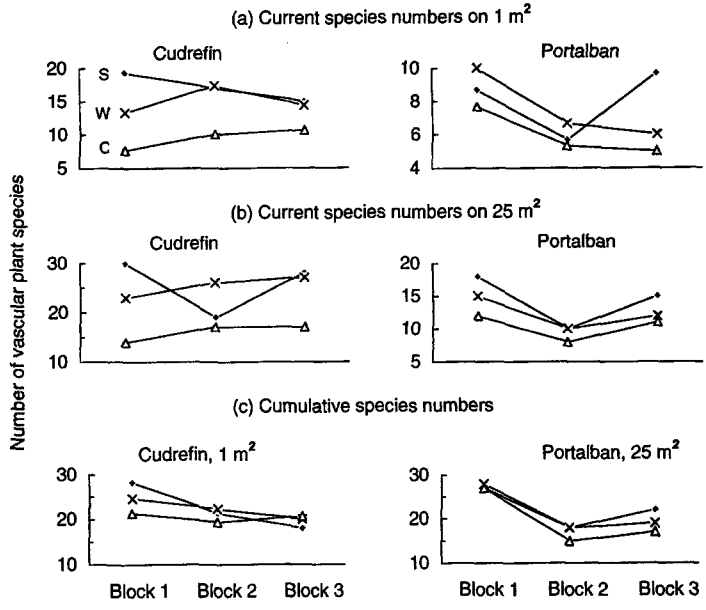

Fig. 6. Interaction plots showing the effects of treatments and blocks on species richness (a, b) in 1996, in quadrats with different size and (c) from 1982 to 1996, counting the total number of species recorded in at least one year during that period. Symbols are:◆: Summer-cut; X: Winter-cut; Δ: Control. Consistent differences between mown and unmown plots were only apparent for current species numbers, and only for the small quadrats in Cudrefin, but for the large quadrats in Portalban.

Table 4. Repeated measures analysis of variance of species numbers (a) in the 1-m^2 quadrats in Cudrefin and (b) in the 25-m^2 quadrats in Portalban, with data from all years.

Source of variation	(a) Cudrefin d.f.	MS	*F* ratio	*P*	(b) Portalban d.f.	MS	*F* ratio	*P*
Between subjects								
Treatment	2	114.38	3.26	ns	2	43.47	7.05	<0.05
Block	2	0.82	0.06	ns	2	201.60	32.69	<0.01
Error	4	35.13	2.49		4	6.17		
Within subjects								
Time	5	21.79	1.88	ns	4	29.17	5.54	<0.05
Time * Treatment	10	20.93	8.43	<0.001	8	3.97	3.40	<0.05
Time * Block	10	11.62	4.68	<0.01	8	5.27	4.51	<0.01
Error	20	2.48	1.53	ns	16	1.17		

Table 5. Analysis of variance of species numbers (a) in the 1-m^2 quadrats in Cudrefin and (b) in the 25-m^2 quadrats in Portalban, after the first four years of the experiment (1985) and after 14 years (1996).

Source of variation	1985 d.f.	M.S.	*F* ratio	*P*	1996 M.S.	*F* ratio	*P*
(a) Cudrefin							
Treatment	2	10.11	1.43	ns	137.93	9.07	<0.05
mown versus unmown	1	16.67	2.36	ns	257.85	16.96	<0.05
summer versus winter	1	3.56	0.50	ns	18.00	1.18	ns
Block	2	22.11	8.29	<0.01	6.37	1.42	ns
Treatment*Block	4	7.06	2.65	ns	15.20	3.39	<0.05
Error	18	2.67			4.48		
(b) Portalban							
Treatment	2	19.11	6.14	ns	14.11	11.04	<0.05
mown versus unmown	1	37.56	12.07	<0.05	22.22	17.39	<0.05
summer versus winter	1	0.67	0.22	ns	6.00	4.70	ns
Block	2	30.78	9.89	<0.01	24.11	18.87	<0.01
Error	4	3.11			5.11		

If the ratio was calculated with cumulative species numbers instead of current species numbers, it was only 1.12 in Cudrefin (1 m^2) and 1.14 in Portalban (25 m^2), and no treatment effects were found ($p > 0.05$).

The species turnover (Fig. 7) was highest for the control plots in Cudrefin, mainly because of high rates of species disappearances. The rates of species appearances were similar across treatments. Conversely, the turnover was highest for winter-cut plots in Portalban. Many new species appeared until 1985 and disappeared between 1985 and 1995. At both sites, the turnover rate for the ten-years period from 1985 to 1995 was about 1.5 times the average annual rate until 1985 in both sites. The turnover rates between 1995 and 1996 were similar to those found during the first years of the experiment.

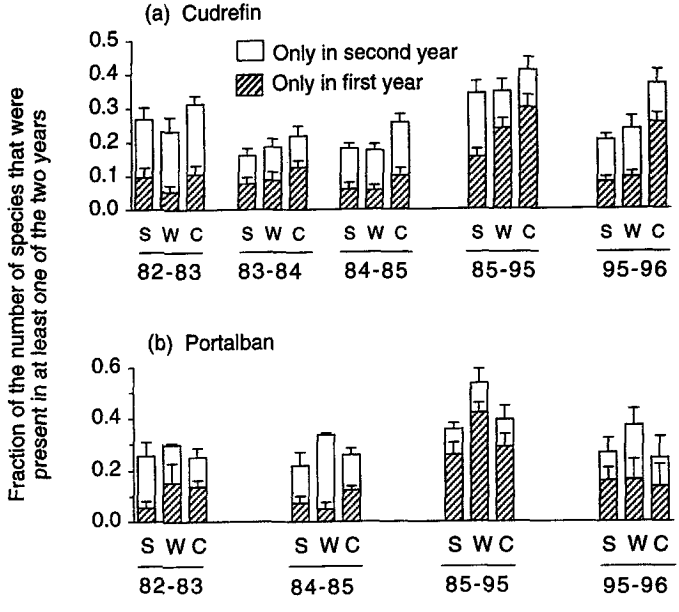

Fig. 7. Average rates of species turnover (a) in the 1-m^2 quadrats in Cudrefin and (b) in the 25-m^2 quadrats in Portalban. For each pair of years, the fraction of species present only in the first year (disappearances) and the fraction of species present only in the second year (appearances) is indicated by the dark and the light grey bars, respectively, together with the standard errors. The total length of the bars represents the rate of turnover.

9.4. Discussion

Short-term versus long-term investigations

Four years after the beginning of the experiment, some treatment effects on the species composition could be established. Treatments explained an increasing fraction of the variance in species composition and species richness, although for species richness this increase was only significant in Portalban. However, if species were considered individually, short-term treatment effects went along with significant long-term effects only for part of them. Thus, the short-term assessment allowed to detect treatment effects at the community level, but it was rather unreliable at the level of individual species.

The 'retrospective' assessment (based on species distribution in 1996) seemed slightly more reliable than the short-term assessment. Treatment effects on species composition and on species richness were significant at both sites, and treatment effects on individual species tended to be more consistent with the long-term changes than effects determined using the 1982–85 data. However, if a retrospective assessment had been attempted after only four years, i.e. in 1985, hardly any treatment effect would have been found. Thus, a 'space-for-time substitution' was only possible if the experiment had lasted for a sufficiently long time period.

We attempted to control spatial heterogeneity through the block design and to reduce the influence of fluctuations on the results by assessing treatment effects with linear models (treatment-by-time interactions). Nevertheless, delayed responses to treatments and unimodal species dynamics did occur. Discrepancies between short-term and long-term responses were probably not due to the low accuracy of percentage cover estimates (Sykes *et al.* 1983), since short-term treatment effects based on counts were not more reliable than those based on percentage cover. This, together with evidence from other experiments (e.g. Tilman 1987b; Magnuson *et al.* 1991) suggests that using even more exact methods to quantify abundances, such as point quadrats (e.g. Stampfli 1991), would not have noticeably improved the predictive value of the short-term assessment. Likewise, using a higher or lower threshold to define 'significant' responses in RDA (instead of 10% explained variance) would hardly have modified the results. With a lower threshold more species would have been found to respond both in the 1982–85 data and in the 1982–86 data, but there would have been more contradictory responses (a treatment appearing favourable in one period and unfavourable in the other). A higher threshold (e.g. 20%, boldface coefficients in Table 1) would have reduced the number of interpretable responses without improving the consistency among the data subsets. The value of 10% has, of course, no general validity: which threshold is appropriate depends on the spatial and temporal heterogeneity, but also on the number and type of variables in the RDA model (ter Braak & Wiertz 1994).

All together, results suggest that differences between short-term and long-term treatment effects were not due to the methods used, but that species

actually responded differently to treatments in the first years and later on. According to Pickett (1991), differences between short-term and long-term observations occur if the phenomena observed depend on slow processes or on rare events, if they are weak compared with background variation or if multiple causality occurs. The first and the last case most probably applied to this experiment.

A decisive slow process was the accumulation of litter in the control plots, particularly the litter of *Cladium mariscus* in two of three control plots in Portalban. The inhibiting effect of litter on plant growth and reproduction was most probably responsible for the decrease in species richness and in the abundance of most species in the control plots (Wheeler & Giller 1982; Carson & Peterson 1990; Facelli & Pickett 1991; Buttler 1992; Stahel, unpublished).

'Multiple causality' means that different processes control the responses of species to management. For example, dynamics of species reproducing mainly by seeds depends (a) on the survival and vitality of adult plants, (b) on opportunities for seeds in the seed bank to germinate, (c) on chances for seed immigration (d) on the establishment of seedlings and (e) on the ability of adults to form new viable seeds. Which of the processes is relevant, and at which time scale differs among species and depends on local site conditions: mowing - especially mowing in summer - produces a lower and more open vegetation structure (Buttler 1992), which generally enhances seed germination and seedling establishment (Maas 1988). However, this can only influence the species composition if viable seeds are in the soil or if new seeds can immigrate. Many fen species form transient or short-term persistent seed banks (Bakker *et al.* 1996b; McDonald *et al.* 1996; but Schopp-Guth 1997), so that no viable seeds of these species were probably present at our sites, abandoned for a long time. Also, the dispersal ability of many fen species is rather poor (Pegtel *et al.* 1996; Pfadenhauer & Klötzli 1996), so that the probability of seed immigration depends on the distance to other sites with that species and on dispersal mechanisms, e.g. related to management (Strykstra *et al.* 1996, 1997). At our sites, seed immigration was probably low. On the other hand, if management prevents reproduction by seeds, effects on species abundances will be delayed if species are long-lived (e.g. *Gentiana pneumonanthe;* Oostermeijer *et al.* 1994; Krenová & Leps 1996).

Importance of the spatial scale

The choice of plot size is crucial in ecological investigations (Magnuson *et al.* 1991). Only the effect of the spatial scale on (apparent) treatment effects on species richness was investigated in this study. The plot size at which significant treatment effects could be found differed between the two sites.

Relatively high rates of appearances suggest that species moved through the experimental site in Cudrefin. and that most of them could immigrate into all plots, including controls ('species carousel model'; van der Maarel & Sykes 1993). However, species were less persistent in unmown plots (high rates of

disappearances), so that their probability to be present in a particular year in a small quadrat was lower there. As a result, small quadrats were less species-rich in the control plots. Conversely, the probability for a species to be present in a large quadrat was relatively high even in the control plots and species numbers on large quadrats did not differ among treatments.

Which quadrat size yielded more correct results? It was the relatively small size of the experimental plots that allowed species to move among them. This means that species numbers on large quadrats rather underestimated the effect of not mowing by overestimating the species richness of control plots. Large quadrats tended to include species that could immigrate from mown into control plots, but not reproduce within the latter, so that they would probably not be found at abandoned sites without adjacent mown meadows. Small quadrats included such species with a lower probability than large ones and consequently reflected the treatment effects more clearly. The situation would be different in large-scale experiments with little migration among plots with different treatments. Species numbers on large quadrats are less susceptible to small-scale fluctuations and indicate the size of the actual species pool (cf. Pärtel *et al.* 1996) more accurately.

The 'carousel model' did apparently not apply in Portalban. In 1996, at least, the effect of mowing on species numbers seemed to be independent of quadrat size, and it was almost the same for current as for cumulative species numbers. This suggests that the control plots were actually unavailable to part of the species, which could not even immigrate, probably due to the abundant litter (Goldberg & Werner 1983; Maas 1988; Facelli & Pickett 1991).

It is well-known that the adequate size of vegetation relevés depends on the vegetation type and on the research question (cf. Dierschke 1994). Our results indicate that different quadrat sizes may also be necessary to investigate the same question in two similar vegetation types. Quadrats of 1 m^2 appeared preferable in Cudrefin, and quadrats of 25 m^2 in Portalban. The ratio of species numbers on 1 m^2 to species numbers on 25 m^2 was almost the same at both sites (0.61 in Cudrefin, 0.58 in Portalban), but the ratio of the mean species number on 25 m^2 (1996 data) to the total number of species ever found at the respective experimental site differed (0.54 in Cudrefin, 0.29 in Portalban). Thus, quadrats of 1 m^2 in Cudrefin included approximately the same fraction of total species number as quadrats of 25 m^2 in Portalban. This may be one reason for the difference in the preferable scale of investigation. However, our results suggest that the choice of the scale also depends on the dynamics of the species and on whether these dynamics are considered 'noise' or part of the process investigated. If treatments affect the persistence of species within plots, while the mobility of species among plots is thought to be 'noise', as in Cudrefin, small quadrats are preferable. If treatments affect the availability of plots to part of the species, whereas within-plot fluctuations are considered 'noise', as in Portalban, large quadrats are more appropriate.

Not only the choice of plot size, but also the question whether to use current or cumulative species numbers depends on the type of dynamics. Cumulative

species numbers may be a better measure of species richness than current species numbers in communities with high species turnover, e.g. in communities of annuals or in dry vegetation types, whose species composition varies with fluctuations in precipitation (e.g. van der Maarel & Sykes 1993). Fens are expected to be more stable because of their high proportion of perennials. The turnover rates at our sites (20-30%) were, indeed, comparatively low. Cumulative species numbers would still be suitable to detect differences in species richness if differences mainly result from a progressive species enrichment in mown plots. This normally happens when mowing is resumed at abandoned sites (Wolf *et al.* 1984; Briemle & Ellenberg 1994; Prach *et al.* 1996). Contrary to expectation, species loss from control plots was the main treatment effect at our sites, which was not reflected in cumulative species numbers.

Validity and practical significance of the results

Guidelines on the management of fen meadows in Switzerland stated that mowing is indispensable to the conservation of the vegetation of these sites, but that it could be periodic (every 2-3 years) at oligotrophic sites (Wildi & Klötzli 1978; Egloff 1984; Bressous *et al.* 1992). The short-term treatment effects in the present experiment lead Buttler (1992) to the same conclusions and this was confirmed by the long-term effects presented here. However, even after 14 years the species composition was still basically the same under all treatments. This contrasted with results of other experiments involving unmown plots (e.g. Wolf *et al.* 1984; Müller *et al.* 1992; Prach *et al.* 1996) and was probably a consequence of the relatively undisturbed hydrology and the nutrient-poor soil conditions at the study sites. Indeed, positive effects of mowing compared with abandonment are generally stronger at sites affected by drainage or eutrophication than at undisturbed ones (Wheeler 1993; Fojt & Harding 1995). A biennial mowing regime would hardly suffice to prevent eutrophication and a spread of tall herbs in most fens of the Swiss Plateau, where such changes even occur at sites mown in late summer every year (Klötzli 1986; Marti & Müller 1993; Brülisauer 1996; Chapter 4).

The aforementioned guidelines also recommended not to mow fen meadows before October or November, unless they are eutrophicated. Likewise, Buttler (1992) concluded from the short-time treatment effects in this experiment that the winter treatment was most favourable to the vegetation. After 14 years, however, we found no clear difference between the summer and the winter treatment. The summer treatment even tended to be more favourable. Several reasons are likely to be responsible for this result:

1. Mowing in summer is known to increase species richness in wet meadows compared to mowing in winter (Bakker & de Vries 1985; Le Nedic & Moret 1990; Rosenthal 1992; Dumortier *et al.* 1996). However, the immigration of species from more intensive grasslands often contributes to this increase (Egloff 1986; Kapfer & Pfadenhauer 1986; Morgan *et al.* 1983). This was not the case in the present experiment: new species observed in 1995 or 1996

were all typical wetland species. Unlike most fen meadows in the Swiss Plateau, our sites were not adjacent to fertilized farmland, so that species from more intensive grasslands could not immigrate.

2. Experimental sites and the surrounding areas had not been mown for ten years before the beginning of the experiment. As a result, they were rather species-poor compared with other fen meadows (Klötzli 1969). Species depending specifically on mowing in summer or in winter, which might have differentiated treatments more clearly, did probably not occur any more.

3. Late-flowering species are considered particularly sensitive to early mowing (Egloff 1984). No late-flowering species occurred at the study sites, except *Gentiana pneumonanthe*. Moreover, if such species had been present, the biennial mowing regime applied since 1987 would have affected them less than mowing every year would have done.

4. Mowing may modify the soil nutrient status and the character of nutrient limitation (Verhoeven *et al.* 1991, 1996), but such changes only occur over a longer time period (Bakker 1989; van der Woude 1994). Preliminary investigations in our experiments did not reveal any differences between mown and unmown plots with respect to nitrogen mineralization and litter decay (S. Stahel, unpublished). Fourteen years of mowing were apparently too short to produce noticeable changes in the soil.

5. Our evaluation was purely botanical. Many animal species are negatively affected by mowing in summer, either because they are injured by the mowing machinery (Bölscher 1992; Claßen *et al.* 1993, 1996) or because the flowers or vegetation structures on which they depend are removed (e.g. Ost 1979; Oppermann 1987; Bosshard *et al.* 1988; Von Nordheim 1992; Huemer 1996). This aspect would also have to be considered when taking decisions on the management of fen meadows.

9.5. Conclusions

The results of this study confirm that "in order to increase the sensitivity of the investigation, more effort would have to be put in increasing the number of plots studied rather than in increasing their size or the degree of sophistication of the relevé method used" (Wildi & Krüsi 1992). However, it is difficult to predict at which spatial scale treatment effects will be most obvious, and therefore using several plot sizes (nested design) in the first years of an experiment may be recommendable (Magnuson *et al.* 1991). Further, increasing the duration of a management experiment should be preferred to increasing sampling effort in one single year or the frequency of investigations during a few years. Finally, as the treatment effects in our experiment appeared to be related to particular site conditions, they can hardly be used to decide on the management at other sites. Different sites may react differently to the same treatments and therefore, management needs to be planned, assessed, and periodically re-evaluated for each site individually.

10. Conclusions

Phragmites australis, an 'invasive' plant in fen meadows ...

An 'invasive' plant species in the context of nature conservation has been defined in the introduction to this thesis (1)[1] as a species (a) becoming significantly more abundant in a large number of sites, (b) spreading spontaneously, but promoted by human influence, and (c) being likely to affect the conservation value of invaded sites.

The spread of *Phragmites* could not be quantified in this study, due to the lack of reliable comparative data. The presence of the species in lakeside wetlands is obviously not new. However, the available qualitative evidence suggests a significant increase in abundance (3), even though this increase might have been overestimated as a consequence of conservationists becoming increasingly aware of the process. A more detailed monitoring would be highly desirable in the future.

The main human influences affecting the vegetation of fen meadows are management, nutrient input and changes to ground water level. The ground water level (within the range encountered in the fens investigated) appeared not to influence the abundance of *Phragmites* (3), whereas nutrient input and a regular mowing in late summer might both have promoted *Phragmites* (7).

The conservation value was, on an average, negatively related to the abundance of *Phragmites* (3). This relation however, seemed to be mainly due to the higher abundance of tall herbs in sites with high abundance of *Phragmites* (4). There was no indication for a dramatic decrease of conservation value caused by an aggressive spread of this species within the study sites. Effects of *Phragmites* on the other species might become apparent over a longer time period, but they would then be progressive and possibly indirect.

... which needs to be controlled ...

The decision to control an invasive plant species depends on the negative impacts expected in case of a (further) increase and on the results expected from taking measures (1). The investigations reported in 3 and 4 suggest that the question must be discussed separately for the alliances *Caricion* and *Molinion* on the one hand, and the alliance *Filipendulion* on the other hand.

In the *Caricion* and *Molinion*, high abundance of *Phragmites* primarily needs to be monitored over a longer time period. No relation between conservation value and abundance of *Phragmites* was found in this study. However, this might be due to the relatively small sample (136 plots) and to the rather low

[1] Underlined numbers refer to the chapters of the thesis and to the references therein. For the sake of brevity references have not been cited again in this chapter.

abundance of *Phragmites* in these alliances compared with the alliance *Filipendulion* or with pure stands of *Phragmites* (cf. 3, 8 and references therein). The abundance was possibly too low for noticeable effects on species composition. More importantly, however, increasing abundance of *Phragmites* seemed associated with a shift towards the alliance *Filipendulion,* rather than with a decrease of conservation value within the alliances *Caricion* and *Molinion* (3, 4). This means that the effect of *Phragmites* on the conservation value of fen meadows was not assessed correctly by only comparing the species richness or species rarity of plots *currently* classified as *Caricion* or *Molinion.*

There was some evidence suggesting that a spread of *Phragmites* might actually trigger a shift towards the alliance *Filipendulion,* i.e. promote tall herbs within *Caricion* or *Molinion* communities. *Phragmites* could do so either by increasing nutrient availability (e.g. by "pumping" nutrients from deeper soil layers to soil surface, cf. 3) or by modifying the relative competitive ability of species with its shade (5). An influence of *Phragmites* on the nutrient economy of these communities would probably be more detrimental than the moderate shading observed at the study sites. In any case, more experimental work is needed to determine whether any of the mechanisms suggested in Chapters 3 and 5 can actually cause a significant promotion of tall herbs by *Phragmites* in fen meadows. If so, a spread of *Phragmites* should be prevented as far as possible.

Monitoring the abundance of *Phragmites* should include measurements of both shoot size and shoot density (8), because shoot size differs more among the alliances than shoot density (3). The abundance of tall herbs must also be considered. Particular attention should be paid to possible changes in soil conditions (especially nutrient availability), because such changes are difficult to reverse (6). They might be either the cause or the consequence of a spread of *Phragmites* (3, 7). The present study suggests that nitrogen might be a key factor. On the one hand, the availability of this element appeared more likely to be influenced by the presence of *Phragmites* than the availability of phosphorus (3). On the other hand, there were indications that *Phragmites* might be promoted by nitrogen inputs more than by phosphorus inputs (7). But again, these are hypotheses calling for experimental confirmation.

In the alliance *Filipendulion* higher abundance of *Phragmites* was directly related to lower conservation value, i.e. lower species richness and a lower proportion of characteristic mire species (3). This relation appeared to be relatively independent of site productivity (4) and competition between *Phragmites* and other species seemed decisive (3, 4). Therefore, reducing the abundance of *Phragmites* appeared likely to increase the conservation value of such sites and rather unlikely to decrease it. Therefore, it is in *Filipendulion* communities that management to reduce the abundance of *Phragmites* should be applied with first priority. Whenever such measures are taken, it is essential to monitor both changes in the abundance of *Phragmites* and in species

composition. A long-term monitoring (at least ten years) is necessary to assess whether a reduction of *Phragmites* and the expected enhancement of conservation value actually occur (cf. 7, 8 and 9), and whether they justify the additional management effort. Indeed, reducing *Phragmites* at strongly invaded *Filipendulion* sites can hardly be expected to lead to a high botanical conservation value (4, 6). Thus, it may (at least in some cases) be more efficient to reduce the frequency of mowing at such sites, which is likely to increase their faunistic conservation value, and to use the available financial means for the maintenance of remaining *Molinion* and *Caricion* sites (6).

... by mowing in summer?

In decisions about management, the effect on the abundance of *Phragmites* is only one aspect, and the results of this study suggest that it is probably not the most important aspect. The presence of tall herbs or grasses was found to be decisive for the conservation value of sites (3). Mowing twice slightly increased the species richness compared with mowing once, as in other experiments conducted under similar conditions (7). No obvious change in species composition (e.g. a shift towards species of other vegetation types) occurred in our experiments (7). Thus, the short-term effect of mowing twice appeared favourable, but on the long term certain typical fen plant species might be suppressed and replaced by species more adapted to early mowing. If possible, such an effect should be avoided.

Mowing in June and in September appeared suitable in productive tall-herb vegetation, where the first aim of management is to create better light conditions for the smaller fen species by reducing overall aboveground biomass. However, this management might not be optimal for only slightly degraded fen meadows that still belong to the alliances *Caricion* or *Molinion*. At the end of August, several fen plant species flowered in plots that had been mown in June, e.g. *Parnassia palustris, Succisa pratensis* or *Serratula tinctoria*. The second cut in early September prevented these species from setting seeds. It seems likely (though not sure) that such a treatment would, on the long term, lead to their disappearance due to a lack of generative reproduction.

Therefore, mowing in June and October would possibly be preferable to mowing in June and September in *Caricion* or *Molinion* meadows. Postponing the second cut until October would probably not significantly reduce the total amount of nutrients removed. In plots that had already been mown in June the vegetation appeared to be still in full growth at the end of August (7), which suggested that only a moderate translocation of nutrients would take place during September. This (presumably moderate) translocation would probably benefit *Phragmites* even less than the other species, since the second harvest contributed less to the total nutrient removal for *Phragmites* than for the other species. Mowing a second time in October would probably allow some of the late-flowering species to complete their annual cycle and, therefore, also be

preferable for various rare insects depending on these plants (references in 9). It would, therefore, be useful to include such a treatment in further mowing experiments and to observe particularly the phenology of the target species.

Additional mowing in June every two years might be preferable to additional mowing every year. This treatment was included in our experiments (7), but after only three years it was not possible yet to evaluate the results (9). Mowing only in June would not be a suitable treatment, as litter would then be present in the following spring and inhibit the growth of small species (references in 9). Mowing only in September seemed not optimal either, because *Phragmites* could already translocate an important part of its nutrients from shoots to below ground parts, and appeared, therefore, to be promoted (7).

All together, results suggest that in fen meadows of the alliances *Caricion* and *Molinion*, annual mowing in September should possibly be replaced by annual mowing in October, associated with an additional cut in June every two or three years (depending on site productivity). If a reduction of *Phragmites* is desired, mowing in June and October might be combined with short periods of grazing by horses or robust cattle in August. At this time the soil is generally dry, and the vegetation is low due to the June cut, so that trampling damage should be limited. The easily accessible young shoots of *Phragmites* (7) would probably be selectively grazed (references in 7). First experience with grazing by highland cattle is currently being made in Swiss fens (Hasler 1996a,b), but implementing a combined management (mowing and grazing) might be an other interesting and profitable experiment for nature conservation.

This thesis has shown how complex and variable the relation between *Phragmites*, fen vegetation and management is. Other studies indicated a similar – if not greater – complexity in the relation between these three elements and the fauna[2]. All available evidence strongly suggests that there is no unique optimal management for reed-invaded fen meadows. Not only does the effect of management depend on several factors, particularly on the vegetation type, the groundwater level and the nutrient supply (6, 7). Spatial and temporal variation in management may be favourable in itself, an idea that is increasingly considered in management plans for nature reserves (A. Keel, pers. comm.). A more variable and flexible management would reflect the dynamic and unpredictable nature of vegetation (1) and could probably help to maintain the richness of the flora and fauna in fen meadows.

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[2] For example Bibby & Lunn 1982; Bosshard *et al.* 1988; Ditlhogo *et al.* 1992; Tscharntke 1992; Kampichler *et al.* 1994; Handke & Menke 1995; Klieber *et al.* 1995; Manhart 1995; Radlmair & Laußmann 1997

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1987-1988	Social service in the home Elisabethenheim (Müllheim, Germany).
1988-1994	Studies in Environmental Sciences at the Swiss Federal Institute of Technology (ETH) in Zürich. Specialization in vegetation science, environmental chemistry, human ecology and nature conservation. Practical training (6 months, 1991-1992) at the "Groupe d'Etude et de Gestion Grande Cariçaie" in Yverdon, responsible for the management and monitoring of a wetland reserve. Diploma thesis on "Landscape perception and evaluation by lay people - significance for nature conservation", supervised by Dr. B. O. Krüsi, WSL, Birmensdorf and Dr. G. Dürrenberger, EAWAG, Dübendorf. Diploma obtained in May 1994.
1990-1994	Teacher training at ETH Zürich for high school teaching in biology, chemistry and environmental education. Diploma obtained in May 1995.
1992-1995	Chemistry teacher at various high schools (Deutsches Gymnasium, Biel; Gymnasium Alpenstrasse, Biel; Kantonsschule Zürcher Unterland, Bülach).
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