Nature Management Experiments in a Derelict Reedmarsh. I: Effects of Winter Cutting

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ABSTRACT

Lowering of the summer water table, eutrophication and dereliction have caused severe ruderalisation of the reedmarsh in the important Belgian wetland site of the Blankaart. The reed vegetation has become totally overgrown by competitive species such as Urtica dioica, Calystegia sepium *and* Calamagrostis canescens. *Management experiments conducted from 1978 to 1986 have shown that a regime of annual winter cutting can substantially reduce the ruderal and nitrophilous character of the vegetation and increase species diversity. The process is mostly linked to the correlated effects of litter removal. The changes in the vegetation are influenced by the position in the zonation/succession. It is argued that, for complete restoration of the vegetation, efforts should be made to raise the summer water table and to stop eutrophication and silting of the pond.*

INTRODUCTION

Species diversity in semi-natural vegetation is usually linked with previous traditional (agricultural) management in relation to specific ecological environmental conditions. The effect is mostly due to the suppression of species which are potential dominants.

It is therefore not surprising that 'ruderalisation' is a well known phenomenon in many derelict or abandoned marshes and fens. It is characterised by the invasion of tall growing herbs ('tall forbs'), ruderals, shrubs, etc., and the subsequent decrease of species diversity. These vegetation processes are mostly caused directly by the cessation of

management and/or changing environmental conditions, such as lowering of the water table (drainage) or eutrophication (Westhoff *et al.*, 1971; Klötzli, 1973; Grime, 1979; Wheeler, 1980, 1983; Gryseels & Hermy, 1981; Wheeler & Giller, 1982; Gryseels, 1985; Gigon & Bocherens, 1985; Rowell, 1986).

A clear illustration of this phenomenon is provided by the loss and degeneration of reedmarsh and rich-fen communities at the Blankaart, a wetland site of international importance (recognized by the RAMSAR Convention) in the lowland region of Belgium, and owned by the 'Belgische Natuur– en Vogelreservaten' as a private nature reserve. Management experiments have been carried out in this reserve since 1978.

This paper examines the effects of seasonal cutting on overgrown, abandoned reed and mixed-fen vegetation, which has also been severely affected by eutrophication and lowering of the water table. The effects of winter cutting are reported in Part I, and of summer mowing in Part II (Gryseels, in press).

STUDY SITE

The study site is located approximately 6 km south of Diksmuide (Province of W. Flanders, Belgium), near the south-western edge of the Polders, a lowland, wet area of pastures and waterways on clay, bordered by the intensively cultivated sandy-silt region of higher elevation.

The site itself consists of a nutrient-rich, shallow pond of about 50 ha, dug out of the peat in the 16th century and now surrounded by 20 ha of reed and mixed-fen vegetation. It is located at the floor of a shallow valley, of which the clay-subsoil is covered by peat, up to 1 m thick near the pond. The pond is fed by six rivulets with very nutrient-rich, silty and muddy water while two others connect the pond with the river Yser.

During winter and early spring the whole valley is usually flooded. These winter floodings are very important ecologically as they provide the marsh with additional nutrients. During the vegetative period the water table is normally just at substrate level, but for about 10 years (since 1975) has been severely disturbed by irregular pumping for agricultural purposes (drainage of the valley) and water supply. This has caused a very low water table in summer (up to 20–30 cm below ground level), but has not prevented winter flooding.

The vegetation of the marsh and fen of the Blankaart has been described in detail by Gryseels (1978, 1985). Inundations with salt water for strategic purposes during the First World War transformed the original oligotrophic water and marsh vegetation into a more mesotrophic swamp, marsh and mixed-fen system. However, during recent decades, eutrophication, lowering of the water table, silting of the pond and cessation of traditional

management have led to the disappearance of the former luxuriant aquatic vegetation (e.g. *Nymphaea alba, Nuphar lutea, Callitriche* div. sp., *Lemna* div. sp., *Hydrocharis morsus-ranae*), a major part of the swamp vegetation (*Scirpus lacustris, Typha angustifolia, Phragmites australis*), and to a substantial modification of the marsh vegetation. The reedmarsh and mixed-fen which have succeeded the (still existing) monospecific, dense reed and (local) *Typha angustifolia* stands along the pond side, have been transformed into a ruderalised, highly nitrophilous reed vegetation, a community where *Phragmites australis, Calystegia sepium* and *Urtica dioica* are (co)dominant, with *Calamagrostis canescens* later in the succession. Productivity of the reedmarsh is very high and it yields an enormous amount of litter (up to 30–40 cm thick). Accompanying plants are common marsh species (e.g. *Solanum dulcamara, Rumex hydrolapathum, Lycopus europaeus, Iris pseudacorus, Carex riparia, Mentha aquatica, Rorippa amphibia*) and tall forbs (e.g. *Symphytum officinale, Filipendula ulmaria, Lysimachia vulgaris, Lythrum salicaria, Thalictrum flavum, Valeriana repens*), which usually grow where the litter mat is broken. Grazing by muskrats (*Ondatra zibethicus*) creates open space and leads to the development of a very different, floating raft-like vegetation with *Carex pseudocyperus*. Some interesting marsh plants have become very rare (e.g. *Sium latifolium, Ranunculus lingua, Lathyrus palustris*). Shrubs (mainly willows) are strongly invading the marsh.

The succession stage generally corresponds with the position in the zonation.

METHODS

Sampling

In the ruderalised reedmarsh and fen, 8 experimental plots (100–200 m^2) were chosen, representing different stages in the vegetation succession, sometimes within one plot (Table 1). Each plot was divided into a variable number of permanent quadrats. The vegetation of these plots was cut every winter from 1977–78 until 1981–82. Relevés were made during summer (July–August) from 1978 to 1982, on the basis of the Braun-Blanquet method (Braun-Blanquet, 1964) with the Londo-scale (Londo, 1976).

Due to practical circumstances, the original vegetation could not be described before the first cutting and its exact composition is thus unknown. However, permanent quadrats in uncut vegetation of the same type near the experimental plots have also been described since 1978 and served as controls.

After 1982, cutting continued on plot I, and plot V was cut again in 1984. Relevés of all plots were made again in July 1986, except for plots III and IV.

TABLE 1

Description of the Plots

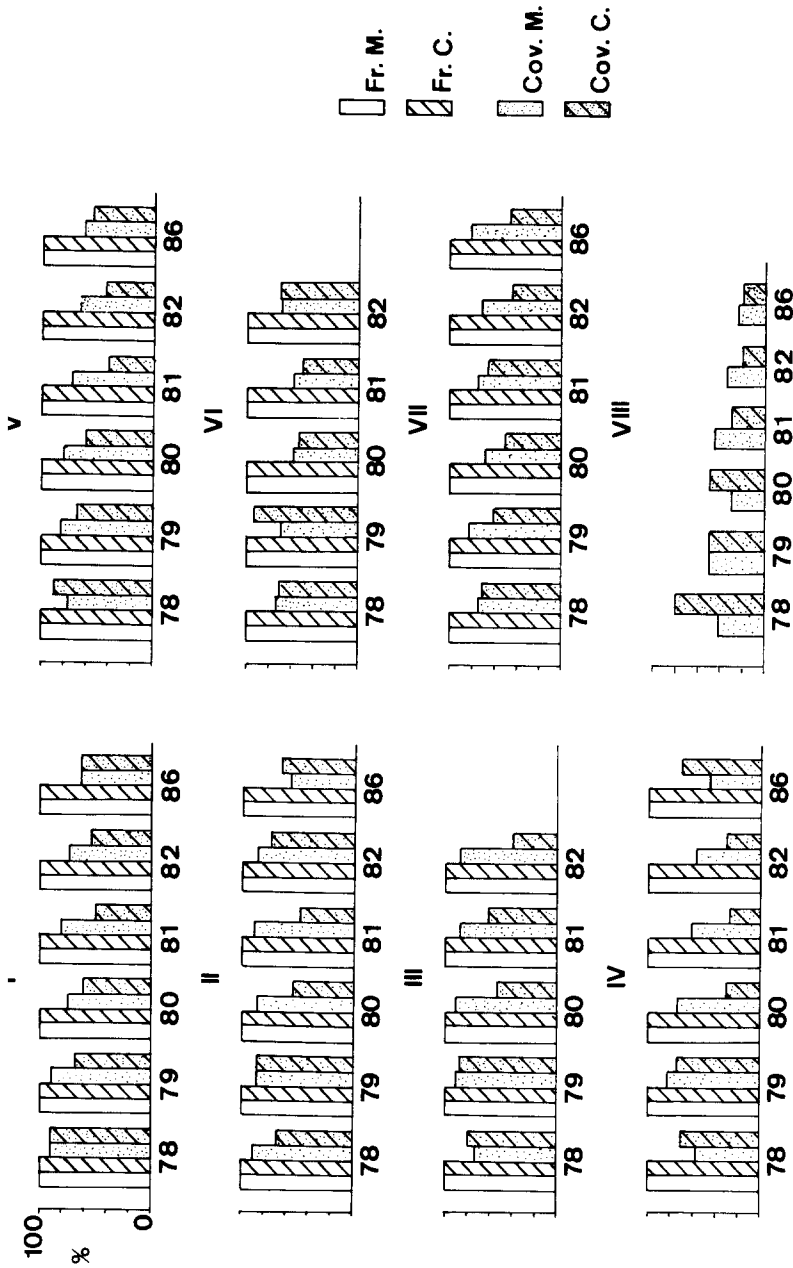|	Plot I	Plot II	Plot III	Plot IV	Plot V	Plot VI	Plot VII	Plot VIII
Surface, m²	300	200	300	150	200	200	100	100
Number of permanent quadrats/ Number of permanent quadrats in control plots	8/4	7/5	9/7	9/3	12/4	8/4	5/4	1/1
Position in the zonation/succession	Full zonation transect along NE-shore	Zonation transect from shore to mixed-fen vegetation		Middle of the succession: between the shore vegetation and the willow shrubs			Isolated plot at the end of the succession	Isolated plot on an old floating raft at the end of the succession
Vegetation type	Transition of the reedswamp dominated by *Phragmites* slightly overgrown by *Calystegia*, into a marsh dominated by *Phragmites*, *Calystegia* and *Urtica*		Same as plots I and II, but more *Calystegia* and *Urtica*	Vegetation of *Phragmites*, *Calystegia*, *Urtica*, locally *Calamagrostis*	Vegetation dominated by *Phragmites*, *Calystegia*, *Urtica*, with other marsh plants and locally transition to *Calamagrostis* mixed-fen vegetation		*Calamagrostis* mixed-fen, no more *Urtica*	*Calamagrostis*-dominated fen
Ecological conditions	Very wet and silty	Very wet and silty	Very wet and silty	Peaty substrate	Peaty substrate	Peat	Peat	Peat
Management	Cut yearly until 1985–86	Cut yearly until 1981–82	Cut yearly until 1981–82	Cut yearly until 1981–82	Cut yearly until 1981–82; cut again in 1983–84	Cut yearly until 1981–82	Cut yearly until 1981–82	Cut yearly until 1981–82
Comment			Not visited in 1986			Not visited in 1986		

All plots have been cut yearly since the winter of 1978–79.

Fig. 1. *Phragmites australis*: frequency (Fr) and mean cover value (Cov) in the managed (M) and control (C) plots (I–VIII).
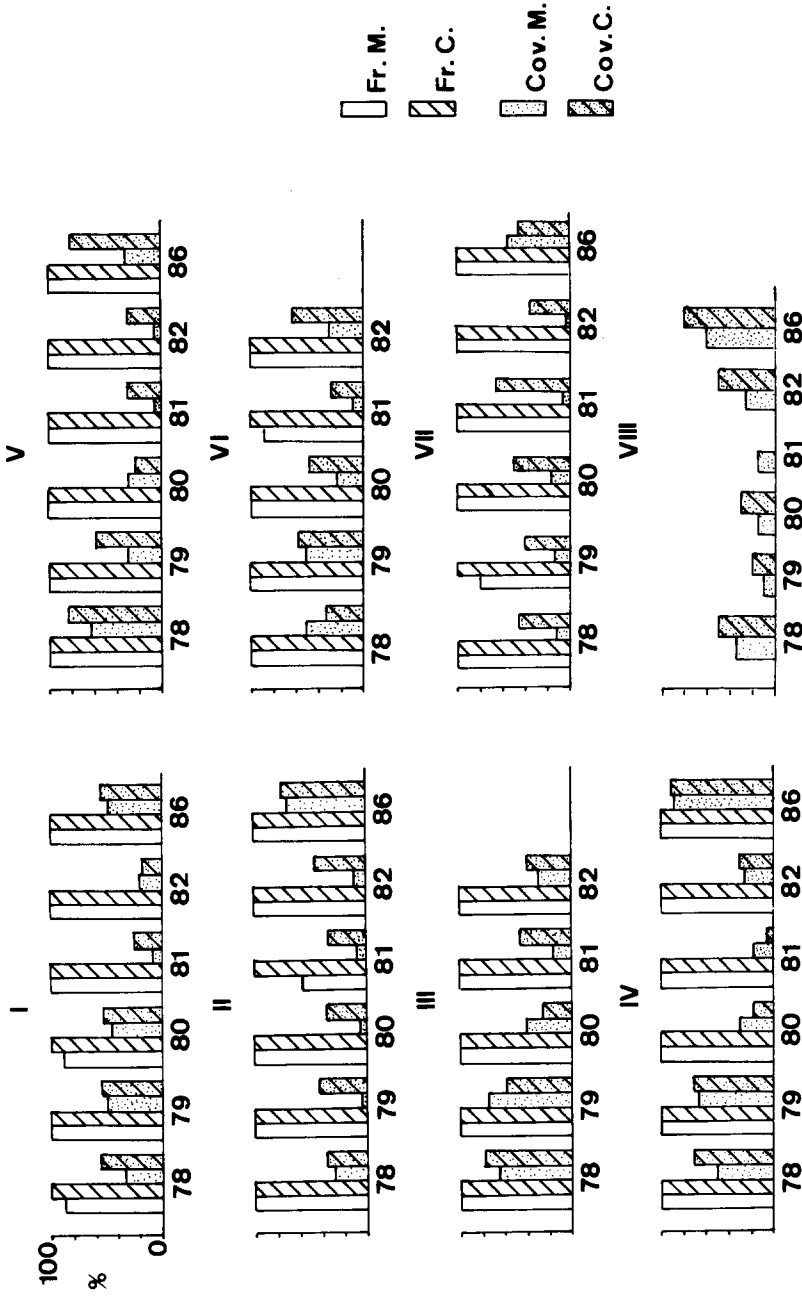
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Fig. 2. *Calystegia sepium*: frequency (Fr) and mean cover value (Cov) in the managed (M) and control (C) plots (I–VIII).
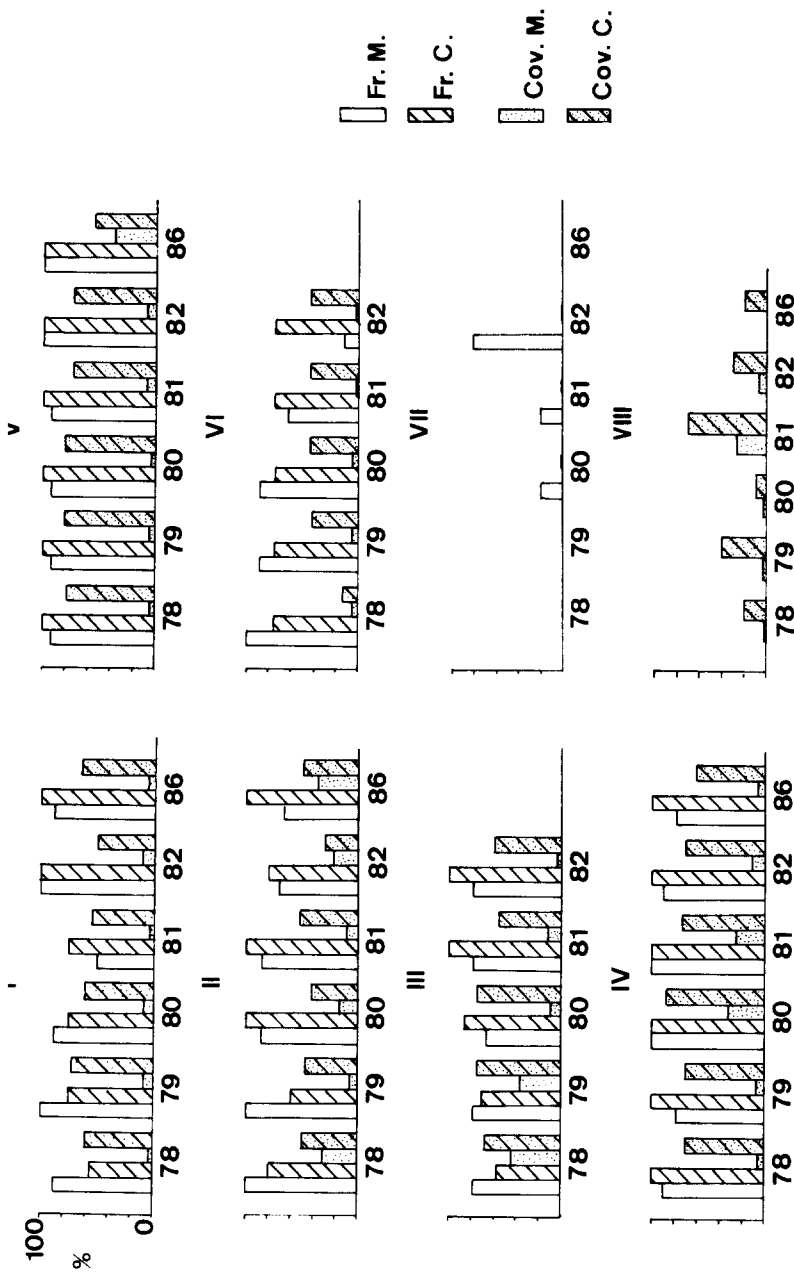
Fig. 3. *Urtica dioica:* frequency (Fr) and mean cover value (Cov) in the managed (M) and control (C) plots (I–VIII).

Analysis

The annual relevés of the permanent quadrats of the eight plots were compared by tables, and were summarised by using 'frequency' and 'mean cover value' (see below) of the species in the quadrats in each plot. These data were used to illustrate the behaviour of original dominant species and the evolution of total species number and species diversity (Figs 1–6).

Data were analysed using various computer programs. The classification of the vegetation samples in tables was obtained by the 'TWINSPAN' program (Hill, 1979a) and samples were ordinated by Detrended Correspondence Analysis (DCA) using DECORANA (Hill, 1979b; Hill & Gauch, 1980). The computer programs were implemented by Hermy (1984). For lack of space only one DCA of the summarised data per plot per year is presented in this paper: the DCA of the relevés (Fig. 7), based on the mean cover value of the species in the plot.

$$\text{Frequency in } \% = \frac{\text{Number of relevés (permanent quadrats) in the plot in which the species is present}}{\text{Total number of permanent quadrats in the plot}} \times 100$$

$$\text{Mean cover value in } \% = \frac{\text{Sum of the cover values (in \%) of the species in the permanent quadrats}}{\text{Number of permanent quadrats in which the species is present}}$$
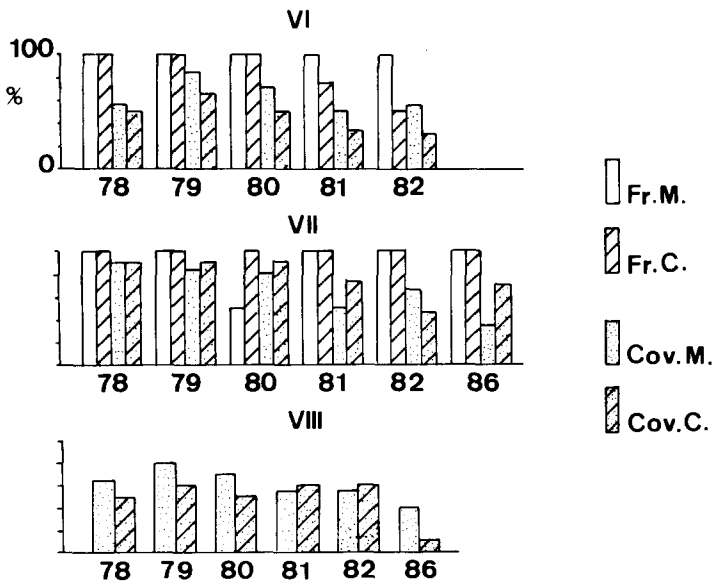

Fig. 4. *Calamagrostis canescens*: frequency (Fr) and mean cover value (Cov) in the managed (M) and control (C) plots (VI–VIII).
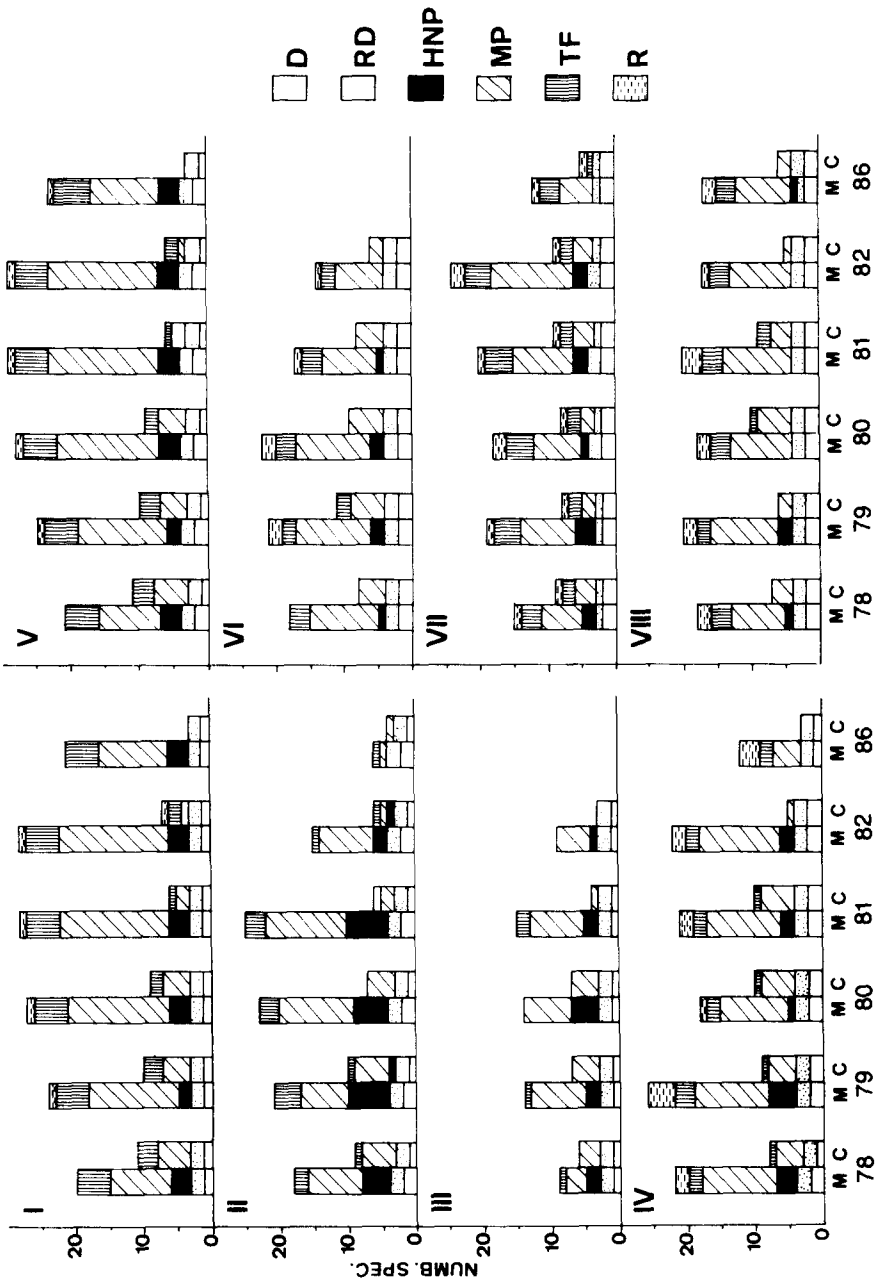
Fig. 5. Change in total species number and species diversity in the different plots. First bar of each year represents the managed plot (M), the second bar represents the control plot (C). D, dominants; RD, ruderal dominants; HNP, hygro-nitrophilous plants; MP, marsh plants; TF, tall forbs; R, rest. (For further explanation on the species groups, see Table 2.)
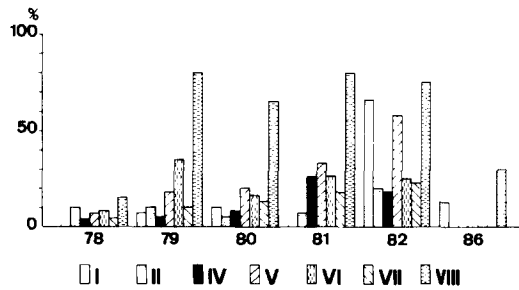
Fig. 6. Mean % cover value of bryophytes in the managed plots (I–VIII). No data are given for plot III (negligible presence of bryophytes).

RESULTS

The effects of cutting are mostly indicated by (1) changes in cover of the (original) dominant species (*Phragmites australis, Urtica dioica, Calystegia sepium, Calamagrostis canescens*) (Figs 1–4), (2) germination, development, higher frequency of a number of species (Fig. 5) and development of a bryophyte layer (Fig. 6).

The vegetation of the unmanaged reedbed changed to a very ruderalised community, in which *Urtica dioica* and *Calystegia sepium* became the dominant species, while reed declined. In contrast, the vegetation of the managed reedbed is evolving into a well-developed reed community, which can be relatively species-rich.
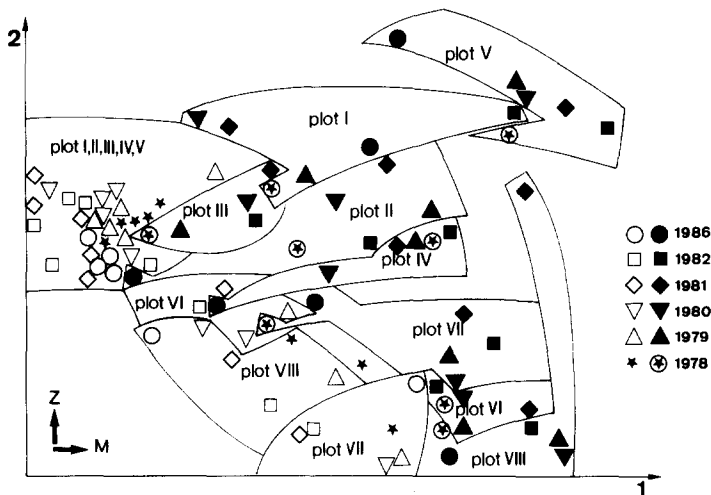

Fig. 7. DCA relevés ordination of the summarized data per plot per year. Arrows indicate two ecological gradients: M, management; Z, zonation. Open symbols, control; closed symbols, managed.

Effect on dominant species

Dominant species in the reedmarsh of the Blankaart all belong to the so-called 'competitors', described by Grime (1979) as plants with great competitive ability, due to their tall stature, extensive lateral spread, large perennating organs, efficient storage organs, rapid extension of leaf and root surface areas. *Phragmites australis* and *Urtica dioica* are typical. Their nature differs according to their different ecology. While *Phragmites* grows here in a normal ecological environment, *Urtica* has to be regarded as a 'ruderal' (not in terms of strategy!) species, illustrating the disturbance of the marsh ecosystem. Grime (1979) has not expressed clear views concerning the strategy of creeping species such as *Calystegia sepium*. In our study, this latter species was seen as a 'competitor', due to the enormous power of vegetative expansion and its ability to reproduce from very small pieces of rhizome. It is, however, similar to *Urtica dioica* in its ruderal character. *Calamagrostis canescens* is to be considered as a 'stress-tolerant competitor'.

In the abandoned reedbed, the cover of *Phragmites australis* (Fig. 1) decreases, in contrast to the cut plots, where it forms a much more vigorous stand. There may be more, thinner stems, and fewer of the very high, thick stems which are regularly found in the unmanaged vegetation. The cut reedbed is more 'homogeneous', of a greater density, composed of healthy, well-flowering plants of the same height (± 2 m). The beneficial effect on reed growth is striking, especially in the wettest plots (I, II, III).

Competition for space and light is also shown in the high presence of *Calystegia sepium* and *Urtica dioica* in the uncut reedbed (Figs 2 and 3). 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. In contrast, these two species are severely restricted in the managed vegetation.

The reaction of *Calamagrostis canescens* is not as clear. A slight increase seems to be followed by a decrease in cover, but a definite decline can also be observed in the uncut controls (Fig. 4). However, the formation of tussocks is more inhibited.

Effect on species richness

Species density is much higher in the cut plots (Fig. 5). Several species groups are responsible for this, each representing a particular phase in the zonation/succession, reflected by their presence in certain plots (Table 2).

'Hygro-nitrophilous' species appear first, mostly therophytes with a high potential growth rate and a ruderal strategy based on rapid curtailment of

TABLE 2

Recognised Species Groups and Their Strategy

Species group	Strategy	Species
Dominants (D)	Competitor Stress-tolerant competitor	*Phragmites australis* *Calamagrostis canescens*
Ruderal dominants (RD)	Competitor (ruderal character)	*Urtica dioica, Calystegia sepium*
Hygro-nitrophilous plants (HNP)	Ruderal Stress-tolerant	*Ranunculus sceleratus, Rorippa islandica, Atriplex prostrata,* *Rumex maritimus, Oenanthe aquatica, Alisma plantago-aquatica, Bidens tripartitus, Polygonum hydropiper, P. persicaria*
Marsh plants (MP)	Different strategies	*Cardamine pratensis, Galium palustre, Scutellaria galericulata, Myosotis cespitosa, M. scorpioides, Poa trivialis, Rorippa amphibia, Epilobium ciliatum, E. parviflorum, E. palustre, Carex pseudocyperus, Rumex hydrolapathum, Lycopus europaeus, Rumex sanguineus, R.conglomeratus, Carex riparia, Iris pseudacorus, Mentha aquatica, Sium latifolium, Polygonum amphibium, Dryopteris carthusiana, Lysimachia nummularia, Typha latifolia, Solanum dulcamara*
Tall forbs (TF)	Competitor	*Lythrum salicaria, Lysimachia vulgaris, Filipendula ulmaria, Valeriana repens, Thalictrum flavum, Epilobium hirsutum, Symphytum officinale*
Bryophytes	Stress-tolerator	*Brachythecium rutabulum, Leptodictyum kochii, L. riparium, Amblystegium serpens, Calliergonella cuspidata, Plagiothecium denticulatum, Eurhynchium praelongum*

Taxonomic nomenclature follows de Langhe *et al.* (1983) and Margadant (1975) for bryophytes.

vegetative growth and diversion of resources into seed production (Grime, 1979). These are the 'pioneers of mud'. Their appearance is most obvious on the open mud-flats in the wettest plots (e.g. plot I) after 2 years of management, when full litter removal has provided open space (e.g. plots II, III). Where *Calamagrostis canescens* is growing (further in the succession), open mud is scarce (only between the tussocks), and so these species are rather rare. In the uncut or only irregularly cut reedbed (Plot V after 1982) hygro-nitrophilous plants are totally absent.

The group of the typical 'marsh plants' includes a wide range of, usually, combined strategy types. The smaller species (e.g. *Galium palustre*, *Myosotis cespitosa*) spread very fast, especially in those plots not located directly at the pond side, and create a homogeneous 'lower field layer' under the higher field layer of reed and other dominants.

Taller marsh plants such as *Carex riparia*, *Rumex hydrolapathum* and *Iris pseudacorus* were mostly already present before the first cutting. After cutting seedlings become frequent, though they mostly remain as juveniles or vegetative in contrast to the unmanaged reedbed, where the few plants present are tall and well-developed. Special note should be made of *Typha latifolia* in plot I, where the species was present from the beginning. After the plot was cut, an enormous vegetative propagation was observed, with more individuals each year, although lower and not as strong as the *Typha* plants in the uncut situation, with the ultimate result that total cover has not significantly changed. Nevertheless, the species tend to suppress the other dominant *Phragmites*, as well as neighbouring marsh species.

'Tall forbs', another group of typical 'competitors', were sparsely represented in the uncut reedbed, but increasing in most of the cut plots, especially in those situated in the middle or at the end of the zonation. However, like the taller marsh plants, they often remain vegetative or juvenile, in contrast to the well-developed individuals in the unmanaged vegetation.

The development of a bryophyte layer in the cut plots is striking, because such a layer is completely absent in the unmanaged vegetation. These bryophytes represent the real 'stress-tolerant ruderal' strategy (Grime, 1979). However, just a few, very common species, mainly *Brachythecium rutabulum*, are present (Table 2).

Effects on the succession phase

The Detrended Correspondence Analysis of the relevés (Fig. 7) shows the effect of cutting in relation to the succession phase in which the plot is located. The ordination gives two important ecological gradients which are responsible for the variation in the vegetation: zonation/succession and

management. The diagonal position of the plots suggests the strong correlation between both ecological gradients. It is clear that the best result is obtained in plot V, situated in the middle of the zonation (Table 1). The divergence between the cut plots illustrates the greater variation and greater species diversity within the managed vegetation, in contrast to the unmanaged vegetation.

Effects after renewed dereliction

In the plots which were derelict after 1982, *Calystegia sepium* again reached high cover values, with a negative effect on the vitality of *Phragmites australis. Urtica dioica* did not recover very fast, and species diversity again decreased, smaller marsh plants and therophytes disappearing.

This is not the case in plot V, which was subjected to an intermittent management regime. Here species diversity is not changing much, while tall forbs and taller marsh plants are reaching their full development. Except for plot VIII, most of the moss layer has been completely destroyed.

Continuing management, as in plot I, does not bring further distinct changes, although *Poa palustris* and *Carex vesicaria*, two interesting marsh plants new for the Blankaart, were first recorded in this plot in 1986. An increase of *Calystegia sepium* was also noticed here.

DISCUSSION

The changing vegetation structure and increasing species diversity: the important role of litter removal

Dominant species
The effect of litter, directly or indirectly, on the development of reed, is correlated with several ecological factors, e.g. temperature, light, infection by parasites and insects hibernating in the litter (Haslam, 1969, 1971a,b, 1972; Klötzli & Züst, 1973; Husak, 1978; Krisch et al., 1979).

The thick litter mat in the abandoned reedbed is responsible for the decline of reed. Only a few, thick buds develop (the stimulating effect of low temperature and frost in the formation of new buds is missing) and penetrate the thick layer of litter (Haslam, 1969, 1972).

In addition, *Phragmites* is affected by the higher nitrification in the uncut reedbed, as this leads to less thick schlerenchymatic tissues in the stem. The reed is thus weaker, more sensitive to damage caused by mechanical action (such as waves and waterfowl), resulting in a decline (Tobler, 1943; Klötzli & Züst, 1973; Grünig, 1979; Sukopp & Markstein, 1981; Moss, 1983).

Parasite and insect infestation also appear to be an important factor in reed decline (Husak, 1978; Skuhravy, 1978; Van der Toorn, 1982; Mook & Van der Toorn, 1982; Van der Toorn & Mook, 1982).

The spectacular decline of *Urtica dioica* can be explained entirely by the removal of the litter mat, since it is in this organic, very loose, superficial layer that the species is rooted. The few *Urtica* plants that can still be found in the cut vegetation are juvenile, recently developed from seed (abundantly present in the seedbank). This explains the still high frequency of the species in the plot. Moreover, *Urtica* was seriously harmed by very long, exceptional floods from September 1984 until April 1985, which were also probably responsible for the poor recovery in 1986.

Removal of litter is also responsible for the decrease of *Calystegia sepium*, but as this species is likewise rooted partly in the superficial soil layer (immediately under the litter), the decline is not as strong. It is mostly the vitality of the species that is harmed. The enormous regenerative power of small pieces of rhizome explains the quick recovery of the species after some years of dereliction.

More difficult to understand is the behaviour of *Calamagrostis canescens*. In abandoned vegetation this species forms large tussocks and produces much litter, and is thus an effective competitor for space. Cutting of the vegetation does not really seem to harm it, but the formation of tussocks and the accumulation of litter is prevented, and both are major factors in the competitive power of the species. There is, however, an external factor which also determines the vitality and abundance of *Calamagrostis*: the water table. This explains the decline of the species in the uncut vegetation— most evident after the exceptional summer floods of July 1980 and 1981. This confirms an earlier observation by Haslam (1973), that a small difference in the water table of only 10 cm can be critical in competition between *Phragmites* and *Calamagrostis*.

The change in the behaviour of these dominants in turn encourages a favourable development of *Phragmites*.

Species diversity
The absence of litter and the lack of competition in the 'lower field layer' of the reedbed in the rather extreme conditions along the pondside (alternation of wet–dry, deposit silt, etc.), provides excellent growth conditions for therophytes with an r-strategy (Grime, 1979) or for other species which prefer similar ecological conditions (e.g. *Oenanthe aquatica*, *Rumex maritimus*). The seedbank is probably very important in the mass-invasion during the first years after cutting, and long-term establishment is dependent on good conditions for seedling emergence and development (surface moisture). That is why these species persist only in plot I; the sudden fall in

1986 was due to less careful litter removal the previous year which limited the open mud-space.

The increase of other 'typical' marsh plants dependent on a wet, nutrient-rich, sheltered surface (e.g. *Galium palustre*, *Scutellaria galericulata*, etc.), can also be explained by the absence of litter, which allows seedling emergence and development of a lower field layer. Most of the smaller species produce plentiful seed which is dispersed easily by water. Once the seed has reached the cut plot, full development is possible, and a seedbank is built up. As litter and shading are negative factors, these marsh species benefit from annual cutting which removes the overwintering crop and litter, so that an open and lit space becomes available for new seedlings and renewed development.

In the uncut vegetation, taller marsh species are often overgrown by the other competitive species and become choked by litter, which inhibits normal development and often also flowering. Only the tallest individuals survive and seedling emergence is impossible. Removal of the litter layer and suppression of the 'ruderal dominant species' allow most of the individuals to develop fully. The same can be noticed with tall forbs, whose increase seems to be rather contradictory. These are typical in an uncut, abandoned, litter-rich marsh vegetation, but are not very frequent in the Blankaart. As competitors in derelict areas, they may not like regular management, but need gaps in the vegetation in order to invade. The cut plot is, one such gap, free of litter and competitive species so that emergence of seedlings is possible. This may occur from the seedbank, but also from seed present in the environment and carried by water or wind.

However, the annual cutting regime is too intensive a management for good development of the taller marsh plants and forbs. Cutting promotes vegetative expansion, more seedlings and juveniles, and less vigorous growth. Under a deep litter mat, only thick buds develop while without litter, all buds are stimulated to growth. This is prevented by an intermittent management regime, or dereliction for a few years.

Propagated vegetative expansion and strong clonal growth of *Typha latifolia* seem to be responsible for the suppression of reed and floristic poverty in the initial *Typha* community developing in plot I, perhaps with some allellopathic influences and autotoxines, as suggested by McNaughton (1968).

Absence of litter and the full light of springtime conditions are also major factors in the development of a bryophyte layer in the cut plots. Nevertheless, the yearly inundation during winter with very silty, nutrient-rich water destroys the newly developed moss layer almost completely, so that it has to be renewed every summer. This limits bryophyte presence to some common 'ruderal' species, and explains the better development of moss

growth on the higher tussocks of reed and *Calamagrostis canescens* which are usually less subject to inundation. It also explains the destruction of mosses after dereliction.

The relation between the effect of management and zonation/succession and the influence on floristic diversity

The beneficial effects of cutting and removal of litter in preserving or creating species richness in the reedbed are clearly linked with the values of above-ground biomass. High values of total crop are associated with low species density, as was discussed by Wheeler & Giller (1982). In the Blankaart, the development of a large total crop is due to the development of a large standing crop and accumulation of large amounts of litter.

With respect to the Broadland fens in Norfolk, England, Wheeler & Giller (1982) have discussed the important effects on species diversity of the net productivity of the vegetation in relation to management regime. They recorded differences between reedbeds, tall forb vegetation and sedge beds. In the Blankaart some ecological parameters have an important effect on species diversity, as clearly suggested by the Detrended Correspondence Analysis (Fig. 7), and by the development of bryophytes (Fig. 6). The influence of cutting is not everywhere the same. The better growth of *Phragmites australis* may be evident in all plots, but not the increase of species diversity and development of mosses.

Influence of management is most clear in plot V, situated in the middle of the zonation (succession) (Table 1). The vegetation is more or less protected from changing ecological factors such as an irregular water table, deposits of silt and mud, while the influence of the very eutrophic water is somewhat limited by the greater distance from the pond side. In contrast, the pondside plots are subject to extreme changes in wetness. Small changes in the water level (e.g. after heavy rain, short drought periods, pumping) have a direct influence and the deposition of silt is very frequent (after each inundation) and important. Hygro-nitrophilous, short-living therophytes here find the more or less ruderal environment in which marsh species of 'stabilized' areas are absent. The beneficial effect on *Phragmites* is linked with the wetter environment (helophytes).

The influence on *Calamagrostis canescens* is not as clear, because changes occur much more slowly in these plots at the edge of the marsh. In the Blankaart, *C. canescens* represents a rather stabilised, extreme 'ruderalised' vegetation type, which is seen as a climax in the succession (rather than colonisation by trees (Gryseels, 1985). Plot VIII is an exception as this is an old floating mat, which intercepts disturbing external influences such as

changing water levels, allowing a faster development to a more species-rich vegetation (e.g. with ferns such as *Dryopteris carthusiana, Athyrium filix-femina*), and where bryophytes (e.g. with *Plagiothecium denticulatum*) can reach high cover values (Fig. 6).

It is thus the stage in succession, and the degree of ruderalisation, which determines vegetation development as a result of management, especially with regard to species diversity and moss development. Plots in the middle of the zonation gave the best response, because (1) they are best protected against changing environmental factors (in contrast to the plots closest to the pond side), and (2) the vegetation is still in evolution (in contrast to the *Calamagrostis canescens* plots at the edge of the marsh).

The rich development of bryophytes is largely a response to the same factors that lead to a rich variety of low-growing vascular plants (e.g. plots V and VIII). This process has also been observed by Wheeler & Giller (1982).

The effect on the declining dominant species (*Urtica dioica, Calystegia sepium*) is similar on all the plots because of the predominant importance of litter removal.

Coexistence of species

The coexistence of several 'dominants' in the uncut vegetation (*Phragmites australis, Calystegia sepium, Urtica dioica*), both in terms of strategy and cover values, is possible because every species has its particular niche, below and above ground. Reed rhizomes grow deepest (up to 1·5 m under substrate level), *Calystegia* roots grow in the upper 20 cm and, in the superficial soil-litter layer, *Urtica* roots are well-developed. A small difference in phenology between *Urtica* and *Phragmites* allows their optimal development (June/July–August). The life form of *Calystegia* as a creeping plant allows exploitation of the 'gap' above the herbaceous canopy which is inaccessible to neighbouring herbs.

Cutting implies litter removal and thus removal of *Urtica* and part of the *Calystegia* roots, which causes their decrease or even disappearance. The cleared space is then invaded by new species, especially from the group of 'marsh plants'. Competition with the only remaining dominant, *Phragmites*, for shade, light, etc., is avoided by the more or less complementary phenology which makes coexistence possible. Most of the accompanying species and mosses have their full development in spring or at the beginning of the summer. Reed, and eventually *Calystegia*, reach maximum development only in summer.

Origin of increased species richness. Limitations to invasion of new species

The increase in species density in the cut plots is not caused by species new to the Blankaart, but by ordinary species already present, although scarce, in the marsh. These are species tolerant of the ruderal character of the Blankaart (irregular flooding), but limited by stress (litter) and competition in an unmanaged reedbed. Cutting suppresses the strength of competitive species.

However, invasion of new species is limited not only by this 'ruderal aspect', but more importantly by the lack of seed, either from the seedbank or from the environment.

Vegetation evolution and syntaxonomy in relation to management

It has been shown that regular cutting and litter removal causes distinct changes in species poor reed vegetation, depending upon the position in the zonation. Near the shore, a monospecific reedswamp develops, in which just a few hygro-nitrophilous therophytes appear during the summer season. Further in the zonation, a mixed reed-fen vegetation develops. Towards the edge of the marsh, more tall forbs and mosses appear. Management causes the zonation to resemble the natural sucession as the extreme ruderal plants such as *Calystegia sepium* and *Urtica dioica*, which were masking this succession, now disappear. This helps considerably to clarify the syntaxonomical interpretation of the vegetation: the reed associations (*Scirpo-Phragmitetum*, several subassociations, see Westhoff & Den Held, 1969; *Angelico-Phragmitetum*, see Wheeler, 1980) can again be recognised, without the disturbing effects of *Calystegietum* associations or ruderal communities dominated by *Urtica dioica*. The syntaxonomical classification of semi-natural vegetation, the floristic composition of which is usually dependent on management practices, often gives such problems.

Implications for future management

Cutting of vegetation, and litter removal, is an efficient way to rehabilitate abandoned reed and mixed-fen vegetation. It is, however, a long-term process requiring at least 4–5 years. In the experiment discussed in this paper, two phases have been recognised. During the first, competitive ruderal species decline, while smaller species rapidly expand. The latter do

not persist (ruderal therophytes), or change rapidly in cover value, and after only 2–3 years their presence is more or less stabilised (e.g. *Galium palustre, Scutellaria galericulata, Epilobium parviflorum*). This is a disturbing phase, a first reaction to the suddenly open surface. During the second phase, an equilibrium is reached between the remaining dominants *Phragmites australis* and—eventually—*Calystegia sepium*, and the accompanying species which reach normal cover values. At the same time, new species invade (e.g. *Poa palustris, Carex vesicaria*). This is a stabilisation phase.

One isolated cutting will not have a prolonged effect, although it may be useful in promoting an existing but declining population (as the open surface encourages seed and juvenile development). The effect will not be sufficient to suppress ruderal-dominant, competitive species. One cutting is usually not sufficient to remove the whole litter layer, particularly when rooted with *Urtica dioica*—the seedbank has also to be depleted. For that reason, burning of the reedbed has little or no effect on species diversity, as only the upper part of the litter layer is scorched.

Dereliction of the managed plot causes a quick development to the original, ruderalised vegetation; less intensive management has an intermediate effect. The reedbed persists very well, but smaller species and mosses disappear, while tall forbs and robust marsh plants reach full development. The intermittent cutting regime in a highly productive environment prevents the latter from choking under the litter.

A continued, yearly cutting seems to give no further distinct change: in plot I, the vegetation in 1986 was not substantially different from that of 1982. This shows that the fen and reed vegetation in the Blankaart will continue to hold a certain ruderal character.

The changed environmental conditions of the area (eutrophication, lowered water table), which have been important causes for degeneration and ruderalisation, still exercise the same influence. Cutting and removal of litter have an effect on some symptoms of ruderalisation, which in turn activate the process (litter accumulation, success of competitive species), but do not affect the fundamental causes of ruderalisation. Management suppresses the process of ruderalisation, but does not eliminate it. Under the same external environmental conditions, management is not able to cause further fundamental changes in the vegetation. Inundations with silty, eutrophic water inhibits not only the development to a more mesotrophic reedbed, but also destroys every new development or process in the vegetation (e.g. those stimulated by bryophyte growth) also observed by Westhoff *et al.*, 1971; Van Wirdum, 1979*a,b*; Wheeler & Giller, 1982; Giller & Wheeler, 1986).

These management experiments show that, as already suggested by Wheeler & Giller (1982), reduction of a large standing crop and litter layer is

a prerequisite for the restoration of derelict fens and for the maintenance of species-rich vegetation. This process is mostly linked with the germination of smaller plants and the suppression of competitive species. The reinstatement of less common species is dependent on the available seedbank and dispersal mechanisms.

In conclusion, available evidence strongly suggests that, for fens and reedbeds which are not buffered against changing environmental conditions, management by cutting is a desirable objective for conservation.

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