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Published in:
Journal of Applied Ecology

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
1996

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
Oomes, M. J. M., Olff, H., & Altena, H. J. (1996). Effects of vegetation management and raising the water table on nutrient dynamics and vegetation change in a wet grassland. *Journal of Applied Ecology*, *33*(3), 576-588.

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Author(s): M. J. M. Oomes, H. Olff and H. J. Altena
Source: *Journal of Applied Ecology*, Vol. 33, No. 3 (Jun., 1996), pp. 576-588
Published by: British Ecological Society
Stable URL: http://www.jstor.org/stable/2404986
Accessed: 19/08/2013 09:27

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Journal of Applied Ecology 1996, **33**, 576–588

Effects of vegetation management and raising the water table on nutrient dynamics and vegetation change in a wet grassland

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Summary

1. The results of a restoration experiment carried out on a permanent grassland on peaty, heavy clay in the Netherlands are described. The experiment started in 1985, 7 years after fertilizer application had ceased, and was designed to provide insight into ecologically significant processes accompanying restoration. An analysis was made of the effect of management regime and of raising the water table on nutrient availability, dry matter production, tissue nutrient concentration, dynamics of species numbers and plant species replacement. Three management practices were compared: cutting and removal (RR), cutting and mulching (MM), sod removal in 1985, and thereafter cutting and removal of the hay (RS). Data are presented on changes during a 5-year period.

2. No trend was discernible in soil pH, total C, N and P in the RR treatment; extractable P and K decreased sharply in the field with the raised groundwater level.

3. Nine years after fertilizer application ceased, dry matter production had fallen from 10–11 to 6–7 t ha^{-1} year^{-1}. In the subsequent 5 years of the experiment it declined to 5–6 t ha^{-1} year^{-1} when all cut biomass was removed, and to about 4 t ha^{-1} year^{-1} after sod removal. Mulching caused an increase to 11 t ha^{-1} year^{-1}. No effect was seen of the raised water level.

4. The dry matter yield of the first June cut in the RR treatment decreased. The tissue K concentration also decreased, but no increase of the tissue P concentration was detected. It was concluded that the availability of K and to some extent of P was more important than N availability in explaining the decrease in dry matter production. The tissue nutrient concentrations were not influenced by the water table.

5. Sod removal to a depth of 5 cm resulted in the lowest productivity and the lowest tissue concentrations of P, while tissue concentrations of N and K were not affected.

6. Raising the water level resulted in a more rapid establishment of species indicative of wet conditions, some of which invaded from nearby ditches.

7. The trends of dominant species are described with a set of response models. The species were ranked from disappearing to colonizing species. The relationship between rank order of replacement and indicator values of species was investigated. Raising the water table resulted in species indicative of wet conditions becoming dominant, independently of vegetation management. The removal of nutrients resulted in the appearance of species with a lower maximal height, indicative of lower P and K availability.

Key-words: grassland management, groundwater, nutrient concentration, response models, restoration.

Journal of Applied Ecology (1996) **33**, 576–588

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Introduction

Current management for the restoration of grassland in Western Europe often aims at transforming productive, species-poor grasslands into less productive grasslands with a high species density (Park 1988; Bakker 1989; Gough & Marrs 1990). These species-rich grassland communities have become rare because of intensification of agricultural practices (fertilization, frequent cutting and lowering of the groundwater table). The first condition that has to be fulfilled is a reduction of the dry matter production to at least 4–6 tonnes ha^{-1} year^{-1} (Oomes 1992). Nutrient availability can be reduced by stopping the application of fertilizer and by removing nutrients from the system by cutting or sod stripping. Furthermore, in areas suffering from drainage high water tables can be restored, possibly slowing down the rate of nutrient mineralization and plant production (Myers, Campbell & Weier 1982; Berendse *et al.* 1994).

Several authors have stressed the importance of the relationships between hydrology, nutrient availability and botanical composition of wetlands (Wassen *et al.* 1990; Wheeler & Shaw 1991; Wheeler, Shaw & Cook 1992; Koerselman, Kerkhoven & Verhoeven 1993). For grasslands, however, experimental studies on the interactive effects of water table and vegetation management on nutrient availability, primary production and botanical composition are still scarce.

This paper reports on a 5-year field experiment, started in 1987. The aim was to analyse the effect on species replacement and ecosystem functioning of several management practices, namely cutting, mulching and sod removal, with or without raising the water table.

SITE DESCRIPTION AND EXPERIMENTAL DESIGN

The experiment was carried out in a grassland area near Wageningen, the Netherlands (51° 54′N; 5° 38′E). The first 20–80 cm of the soil consists of peaty clay, overlying peat. At the beginning of this century, the vegetation was a species-rich *Junco–Molinion** grassland (D. M. de Vries, unpublished data). After 1945, the area was drained and levelled for agricultural purposes. From 1968 to 1978, the average annual applications of N, P and K fertilizer were 300, 33 and 125 kg ha^{-1} year^{-1}, respectively. The grassland was cut several times during a year and/or was grazed by cattle. The average yield of this productive, species-poor grassland was 10–12 t ha^{-1} year^{-1}. Restoration management started in 1978 when fertilizer application was stopped, and since then the above-ground biomass has been cut and removed twice yearly in June and September. For a detailed lay-out of the experiment, see Oomes (1991).

In August 1985, 7 years after fertilizing ceased, a field of 13 ha was divided in subareas of 1·5–2·0 ha, in which the groundwater level could be manipulated independently. Two of these subareas were studied here: in one the water table was restored to its former high level ('wet field') by embankment to retain rain water and in summer additional water was supplied by allowing groundwater to infiltrate from the surrounding ditches through a drainage system. The water was pumped up from a depth of 60 m; it contained small amounts of N, P and K (respectively 0·13, 0·20 and 0·93 mg L^{-1}) and a relatively large amount of Ca (26·0 mg L^{-1}), with a pH of 7·6. In the second field the water table was not manipulated ('dry field') and no measures to retain or infiltrate water were taken, so the groundwater level followed the fluctuations of the surrounding agricultural grassland. The groundwater level was recorded daily, and the mean course over the period 1988–91 is shown in Fig. 1. The mean difference between the wet and dry field was 20–30 cm; the soil in the wet field was totally water-saturated in winter and spring.

The grassland management treatments were started in 1987, 9 years after stopping the fertilization and one growing season after raising the groundwater level. The three treatments were: (i) cutting in June

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*Names of plant associations (syntaxa) follow Westhoff & den Held (1969); names of species follow Heukels & van der Meijden (1983).

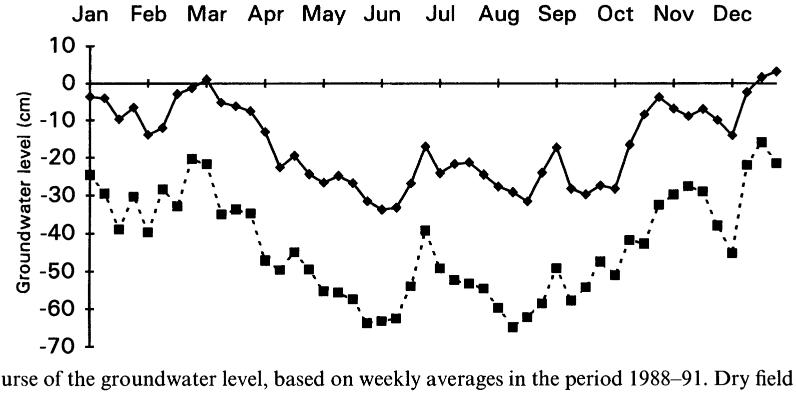

Fig. 1. Seasonal course of the groundwater level, based on weekly averages in the period 1988–91. Dry field (■), wet field (◆).

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and September and removing the biomass from both cuts (RR); (ii) cutting in June and September, but leaving the nutrients in the system by mulching the chopped biomass (MM); (iii) cutting in June and September the vegetation that re-established after the sod had been removed to a depth of 5 cm in 1985 (RS), the hay being removed. The cutting and mulching treatments were carried out on the wet and dry fields on five replicate plots of 100 m^2 each, in a block design, and the treatments were randomized within the blocks. Sod removal treatment involved one plot of 375 m^2 in each field.

SOIL AND VEGETATION ANALYSIS

Soil samples were collected from the RR plots only, in each field in April 1986, 1989 and 1991 by taking at random 10 cores per plot, each of 2 cm in diameter and 10 cm in depth; the 50 cores from each field were pooled. Soil pH was determined by adding 10 g soil to 25 ml water or 1 M KCl, and organic matter after loss-on-ignition at 850°C over 2·5 h. Water-soluble P was measured after shaking 1·0 g dry soil vigorously in 72 ml H_2O for 1 h; K extractable after shaking 10·0 g of dry soil for 1 h in 100 ml 0·1 M HCI + 0·2 M oxalic acid.

The above-ground biomass of each plot was determined at each harvest by cutting a strip of 15 m^2, the fresh weight of which was determined. In a subsample of 500 g fresh material, the dry matter content was measured and a representative sample was taken for N, P and K analysis following the methods described by Williams (1984).

The species composition of the vegetation was described by frequency analysis (de Vries 1937). Twenty samples of 0·25 dm^2 were taken from each of the 100-m^2 plots under the RR or MM treatment, 50 samples were taken on the two plots with the RS management. Each sample was sorted to species and the frequency of occurrence of each species in the 20 or 50 samples was calculated. Additionally, each year a complete list of all plant species in each plot was made, since only 60–70% of all species present were found in the frequency samples.

STATISTICS

The results consist of two sets of data. One set is the RR and MM plots, replicated five times on the wet and dry fields. This allows a mixed-model ANOVA (Genstat 5 Committee 1987), with Management as a fixed effect (two treatments) and the following block structure: plot (nested within field/water table, five replicates, 16 d.f. for the error term); year (nested within plot, 5 years, 99–19–16 = 64 d.f. for the error term) and harvest month (nested within year, two harvests within a year, 199–99–16 = 84 d.f. for the error term). The water table effect could not be tested, since it was not replicated and could not be separated from the random effect of the field. The 4 degrees of freedom for the year effect were partitioned into two terms using polynomial contrast, where the first term (year 1) then represents the linear change with time of the dependent variable (see Hays 1988).

The dynamics of species numbers for species which disappeared or became newly established was analysed as described above, except that the strata harvest and year were not present, using the number of newly established species and the number of those that disappeared at the end of the experiment as dependent variables.

The other data set is the RS treatment on each field which was not replicated, so the effect of this treatment can only be compared qualitatively with the other treatments.

Data were not transformed since differences between variances of means appeared to be small and transformation would hamper interpretation of the polynomial decomposition of the year effect.

CALCULATION OF SPECIES TRENDS

The temporal changes in occurrence of individual species were described using a set of hierarchical models for species response analysis as proposed by Huisman, Olff & Fresco (1993) and used by Olff, Huisman & van Tooren (1993). The probability of occurrence of each species as a function of time $p(t)$ in each combination of hydrology and grassland management was fitted to one of the following general response models:

$$p(t) = \frac{1}{1+e^{a}} \qquad \text{eqn 1}$$

$$p(t) = \frac{1}{1+e^{(a+bt)}} \qquad \text{eqn 2}$$

$$p(t) = \frac{1}{1+e^{a+bt+ct^2}} \qquad \text{eqn 3}$$

where a, b and c are the parameters to be estimated. A parameter was only included in the model if its inclusion improved the fit significantly. These curves merely describe the observed changes. However, they have been shown to be useful in various studies on vegetation succession (see Huisman *et al.* 1993). The parameters were estimated by logistic regression, with the parameter selection based on a χ^2 test (Jongman, ter Braak & van Tongeren 1987; Huisman *et al.* 1993; Olff *et al.* 1993). To ascertain the explained variance of the response model, R^2 was calculated from the observed frequency of occurrence in each year and the probability 'predicted' by the model (see Table 5). We did not use the two additional models suggested by Huisman *et al.* (1993) because of the relatively short time span of the present study (6 years). The parameters of the response models were used to rank species in their replacement order.

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This rank was correlated with the order of some plant characteristics by Spearman's rank correlation. The first group of species followed equation 2, with a positive sign for the parameter *b* (decreasing throughout the time interval). These species were ranked according to a decreasing value of *b*, with the fastest decreasing species being ranked first. The next group comprised the species which best fitted equation 3 (species which increased and then decreased).

We calculated the year in which each species reached its highest frequency percentage following Jongman *et al.* (1987) and ranked species accordingly. The last group of species had negative values of *b* and best fitted equation 2 (increasing species). These species were ranked according to decreasing values of *b* so that those showing fastest increase came last. Species where equation 1 fitted best (no trend) could not be ranked. The order of species replacement obtained this way at each combination of grassland use and level of the water table was then investigated further by calculating rank correlation coefficients between species ranks and various species traits, obtained from the literature.

Results

SOIL CHARACTERISTICS

The changes with time in soil characteristics of the 0–10 cm layer of the RR plots are given in Table 1. Most soil variables did not show a trend. However, water-soluble P and extractable K decreased sharply in the field with a shallow groundwater table, but showed a much smaller decrease in the field with the deeper groundwater table.

ABOVE-GROUND STANDING CROP AND TISSUE NUTRIENT CONCENTRATIONS

The dry matter yield was strongly affected by management (mulching or cutting) and by the harvest month (June, September: Table 2). Furthermore, the rate of change in dry matter yield over the 5-year period was significantly different between these two management practices (a large Year 1 × management interaction: Table 2). For the mulching management (MM), the dry matter yield increased significantly over the 5-year period in both the June and September cuts (Table 3, Fig. 2a). This increase was larger for the September cut than for the June cut (Table 3). When the cut material was removed (RR), the yield in June fell significantly, but the September yield did not decrease. By comparison with Treatment RR, sod removal (RS) resulted in a lower yield of the June cut, especially in the dry field (Fig. 2a).

The tissue nutrient concentrations were generally lower in June than in September, but this difference diminished during the experiment (Tables 2 and 3, and Fig. 2b–c).

Tissue N concentrations were strongly affected by the management practice and by the harvest month (Table 2). The rate of change over the 5-year period strongly depended on the time of cutting (a strong Year 1 × management and Year 1 × harvest month interaction, Table 2). The tissue N concentration generally decreased in the September cut, while small increases were found in the June cuts, independent of the water table (Table 3, Fig. 2b). The N concentration in the RS treatment showed the same tendency.

Tissue P concentrations generally decreased during the experiment (a strong year 1 effect, Table 2, Fig. 2c). This decrease was greater in the September cuts than in the June cuts (a large harvest month × Year 1 interaction, Table 2).

Table 1. Soil characteristics of the 0–10 cm layer in the RR treatment (percentages are gravimetric)

	Dry			Wet		
	1986	1989	1991	1986	1989	1991
pH (in KCl)	4·8	4·6	4·8	4·9	4·7	4·7
pH (water)	5·7	5·4	5·5	5·7	5·4	5·5
Clay* (%)	54	–	49	46	51	51
Organic matter (%)	23·8	30·0	26·9	21·3	28·3	27·7
Total C (%)	13·7	11·5	14·3	11·5	14·2	12·6
Total N (%)	1·21	1·16	1·31	1·11	1·24	1·36
Total P (%)	0·20	0·15	0·22	0·17	0·11	0·17
Water-soluble P†	103	94	84	75	47	34
Extractable K†	14	13	12	11	7	5
C/N ratio	11·3	9·9	10·9	10·4	11·5	9·3

*Particles $< 2 \times 10^{-6}$ m; †mg per 100 g dry soil.

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Table 2. Analysis of variance of the effect of management, water table, year and harvest on above ground dry matter yield (DMY) and above-ground tissue concentrations of nitrogen (N), phosphorus (P) and potassium (K). The experiment was analysed as a block design, where the factor harvest was nested within year, years were nested within plots and plots were nested within the treatment water table. Two fields with different water tables were used. Therefore, the main effect of water table could not be calculated. The year effect (d.f. = 4) was partitioned into two polynomial terms, in which the first term (Year 1) represents the linear trend of the dependent variable with time, while Year 2 incorporates all higher order effects

Effect	d.f.	*F*-values for each dependent variable			
		DMY	N	P	K
Plot within field stratum					
Management	1,16	236·01***	66·30**	33·39***	107·64***
Management × water table	1,16	1·23NS	2·97NS	0·01NS	0·10NS
Year within plot within field stratum					
Year	4,64	19·94***	21·80***	60·65***	83·44***
Year 1 – linear effect	1,64	24·48**	9·10**	88·34***	284·15***
Year 2 – other effects	3,64	18·43**	26·03***	51·43***	16·53***
Year × water table	4,64	6·99***	1·45NS	11·02***	3·85**
Year 1 × water table	1,64	0·84NS	0·73NS	35·54***	9·29**
Year 2 × water table	3,64	9·04***	1·69NS	2·85*	2·04NS
Year × management	4,64	42·22***	10·61***	9·39***	12·47***
Year 1 × management	1,64	167·81***	39·13***	33·54***	19·03***
Year 2 × management	3,64	0·35NS	1·11NS	1·34NS	10·28***
Year × water table × management	4,64	0·47NS	0·31NS	1·04NS	1·81NS
Year 1 × water table × management	1,64	0·01NS	0·01NS	0·35NS	0·01NS
Year 1 × water table × management	3,64	0·62NS	0·041NS	1·27NS	2·41NS
Harvest within year within plot within field stratum					
Harvest	1,84	465·88***	543.06***	326.32***	75·84***
Harvest × year	4,84	18·15***	35·88***	61·52***	62·61***
Harvest × Year 1	1,84	51·50***	115·38***	114·57***	180·11***
Harvest × Year 2	3,84	7·04***	9·38***	43·83***	23·04***
Harvest × water table	1,84	20·59***	0·14NS	4·24*	1·80NS
Harvest × management	1,84	3·37NS	0·93NS	1·29NS	21·77***
Harvest × water table × year	4,84	2·87NS	5·15***	4·62**	3·20*
Harvest × water table × Year 1	1,84	4·16*	0·64NS	0·01NS	5·20*
Harvest × water table × Year 1	3,84	2·45NS	6·65***	6·16***	2·53NS
Harvest × management × year	4,84	1·91NS	1·77NS	2·26NS	8·94***
Harvest × management × Year 1	1,84	1·15NS	3·16NS	2·83NS	24·63***
Harvest × management × Year 2	3,84	2·16NS	1·31NS	2·07NS	3·71*
Harvest × management × water table	1,84	0·23NS	1·64NS	1·62NS	0·48NS

F-values are given, with their level of significance: $^{*}P < 0·05$, $^{**}P < 0·01$, $^{***}P < 0·001$; NS, not significant.

Tissue K concentrations also generally declined over the study period (a large Year 1 effect, Table 2). An exception was an observed increase in K concentration in June in both fields under mulching (Table 3). Whenever the K concentration decreased, the decrease was greater in the wet field (Table 3).

DYNAMICS OF SPECIES NUMBERS

The total number of species in each plot was slightly lower in 1992 than in 1987 ($F_{1,18} = 5·29$, $P < 0·05$, Table 4). The effects of vegetation management (mulching or cutting) and the interaction year × management were not significant ($F_{1,17} = 1·57$, $P = 0·23$ and $F_{1,18} = 1·23$, respectively). The influence of water table could not be tested, but seemed to be minor. However, when the numbers are split into species present in both years, new species and species disappearing, the effect of grassland management and water table becomes clear. The RR plots had more new species than the MM plots ($F_{1,17} = 5·31$, $P < 0·05$, Table 4), but nearly all were found on the wet field. So raising the water table enhanced the number of new species in the RR treatment, but the significance of this effect could not be tested. The number of species lost did not differ between management practices ($F_{1,17} = 0·73$, $P = 0·40$), nor did the number of species present in both 1987 and 1992 ($F_{1,17} = 0·18$, $P = 0·68$).

Two years after sod removal, the newly established vegetation within 375 m^2 consisted of 37 plant species in the wet field and 49 in the dry field. In 5 years the species density did not change, but changes in species numbers in the dry field were much greater than in the wet field. In both fields 24 species that did not occur in the undisturbed grasslands and their surroundings were found. They included several species which are very rare in the Netherlands, namely *Carex oederi*, *C. pallescens*, *Eleocharis palustris* and *Viola persicifolia*.

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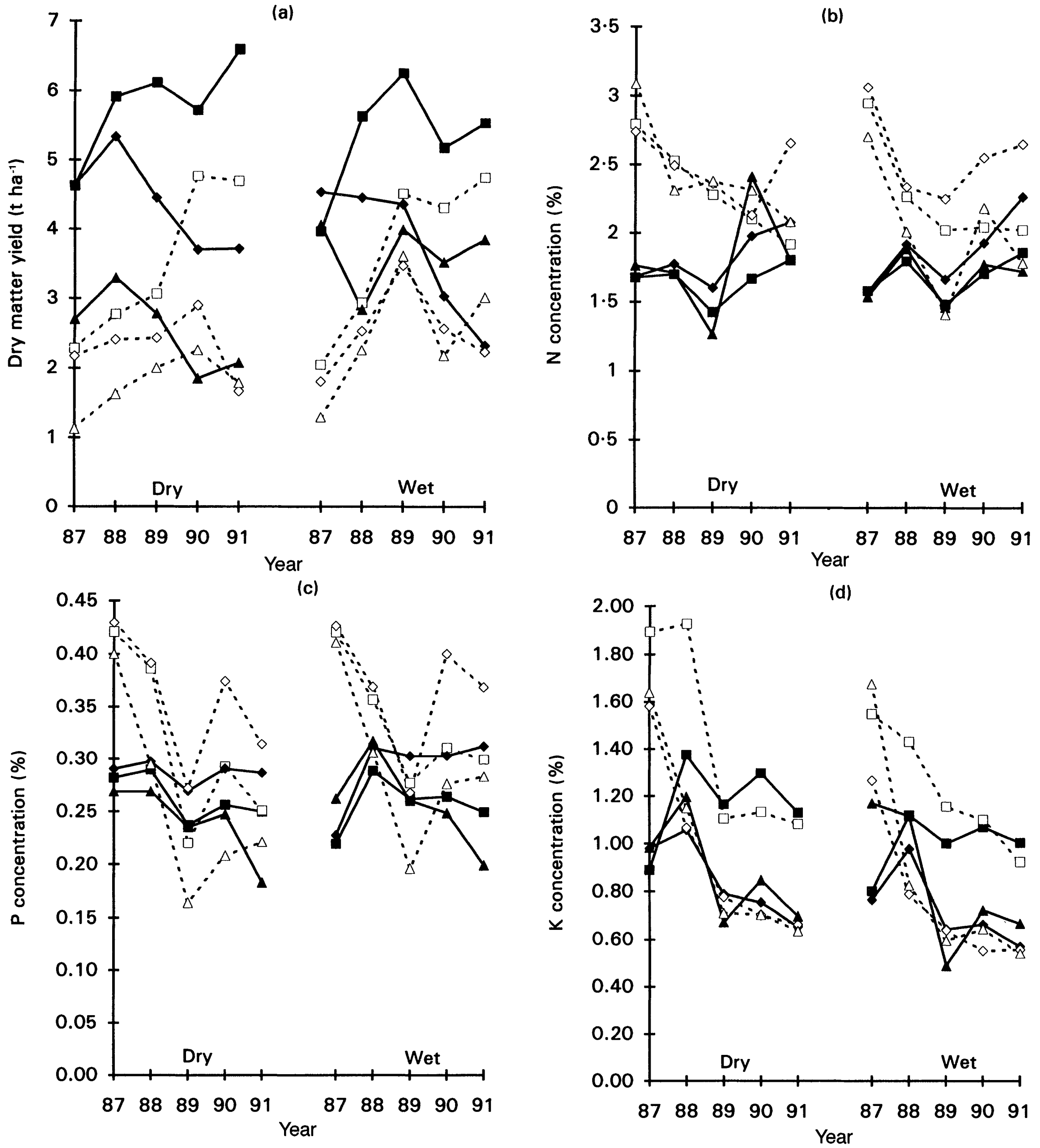

Fig. 2. (a) Mean annual dry matter yield and (b), (c) and (d) mean content of N, P and K respectively for June (solid line) and September (dashed line) cuts in the grassland at several combinations of groundwater table and management. ◆, ◇, two cuts, hay removed (RR); ■, □, two cuts, biomass mulched (MM); ▲, △, sod removed in 1985, from 1987 two cuts, hay removed (RS).

DYNAMICS OF SPECIES ABUNDANCE

Seventeen species occurred sufficiently frequently to allow logistic regression analysis. Fig. 3 shows the fitted curves of 10 frequently occurring plant species. In Tables 5 and 6 the parameters of the response models are given, based on the most appropriate model; R^2 is given as an indication of the explained variance. The plant species are arranged per management treatment in the order of successional replacement. The data of the RS treatment are for a shorter period of 4 years, so equations 2 or 3 fitted significantly better than equation 1 for only a small number of species.

At the beginning of the experiment the co-dominant species in order of importance were *Poa trivialis, Lolium perenne, Agrostis stolonifera, Poa pratensis, Bromus hordeaceus* ssp. *hordeaceus* and *Rumex acetosa.* The following species were abundant: *Ranunculus repens, Taraxacum officinale, Cardamine pratensis, Stellaria media* and *Elymus repens.* Figure 3a shows that the RR management in the dry field resulted in a dominance of *Alopecurus pratensis, Rumex acetosa, Poa trivialis* and *Agrostis stolonifera.* In the wet field, the eutrophic species decreased faster and *Cardamine pratensis* increased to a higher frequency than in the dry field (Table 6). *Agrostis stolonifera, Alopecurus geniculatus* and *Ranunculus repens* increased rapidly. These four species, together with

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Table 3. Analysis of variance testing the rate of change over 5 years of above-ground dry matter yield (DMY, g m^{-2} $year^{-1}$), and tissue concentrations (g kg^{-1} $year^{-1}$) of N, P and K for all combinations of water table, management and cutting date

				Dependent variable			
Water table	Management	Cutting date		DMY	N	P	K
Low	Mulching 2 × (MM)	June	*a*	26·81	0·47	0·03	0·35
			t	2·76**	2·00*	1·4NS	2·49*
		September	*a*	67·61	−2·07	−0·29	−1·58
			t	10·61***	−6·79***	−5·73***	−6·09***
	Cutting 2 × (RR)	June	*a*	−58·26	1·39	0·16	−0·71
			t	−6·00**	5·98***	6·47***	−4·96***
		September	*a*	8·84	−0·62	−0·09	−1·65
			t	1·38NS	−2·02*	−1·69NS	−6·36**
High	Mulching 2 × (MM)	June	*a*	37·41	0·23	−0·10	0·40
			t	3·85***	0·97NS	−3·94***	2·81**
		September	*a*	68·07	−2·17	−0·43	−2·42
			t	10·69***	−7·11***	−8·59***	−9·31***
	Cutting 2 × (RR)	June	*a*	−34·74	0·99	−0·02	−3·02
			t	−3·58**	4·25***	−0·58NS	−6·70***
		September	*a*	−5·25	−0·53	0·25	−2·20
			t	−0·82NS	−1·73NS	−4·92***	−8·46***

Parameter estimates of the slopes *a* of each ANOVA are given, representing the annual rate of change of the dependent variable, for each combination of levels of the variables cutting date, management and Field. The *t*-values test the significance of the deviation of each from zero.The parameters were estimated as the linear polynomial terms of the year effect and were calculated within the appropriate levels of management and water table in a factorial design. Block effects were ignored in this analysis and a separate ANOVA was calculated for each cutting date. Levels of significance: *** $P < 0{\cdot}001$, ** $P < 0{\cdot}01$; * $P < 0{\cdot}05$; NS, not significant.

Table 4. Effect of management on the dynamics of number of plant species on a wet and dry field from 1987 to 1992. RR = two cuts, hay removed; MM = two cuts, biomass mulched; RS = sod removed in 1985, from 1987, two cuts, hay removed. RR, and MM mean and SE of mean of five replicates of 100 m^2. RS one plot of 375 m^2

	Treatment									
	Dry					Wet				
	RR		MM		RS	RR		MM		RS
Number of species	Mean	SE	Mean	SE		Mean	SE	Mean	SE	
1987	20·2	0·9	20·6	0·4	49	19·2	0·8	18·2	0·7	37
1992	17·8	0·7	18·0	0·6	51	20·2	1·2	16·8	0·9	37
Constant	14·8	0·8	14·6	0·5	29	13·4	0·6	14·4	0·6	24
New	3·0	0·7	3·4	0·2	22	6·8	0·8	2·4	0·5	13
Disappearing										
Number	5·4	0·2	6·0	0·6	20	5·8	0·7	3·8	1·1	13
% of 1987	26·8	0·9	29·2	3·1	40·8	30·2	3·2	20·9	5·6	35·1

Poa trivialis and *Rumex acetosa,* became co-dominant in 1992.

In 1989, 4 years after sod removal, the vegetation in the RS plots was totally different from the initial grassland (Tables 5 and 6). After 7 years, in 1992, the vegetation in the dry field was dominated by *Poa trivialis*, *Agrostis stolonifera, Ranunculus repens*, *Alopecurus pratensis*, *Elymus repens* and *Trifolium repens.* In the wet field, the first three species together with *Alopecurus geniculatus* and *Juncus* spp. became dominant.

RELATION BETWEEN REPLACEMENT AND INDICATOR VALUES OF SPECIES

Tables 5 and 6 rank the dominant plant species for each treatment from early and quickly disappearing to late established and quickly increasing species. Table 7 gives the Spearman rank correlation between species ranks in the replacement series between treatments and various indicator values and plant characteristics. Constant or indifferent species were excluded from this analysis. It was found that the species sequence

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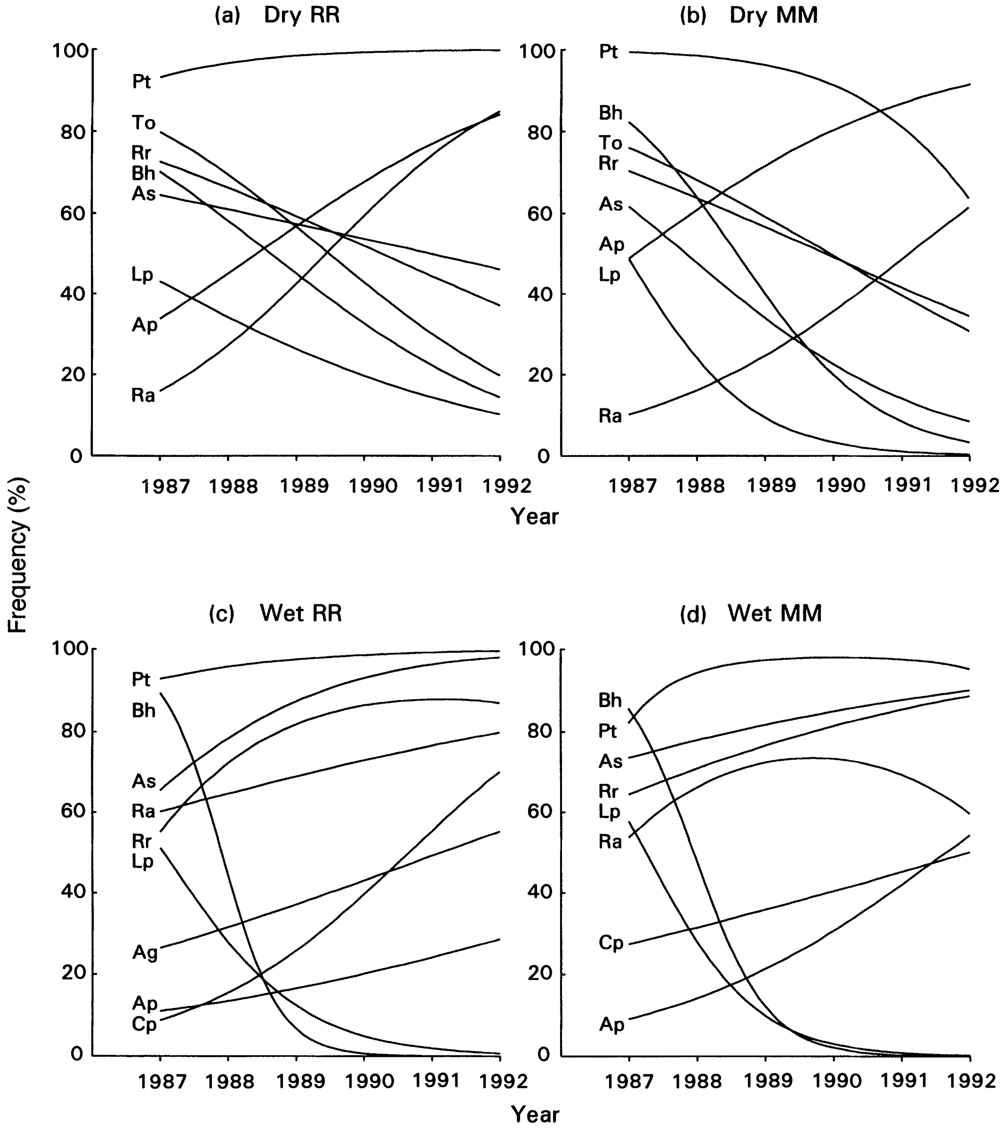

Fig. 3. Modelled frequency percentage of some frequently occurring species in the grassland at several combinations of groundwater table and management. Ag = *Alopecurus geniculatus*, Ap = *Alopecurus pratensis*, As = *Agrostis stolonifera*, Bh = *Bromus hordeaceus* ssp. *hordeaceus*, Cp = *Cardamine pratensis*, Lp = *Lolium perenne*, Pt = *Poa trivialis*, Ra = *Rumex acetosa*, Rr = *Ranunculus repens*, To = *Taraxacum officinale*. See Fig. 2 for treatment codes.

in the dry RR plots did not correlate with the species sequence in the other three treatments (Table 7). So each treatment placed the species in a new sequence, the most aberrant sequence being in the wet MM plots. The rise in water table caused a sequence that was correlated positively with the soil moisture indication values of Ellenberg (1974) and Kruijne, de Vries & Mooi (1967), showing that species that appeared later in these plots were characteristic of wet conditions. This effect was independent of the vegetation management (removing the cut biomass or mulching). In the wet field we found no correlation with soil fertility indication, as given by Kruijne *et al.* (1967) or Clausman, van Wijngaarden & den Held (1984). Species appearing under dry conditions were indicative of the reduced availability of P and K. In contrast to expectation, the effect was especially marked under mulching. Only in treatment RR was a negative correlation found with maximum plant height (Grime *et al.* 1988), indicating that later species in the sequence were shorter.

Discussion

In 1987, 9 years after fertilizing ceased, the dry matter production had decreased from 10–11 to 6–7 t ha^{-1} $year^{-1}$. In the subsequent 5 years of the experiment, it declined further to 5–6 t ha^{-1} $year^{-1}$. In the field where the groundwater level was raised, the N mineralization in the soil decreased (Berendse *et al.* 1994). Nevertheless, this decrease resulted in a negligibly lower annual dry matter production, indicating that N availability is of less importance during this phase of soil impoverishment on this heavy clay soil with a high

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Table 5. Rank order of plant species in the replacement series, caused by different management treatments in the dry field. RR = two cuts, hay removed; MM = two cuts, biomass mulched; RS = sod removed in 1985, from 1987 two cuts, hay removed. The order is derived from parameter *b* of the model. The predicted and observed frequencies in 1987 and 1992 are also given. The explained variation of the model for each species is expressed as the R^2 of the regression of values predicted by logistic regression against the observed values

			Frequency (%)				
			1987		1992		
	Year of maximum	*b*	Predicted	Observed	Predicted	Observed	R^2
Dry RR							
Taraxacum officinale	87·0	2·77	80	82	20	22	0·66
Bromus hordeaceus	87·0	2·63	70	74	14	19	0·46
Elymus repens	87·0	2·13	58	56	14	17	0·33
Lolium perenne	87·0	1·88	43	41	10	11	0·25
Ranunculus repens	87·0	1·50	73	76	37	47	0·20
Poa pratensis	87·0	1·24	65	85	35	54	0·17
Agrostis stolonifera	87·0	0·75	64	69	46	43	0·07
Holcus lanatus	90·0		0	0	0	0	0·48
Alopecurus geniculatus	92·0	−2·12	0	2	4	7	0·30
A. pratensis	92·0	−2·34	34	29	84	80	0·56
Cardamine pratensis	92·0	−2·35	1	0	5	5	0·15
Rumex acetosa	92·0	−3·39	16	18	85	89	0·38
Poa trivialis	92·0	−3·78	93	92	100	100	0·39
Cerastium fontanum	92·0	−4·78	1	3	38	40	0·67
Dry MM							
Lolium perenne	87·0	5·47	48	42	0	0	0·67
Bromus hordeaceu	87·0	4·88	82	93	3	4	0·69
Poa pratensis	87·0	4·77	78	87	3	11	0·76
P. trivialis	87·0	4·48	99	98	64	61	0·59
Agrostis stolonifera	87·0	2·84	61	71	9	13	0·49
Cerastium fontanum	87·0	2·29	5	8	0	3	0·29
Taraxacum officinale	87·0	1·96	76	81	31	33	0·43
Ranunculus repens	87·0	1·50	70	87	35	66	0·15
Cardamine pratensis	91·1		0	0	12	14	0·47
Alopecurus pratensis	92·0	−2·44	49	51	92	90	0·51
Rumex acetosa	92·0	−2·63	10	11	61	57	0·53
Holcus lanatus	92·0	−3·14	0	1	10	12	0·42
Alopecurus geniculatus			0	0	0	0	
Elymus repens			50	52	50	52	
Dry RS							
Bromus hordeaceus	89·0	3·23	59	54	5	2	0·94
Cardamine pratensis	90·2		4	4	19	18	0·99
Elymus repens	92·0	−0·97	29	20	52	48	0·47
Trifolium repens	92·0	−1·26	44	42	74	78	0·67
Alopecurus pratensis	92·0	−1·76	17	14	54	54	0·94
Agrostis stolonifera	92·0	−2·65	33	36	87	86	0·93
Alopecurus geniculatus			2	0	2	2	
Cerastium fontanum			2	14	2	26	
Lolium perenne			6	12	6	8	
Poa pratensis			15	14	15	10	
Holcus lanatus			22	16	22	26	
Rumex acetosa			40	44	40	42	
Taraxacum officinale			40	36	40	50	
Ranunculus repens			90	98	90	92	
Poa trivalis			96	98	96	94	

organic matter content. The relatively small changes in the N content of the dry matter and in the total N yield, independent of management or water table, also indicate that in this system the N availability does not determine the decrease in dry matter production during soil impoverishment.

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Table 6. Rank order of plant species in the replacement series, as presented in Table 5, but in the wet field

			Frequency (%)				
			1987		1992		
	Year of maximum	b	Predicted	Observed	Predicted	Observed	R^2
Wet RR							
Bromus hordeaceus	87·0	11·9	89	98	0	0	0·88
Cerastium fontanum	87·0	7·34	44	50	0	2	0·73
Lolium perenne	87·0	4·98	51	51	1	0	0·75
Poa pratensis	87·0	4·17	66	71	3	2	0·72
Elymus repens	87·0	2·86	14	14	1	0	0·27
Taraxacum officinale	87·0	2·62	49	57	7	7	0·58
Ranunculus repens	90·1		55	51	87	91	0·37
Rumex acetosa	92·0	−0·96	60	60	80	78	0·16
Alopecurus pratensis	92·0	−1·18	11	11	29	25	0·15
Alopecurus geniculatus	92·0	−1·23	26	19	55	70	0·13
Poa trivialis	92·0	−2·72	93	91	99	98	0·41
Cardamine pratensis	92·0	−3·18	9	12	70	67	0·58
Agrostis stolonifera	92·0	−3·23	65	63	98	99	0·48
Holcus lanatus			5	5	5	4	
Wet MM							
Cerastium fontanum	87·0	10·6	43	42	0	0	0·81
Bromus hordeaceus	87·0	9·38	86	93	0	1	0·91
Lolium perenne	87·0	6·28	58	56	0	0	0·85
Poa pratensis	87·0	5·35	59	54	1	2	0·69
Taraxacum officinale	87·0	2·04	47	59	10	12	0·41
Elymus repens	87·0	1·55	11	13	3	2	0·1
Rumex acetosa	89·7		54	57	60	62	0·14
Poa trivialis	90·1		82	82	95	95	0·44
Cardamine pratensis	92·0	−0·97	27	35	50	50	0·07
Ranunculus repens	92·0	−1·46	64	54	89	93	0·31
Agrostis stolonifera	92·0	−1·88	73	68	95	95	0·37
Alopecurus pratensis	92·0	−2·46	9	8	54	44	0·62
A. geniculatus			19	51	19	26	
Holcus lanatus			1	0	1	0	
Wet RS							
Alopecurus geniculatus	89·0	2·18	63	78	16	36	0·47
Trifolium repens	89·0	1·97	51	58	13	24	0·64
Cardamine pratensis	90·6		9	12	13	10	0·62
Agrostis stolonifera	92·0	−2·18	77	72	97	96	0·73
Juncus articulatus	92·0	−3·62	2	0	36	34	0·98
Ranunculus repens	92·0	−3·74	83	84	100	100	0·99
Holcus lanatus			1	0	1	0	
Poa pratensis			1	4	1	0	
Elymus repens			5	4	5	4	
Rumex acetosa			10	8	10	6	
Taraxacum officinale			10	10	10	6	
Alopecurus pratensis			10	6	10	18	
Juncus effusus			27	22	27	30	
Poa trivialis			90	96	90	80	

The decrease in P and K availability is indicated by the decrease in the total annual nutrient yield (Oomes & Altena 1994). However, an analysis of the concentrations allowed us to predict which nutrient was or would become limiting for the dry matter production. It appeared important to distinguish both cuttings; most informative was the course in time of the nutrient concentrations of the first cut. A decreasing nutrient availability is indicated by a decrease in nutrient content when the dry matter yield remained constant or declined. A decrease with time in the dry matter yield from the RR and RS treatments occurred only in the June cut. The yield of the September cut was constant or increased. Only the K content of both

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Table 7. Spearman rank order correlation coefficients between the rank order of the species in the replacement series of each treatment and several plant characteristics. Species without a significant trend have been excluded; *n*, number of species involved. Treatment codes as Fig. 2

	Dry				Wet			
	RR	*n*	MM	*n*	RR	*n*	MM	*n*
Dry, RR	—	—	0.38	12	0.44	13	0.21	12
Ellenberg (1974)								
Humidity	0·49	12	0·45	10	0·78**	11	0·74*	10
Kruijne *et al.* (1967)								
Humidity	0·27	14	0·68*	12	0·78**	13	0·80**	12
P indication	−0·39	14	−0·58*	12	0·05	13	0·01	12
K indication	−0·26	14	−0·64*	12	0·10	13	−0·10	12
Clausman *et al.* (1984)								
Fertility indication	−0·39	14	−0·27	12	0·27	13	0·31	12
Grime *et al.* (1988)								
Height	−0·66**	14	0·5	12	−0·43	13	−0·16	12

Levels of significance: **$P < 0{\cdot}01$; *$P < 0{\cdot}05$.

cuts decreased sharply; the P content of the first cut was constant (RR) or decreased (RS). This indicates that the K availability in this system was decreasing, and the low concentration (de Wit, Dijkshoorn & Noggle 1963; Knauer 1963) shows that K was probably limiting the dry matter production. Knauer (1963) estimated that average concentrations of N, P and K in a June cut of 1·29, 0·24 and 1·93%, respectively, indicate a low nutrient availability. This K limitation has also been found in other restoration experiments on peaty and sandy soils (Kapfer 1988; Olff 1992). Such a declining and low availability can only be deduced from the low concentration, but can hardly be seen in the changes in extractable K contents in the soil. The decrease in dry matter yield and the constant P concentration in the biomass of the first cut of RR indicate that the P availability decreased, but the concentration was still relatively high. The measured decline in water-soluble P in both fields agrees with this; the relatively sharp decline in the wet field might be due to P being fixed in the soil by the Ca-rich groundwater (Koerselman *et al.* 1993).

Returning the nutrients by mulching the biomass instead of removing it caused a recirculation of nutrients, K recirculating faster than N and P (Oomes 1991). Only in the first cut did the recirculation raise the dry matter production and K content, but not the N and P concentration. So the return of nutrients, and especially of K, was very effective in the first part of the growing season. In the second part, the dry matter yield also increased, but then the concentrations decreased, showing that the nutrient availability became lower.

After the sod had been stripped to a depth of 5 cm, the P content and the total annual N and P yield in the biomass from both cuts were lower than without sod removal. However, 7 years after sod removal the annual dry matter yield was hardly any lower. Nevertheless, this can be an effective way to restore a species-rich grassland, because the P concentration and yield in the biomass were lower than that of the undisturbed grassland, so that a co-limitation by P can be expected earlier.

In 1987 the dry matter production in the RR treatment was sufficiently low for an increase in species density to be expected (Oomes 1992). However, no such increase occurred. The 'extensification' of the grassland use led to a relatively high loss of species preferring more fertile conditions. In the wet field this loss was compensated by wet species that invaded from nearby ditches. However, the invasion of new species from the surrounding grassland area was low, because of limitations in seed dispersal; furthermore there were few sources of native flora (van Dorp 1992, 1996). The appearance of many new and rare species in the RS plots suggests that these were still present in the seed bank. For some years, sod removal created an open sward of low productivity and, hence, favourable conditions for the establishment of species. However, the loss of species was also great. The higher species density in the dry field after sod stripping is mainly attributable to historical differences before grassland improvement and to some extent to the lower production of the vegetation that regenerated. Mulching the biomass provided a large amount of litter and boosted dry matter production. Nevertheless, the fraction of species that disappeared was no higher under mulching, so the probability of disappearance did not increase, despite the litter produced.

An analysis of the changes in the occurrence of plant species showed that, even in the short term, a rise in groundwater level results in species being replaced by those indicative of wet growing conditions. The rank correlations showed further that the replacing species are shorter and are indicative of relatively nutrient-poor sites. This effect was clearer in the dry field. However, nutrient enrichment by mul-

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ching also caused a replacement by species indicating lower fertility, namely *Alopecurus pratensis, Ranunculus repens* and *Rumex acetosa*. This suggests that other plant characteristics, such as their ability to colonize open places covered by litter, are also important.

The results have implications for restoration management. Sod removal can be an effective treatment. The open sward with its low productivity permits, in the short term, establishment of new and sometimes very rare species from the soil seed bank and from ditch banks. In the longer term, however, on a clay soil with a high content of organic matter, the yield may increase again if the layer removed is too thin. A rise in groundwater level may cause a faster decrease in nutrient availability and productivity. However, this greatly depends on the depth of the water table, the quality of the water and the soil characteristics. More research has to be done to elucidate these interactions.

In the short term of 5 years, a raised water level caused dry species to disappear and be replaced by wet species. New species could establish, the dry matter production apparently being already sufficiently low to allow the invasion of new species (Oomes 1992); but the further increase in species density is limited by the small species pool in the surroundings and the short distance of seed dispersal.

In relatively productive systems (> 6–7 tons ha^{-1} year^{-1}) it is necessary to remove all mown biomass, because the return of nutrients by mulching enhances grassland production and limits the establishment of new species.

The process of soil impoverishment can be described by the decline in the dry matter and nutrient yield. However, data on nutrient content are necessary to ascertain the causes of this decline and to trace nutrient limitation. This knowledge must be the basis for a management strategy aimed at soil impoverishment.

Acknowledgements

J.C.M. Withagen is gratefully acknowledged for his assistance in applying the curve-fitting technique. We thank J.G. Heij for analysing the botanical samples, and F. Berendse and J.J.M.H. Ketelaars for their comments on the manuscript. Mrs. J. Burrough revised the English text.

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Received 3 May 1994; revision received 10 July 1995

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