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LONG-TERM DYNAMICS OF STANDING CROP AND SPECIES COMPOSITION AFTER THE CESSATION OF FERTILIZER APPLICATION TO MOWN GRASSLAND

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SUMMARY

(1) Current agricultural overproduction in Western Europe has led to an increase in the area of unfertilized grassland. This paper reports an experiment where fertilizer application was stopped to try to restore former species-rich vegetation.

(2) Standing crop and species composition of three different fields were studied during the first 14 years after cessation of fertilizer application. In two fields on peaty soil a strong decrease in standing crop (from 800 to 300 g m^{-2}) was observed but in a field on sandy soil, the initial production of 300 g m^{-2} did not decrease. The deviations from the mean between years were significantly correlated to the potential water surplus in the growing season in this latter field, but not for the two fields on peaty soil. The species composition changed gradually in all fields.

(3) In the two fields with decreasing standing crop, species-richness per field and per 4-m^2 plot increased markedly during the 14 years. A maximum of forty species was observed after 8 years in the field on sandy soil.

(4) Several species reached their maximum cover during these successions. The dynamics of species replacement was described using a Gaussian response model for each species. Species indicating nutrient-poor conditions entered earlier in the successional sequence with cutting twice a year and in the field on sandy soil. The results are discussed with regard to diversity−productivity relationships, nutrient cycling and adaptations of species to nutrient-poor conditions.

INTRODUCTION

General theories on the relationship between standing crop and species diversity predict a unimodal relation, with an optimum at intermediate levels (Grime 1979). However, several restraints can be put on this general rule. Firstly, the scale of measurement seems to be an important determinant of its form. The relationship is often present when different vegetation types are combined in one graph (e.g. Al Mufti *et al*. 1977; Willems 1983; Vermeer & Berendse 1983) but seems to be absent within vegetation types (Moore & Keddy 1989; Ter Heerdt, Bakker & De Leeuw 1991). The problem in combining productivity and diversity data from different vegetation types in different sites is that many correlated factors, such as vegetation history, management, soil conditions and grazing, co-vary with productivity. This makes it difficult to formulate mechanistic causes for this relationship, such as variation in the intensity of competition and environmental heterogeneity. Secondly, the optimal level of standing crop at which the highest diversity is found varies from 50 to 1500 g m^{-2} (Wisheu & Keddy 1989 and references therein). This implies that although an optimum is found in different studies, its position is very dependent on

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the characteristics of the local ecosystem.

This study examined changes in standing crop, species-richness and vegetation composition of three different grassland sites during the first 14 years following cessation of fertilizer application. Recent restrictions on the yields of dairy products and the demands of nature conservationists have increased the area of grassland taken out of agriculture in the Netherlands. One option for the further use of such 'unwanted' grassland has been to restore the former species-rich hay-field communities found before the application of artificial fertilizers which began in the 1920s. These communities were found at sites with marginal agricultural use, e.g. haymaking once a year without fertilizer application. Adding fertilizer to moist grassland communities beside small streams in the northern Netherlands increased the above-ground standing crop prior to hay-making to $c.$ 1000 g m^{-2}. This led to a decrease in species-richness (Bakker 1989). The cessation of fertilizer application presumably reduces nutrient availability and, therefore, reduces peak standing crop (with continued mowing). This makes it possible to investigate the relationship between peak standing crop and species diversity without extrapolating over different sites. Decreasing productivity could then be used to monitor the potential for regeneration of species-rich communities (Willems 1980). The changes in species composition can also yield information on the mechanisms of the changes occurring. The results could be used to formulate further hypotheses on the causes of the changes in species composition, e.g. changes in competitive relationships between species when the nutrient supply rate is decreased.

METHODS

Study area

The hay-fields studied are in the Drentse A Nature Reserve, The Netherlands (53°N, 6°42'E). The current experiment used two sites: the Loefvledder site which is in a stream valley on a peaty soil receiving some seepage water, and the Westerholt area which is situated on upland sandy podzol. Both sites had been fertilized hay-fields until 1972 (artificial fertilizer with 150−250 kg N and K and 25−75 kg P ha^{-1} year^{-1}), when fertilizing was stopped but hay-making continued. In Loefvledder, we compared two 50 × 10 m experimental fields which have had different management since 1972. One field has been cut for hay once a year in July (field L1) and the other has been cut twice a year, in July and in September (field L2). At the Westerhold area, a 20 × 10 m experimental field was studied which had been cut for hay once a year in July (field W1). Soil characteristics of the three fields are given in Table 1. Above-ground standing crop was estimated in each field from 1973 to 1988, just before hay making, by clipping ten 20 × 20 cm samples at the soil surface. These were oven-dried at 70 °C (24 h) and weighed.

Vegetation composition was determined yearly in June from 1974 to 1988 by estimating the percentage cover of each species on a decimal scale in 2 × 2 m^2 permanent plots (six plots per field). Plant nomenclature follows Van der Meijden et al. (1983).

Productivity changes

To test for changes in above-ground production as estimated by standing crop,

over time in each field, we used the exponential model

$$Y(t) = Y_0 e^{(-bt)} \tag{1}$$

where the yield (Y) in year t is a decreasing function of the parameters Y_0 (production at the moment of cessation of fertilization) and b (rate of decrease). To examine precipitation effects on production, the residuals of the regression model were correlated in a linear regression to the potential water surplus (rainfall minus Penman (1948) evaporation of the second quarter of each year (April–June, this being the main growing season)). When the regression was not significant, the deviations from the mean were analysed as residuals from the mean.

Some data on the nitrogen budget of the Loefvledder site were obtained from Bakker (1989) and Grootjans, Schipper & Van der Windt (1985).

TABLE 1. Soil characteristics at two different depths of three fields in 1974 and in 1982

Soil type	Field L1 Peaty soil				Field L2 Peaty soil				Field W1 Podzol			
Year	1974		1982		1974		1982		1974		1982	
Depth (cm)	0–5	5–20	0–5	5–20	0–5	5–20	0–5	5–20	0–5	5–20	0–5	5–20
pH (in KCL)	5·3	4·1	4·9	4·3	5·6	4·1	5·0	3·9	4·5	4·4	3·8	–
Total N (mg N $100\,g^{-1}$ dry soil)	0·8	0·7	0·6	0·4	0·7	0·6	0·4	0·5	0·2	0·3	0·2	–
Total P (mg P_2O_5 $100\,g^{-1}$ dry soil)	380	310	200	150	390	320	220	210	65	80	40	–
Exchangable K (mg K_2O 100 g^{-1} dry soil)	13	10	7	3	13	9	5	2	3	8	3	–
C/N tatio	19	21	22	24	21	21	24	27	27	20	25	–

– Not measured.

Changes in species composition

The changes during succession were analysed using a Gaussian response curve, where the mean cover of a species in a field (COV) is a function of time (t) according to the equation

$$COV = C_m \exp\left(\frac{-t^k - t^{*k}}{s}\right)^2 \tag{2}$$

where k is the skewness of the function, t^* is the year of maximum cover, C_m is the maximum cover in this year and s is the standard deviation (width) of the curve. The parameters of the function were computed by iteration using the VEGROW program package for the analysis of vegetation data (Fresco 1989). The fit of the model for each species was tested as the product moment correlation coefficient (r) between the observed and predicted data. Species which did show a significant trend in a field were characterized by their mean cover over the entire period for each field.

Species-richness and rate of succession

Two measures of species-richness were analysed: the number of higher plant

species per field in a specific year, and the mean number of species per plot. The rate of successional change was computed as the percentage dissimilarity for each year with the median of the preceeding three years (D_p) and the dissimilarity with the first year (D_f). The average cover per field of each species was used for the computation of the dissimilarities between years. All species were used in these computations. The first estimate D_p gives a smoothed rate of change, while the second estimate D_f shows the cumulative result of all preceeding changes for each year. Percentage dissimilarity between two samples i and j was estimated from

$$D = 200 \sum_k \min (y_{ki}, y_{kj})/(\sum_k y_k i + \sum_k y_k j) \qquad (3)$$

where y_{ki} is the mean abundance of the kth species in year i, and y_{kj} is the mean abundance of the kth species in year j (Van Tongeren 1987). The mean percentage cover of each species was square root $\times 100$ transformed before calculating D.

RESULTS

Standing crop

The two fields on peaty soil (Loefvledder) showed a strong decrease in standing crop in July (first cut) from $c.$ $800\,\text{g m}^{-2}$ to $300\,\text{g m}^{-2}$ over the study period (Fig. 1a, b). The negative exponential model was a good description of the observed changes in the Loefvledder site $(R = -0.77, P < 0.001$ for L1, $R = -0.75, P < 0.001$ for L2).
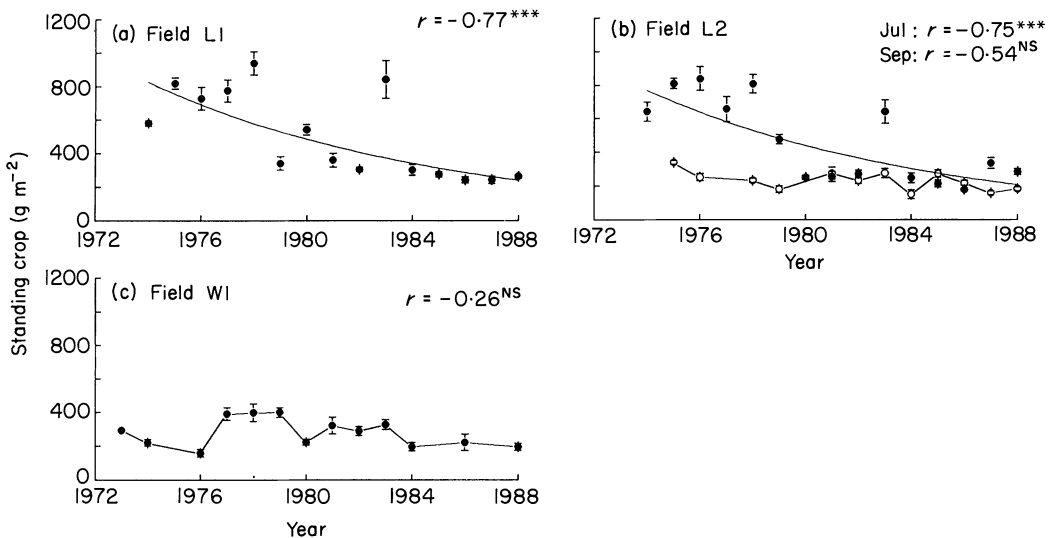

FIG. 1. Changes in the standing crop (mean $\pm$ S.D., $n = 10$; g m^{-2}) in July of three fields differing in management and/or soil conditions. Fertilizer application was stopped in 1972 while hay-making continued. Standing crop changes are given for (a) the Loefvledder site on peat soil with July hay-making. (b) the same site with July and September hay-making, and (c) the Westerholt site on sandy soil with July hay-making. The standing crops at the first cut in July ($\bullet$) and the second cut in September ($\circ$) are given. The line gives the exponential model (if significant) for each field, with its correlation coefficient. N.S., not significant; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

The variation between years in standing crop was larger in the beginning than in the later years (Fig. 1a, b). The extremely high standing crop in 1983 in both fields could be ascribed to the very wet summer of this year (Bakker 1989). The decrease in yield of the second cut of field L2 in September was not quite significant ($r = -0.54$, $P = 0.06$).

The standing crop of field W1 on sandy soil (Westerholt) showed no significant decrease from its initial value of approximately $300 \, \text{g m}^{-2}$ in 1972 (Fig. 1c, $r = -0.26$). The standing crop in this field was also less variable during the study period. The residual variation from the regression model of the standing crop changes in fields L1 and L2 was not correlated to the rainfall deficit in the growing season (Fig. 2a−c). Apparently only the extreme deviations were related to this factor. Although much less variable, the residuals for field W1 were correlated to the rainfall deficit ($r = 0.55$, $P < 0.05$, Fig. 2d). This positive correlation suggests that a higher standing crop was found in wetter years.

Because of the higher cutting frequency, more nitrogen was removed per year from field L2 (Table 2). This was, however, a very small fraction of the large amount of N stored in the soil and was partly compensated for by atmospheric deposition and net mineralization (Table 2). Most available N was from the fertilizer. Lower nutrient availability as a result of cessation of fertilizer application is therefore the most likely cause of the decrease in standing crop and the trigger for species replacement.
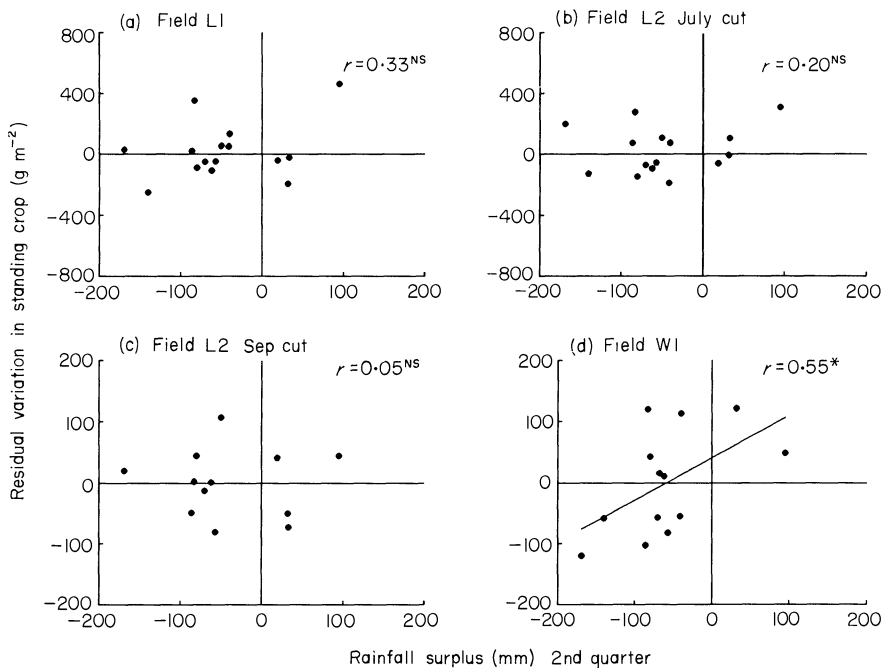
FIG. 2. Relationship between residual variation in standing crop for the three fields from Fig. 1, and the potential water surplus in the second quarter of each year (April−June) of (a) Loefvledder field L1, (b) Loefvledder field L2 first cut in July, (c) Loefvledder field L2 second cut in September, (d) Westerholt field W1. Potential water surplus was defined as the rainfall minus Penman (1948) evaporation. The linear correlation coefficient is given for each field. Abbreviations and levels of significance as in Fig. 1.

Table 2. Nitrogen budget (levels in g m^{-2} and rates in g m^{-2} year^{-1}) for the two Loefvledder fields. Data were measured in 1975, 3 years after cessation of fertilizer application

Parameter	Pool size	Supplied	Removed
Field L1			
Total present in soil (0–20 cm)	475		
Fertilization		20–30	
Atmospheric deposition		5	
Net mineralization		(5)	
Removed by cutting			11
Field L2			
Total present in soil (0–20 cm)	475		
Fertilization		20–30	
Atmospheric deposition		5	
Net mineralization		(5)	
Removed by cutting			16

Fertilizer addition rates refer to the initial situation. Mineralization values are from another study site, and are therefore only indicative. Data are from Grootjans (1985, mineralization values) and Bakker (1989, all other data).

Species-richness and rate of succession

Both estimates of species-richness increased significantly in the two Loefvledder fields over the study period (Fig. 3). The increase started earlier in field L2 than in field L1 (Fig. 3a, b). The mean number of species per plot decreased with time in field W1, while the number of species per field did not change significantly (Fig. 3c). A possible peak of about forty species was found after 8 years in field W1 (Fig. 3c), after which the number decreased to the initial level of thirty.

In all three fields, cumulative dissimilarity from the first year (D_f) increased to approximately 60% by 1988 (Fig. 4). However, cumulative differences (dissimilarity with the median of the three preceding years. D_p) in both estimates of species-richness were less variable at Westerholt than at Loefvledder (Fig. 4). The earlier increase in species-richness in field L2 was reflected in a higher rate of succession during the first 2 years (Fig. 4). The rate of succession in field W1 during the first few years was much lower than in fields L1 and L2 (Fig. 4).

Changes in species composition

Holcus lanatus initially dominated fields L1 and W1, and *Agrostis stolonifera* field L2 (Figs 5–7, Table 3). Almost all species which covered more than 1% in field W1 (Table 3) showed a significant trend (Fig. 7). For fields L1 and L2, about half of these species showed a trend (Table 3, Figs 5 & 6). Non-directional fluctuations probably occurred more often on the peat soil than on the sandy soil. The dominants of field L1, *Holcus lanatus*, *Agrostis stolonifera* and *Festuca rubra* were largely replaced by *Ranunculus repens*, *Rumex acetosa*, *Rhinanthus angustifolius*, *Anthoxanthum odoratum* (Fig. 5). Similar changes occurred in field L2 (Fig. 6), except that *Holcus lanatus* did not change significantly. A difference between fields L1 and L2 was that
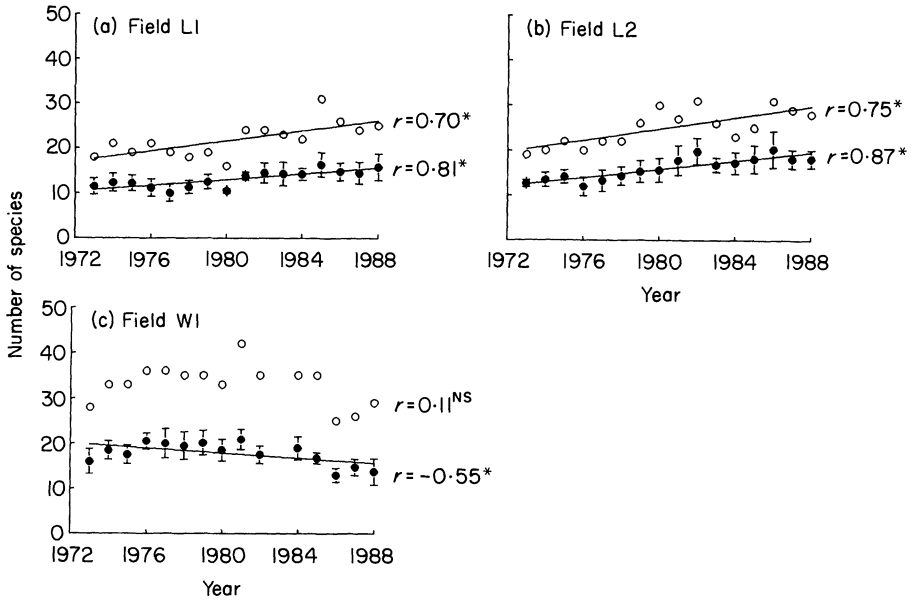
FIG. 3. Changes in species-richness as number of species in July per field (○) and mean number of species per plot (●, with S.D.) for the three hay-fields from Fig. 1 (conventions as in Fig. 1).
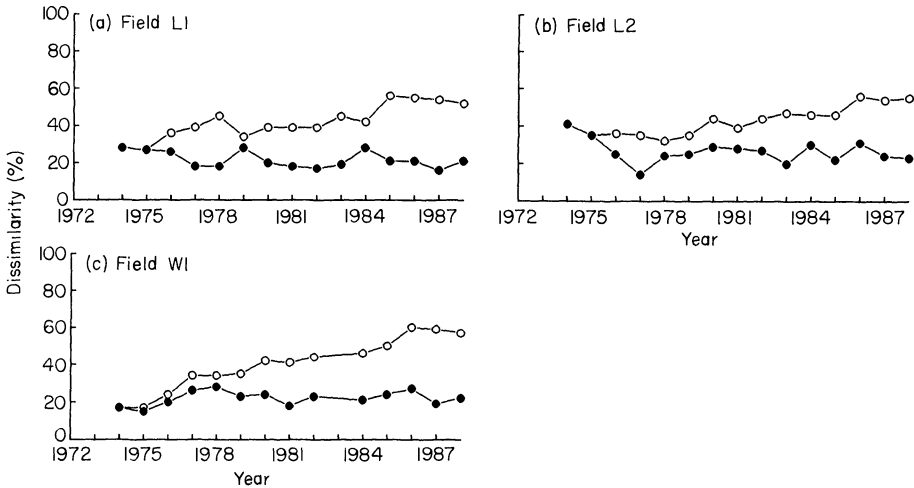
FIG. 4. Rate of succession in the three hay-fields from Fig. 1, expressed as the % dissimilarity of each year with 1973 (D_f, open symbols) and the median dissimilarity with the preceeding 3 years (D_p, ●).

the increasing species *Ranunculus repens, Anthoxanthum odoratum* and *Plantago lanceolata* appeared earlier in L2 (Figs 5 & 6). The peak in species-richness in field W1 noted earlier can probably be ascribed to the fact that many species initially
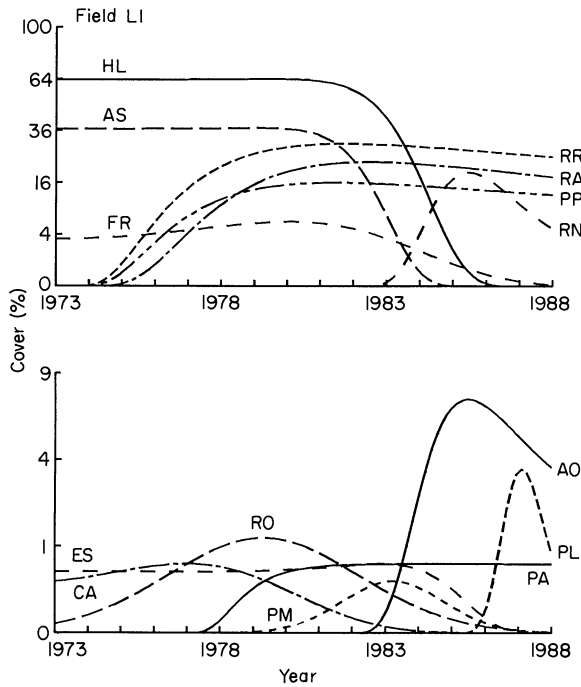
FIG. 5. Dynamics of species replacement in field L1. Fitted curves are given for each species according to a Gaussian response model (eqn (2)). Only those species which significantly changed with time are given. The % cover of each species was square root × 10 transformed before calculating the response curves. Abbreviations of the species names: HL, *Holcus lanatus*; AS, *Agrostis stolonifera*; RR, *Ranunculus repens*; RA, *Rumex acetosa*; PP, *Poa pratensis*; RN, *Rhinanthus angustifolius*; FR, *Festuca rubra*; ES, *Epilobium spp.*; CA, *Cirsium arvense*; RO, *Rumex obtusifolius*; PM, *Plantago major*; AO, *Anthoxanthum odoratum*; PL, *Plantago lanceolata*; PA, *Potentilla anserina*.

TABLE 3. Mean % cover of species during 1973–88

Species	Field L1		Field L2		Field W1	
Holcus lanatus	17·6	(T)	21·7		17·6	(T)
Ranunculus repens	13·1	(T)	22·6	(T)	6·5	(T)
Agrostis stolonifera	9·6	(T)	10·1	(T)	0·6	(T)
Rumex acetosa	9·0	(T)	3·7	(T)	4·1	(T)
Poa pratensis	7·9	(T)	1·8		2·9	(T)
Festuca rubra	2·9	(T)	1·1	(T)		
Festuca pratensis	2·8		2·3			
Rhinanthus angustifolius	2·4	(T)	3·0		2·3	
Poa trivialis	2·3		7·7		1·2	
Anthoxanthum odoratum	1·0	(T)	3·9	(T)	5·1	(T)
Agrostis capillaris	0·4		2·5	(T)	7·3	(T)
Cardamine pratensis	0·8		1·6			
Plantago lanceolata	<0·1	(T)	0·4	(T)	1·1	(T)

Only species for which the mean cover in any field exceeded 1% are listed. Species which showed a significant change with time as graphed in Figs 5–7 are annotated with (T).
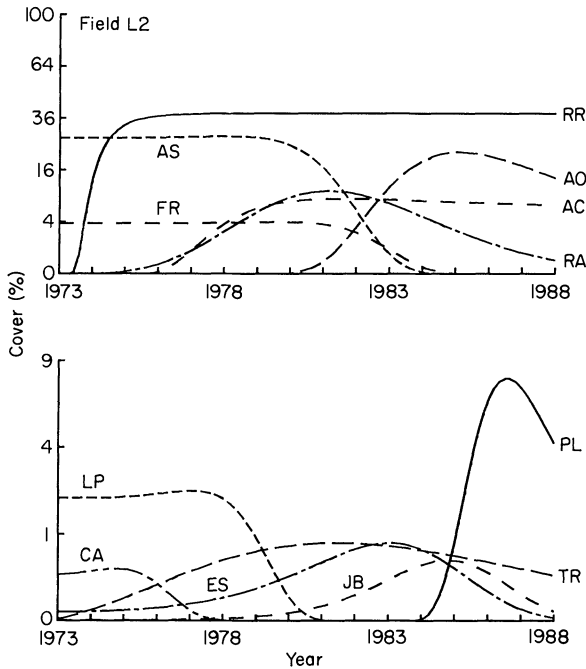
FIG. 6. Dynamics of species replacement in field L2 (details as in Fig. 5). Further species abbreviations: AC, *Agrostis capillaris*; LP, *Lolium perenne*; JB, *Juncus bufonius*; TR, *Trifolium repens*.

present were disappearing by 1980, while others appeared (Fig. 7). *Holcus lanatus*, *Taraxacum* spp. and many grasses initially present were replaced by *Agrostis capillaris*, *Anthoxanthum odoratum*, *Plantago lanceolata*, *Ranunculus repens* and *Leontodon autumnalis* (Fig. 7). *Agrostis capillaris* and *Plantago lanceolata* entered the succession earlier in field W1 than in L1 and L2. Furthermore, no new species entered field W1 after 1980, indicating that the successional replacement there had already proceeded further by the start of the experiment than in L1 and L2.

DISCUSSION

The two fields in the Loefvledder area had a large decrease in standing crop and an increase in species-richness following the cessation of fertilizer application. In both fields, the major increase in species-richness began when the standing crop had dropped below ± 400 g m^{-2}. Changes in productivity and diversity occurred earlier in field L2, possibly because of a higher rate of removal of nutrients from this field as it was cut twice a year. In a comparable experiment, Oomes (1990) studied the standing crop and number of species after cessation of fertilizer application to hay fields on a heavy clay soil and on a humic sandy soil. These grasslands were more productive at the start of the experiment (1200 g m^{-2}), and standing crop did not decrease below 500–600 g m^{-2}. No changes in the number of species were observed after 14 years, indicating that a peak standing crop < 400 g m^{-2} is necessary for an
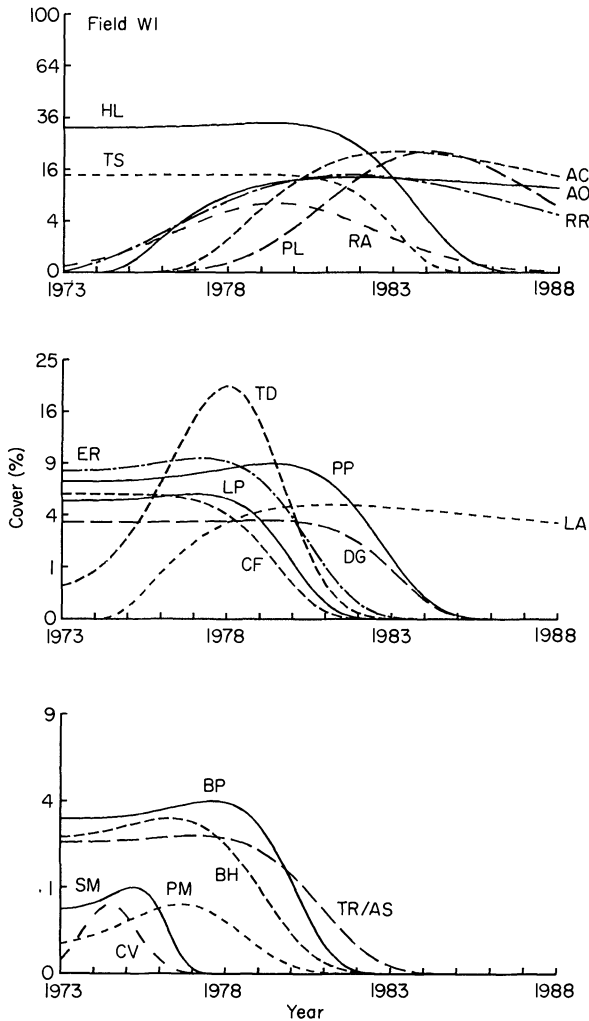
Fig. 7. Dynamics of species replacement in field W1 (details as in Fig. 5). Further species abbreviations: TS, *Taraxacum spp.*; TD, *Trifolium dubium*; ER, *Elymus repens*; CF, *Cerastium fontanum*; DG, *Dactylis glomerata*; LA, *Leontodon autumnalis*; BP, *Bellis perennis*; BH, *Bromus hordeaceus*; CV, *Cirsium vulgare*; SM, *Stellaria media*.

increase in species-richness. The results from field W1 indicate that productivity fluctuations can be determined by year-to-year variation in weather conditions, as was also found by De Leeuw, Olff & Bakker (1990) for a salt-marsh vegetation.

An increase in the number of species was found per field and per 4-m^2 plot. This indicates that the increase in number of species per field was not caused by an increase of the number of vegetation types within a field (see Wisheu & Keddy 1989; Ter Heerdt, Bakker & De Leeuw 1991). The initial low standing crop ($\pm\,300\,\mathrm{g\,m^{-2}}$) and relatively high species-richness (thirty species) of field W1 were comparable to the final values of fields L1 and L2. Species which occurred in all three fields entered

the succession earlier in field W1. Therefore, it is likely that field W1 was already subject to marginal agricultural use prior to the start of the experiments.

Species replacement, expressed as dissimilarity (*D*), appeared to be gradual (Fig. 4). The increase in the number of species was however delayed during the first years in field L1 (Fig. 3), but not in field L2. It is remarkable that the rate of species replacement was fastest in field W1, while standing crop did not change much. A possible explanation for this might be a shift in limitation from nitrogen to other nutrients such as phosphate or potassium, or vice versa. Changes in the relative availability of nutrients might cause successional changes in species composition without changing total productivity (Tilman 1982). The level of optimal species-richness found in field W1 could indicate a point where many species were limited by different nutrients.

The partial lack of correspondence between the time of the decrease in standing crop, and the timing of species replacement suggest that part of the dynamics of species replacement might be due to differences in colonization ability between species. The cessation of fertilizer application probably functions as a trigger for the observed vegetational succession, but is probably not fully determining its further progress. The differences between fields L1 and L2 in the sequence of species replacement with time might be due to the difference in vegetation structure between the fields. Cutting twice a year will lead to a more open vegetation structure, especially in spring, than cutting only in July (Bakker 1989). Species adapted to nutrient-poor conditions might be poor competitors for light (Tilman 1988), which possibly allows them to enter the successional sequence earlier in field L2 than in L1. It is clear that in the present successional sequence, species indicating nutrient-rich conditions such as *Holcus lanatus, Lolium perenne, Agrostis stolonifera, Elymus repens* and *Dactylis glomerata* were replaced by species indicating poorer conditions, (*Agrostis capillaris, Rhinanthus angustifolius, Anthoxanthum odoratum* and *Plantago lanceolata*). It is likely that this species replacement is mainly caused by changing competitive relationships dependent on nutrient-supply rate and vegetation structure. Which plant traits (such as relative growth rate, allocation patterns and plant architecture, as well as the plasticity of these traits) are predictors of this habitat-dependent outcome of competition needs evaluating. Olff, Van Andel & Bakker (1990) studied growth and allocation patterns of some species from this successional series, and did not find a lower shoot:root ratio in species from the poorer successional stages, as suggested by Tilman (1988). A similar result was found by Berendse & Elberse (1990).

The constant low yield of field L2 at the second cut suggests that the high productivity of this field in the first 7 years was mainly caused by higher nutrient availability in the first part of the growing season. Nitrogen is probably the major limiting nutrient in these grasslands (Pegtel 1987). The gradual decrease in standing crop may be due to a gradually decreasing nutrient availability after the application of fertilizers was stopped. The high mobility of nitrogen in the soil makes it unlikely that this high productivity was caused by fertilizer nitrogen remaining in the soil. If this was the only determinant of productivity, then the standing crop would be expected to decrease immediately after the cessation of fertilizer application in 1972. The observed gradual decrease in productivity, and presumably nitrogen supply rate, may be due to indirect effects of dominant species on nutrient cycling parameters, such as nitrogen mineralization (Berendse, Bobbink & Rouwenhorst 1989; Wedin 1990). The dominant species from the fertilized stages could produce litter with high N and low lignin concentration, which should lead to higher net N mineralization rates than

the litter of species found later in the succession. These hypotheses are currently being tested in fertilizer addition experiments. The high groundwater table of the partly anaerobic peat soil in the Loefvledder area (Bakker 1989) might cause slow decomposition and nitrification in deeper soil. Some information on nitrogen cycling for the Loefvledder field is summarized in Table 2. Although as yet incomplete, these data suggest that fertilizer addition to these grasslands is by far the most important determinant of nutrient availability compared to the probably very slow natural mineralization rates. These roughly equal the average atmospheric deposition rates of nitrogen. Furthermore, it appears from Table 2 that these peat soils have a very large pool of organic nitrogen. Lowering the ground water table in these areas can, therefore, cause large increases in the mineralization of N from peat (Grootjans, Schipper & Van der Windt 1985). The changes in the total pool size of N, P and K during the successional sequence were very small (Table 1, and see Bakker 1989). The amount of N which is removed from the system by hay-making is very small compared to the total pool size. It can however be an important part of the available fraction.

It can be concluded from the results that the main aim of this research was achieved: increasing the species diversity by decreasing the standing crop. However, the mechanisms behind the decreases in standing crop and replacement of species cannot yet be determined. More information on other sources of N loss, such as denitrification and leaching to groundwater, and on seasonal patterns of mineralization rates and uptake by the vegetation, are needed.

ACKNOWLEDGMENTS

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