Reversion of grassland vegetation following the cessation of fertilizer application

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Abstract. Tadhams Moor in Somerset, England, is an exceptionally rich wetland site which has been mown for hay for many years, with stock grazing the aftermath, but with no history of any fertilizer use. A randomized blocks field experiment (1986-1989) was used to study the effects of five levels of nitrogen input treatments: 0 = control, 25, 50, 100 and 200 kg of N fertilizer per ha per yr. In Phase II of the experiment (1990-1993), each plot was split into two subplots. The allocated fertilizer treatment for the plot was continued in one, randomly selected, subplot but the treatment was discontinued in the other subplot. The experiment not only identified and quantified the changes occurring in the vegetation of hay meadows under different levels of N input, it also provided valuable insight into the dynamics of the sward upon the discontinuance of the treatments. The data for Phase II were used to estimate the time required by the changed vegetation (under different nitrogen treatments) to revert to a state comparable to that prevailing in the control plots. A method for estimating reversion times is described. The main difficulties in estimating the reversion times are identified, the choice of robust vegetation variables being critical. Reversion time estimation methods are presented and used to obtain working estimates for the four nitrogen treatments, applied for 5 yr. These estimates are 3, 5, 7 and 9 yr respectively. The validity of the estimates of 3 yr for the lowest nitrogen input treatment (25 kg/ha/yr) was checked using the available post cessation data.

Keywords: Meadow; Nitrogen; Vegetation recovery.

Nomenclature: Smith (1978) for mosses; Stace (1991) for vascular plants.

Introduction

By 1984, the extent of unimproved pasture in England and Wales was only 3% of that present prior to World War II (Fuller 1987). It was known that fertilizer application stimulated sown grasses at the expense of indigenous species (Fuller 1987; Rabotnov 1977) and that fertilized swards supported different plant communities to those mown or grazed but not fertilized (Ellenberg 1988). However, experimental data on the effects of

fertilizer on the botanical composition of British semi-natural grasslands were sparse, and almost absent for wet grasslands of the types found on the Somerset Levels and Moors. More recently, interest has developed in habitat re-creation and rehabilitation, and hence on the effects of decreasing fertilizer use. In 1986, the Ministry of Agriculture, Fisheries and Food (MAFF) designated the Somerset Levels and Moors as an Environmentally Sensitive Area (ESA). One aim of the ESA prescription was to assess the potential for enhancing biodiversity, whilst retaining agricultural management (Anon. 1992). It was suggested that this might be achieved partly by reducing or eliminating fertilizer applications, in a manner similar to that practised in Dutch nature management (Bakker 1987, 1994). Together with English Nature (EN) and the Department of Environment (DoE), MAFF commissioned an experimental study of the effects of a wide range of rates of fertilizer application at Tadhams Moor in Somerset (51° 12' N; 2° 49' W), where an exceptionally rich meadow occurred on low-lying peaty soils. The grassland at Tadhams had been mown for hay for many years, with stock grazing the aftermath, but there was no history of fertilizer use. The fields supported a mosaic of grassland types, with two communities of the National Vegetation Classification prominent: MG5, *Centaureo-Cynosuretum cristati*, and MG8, *Senecioni-Brometum racemosi* (Rodwell 1992).

While some of the fertilizer treatments in the classic Park Grass Experiments at Rothamsted were discontinued after a few decades (Williams 1978), most of the experimental studies of changes following the end of nitrogen application have taken place in the Netherlands (Bakker 1987, 1994; Olff & Bakker 1991; Olff et al. 1994; Oomes 1990, 1992). The Dutch studies not only involve wet mesotrophic grasslands similar to those at Tadhams Moor, but also communities similar to MG6: *Lolium perenne-Cynosurus cristatus*, MG7: *Lolium perenne*, and M24: *Molinia caerulea-Cirsium dissectum* (Rodwell 1991, 1992). However, the sites investigated in the Dutch experiments were managed by hay-cutting or grazing post-cessation, rather than the combined July hay-cut and aftermath grazing practised at Tadhams.

Objectives and hypotheses to be tested

The experiment was conducted in two phases. During Phase I (1986-1989), the principal objective was to measure the impact of nitrogen fertilizer on sward composition, and to ascertain whether there was a 'safe' level of nitrogen that could be applied to species-rich grassland without reducing floristic diversity. In Phase II (1990-1993), three objectives were addressed: (1) to assess the longer-term impact of nitrogen application; (2) to investigate the changes in sward composition after the cessation of fertilizer application; and (3) to estimate the time required for the vegetation in plots subject to different fertilizer treatments to revert to a composition similar to that in the plots which received no application of fertilizer i.e. to estimate the vegetation reversion times. This paper is concerned with the reversion of vegetation after fertilizer input had been discontinued, and focuses in particular on the estimation of the vegetation reversion times after the cessation of fertilizer application. To that end, a method is advanced for estimating recovery times for vegetation following some perturbation; in the present case that perturbation stemmed from four years of fertilizer use.

In a review of a wide range of studies on the relationship between fertilizer addition and species abundance, Marrs (1993) concluded that species diversity was reduced whenever the original ecosystem was relatively species-rich, but that in species-poor communities, the application of fertilizers increased species diversity, a finding which was consistent with the 'hump-back' model developed by Grime (1979). Using this model, elimination of nitrogen input, resulting in (possibly gradual) reduction of both nutrient availability and hay yield, would be predicted to lead to increased species-richness (Oomes 1992). The results of the latter study indicate that maximum species-richness was achieved at between 4 and 6 tonnes/ha dry matter. In 1990, fertilized grassland at Tadhams Moor comprised vegetation which had changed as a result of nitrogen input. The vegetation in N-treated plots was expected to be, and was, different from that in unfertilized (control) plots in at the beginning of Phase II, and varied with the levels of the nitrogen input. In 1990, dry-matter yields were ≥ 7 tonnes/ha wherever nitrogen had been applied, and there was a significant suppression of species richness at high levels of fertilizer (Mountford et al. 1993, 1994). Once fertilizer treatment ceased at Tadhams, it might be postulated that the vegetation would revert, over a period of time, to a composition indistinguishable from that found in adjacent untreated swards, with restored high species diversity, and a dry matter yield comparable with the controls (i.e. ca. 4.5 - 5 tonnes/ha). In a closed sward of the type found at Tadhams Moor, where

regeneration niches are restricted, increased diversity following the cessation of fertilizer use would be more likely to result from changes in the relative extent of long-lived perennials, rather than the recruitment either of new species, or of species lost to that sward during Phase I. Thus whilst the number of species per m² might increase, the total number of species within the plot might not recover. However, the cessation of fertilizer input might simply trigger change, rather than determine the precise outcome of such change (Olff & Bakker 1991). Further, it was anticipated that the vegetation in previously treated plots may show a trend towards a new equilibrium, and could also be subject to trends and fluctuations induced by external environmental factors.

Methods

Study area and experimental design

The field experiment at Tadhams consisted of three randomized blocks, with five plots in each block. The plots within the blocks received at random five nitrogen treatments. During the years 1986-1989 the experimental treatments were: $T_1 = \text{control} = N_0 = \text{no fertilizer applied}$, cut for hay in early July and aftermath grazed; $T_2 = N_{25} = 25$ kg of nitrogen fertilizer per ha applied annually, cut for hay in early July and aftermath grazed, and phosphorus (P) and potassium (K) removed in the crop replaced. Treatments $T_3 = N_{50}$, $T_4 = N_{100}$ and $T_5 = N_{200}$, were the same as the treatment T_2 , but with 50, 100 and 200 kg of N fertilizer per ha per yr (Mountford et al. 1993).

Phase II of the experiment commenced in 1990, where each of the 15 plots was divided into two subplots (Mountford et al. 1994). One subplot (N^+) continued to receive the same nitrogen treatment that had been applied annually from 1986 to 1989. In the other subplot (N^-) all fertilizer application ceased. The methods used for recording the floristic composition of subplots were the same as those used in Phase I (Mountford et al. 1993). Objective (1) was addressed within the N^+ subplots, whereas objectives (2) and (3) were dealt with in the N^- subplots.

Vegetation pattern at the end of Phase I

Mountford et al. (1993) have described the effects of the fertilizer treatments during the Phase I of the experiment. Fertilizer encouraged grasses, particularly *Lolium perenne* and *Holcus lanatus*, which came to dominate the sward at the expense of most other species. In plots receiving high levels of nitrogen, the sward became taller, and all measures of species diversity declined.

Only a very few forbs (e.g. *Rumex acetosa*) maintained or increased their cover. All *Carex* species, *Juncus* species and mosses became less common in plots treated with nitrogen, producing an apparently more mesotrophic sward. Short-lived species and low-growing wetland forbs also declined with increased nitrogen, possibly because of shading by tall grasses. Legumes decreased under high levels of nitrogen, but remained common in plots receiving only 25 kg of N per yr, where replacement levels of P and K were applied after cutting. During Phase II, agriculturally productive grasses (*Lolium perenne*, *Holcus lanatus*, *Phleum pratense* and *Bromus hordeaceus*) continued to spread in the N⁺ subplots, developing into a coarser sward. Other species (including all sedges, rushes, bryophytes and the majority of forbs) were most common where no nitrogen was applied and rarest where high N levels were applied. A number of measures of species diversity decreased with increased nitrogen - this effect becoming more significant with time. In 1992 and 1993, species richness was significantly reduced even under the lower rate (25 kg N/ha/yr) of nitrogen application from 1986.

Statistics

Recovery of vegetation: composition of the sward

In Phase II the field observations provided data on the following variables:

- (1) mean number of plant species per 1-m² quadrat, M ;
- (2) total species richness, i.e. the total number of species on 16 1-m² quadrats, S ;
- (3) flowering species richness - calculated as for S but including only those species which were in flower at the time of observation, S' ;
- (d) Simpson's index of diversity, I , (see Mountford et al. 1993); and
- (e) percentage cover p_i for individual named species i .

In Phase I the plot measurements had been based on 24-m² quadrats. The change to 16 1m² quadrats in Phase II introduced no bias in percentage cover values of individual species, nor in the community variable M . However, the community variables S , S' and I depend also on the number of quadrats.

For the years 1991-1993 the data consisted of 15 observations (X_{ij}) from subplots where the original treatments were continued, and 15 observations (Y_{ij}) from subplots where the original treatments were discontinued. For each year, these data were analysed separately as observations arising from a randomized block experiment. The standard ANOVA provided the variance-ratio test (via the $F_{4,8}$ distribution) to test the null hypothesis of equality of the experimental treatments. If

this null hypothesis was rejected, then each N treatment ($T_2 - T_5$) was compared with the control (T_1) using Student's t -test. In addition, for every variable the significance of the linear effect of nitrogen levels was also examined ($F_{1,8}$). The comparison of the effects of discontinuing the treatments with the continuation of the original treatments was based on the differences $Z_{ij} = Y_{ij} - X_{ij}$, which were analysed using the simple one-way classification ANOVA model. The results from the analyses of only the Y -variables concern us here.

Year of cessation and data of interest

Fertilizer treatments ceased after 1989 in the N⁻ subplots. For each vegetation variable, the relevant data were the 15 observations from the 15 plots in year 0 (1990) and 15 observations from the N⁻ subplots in years 1, 2 and 3 (1991-1993). Since there were five treatments, these 60 observations were categorized as five sets of 12, and denoted by $N0_{ij}$, $N25_{ij}$, $N50_{ij}$, $N100_{ij}$ and $N200_{ij}$ with $i = 1, 2, 3$ (replicates) and $j = 0, 1, 2, 3$ (yr).

Reversion times

There is some difficulty in establishing the point at which reversion is complete following the end of fertilizer use, since it cannot be stated with certainty what the composition of the sward would have been had fertilizer not been applied. However, a practical and reasonable approach is to assume that this hypothetical and unobserved vegetation state can be described by observations derived from the untreated (control) plots. If, as a result of the discontinuance of nitrogen input, the vegetation in the subplots were to revert to a composition similar to that in the control plots, then it is reasonable to suppose that the reversion times will be different for the vegetation in plots which have received different inputs of N. If these reversion times are denoted by R_{25} , R_{50} , R_{100} and R_{200} , it is likely that $R_{25} < R_{50} < R_{100} < R_{200}$. It should be noted that by definition $R_0 = 0$.

Choice of vegetation variables

Three types of variable have been used: percentage cover of individual species; community variables: M , S , S' and I ; and groups of species.

Percentage cover of individual species

The estimates of the reversion times R_k for each species were formally obtained, although it was expected that a proportion of the individual estimates would be unsatisfactory. It was considered likely that after discarding those estimates which were clearly unsatisfactory, the remaining estimates might corroborate

the estimates obtained using the other (more robust) variables. This analysis was restricted to the 101 species which were observed in all four years 1990-1993.

Community variables - M, S, S' and I

These variables represent important attributes of the entire plant community. Hence, the estimates of the reversion times (R_k , $k = 25, 50, 100, 200$) should generally make sense.

Groups of species

The percentage cover of a number of species may be pooled to obtain the 'percentage cover' of a group of species. The number of species in each group will be smaller than the number in the community variables. However, the species making up the groups may be chosen deliberately for the purpose of estimating R_k . The results obtained should be more trustworthy than those based on individual species, not only because the data for the grouped variables will be less sparse, but also because the chance variations in the percentage cover of the species within the group might tend to cancel out. Thus if, for example, species A and B belong to the same group, then the percentage cover value for the group will be robust to the changes in the percentage cover of the species A and B, if these changes were in opposite directions i.e. if one of the species tended to increase at the expense of the other.

The actual grouping of species can be carried out using a variety of criteria e.g. growth form (Raunkiaer 1937), the C-S-R system (Grime et al. 1988) or higher taxonomic units (orders, families, etc). For this paper, the approach for grouping the species was based partly on higher taxonomic units (grasses, forbs, bryophytes, sedges and rushes) and partly on the ecological indicator values for the individual species (Ellenberg 1988). In the Ellenberg system, the Nitrogen value (N) of a species is a 9-point scale, reflecting occurrence of the species along a gradient of available nitrogen during the growing period. This ranking is based on considerable experimental and field observation and was believed to be a reliable criterion for grouping species. The N ranking was thought to be appropriate to the present study, since it reflects the understanding of how different species might react to different levels of nitrogen. Species were allocated to seven groups using an N indicator value of 6 as a threshold to separate species thought to respond well to fertilizer application ($N \geq 6$) from those more typical of nitrogen deficient soils ($N \leq 5$). A similar approach, classifying species in terms of their association with rich, intermediate or poor soils, was employed by Bakker (1987), who found that use of the poor:rich ratio reduced the apparent large year-to-year oscillations due to individual species, achieving a more consistent trend.

Estimation of the reversion times (R_k)

As pointed out earlier, for each variable, the relevant data were the observations $N0_{ij}$, $N25_{ij}$, ..., $N200_{ij}$ with $i = 1, 2, 3$ (replicates) and $j = 0, 1, 2, 3$ (yr). Similar data for the grouped variables were obtained by summing the observations for appropriate species. To obtain the estimates of the reversion times for a particular variable, the approach used was to separately fit simple straight line models to the scatter of $N0_{ij}$, $N25_{ij}$, $N50_{ij}$, $N100_{ij}$ and $N200_{ij}$ respectively (12 points) against time measured in years: $t = 0, 1, 2, 3$. Thence for a given nitrogen treatment, an estimate of the reversion time is given by noting the time point when the trends fitted to the data under that treatment and the control treatment meet.

To illustrate the estimating procedure, denote the five fitted straight line models by:

$$N_0 = a_0 + b_0 \cdot t \quad (1)$$

$$N_{25} = a_{25} + b_{25} \cdot t \quad (2)$$

$$N_{50} = a_{50} + b_{50} \cdot t \quad (3)$$

$$N_{100} = a_{100} + b_{100} \cdot t \quad (4)$$

$$N_{200} = a_{200} + b_{200} \cdot t \quad (5)$$

To obtain the estimate of R_{25} we consider the two trend lines (1) and (2). At the time when these two lines meet, N_0 must equal N_{25} and hence

$$a_0 + b_0 \cdot t = a_{25} + b_{25} \cdot t \quad (6)$$

from which an estimate of R_{25} is provided by

$$t = (a_0 - a_{25}) / (b_{25} - b_0). \quad (7)$$

In general, the estimate of R_k will be given by $(a_0 - a_k) / (b_k - b_0)$ for $k = 25, 50, 100, 200$. An approximation for the standard error of the estimate of the reversion time is presented in App. 1. It should be noted that the estimates of reversion times are from the date of cessation of treatment (i.e. 1990). The reversion times, measured from the time of the last application of the treatment will be one year greater.

Smoothing and combining of the estimates

The estimates obtained can be smoothed using the reasonable assumption $R0 < R25 < R50 < R100 < R200$. Firstly, it is useful to plot the estimated R_k values against the nitrogen treatment levels. This should describe an increasing relationship. If so, a monotonic increasing model, fitted to the observed points, can provide smoothed estimates of the R_k values.

Since the reversion times can be estimated using a number of vegetation variables, there will be as many sets of estimates of R_k as there are vegetation variables

used. A simple approach is to combine these results by obtaining a set of mean R_k values. However, the approach can be improved by first examining the individual estimates and discarding those estimates which can readily be identified as unsatisfactory. Thus, for example, an estimate $R = -20$ is unsatisfactory because a negative estimate is not meaningful. Similarly, a series of estimates such as $R_{50} = 5$, $R_{100} = 50$ and $R_{200} = 20$ clearly breach the inequality in R_k values mentioned above; comparing these series with estimates obtained using other vegetation variables might point to (for example) the estimate $R_{100} = 50$ yr as being unsatisfactory (as a likely large overestimate). An examination of the relationship between the various sets of R_k values (using different vegetation variables) and nitrogen levels simultaneously on a composite plot may identify obviously unsatisfactory estimates. A smooth curve describing the relationship between the R_k values and the nitrogen levels in the composite scatter-plot provides the estimates of the R_k values, based on all results.

The above approach can be improved. First, care should be taken to ensure that a particular vegetation variable is not being given too much weight by (perhaps inadvertently) using essentially the same variable repeatedly under a different name e.g. community variables S and S' might be correlated. In the case of grouped variables, the same species might contribute to the results for different groups. In the present study, the groups were of mutually exclusive species, hence avoiding this problem. Secondly, the results for some variables might be expected to be more reliable e.g. the results for the community variables might be more reliable than those for the cover values of individual species. Hence, separate composite plots should be obtained for the different sets of variables (community variables, grouped variables, individual species). These plots provide separate average estimates under the three types of variables. Overall estimates of the reversion times can be obtained from these separate averages.

Results

Composition of the sward after fertilizer discontinuance

In studying the composition of the sward within the N^- subplots after the cessation of the fertilizer treatments, any treatment effects displayed clearly refer to the fertilizer applied during Phase I. In 1993, the total numbers of positive (25) and negative linear trends (104) (in relation to the levels of nitrogen applied before 1990) in the N^- subplots were very similar both to the corresponding totals in 1993 for the N^+ subplots, and to those for N^+ and N^- subplots in 1991. For all four

community variables, the linear trends against nitrogen levels remained significantly negative in all four years i.e. subplots which had received nitrogen during Phase I were poorer in species and less diverse than the controls.

In 1993, seven species showed a significant positive linear trend with past N use in the N^- subplots:

<i>Agrostis capillaris</i>	<i>Anthoxanthum odoratum</i>
<i>Holcus lanatus</i>	<i>Lolium perenne</i>
<i>Rumex acetosa</i>	<i>Stellaria graminea</i>
<i>Trifolium repens</i> .	

All except *S. graminea* and *T. repens* had shown this trend in 1992. In contrast, 11 species showed a significant negative linear trend with N applied in Phase I:

<i>Bellis perennis</i>	<i>Carex disticha</i>
<i>C. flacca</i>	<i>C. hirta</i>
<i>Dactylorhiza praetermissa</i>	<i>Festuca rubra</i>
<i>Lychnis flos-cuculi</i>	<i>Lysimachia nummularia</i>
<i>Myosotis discolor</i>	<i>Calliargon cuspidatum</i>
<i>Climacium dendroides</i> .	

For the seven groups of species used for estimating reversion times, grasses known to favour nitrogen-rich sites (groups 1a and 1b) showed a positive linear trend with nitrogen in 1991 and 1992 (though less significant in 1992). In 1992 and 1993, as *H. lanatus* and *L. perenne* declined in the N^- subplots; their place was taken by *A. capillaris* and *Cynosurus cristatus* (group 2), resulting in a significant positive trend with N applied during Phase I.

During Phase II a contrasting trend was observed in groups 5 (*Cyperaceae* and *Juncaceae*) and 6 (mosses), which both showed a significant negative trend with nitrogen. The significance of this trend diminished with time for group 6. The remaining groups 3 and 4 consisted of forbs, but were expected to respond in opposite ways to the cessation of fertilizer. Group 3 species were predicted to benefit from fertilizer application, but showed no significant trend in Phase II. Group 4 species were expected to increase as the vegetation recovered from fertilizer, and by 1993 the group showed a significant positive trend with past N, reflecting an increase in N-intolerant species as N-demanding species declined.

Estimated reversion times for vegetation

Table 1 shows the estimates of the reversion times based upon the community variables (M , S , S' and I) and the seven species groups. Examples of the estimates of reversion times based on some of the individual species are given in Table 2. These tables also show, for each fertilizer treatment of Phase I, the mean estimate and its standard error, using the particular type of vegetation variables.

The estimates based upon the community variables and species groups were expected to be more efficient than those based upon individual species. However, for all variables, there were a number of estimates which were clearly unsatisfactory e.g. for the variable *S*, the estimate of nearly 50 yr for R_{50} appeared to be too large, whilst the other estimates were negative! A free-hand curve showing the relationship between past N application and reversion time based upon *M*, *S'* and *I*, was found to correspond closely to the estimate based solely on *M* (mean number of species per m² quadrat) (Fig. 1). Using the same approach for the species groups, there was wider divergence between the curves based upon each group. The curve for the average reversion time, however, based upon all species groups was very close to that derived from the community variables (Fig. 2).

As expected, the estimates based on individual species were much more varied and included many unsatisfactory results; these were omitted from the final composite plot (Fig. 3). It is interesting to note that species producing the unsatisfactory results (particularly *Lysimachia nummularia* and *Prunella vulgaris*) are normally absent from areas with high N availability, and were severely reduced during Phase I. Continued decline or virtual extinction following cessation of fertilizer use was associated with estimates of reversion times which were either negative or very large, and hence unsatisfactory. The (unrejected) estimates of reversion times based upon single species tended to be lower than those which employed groups of species, or

measures of species richness and diversity. A free-hand curve was drawn, based on individual species results, to describe the smoothed relationship between past N treatment and reversion time.

The curves describing the smoothed relationship between past N and reversion time (Figs. 1–3), were redrawn and an overall average estimate of reversion time was derived which corresponded closely to that based upon community variables. The resulting working estimates for the reversion times (from 1990) are ca. 3 yr for the N_{25}^- subplots, 5 yr for the N_{50}^- subplots, 7 yr for the N_{100}^- subplots and 9 yr for the N_{200}^- subplots.

Discussion

Composition of the sward

The residual effect of fertilizer in the N^- subplots, nearly four years after the last application of N, was evaluated. In 1993, the relative totals of positive and

Table 1. Estimates of vegetation reversion times (yr) based on community variables and species groups. Estimates judged as unsatisfactory are in bold. Means and standard errors are obtained using only the satisfactory estimates.

Treatment (1986-1990)		Vegetation				
Variable	0*	25	50	100	200	
Community variables:						
<i>M</i>	0	1.7	5.3	7.3	10.1	
<i>S</i>	0	-1.8	49.5	-38.9	-41.4	
<i>S'</i>	0	-1.0	8.5	12.5	-18.8	
<i>I</i>	0	-1.1	3.0	50.0	6.4	
Mean	0	1.7	5.6	9.9	8.3	
S.E.	0	-	1.5	2.6	1.9	
Species groups:						
Group 1a	0	3.5	4.9	4.6	3.9	
Group 1b	0	5.9	-17.9	5.9	4.2	
Group 2	0	7.6	3.1	8.7	1.1	
Group 3	0	3.1	-8.6	13.4	1.7	
Group 4	0	23.8	0.8	4.5	-2.1	
Group 5	0	1.4	20.7	5.8	-63.8	
Group 6	0	1.5	15.7	11.6	16.6	
Mean	0	3.8	7.9	7.8	8.2	
S.E.	0	1.0	3.9	1.3	4.2	

* Recovery time for control treatment = 0 yr.

Table 2. Estimates of recovery times (yr) based on percentage cover of some of the individual species. Estimates judged as unsatisfactory are in bold. Means and standard errors are obtained using only the satisfactory estimates.

Treatment (1986–1990)					
Species used	0*	25	50	100	200
<i>Agrostis capillaris</i>	0	5.6	2.2	2.8	0.4
<i>Anthoxanthum odoratum</i>	0	– 4.6	1.6	– 0.7	– 0.2
<i>Bellis perennis</i>	0	0.7	2.2	0.3	– 1.1
<i>Bromus hordeaceus</i>	0	8.8	– 0.6	3.1	3.0
<i>Cardamine pratensis</i>	0	0.3	1.0	0.7	0.1
<i>Carex disticha</i>	0	2.0	4.1	9.3	38.0
<i>C. flacca</i>	0	7.2	5.1	7.9	6.9
<i>Centaurea nigra</i>	0	– 3.6	9.2	– 11.6	– 5.2
<i>Cerastium fontanum</i>	0	5.8	6.3	5.3	3.2
<i>Cynosurus cristatus</i>	0	– 3.7	8.3	– 2.4	4.3
<i>Eleocharis palustris</i>	0	3.3	4.6	6.2	6.3
<i>Festuca rubra</i>	0	3.7	5.2	24.9	12.5
<i>Filipendula ulmaria</i>	0	– 0.2	3.4	0.6	1.2
<i>Galium aparine</i>	0	– 1.8	5.4	1.4	1.4
<i>G. palustre</i>	0	4.7	4.1	22.1	4.2
<i>Holcus lanatus</i>	0	3.4	16.6	11.1	5.0
<i>Juncus effusus</i>	0	1.5	11.9	1.6	8.9
<i>Lolium perenne</i>	0	3.7	4.5	4.0	4.0
<i>Lysimachia nummularia</i>	0	0.6	– 7.9	– 3.6	– 2.9
<i>Persicaria amphibia</i>	0	0.9	– 1.3	1.6	3.6
<i>Plantago lanceolata</i>	0	– 3.7	3.7	– 7.9	4.1
<i>Poa trivialis</i>	0	2.9	3.9	3.7	3.0
<i>Prunella vulgaris</i>	0	36.5	– 21.0	– 76.6	60.5
<i>Ranunculus acris</i>	0	0.3	– 3.6	1.3	2.3
<i>Rumex acetosa</i>	0	3.0	3.4	3.4	5.0
<i>Stellaria graminea</i>	0	15.8	1.9	13.9	0.2
<i>Trifolium pratense</i>	0	2.0	2.3	– 1.3	10.6
<i>T. repens</i>	0	3.1	8.8	1.2	1.7
<i>Brachythecium rutabulum</i>	0	0.9	5.8	6.1	6.4
<i>Calliargon cuspidatum</i>	0	1.3	1.1	10.2	33.0
Mean	0	3.0	5.0	5.7	5.3
S.E.	0	0.5	0.6	1.0	0.7

* Recovery time for control treatment = 0 yr.

Fig. 1. Composite plot showing estimates of reversion times based on M , S' and I (see Table 1). $M = \circ$; $S' = \square$; $I = \triangle$; Average = $\blacktriangle$. Erratic estimates are not shown (see text).

Fig. 2. Composite plot showing estimates of reversion times based on the % cover of groups of species (Table 1). 1a = $\square$; 1b = $\blacksquare$; 2 = $\triangle$; 3 = $\blacktriangle$; 4 = $\diamond$; 5 = $\blacklozenge$; 6 = $\circ$; Average = $\bullet$.

negative trends with N applied during Phase I had remained unchanged from 1990/1991, indicating that, despite the cessation of nitrogen application, most species continued to be more abundant in the control subplots than in the plots to which fertilizer was applied between 1986 and 1989. The results of the Tadhams Moor study reported here derive from a relatively short-term experiment, and studies in other grassland types suggest that the effect of past fertilizer application may be discerned many years after cessation e.g. > 30 yr in a Swiss montane *Nardetum* (Hegg et al. 1992), or 17 yr after fertilizer had ceased in a *Centaureo-Cynosuretum cristati* meadow in Lincolnshire (Silvertown et al. 1994). Thus, although there was evidence that the N^- subplots were diverging from those where fertilizer application continued, clear effects of past treatment were still observed in 1993, indicating that reversion was certainly not complete where high levels of N had been applied.

In Phase II, both M and I increased for the N^- subplots which by 1993 were distinctly more diverse than the N^+ subplots. The apparent rate of increase in M (ca. 1 species/m²/yr in all treatments) was faster than that reported for peat in the Netherlands (1 species / 4 m² in four years) (Bakker 1987). Further evidence of sward

reversion in the N^- subplots derives from comparison of results for agricultural productivity with changes in the value of M (Mountford et al. 1994). Productivity fell during Phase II, as values for M increased, and were all in the range 3.8 - 5.5 tonnes/ha i.e. within the bounds associated with species-rich communities (Oomes 1992; Smith 1994).

Comparison of changes in individual species observed at Tadhams following cessation, with those reported by other workers indicate that whilst some trends are consistent between studies, others conflict. Differences may partly result from variation in site conditions e.g. *Holcus lanatus* responded differently in two Dutch studies (Bakker 1987; Olff & Bakker 1991). Other differences from trends reported elsewhere may reflect the relatively short length of time that the Tadhams has been monitored post-cessation. Certainly there is evidence from the Netherlands that some trends may not become apparent until at least 10 yr after cessation (Olff & Bakker 1991).

One further factor which may contribute to the continued influence of past nitrogen regimes observed in 1993 was the marked increase in *Anthoxanthum odoratum*, and particularly in *Agrostis capillaris*, during

Fig. 3. Composite plot showing estimates of reversion times based on the percentage cover of selected species (see Table 2). Individual species = $\square$; Average = $\blacksquare$.

Phase II to greater cover than in 1986 prior to the introduction of fertilizer treatments. This rapid recovery in two grasses typical of infertile soils may partly explain why most other species continued to show a negative trend with past nitrogen. The behaviour of *A. capillaris* at Tadham conflicts with the long-term decline post-cessation reported for peat (Bakker 1987), but agrees with similar work on sandy soils (Olff & Bakker 1991).

Reversion times

Environmentally induced trends and fluctuations

The observations from the control subplots (i.e. the NO_{ij} values) should show no treatment induced trends. However, if Phase II coincided with an external trend (e.g. steady increase or decrease in temperature, rainfall etc), then this might induce a trend in the values of the vegetation variables. With only a few years' data, such fluctuations can also induce spurious trends in time. The comparison of the trends in NK_{ij} values (Eqs. 2 - 5) with the trend in NO_{ij} values (Eq. 1) tend to cancel out such effects. This is because the procedure used is algebraically identical to first obtaining the differences DK_{ij} defined by $(NK_{ij} - NO_{ij})$ and then estimating the rever-

sion times R_k from the time point when the trend in the DK values meets the time-axis (x-axis).

Choice of variables

The estimates of reversion times obtained using the individual species percentage cover variables were expected to contain many untrustworthy estimates. In contrast, the community variables and the percentage cover of carefully defined groups of species should yield more reliable estimates. However, the data were obtained using 24 quadrats in year 0, but 16 quadrats in subsequent years. This should not introduce any bias in the percentage cover variables (individual species or groups of species) or in the community variable M . The bias introduced in the results for S , S' and I might be reduced, to some extent, by the implicit differencing mentioned above, but Table 1 shows that for these variables, eight out of the 12 estimates appear unsatisfactory. Discarding even obviously unsatisfactory estimates is a subjective approach which may introduce some bias. However, such bias can be tolerated as a price for removing gross errors in the estimates.

Further improvements using observations over many years

One factor which effects the efficiency of this estimation approach is that some of the nutrients applied during the treatment phase of the experiment may continue to remain available to the vegetation even after the cessation of any further input of N (and replacement P/K) to the soil. Even more importantly, there is much evidence that fertilizer residues can build up in the soil after continuous application, and that this is particularly the case for phosphorus (Marrs 1993). Hence, those species which should begin to increase or decrease as a result of the non-availability of nitrogen may not do so immediately. The considerable 'inertia' in sward composition after fertilizer application has ceased owes much to an enhanced phosphorus status and its is estimated that it would take >13 yr following cessation before the P status declined to the levels current prior to the application of fertilizer (Mountford et al. 1994). Thus the assumption of an immediate progress towards reversion, implied in the fitted straight line models (Eqs. 1 - 5), may not hold, introducing a bias in the estimates of the R_k values. It can be argued that if the estimates of reversion time turns out to be some positive number of years, then the bias due to this complication is likely to be positive, tending to inflate the estimates. However, in many instances, perhaps partly because of the continued availability of nitrogen applied during Phase I (and also because of the changed nature of the vegetation by the end of Phase I) the vegetation in the previously treated

subplots continued to diverge from that in the control subplots. In such cases, the fitted linear trend lines will be extrapolated backwards in time for them to meet, and hence estimates of reversion times will be negative. With only three years' data after the discontinuance of fertilizer treatment, it is also possible for the estimates of the slopes in the fitted models to be sufficiently in error so as to yield negative estimates of reversion times. However, this problem of negative estimates should disappear if there were data for a large number of years after the discontinuance of fertilizer treatment.

The simple straight-line models (Eqs. 1 - 5) used here, readily provide a finite and estimable meeting time of the different fitted lines. However, from the botanical point of view, it might be more realistic to use non-linear models e.g. exponential or logistic. Such models are asymptotic to the time-axis (x-axis), and their use would require an acceptable definition of 'convergence' of the fitted models for the data from control and treated subplots. The course of reversion will differ between species, requiring the use of different types of model. In an analysis of hay-field succession following the cessation of fertilizer use in the Netherlands, Huisman et al. (1993) assessed how five types of model fitted observed trends over 25 yr in the percentage cover of different species. Examples of four species, all of which are frequent on the Tadham site, were found to fit best with three different models. At Tadham, use of non-linear models (with more parameters) would require post-cessation data extending over a greater number of years.

Reliability and usefulness of estimates

The estimates of reversion time, 3, 5, 7 and 9 yr for R_{25} , R_{50} , R_{100} and R_{200} , respectively are in good agreement with the means (bearing in mind the standard errors) presented in Tables 1 and 2. Also, it should be noted that the estimate R_{25} suggests that the vegetation in N_{25}^- subplots should have recovered by 1993. If so, the 1993 results should fail to separate the N_{25}^- and N_0^- subplots. Analysis of individual species data revealed only two species (*Carex flacca* and *Ranunculus acris*) whose cover in the N_{25}^- subplots was significantly different to the controls, thus providing some corroboration for the estimate of ca. 3 yr for R_{25} .

Though App. 1 enables the calculation of the standard errors for all individual estimates (such as those given in Tables 1 and 2), this approach is deliberately not used generally here because the approach is strongly model-dependent, and ought only to be used for analysing data over many years. However, since the overall estimates of reversion times are very close to those based on the community variable M (Table 1, line 1), we used App. 1 to also obtain the standard errors for the

reversion estimates based on M . Corresponding to the estimates 0, 1.5, 5.3, 7.3 and 10.1, the estimated standard errors are 0, 1.8, 4.8, 7.6 and 10.1, which are of comparable magnitude to the estimates. It is useful to note that an estimate plus twice its standard error should approximately provide an estimate of the upper 95 % confidence limit for the *true* reversion time; and, since these limits are 0, 5.3, 14.9, 22.5 and 30.3, the true reversion times following an application of the four fertilizer treatments for four years are unlikely to exceed respectively 5, 15, 23 and 30 yr.

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App. 1. The standard error of t , the estimate of R_k in yr.

1. As described in the text, using the fitted models (1) - (5), the estimate of R_k is given by $t = (a_0 - a_k)/(b_k - b_0)$. Hence, variance (t) = variance $[(a_0 - a_k)/(b_k - b_0)]$.

2. Suppose the fitted models had been parametrised as $Nk = A_k + B_k(t - t')$, in which $A_k = a_k + b_k t'$ and $B_k = b_k$. Then, under the standard regression theory A_k will be statistically independent of B_k . Also A_0 and B_0 will be statistically independent of A_k and B_k , for $k = 25, 50, 100$ or 200 , because A_k and B_k are obtained using different observations from those used to obtain A_0 and B_0 . Under this parametrisation, R_k will be estimated from $(t - t') = (A_0 - A_k)/(B_k - B_0)$.

Hence, variance $(t - t') = \text{variance} [(A_0 - A_k)/(B_k - B_0)]$. Since t' is a constant, variance (t) = variance $[(A_0 - A_k)/(B_k - B_0)]$.

3. From the two expressions for the variance of t in 1 and 2 above:

$$\text{variance} [(a_0 - a_k)/(b_k - b_0)] = \text{variance} [(A_0 - A_k)/(B_k - B_0)].$$

4. A well-known approximation in statistical theory dealing with the ratio $R = N/D$ (where N = Numerator and D = Denominator) is that if N and D are statistically independent, then the variance of R is given by:

$$\text{var}(R) = (N^2/D^2) \{ [\text{var}(N)/N^2] + [\text{var}(D)/D^2] \}.$$

5. In the present case, $N = a_0 - a_k$ and $D = b_k - b_0$. Hence, $\text{var}(N) = \text{var}(a_0 - a_k) = \text{var}(a_0) + \text{var}(a_k)$ and, $\text{var}(D) = \text{var}(b_k - b_0) = \text{var}(b_k) + \text{var}(b_0)$.

6. The estimates of a_0 , a_k , b_0 and b_k and their variances (obtained from the linear regression models and analyses) together with the results 4 and 5 above give variance (t), where t = estimate of R_k . The square root of variance (t) gives the standard error of t .