Temporal changes in a grassland sward

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Extracted from the Proceedings of the Somerset Archaeological and Natural History Society for 2015.

Volume 159

Produced in Great Britain by Short Run Press, Exeter.

1SSN 0081-2056

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JOHN CROTHERS

INTRODUCTION

When I was in my teens, my father delegated to me the responsibility for mowing our lawn. He was concerned about the abundance of moss (species never determined) and imagined that it could be eliminated by ever-more-frequent mowing. At the time I had no reason to doubt his management plan. If only I had had available, then, the data that I present in this paper!

When, in 1967, the Field Studies Council established its ninth Residential Field Centre in Nettlecombe Court, Dr John Carthy, the Scientific Director, was keen to encourage an experimental approach in the field teaching of ecology (to augment the traditional observational recording) and negotiated the inclusion of a small area of Court Field adjacent to the old croquet lawn within the lease (Fig. 1). It was much easier to devise a worthwhile botanical experiment for that site than any zoological alternative, so most of the area was given over to a long-term investigation into the effects of different mowing regimes on a previously uniform grassland sward.

It must be emphasised that this was always envisaged as a teaching experiment; nobody ever imagined that it might generate data of wider interest. After all, the data were to be collected by students and thus, according to the perceived wisdom of the 1960s, expected to contain so many errors as to be worthless for further study. Undoubtedly, there are errors in the data set under consideration but, I contend, they do not materially influence the conclusions to be drawn from the data.

METHODS

The students

As all the data that form the meat of this paper were collected by students, it is worth recording who they were and why they collected them.

The Field Studies Council is an educational charity founded, as the Council for the Promotion of Field Studies, in 1943 thanks to the determination of a London County Council Inspector of Schools, Francis Butler. Placed in charge of a group of evacuee children in the autumn of 1939, Butler became forcibly aware of their ignorance concerning almost everything about the countryside and of the absence of anybody who might enlighten them. In his vision for a post-war education system he foresaw a network of residential Field Centres across the Country staffed by natural historians.

The problem, of course, was how to finance the vision and the embryo Council's first four Centres faced some very lean years in the early 1950s. Better times followed the introduction of a fieldwork component into A-level Biology and Geography syllabi. The Council offered courses to suit that component and more Centres were opened.

In the late 1960s, week-long (Wednesday to Wednesday) A-level field courses were arranged in almost every week from March until October (although June and August were always slack months). Demand for places on the courses was such that schools were rationed to two or three places and the students were not accompanied by their own staff. As each course was made up of a mixture of first and second year students, probably studying a range of syllabi, it was impossible to 'teach to the syllabus.'

Later on, when supply of courses more nearly matched the demand for them, a school would book a course for the whole A-level class (often on an annual basis) and the school staff became closely involved with preparation and delivery of the course.

Whilst most of the data were collected by A-level students, some are thanks to a Middle School (observed by Post Graduate Certificate in Education students) and others to various Open University Summer Schools.

Comparatively few of the students lived in Somerset; most being from the London area or the Midlands. The only things they had in common were their temporary residence in Nettlecombe Court and the fact that they had never done any investigation of grassland before.

Fig. 1 The newly-enclosed Experimental Plot, 30 March 1968, before the plots had been marked out. It appeared to be reasonably uniform in nature, although the land at the foot of the slope presumably received more nutrients from run-off at times of heavy rain. At this time, the rest of Court Field was let for grazing each summer

Experimental Design

The general layout of the experiment (Fig. 2) was modelled on a comparable set of plots that had been devised at Preston Montford Field Centre (Shropshire) by Charles Sinker (and were well established when I first saw them in 1964); modified, of course, to fit the area available and the plants present.

The object of the exercise was to teach a particular method of recording plant abundance. Nothing is much more boring than to be taught a technique in the abstract; so a long-term experiment was established to compare four 'treatments' applied to the sward of the experimental plot.

It didn't matter what the treatments were, provided they altered the vegetation in different ways and, as the Field Centre already owned grass cutting machinery, the obvious solution was to apply different mowing regimes.

The experimental plot had been mown, along with the rest of Court Field in the autumn of 1967 and appeared fairly homogeneous in March 1968 (Fig. 1) but there were probably local differences in

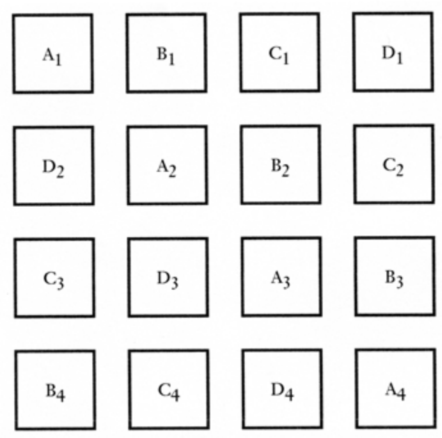

Fig. 2 The 4x4 Latin Square. Each plot was 10 feet square and separated from its neighbours by paths 4 feet wide. 'A' plots were mown fortnightly during the growing season (as was the croquet lawn), 'B' plots annually in June, 'C' plots were unmown whilst the turf was removed from the 'D' plots which were then left unmown

soil depth, drainage, nutrient levels or whatever so, to cancel these out as far as possible, sixteen plots were marked out; four each of treatments A, B, C, D arranged in a Latin Square so that each treatment occurs once in each column and in each row (Fig. 2).

The 'A' plots were mown fortnightly during the growing season, at the same setting as for the croquet lawn. The 'B' plots were mown annually, in June, when local farmers took their hay crop. The 'C' plots were left unmown, whilst the turf was removed from the 'D' plots which were then left unmown. I realised, too late, that I should have randomised the order of the treatments within the rows – because there is a diagonal alliance (across the slope).

Data Collection

No previous experience of British plant species could be assumed (on the part of the students) so identification could have presented a problem, especially in the closely mown 'A' plots. Being more interested in teaching the technique than in the results, at least initially, I decided to work with six distinctive taxa: Cock's-foot (*Dactylis glomerata*); Yorkshire Fog (*Holcus lanatus*); Creeping Buttercup (*Ranunculus repens*); White Clover (*Trifolium repens*); Yarrow (*Achillea millefolium*) and moss – almost all Springy Turf-moss (*Rhytidiadelphus squarrosus*). In addition there were two 'dustbin' categories: 'other grasses' and 'other plants apart from grasses'.

The number of taxa (eight) was selected for convenience. The class would be divided into eight groups; each group would sample two adjacent plots then, back in the lab, when the data had been pooled (initially on the blackboard, latterly on a computer) each group would be allocated a taxon and asked to explain in what way (and why) the different mowing regimes had altered the performance of 'their' plant.

On each sampling occasion, percentage cover of each of the eight taxa was recorded at 100 randomly-distributed point quadrats in each plot (see Chalmers and Parker (1989) for a description of the method). Point quadrats were preferred to frame quadrats because their use does not, of itself, alter plant cover and because they greatly reduce the subjective element in sampling. Most of the plot area could be sampled when kneeling on the surrounding path and trampling was further reduced by placing the central pin of the quadrat in each of 25 randomly-selected positions and examining 4 points about it, at the corners of an imaginary square. This experimental design is an example of stratified random sampling.

A degree of scepticism was expressed by most groups of students as to whether it is possible for records taken at 100 points to represent the vegetation in 100 square feet of plot. But all sampling regimes are a compromise between the ideal number of samples versus the damage caused to the site by sampling and the time involved. In general, the longer it takes the poorer the quality of the result.

To counter this scepticism, I decided to keep a record of the data obtained by each course – to be able to show that comparable figures were obtained each time. Moreover, we thought that people would take more care if they knew that their data would be kept and used over and over again.

When using a point quadrat, you lower your point – 'a position with no area' – mounted at the tip of a sharpened pin into the vegetation until it touches something. It might seem obvious simply to record what the 'something' was that was first hit by the pin. However, this was found to lead to mistaken conclusions regarding the nature of the plant communities present.

Table 1 shows the first three data sets, recorded using the 'first hit' technique. Comparing the average figures, the first set, taken before any 'treatment' had been applied, confirm that we were studying grassland and that there was little difference between the plots (moss averages are 4, 7 and 2). But in the third data set it seems that moss had disappeared whereas simple observation would suggest that moss was thriving. Clearly, 'first hit' recording is akin to surveying rain forest by satellite imagery; only the canopy vegetation is recorded.

The solution appeared to be to record all the plants touched by the point as it was lowered through the sward (Table 2). (This change coincided with a visit from Charles Sinker "You can't simply call it all grass!")

As expected, moss reappeared in the record but, very soon, the sheer volume of data became excessively tedious to collect. That group on 6 July 1968 spent seven hours (in total) on the plots – it was a fine day – and I am very grateful to them because they unequivocally established the fact that this is an impractical technique. Very few groups of students would have stuck at it for so long and in the real world, it would be unaffordable.

TABLE 1 – THE FIRST THREE SETS OF DATA, SCORING ‘FIRST HIT’ ON EACH TAXON. THE ‘D’ PLOTS WERE BARE GROUND AT THIS TIME. (from Crothers, 1991)

	A Plots					B Plots					C Plots				
	1	2	3	4	Av.	1	2	3	4	Av.	1	2	3	4	Av.
1. April 1968 – only the paths had been mown.															
grass	88	90	74	44	74	78	92	77	56	76	87	92	80	73	83
moss	1	1	9	6	4	0	0	7	22	7	0	0	0	7	2
buttercup	3	5	8	11	7	10	5	6	2	6	2	3	11	4	5
clover	0	0	6	19	6	4	0	8	13	6	0	0	0	10	3
yarrow	0	1	1	2	1	0	0	1	0	0	0	1	3	0	1
other plants	0	1	0	0	0	0	1	1	0	1	0	1	1	3	1
2. 6 May 1968 – after the first mowing of the A plots (29 April)															
grass	92	95	74	71	83	76	75	65	66	71	76	55	68	51	63
moss	0	0	3	1	1	0	0	5	2	2	1	9	0	5	4
buttercup	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
clover	0	0	6	38	11	3	5	24	21	13	0	5	0	16	5
other plants	3	2	12	13	8	4	8	5	11	7	0	1	5	4	3
3. 20 May 1968 – after the second mowing of the A plots (6 May)															
grass	98	98	85	51	83	96	97	91	96	95	93	90	88	84	89
moss	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
buttercup	2	1	3	7	3	2	3	4	2	3	7	4	4	3	5
clover	0	0	10	31	10	2	0	4	2	2	0	5	0	13	5
other plants	0	1	2	0	1	0	0	0	0	0	0	1	2	0	1

TABLE 2 – THE SECOND ATTEMPT, SCORING 'ALL HITS' ON EACH TAXON. (from Crothers, 1991)

	A Plots					B Plots					C Plots					D Plots				
	1	2	3	4	Av.	1	2	3	4	Av.	1	2	3	4	Av.	1	2	3	4	Av.
4. 25 May 1968 – after the third mowing of the A plots.																				
Cock's-foot	6	14	16	18	14	38	27	7	16	22	55	30	26	1	28					
Yorkshire Fog	7	5	3	1	4	16	3	0	11	8	17	11	11	6	11					
other grasses	95	86	90	84	89	72	88	79	69	77	86	59	97	96	85					
moss	3	7	18	19	12	5	0	37	24	17	0	19	2	37	15					
Buttercup	6	10	18	19	13	6	6	19	25	14	4	18	8	7	9					
White Clover	1	0	15	55	18	7	2	16	24	12	0	8	0	35	11					
Yarrow	0	4	1	1	2	0	0	5	8	3	0	4	3	1	2					
other plants	0	1	0	3	1	1	0	0	0	0	0	0	0	1	0					
5. 22 June 1968 – A plots mown 5 times, B Plots once.																				
Cock's-foot	0	18	37	13	17	25	49	35	32	35	11	17	18	5	13	0	0	0	0	0
Yorkshire Fog	5	10	32	7	14	7	41	23	45	29	27	23	41	58	37	3	6	0	12	5
other grasses	50	28	26	72	44	45	48	25	231	87	67	20	141	588	204	18	45	95	46	51
moss	7	16	0	15	10	0	0	4	41	11	0	0	28	53	20	6	0	49	0	14
Buttercup	17	0	10	21	12	26	23	9	10	17	0	4	31	14	12	1	13	21	47	21
White Clover	11	0	16	47	19	12	10	13	18	13	1	5	5	55	17	5	4	1	5	6
Yarrow	0	0	0	3	1	12	12	2	2	7	0	0	0	0	0	0	4	0	15	5
other plants	0	6	0	9	4	0	2	0	0	1	1	0	0	0	0	3	11	2	18	9
6. 6 July 1968 – A plots mown 6 times, B Plots once.																				
Cock's-foot	49	99	0	0	37	69	99	34	37	60	63	169	92	4	82	27	26	4	0	14
Yorkshire Fog	23	3	0	0	7	27	25	40	0	23	28	88	24	24	41	30	2	14	1	12
other grasses	77	184	259	362	221	239	377	476	240	333	465	1115	885	1064	882	222	420	214	220	269
moss	0	2	24	36	16	0	2	18	15	9	4	4	1	35	11	43	47	52	59	50
Buttercup	11	7	20	15	13	7	5	18	2	8	2	17	17	32	17	4	6	18	42	18
White Clover	9	0	17	91	29	10	1	42	38	23	0	4	0	51	14	48	10	1	9	6
Yarrow	0	4	2	1	2	0	0	13	5	5	0	0	0	0	0	2	2	2	0	2
other plants	1	0	1	4	2	4	2	8	3	4	3	2	3	5	3	1	2	15	6	6

TABLE 3 – AN EARLY EXAMPLE OF THE SYSTEM USED IN ALL SUBSEQUENT YEARS, SCORING 'FIRST HIT ON EACH TAXON' (from Crothers, 1991)

	A Plots					B Plots					C Plots					D Plots				
	1	2	3	4	Av.	1	2	3	4	Av.	1	2	3	4	Av.	1	2	3	4	Av.
9. 27 August 1968.																				
Cock's-foot	26	33	33	25	29	37	37	27	20	30	55	68	60	2	46	2	9	0	1	3
Yorkshire Fog	12	2	0	25	10	19	0	8	15	11	0	22	12	0	9	24	4	0	2	8
other grasses	24	75	99	86	71	88	97	79	75	85	87	99	85	99	93	99	41	97	97	84
moss	13	15	46	99	43	12	2	64	40	30	6	7	5	15	8	71	35	50	27	46
Buttercup	13	23	28	60	31	15	22	63	13	28	6	26	16	27	19	4	12	27	67	28
White Clover	10	1	21	59	23	4	1	42	38	21	0	1	0	15	4	31	20	6	15	18
Yarrow	1	5	8	23	9	0	0	14	0	4	0	2	0	0	1	1	6	0	3	3
other plants	0	0	6	19	6	0	4	10	15	7	1	3	6	0	3	32	10	0	3	11

TABLE 4 – A LATER SET OF DATA TO ILLUSTRATE THE OBVIOUS LONG-TERM CHANGES
ONLY SEVEN GROUPS OF STUDENTS WERE AVAILABLE, SO TWO PLOTS WERE NOT SAMPLED ON THIS OCCASION

	A Plots					B Plots					C Plots					D Plots				
	1	2	3	4	Av.	1	2	3	4	Av.	1	2	3	4	Av.	1	2	3	4	Av.
231. 13 July, 2001.																				
Cock's-foot	0	0	0	0	0	0	3	3	3	2	0		0	9	3		0	14	0	5
Yorkshire Fog	11	71	0	0	21	45	4	1	1	13	19		3	25	16		28	0	3	10
other grasses	91	1	90	83	66	19	72	41	73	51	70		80	55	68		97	72	54	74
moss	75	7	0	28	28	5	5	39	26	19	10		20	1	10		43	7	8	19
Buttercup	0	3	0	1	1	26	2	0	9	9	0		5	4	3		0	5	0	2
White Clover	50	33	84	75	61	25	2	0	0	7	0		0	0	0		34	3	19	19
Yarrow	41	0	23	67	33	14	3	32	55	26	4		29	24	19		29	23	4	19
other plants	21	19	23	35	25	11	81	24	35	38	34		47	31	37		44	33	5	27

The compromise was to score 'first hit on each taxon' (Table 3). There is nothing surprising about this conclusion, but comparable tables displaying what happens otherwise are rarely published. One positive feature is that the maximum score for each taxon is 100 so the averages make sense in ordinary English. Thus, in Table 3, Cock's-foot showed 46% cover of 'C' plots compared to 29% and 30% in 'A' and 'B' but only 3% in the 'D' plots. In other words, this large tussock-forming grass grows best when unmown but was slow to colonise from seed.

Table 4 displays the data from the last summer group of students taught by me on the plots. Clearly there had been changes over the years. Cock's-foot is rare or absent and the 'other plants' category is the second most abundant, but the feature that surprised me most was the differences that remained between the 'C' and 'D' plots which were 'managed' in exactly the same way throughout the 33 years between data in Tables 3 and 4 (for example, Fig. 3). The past history of a site has a much greater influence on the present vegetation than is often appreciated.

Looking at any of these data sets, one suspects that one can see errors. In Table 4, for instance, the group studying 'A2' appear to have had problems in identifying Yorkshire Fog; 71% cover in an 'A' plot is highly unlikely but the associated 1% cover of 'other grasses' is simply wrong. Such discrepancies, if less dramatic, were apparent whenever the class results were compiled, and those inclined to doubt the value of surveying by the use of point quadrats (or of student data) were quick to discredit the results. That was the original reason why I kept the data and was often able to produce very comparable figures for a similar date in a previous year.

Data presentation

I have 230 sets of data recording percentage cover of the eight taxa, spanning 33 years; a considerable improvement on the 120 sets available for an earlier paper (Crothers 1991).

To take account of the obvious seasonal changes that occur every year, I worked with separate annual averages for spring (February to April), summer (May to July) and autumn (August to October) in all the years for which sufficient data had been recorded. The summer record is the most complete and so I will concentrate on that. At the outset, we assumed (as most people who design experiments assume) that the different mowing regimes would account for the differences in plant cover and so I summarised the data in the form of pie charts (e.g. Fig. 3).

A glance at Fig. 4 shows that, whilst the mowing regime has had an effect, it is certainly not the only variable affecting plant performance. The same glance confirms that these are 'noisy' data. They contain errors, as was always to be expected, which tend to obscure the overall picture. The figures plotted in Fig. 4 are the average percentages cover recorded from May to July in the year concerned. But the number of data sets involved in those averages varies considerably. To smooth out some of these wilder fluctuations, I then calculated three year averages. Thus in Fig. 5, and subsequently, the value shown for 1990 is the mean of 1989+1990+1991, that for 1991 is the mean for 1990+1991+1992, and so on. (I used this technique to similarly smooth the student data on the growth of Common Top-shells on Gore Point (Crothers 2001).)

A common first reaction to a graph such as Fig. 11 is to assume the involvement of a weather-related factor. There is no shortage of local weather records available as a Meteorological Office Class 3 climatological station was established in the Experimental Plot in the spring of 1968 (Ratsey 1973) and data were recorded at 0900 GMT daily throughout the period concerned. Suffice it to say that the vegetational fluctuations do not relate to anything in the met data that has been identified to date. Many people have looked, including members of Met. Office staff.

RESULTS

Cock's-foot (*Dactylis glomerata*)

This large, perennial, tussock-forming grass was the dominant plant in the grassland of Court Field when the experiment began and had been an important component of the seed mixture sown during the early 1960s when the former Deer Park was reclaimed for agriculture. It produces more bulk than any other of our grasses (Moore 1966) and is thus a useful forage crop for cattle.

We had expected this plant to dominate the 'C' plots, initially, for it to follow suit in the 'D' plots later on and for it to be depressed by mowing. In fact (Fig. 3) overall cover in 'B' and 'C' plots was essentially the same.

Its success in 'B' plots can be ascribed to the fact that the maximum spurt of growth in *D. glomerata* occurs from mid-April to mid-May (Moore 1966). So, by the time the plots were cut in June the

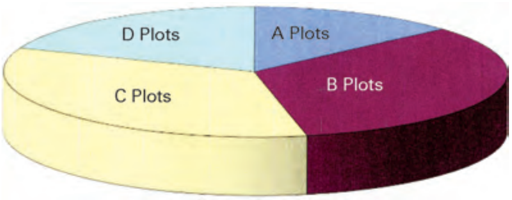

Fig. 3 The overall distribution of cock's-foot in the grass plots during summer, 1969–2001

tussocks had replenished their food stores and were so large that it was impossible to mow the 'B' plots as closely as the 'A's.

Conventional lawn grasses have their growing points at, or just below, the ground surface so that mower blades do not damage them but instead slice through the lamina of the leaves. The growing point in a Cock's-foot tussock is well above the ground surface and is removed or damaged by lawn mowing. No tussocks survived for long in the 'A' plots in those early years. Note the very low cover in 1971 (Fig. 4). I suspect that the subsequent increase in its cover of the 'A' plots reflects a change in management practice.

When the Field Centre opened we inherited a large (and extremely heavy) cylinder lawn mower from the previous tenant. It cut through grass tussocks with ease. When that mower died, it was replaced by a series of Flymo rotary mowers that floated over the ground on the hovercraft principle. They were much less laborious to use but they did not cut as close to the ground as their predecessor – as is revealed by the rise of Cock's-foot in the 'A' plots during the late 1970s. Eventually we realised that it was a false economy to use equipment designed for domestic gardens at Nettlecombe Court and we turned to wheeled rotary mowers; their arrival saw Cock's-foot cover drop down again.

The 'B' plots were cut with a mechanical scythe (when it could be persuaded to work), by a traditional scythe or with shears. In all cases most of the tussocks survived unscathed.

But the main impression conveyed by Figs 5-7 is of a plant diminishing in abundance and this is confirmed by Fig. 8. One possible explanation is

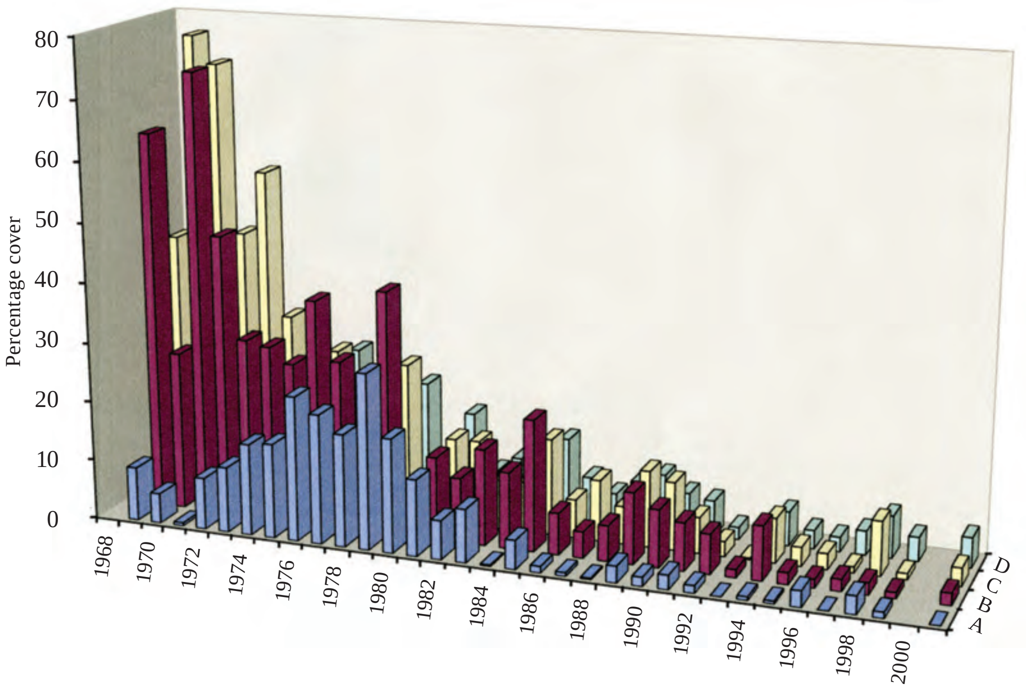

Fig. 4 Fluctuations in the abundance of cock's-foot (Dactylis glomerata) *under the four treatments, over time. 'A' plot data are in the foreground, with 'B' and 'C' plots behind them leaving 'D' plots in the background. The bars represent annual averages of the data collected in summer (May–July).*

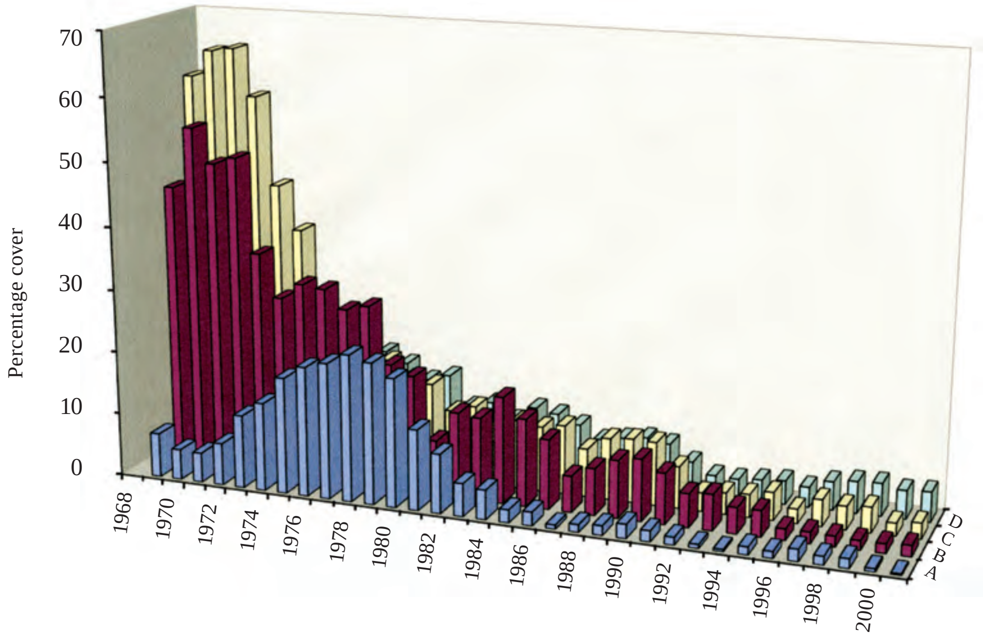

Fig. 5 Fluctuations in the abundance of cock's-foot (Dactylis glomerata) *under the four treatments, over time. 'A' plot data are in the foreground, with 'B' and 'C' plots behind them leaving 'D' plots in the background. ('D' is not visible before 1977.) The bars represent smoothed averages of the data collected in summer (May–July).*

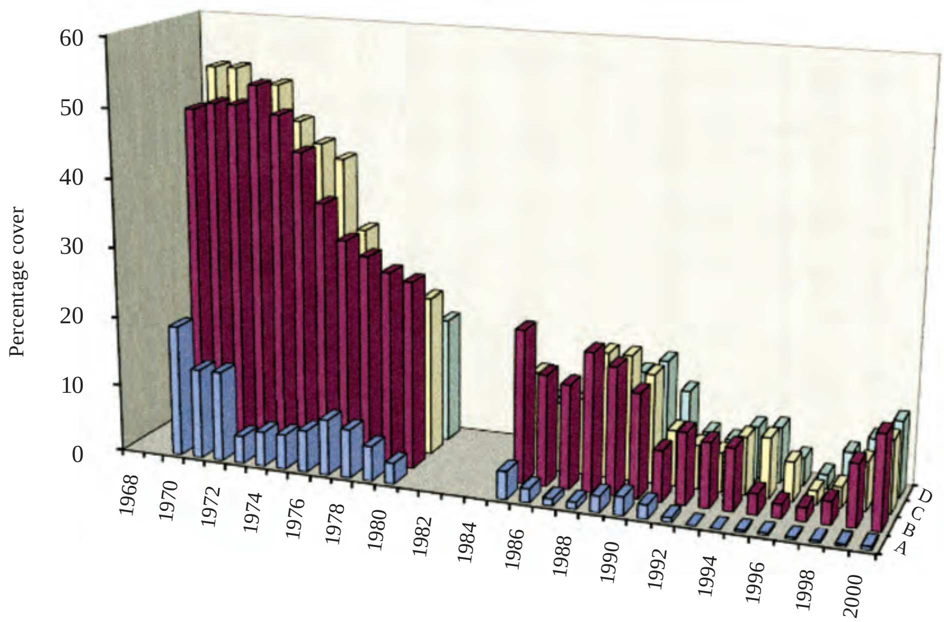

Fig. 6 The comparable plot of the available spring (February–April) data

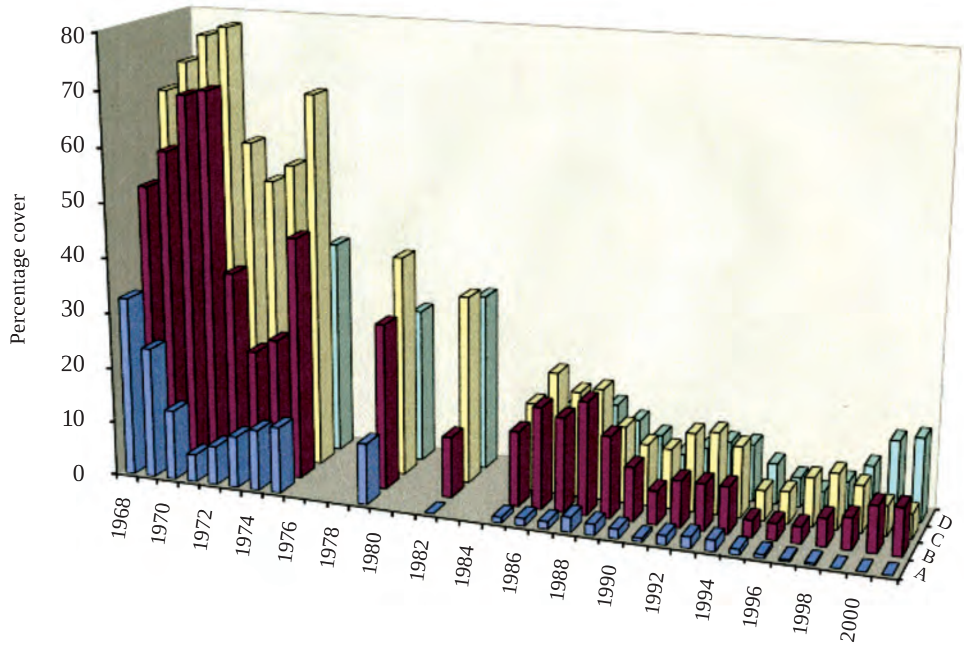

Fig. 7 The comparable plot of the available autumn (August–October) data.

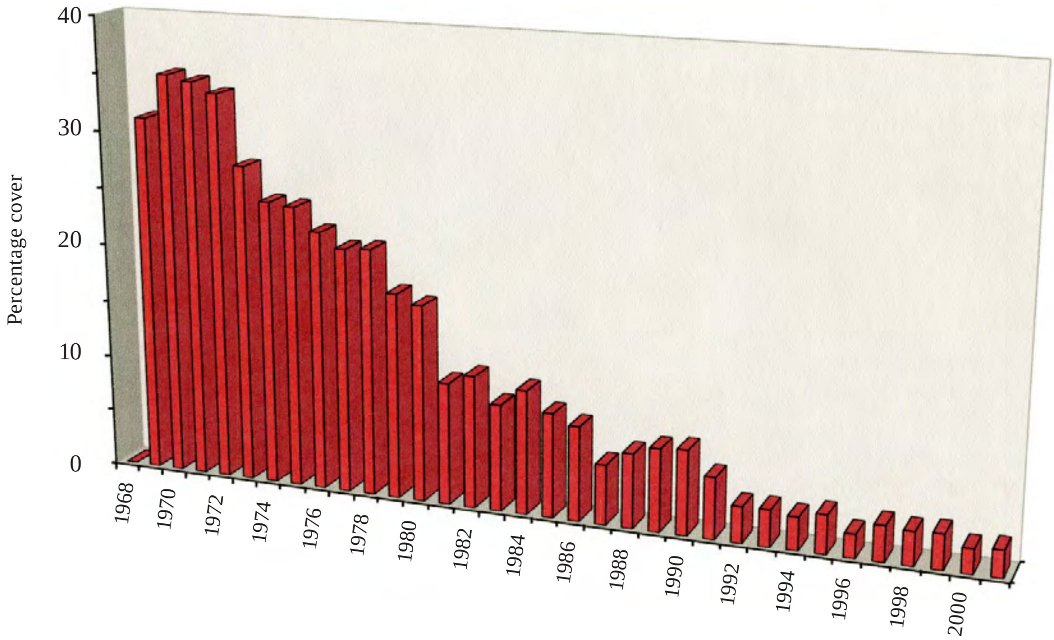

Fig. 8 Overall mean fluctuations in the abundance of cock's-foot (Dactylis glomerata) *in summer, 1969–2001*

given by Moore (1966) who stresses the importance of controlling the rampant summer growth which could be damaged by frost. In the 1970s, farmers were recommended to plough and re-seed grass leys containing Cock's-foot every ten years (W. W. Ker *pers. comm.*) and to fertilise regularly. It will be noted that the peak abundance of Cock's-foot in Figs 4-8 occurred in 1969 or 1970, ten years after sowing. No fertiliser was applied to the plots after 1967.

Cock's-foot flowered regularly in the 'C' plots but did not colonise freely from seed (some commercial strains are known to be infertile). The 'D' plots colonised very slowly, vegetatively, from the margin. Overall, we see the fate of an introduced species, deprived of the added fertiliser that it requires in order to thrive, steadily diminishing over time.

Yorkshire Fog (*Holcus lanatus*)

This grass had proved to be an invasive species in the Preston Montford plots (C. A. Sinker *pers. comm.*), coming to dominate in his equivalent of the 'B' plots. The other reason for selecting it for study was its ease of identification – the only 'hairy' grass present and with pink 'pyjama stripes' on its white leaf-bases. It would not have been included in the original seed mixture because it is unpalatable to farm stock except when very young.

Yorkshire Fog produces copious quantities of seed and is a rapid coloniser of disturbed ground; by the autumn of 1969, it was actually the most abundant species in the 'D' plots although Fig. 9 shows that overall it has performed best in the 'C' plots.

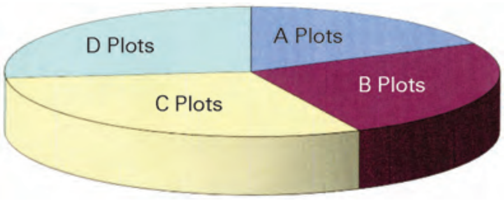

Fig. 9 The overall distribution of Yorkshire fog in the grass plots during summer, 1969–2001

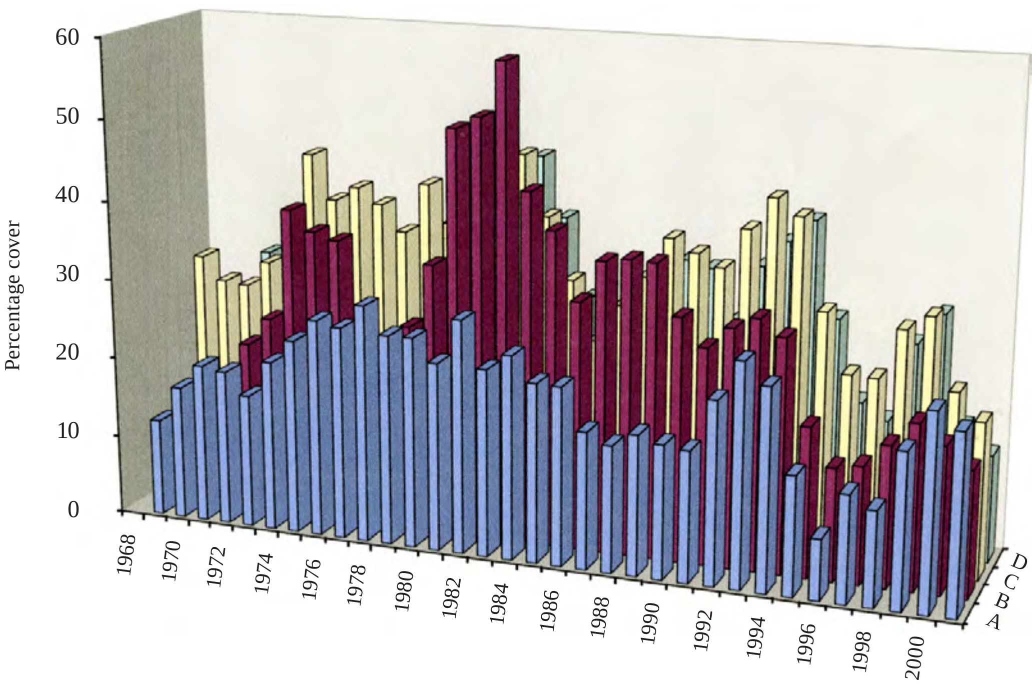

Fig. 10 Fluctuations in the abundance of Yorkshire Fog (Holcus lanatus) *under the four treatments, over time. 'A' plot data are in the foreground, with 'B' and 'C' plots behind them leaving 'D' plots in the background. The bars represent smoothed averages of the data collected in summer (May–July).*

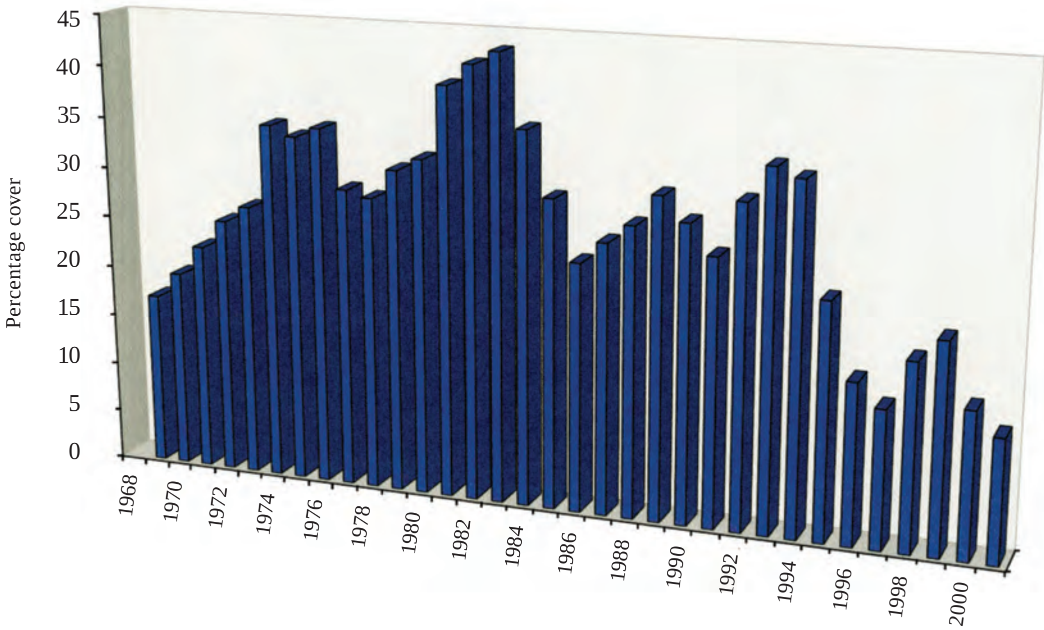

Fig. 11 Overall mean fluctuations in the abundance of Yorkshire Fog (Holcus lanatus) *in summer, 1969–2001*

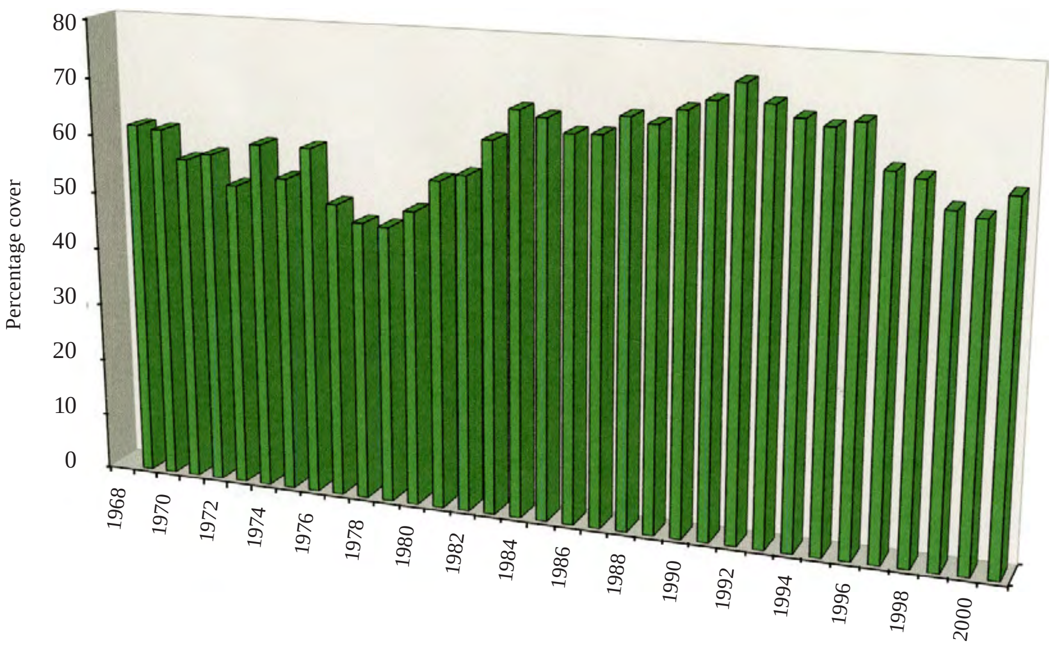

Fig. 12. Overall mean fluctuations in the abundance of other grasses in summer, 1969–2001.

Neither Fig. 10 nor Fig. 11 suggests that theFexperimental treatments were the controlling factor operating on the performance of this grass. Up until 1983, the plot shows a progressive increase in percentage cover, to be replaced by an overall decline, complicated by a pattern of cyclical fluctuations. This pattern was initially interpreted (Crothers 1991) to be a response to the decline in Cock's-foot (Fig. 12). That may, indeed, have been a factor, but the subsequent overall decline requires a different explanation.

'Other grasses'

It is difficult to draw many conclusions about a 'dustbin category' such as this because there are so many unknowns. The pie chart (not included) is so nearly perfectly divided into quarters as to suggest that, between them, these 'other grasses' successfully exploited the entire available habitat.

When compared with Fig. 8 (Cock's-foot peaked in 1970) and Fig. 11 (Yorkshire Fog peaked in 1983) the 'other grasses' peak (Fig. 12) was delayed until 1992. Unable to dominate either of the large perennial species (let alone both of them together) they only came into their own when the others were both in decline. (Which does not explain why they, too, were in decline after 1996.)

The student data can tell us no more, but there were other surveys of the plot flora. On 19 March 1969, Charles Sinker examined the 'D' plots one year after the start of the experiment. By far the most successful colonist, covering more than 25% of each plot, was Creeping Bent (*Agrostis stolonifera*). Yorkshire Fog was the next commonest grass, well-established but less than 12.5% cover. Scattered individuals of Common Bent (*Agrostis capillaris*), Sweet Vernal-grass (*Anthoxanthum odoratum*), Meadow Foxtail (*Alopecurus pratensis*), Cock's-foot, and Perennial Rye-grass (*Lolium perenne*) were also noted.

The plant list for all plots compiled by Dr D. H. (Kery) Dalby in July 1978 confirmed the continued presence of *A. odoratum* and *L. perenne* and added Soft Brome (*Bromus hordeaceus*), Crested Dog's-tail (*Cynosurus cristatus*), Red Fescue (*Festuca*

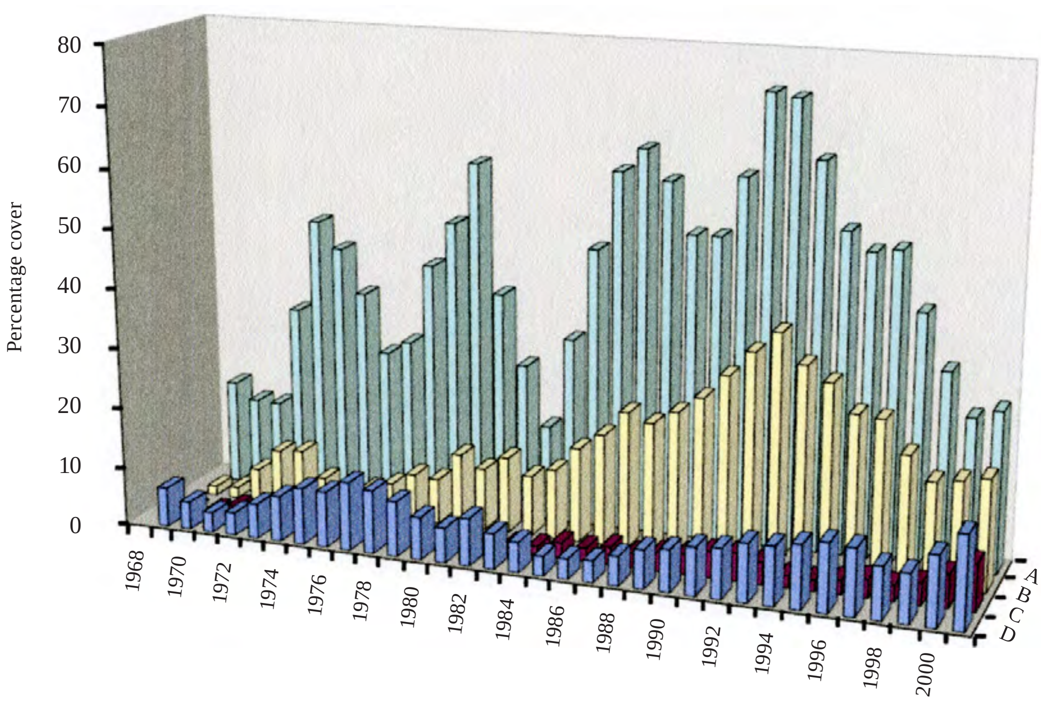

Fig. 13 Fluctuations in the abundance of moss (Rhytidiadelphus squarrosus) *under the four treatments, over time. 'D' plot data are in the foreground, with 'C' and 'B' plots behind them leaving 'A' plots in the background. The bars represent smoothed averages of the data collected in summer (May–July)*

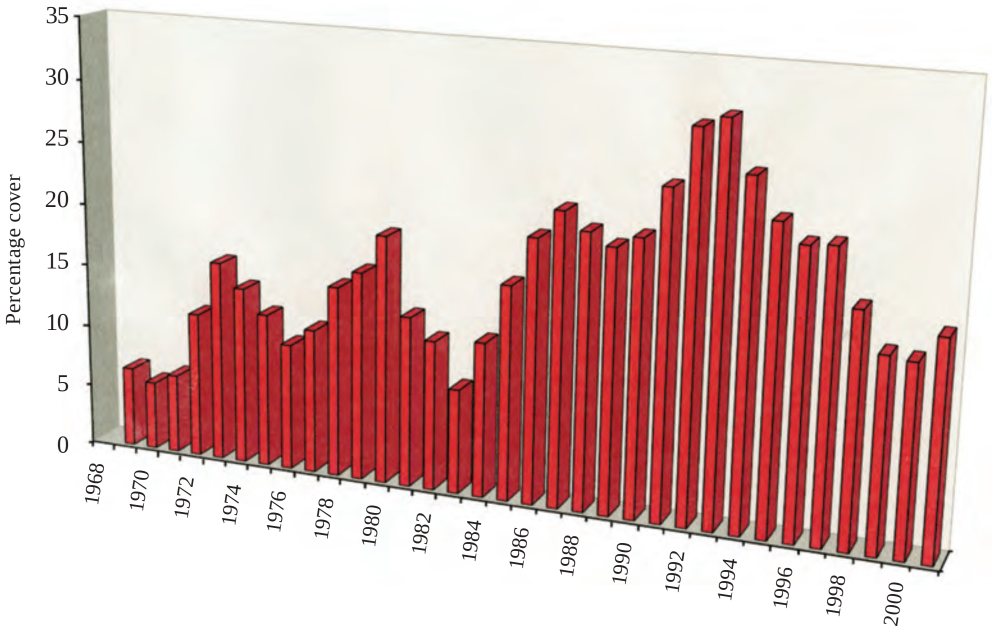

Fig. 14 Overall mean fluctuation in the abundance of moss (Rhytidiadelphus squarrosus) *in summer, 1969–2001*

rubra), Small Sweet-grass (*Glyceria declinata*) and Annual Meadow-grass (*Poa annua*).

Several lists drawn up between 1988 and 1990 confirmed the continued presence of *A. capillaris, A. odoratum, A. stolonifera*, and *F. rubra* whilst adding Wavy Hair-grass (*Deschampsia flexuosa*) and Timothy (*Phleum pratense*).

In July 1997, Dr Charles Turner found *A. odoratum* to be the most widespread 'other grass', it being present in all 16 plots whilst *F. rubra* was present in all 'B', 'C' and 'D' plots. The only other species recorded was Smooth Meadow-grass (*Poa pratensis*).

Nobody would ever claim to have found all the species present in a non-destructive sample taken on a single day, so nobody should attempt to read too much into the last few paragraphs. But the overall appreciation would appear to be that the most successful coloniser of the bare ground in the 'D' plots had given way to a predominance of Sweet Vernal-grass and Red Fescue, the picture being complicated by the occasional appearance of various other species.

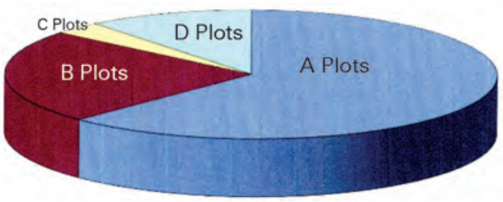

Fig. 15 The overall distribution of moss in the grass plots during summer, 1969–2001

Moss

As would be expected, moss performed much better in the mown than in the unmown plots (Figs 13 and 15) because its low growth-form is easily shaded out by taller vegetation; although it performed much better in the 'D' plots than in the 'C', having been given that opportunity to colonise bare ground in March 1968. (Note that the plot order in Fig. 13 has been reversed so that the 'A' plots are at the back to allow the other data to be seen.)

I don't think anybody, in 1968, would have expected the data to show episodic fluctuations of abundance in the 'A' plots but not, to the same extent, in the others. The overall long-term fluctuation is best appreciated in Fig. 14 which uses the (summer) data from all of the plots.

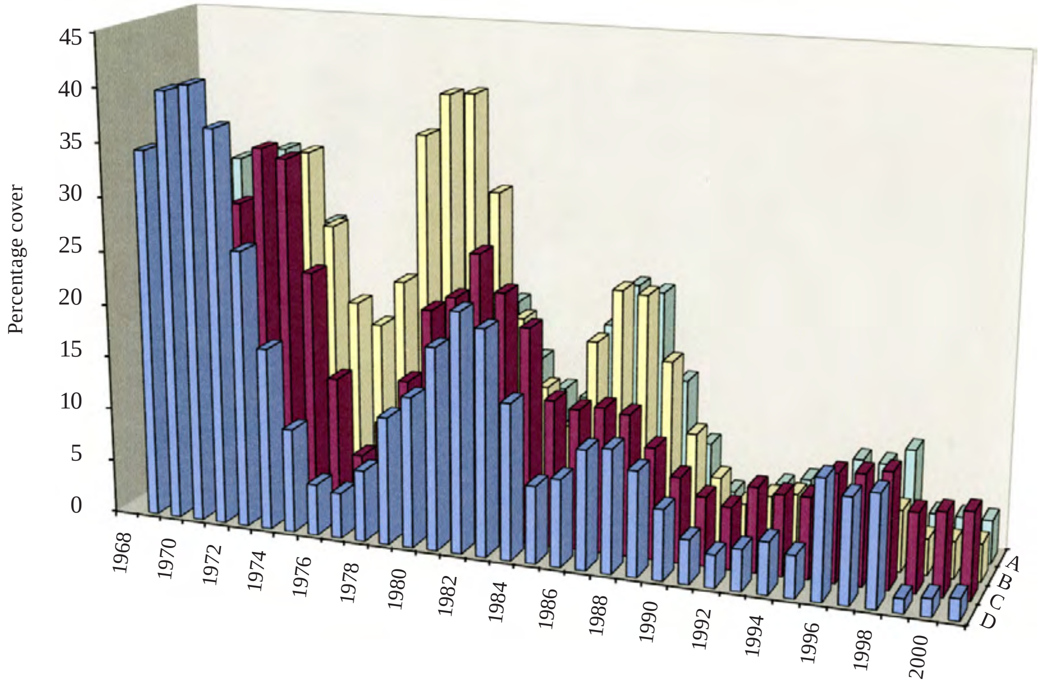

Fig. 16 Fluctuations in the abundance of Creeping Buttercup (Ranunculus repens) *under the four treatments, over time. 'A' plot data are in the foreground, with 'B' and 'C' plots behind them leaving 'D' plots in the background. The bars represent smoothed averages of the data collected in summer (May–July)*

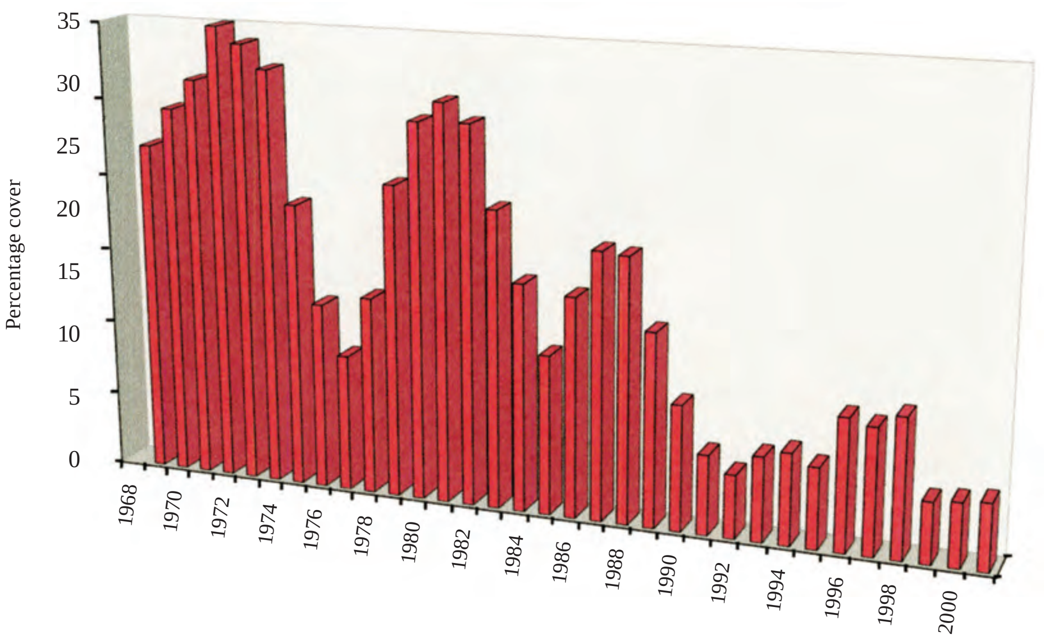

Fig. 17 Overall mean fluctuations in the abundance of Creeping Buttercup in summer, 1969–2001

Springy Turf-moss (*Rhytidiadelphus squarrosus*) was, seemingly, the predominant species although a Haircap (*Polytrichum* sp.) and Neat Feather-moss (*Pseudoscleropodium purum*) were recorded on two occasions, and Rough-stalked Feather-moss (*Brachythecium rutabulum*), Pointed Spear-moss (*Calliergonella cuspidata*) and Taper-leaved Earth-moss (*Pleuridium acuminatum*) were recorded once only.

Creeping Buttercup (*Ranunculus repens*)

This, seemingly the only species of *Ranunculus* to be present in the plots in 1968, was originally chosen as one of the study taxa because its distinctively-shaped leaves rendered it easy to identify. A common agricultural weed, it would not have been (intentionally) included in the seed mixture sown in Court Field when it was reclaimed for agriculture in 1960. It was well-established by 1969 (Figs 16 and 17) and, according to Charles Sinker, was the third most abundant coloniser of the 'D' plots in March that year (after *Agrostis stolonifera* and *Holcus lanatus*).

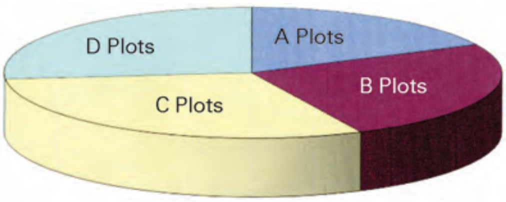

Fig. 18. The overall distribution of Creeping Buttercup (Ranunculus repens) *in the grass plots during summer, 1969–2001*

Figure 18 reflects its ability to prosper under most grassland conditions; a vegetative reproduction strategy, based on runners very close to the ground surface, facilitates colonisation of bare surfaces and survival of mowing whilst an ability to grow tall when supported by the surrounding vegetation ensures its survival in the long-grass 'C' and 'D' plots. I was interested to see that it fared least well in the, intermediate, 'B' plots – yet, at the beginning of this century, it was most abundant there.

However, the commanding impression from Fig. 17 is of the cyclical nature of the fluctuations in abundance of this plant down the years. Fig. 16 is, arguably, the most complicated of the equivalent graphs presented here because peak abundances shifted from 'A' plots via 'D' plots to 'C' plots and, ultimately, to 'B'. In short, the experimental 'treatment' was almost entirely coincidental to the performance of this plant at this site – a conclusion that I had not envisaged in 1968!

A brief comparison of Fig. 17 with the equivalent plot for moss (Fig. 14) shows a quasi-reciprocal relationship: one declining whilst the other increases, yet both peaking at much the same time.

White Clover (*Trifolium repens*)

Figures 19 and 20 demonstrate very clearly that this is a plant of short grassland, much better suited to a lawn than a pasture. The stem of this clover grows across the ground very close to the surface, rooting from the nodes and the height of the leaf surface is a function of petiole length alone. In short, this is a plant very well adapted to survive sheep or rabbit grazing (and therefore lawn-mowing) but as a consequence depends on such activities for it to receive adequate illumination.

It might appear surprising, therefore, to find it growing in a sward dominated by a large grass (Cock's-foot) but both had been sown together when the land was reclaimed for agriculture. "It is usual to include one or more of the clovers in association with grasses. Being leguminous, clovers utilise the nitrogen of the atmosphere and when the root residues are mixed with the soil, nitrogen is subsequently released for the use of other plants" (Moore 1966). Moreover, the clover helps to knit the sward together and, being richer in protein over a longer period of the growing season than are grasses, they improve the feeding value of the herbage. Moore goes on to say that wild White Clover was considered an essential ingredient of all seed mixtures intended for three-year or longer leys.

There is no doubt that this species performs best in the 'A' plots, where the regular mowing prevents the development of tall vegetation that would have

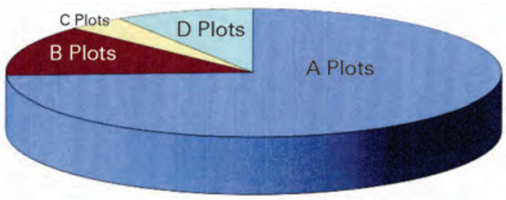

Fig. 19 The overall distribution of White Clover (Trifolium repens) *in the grass plots during summer, 1969–2001*

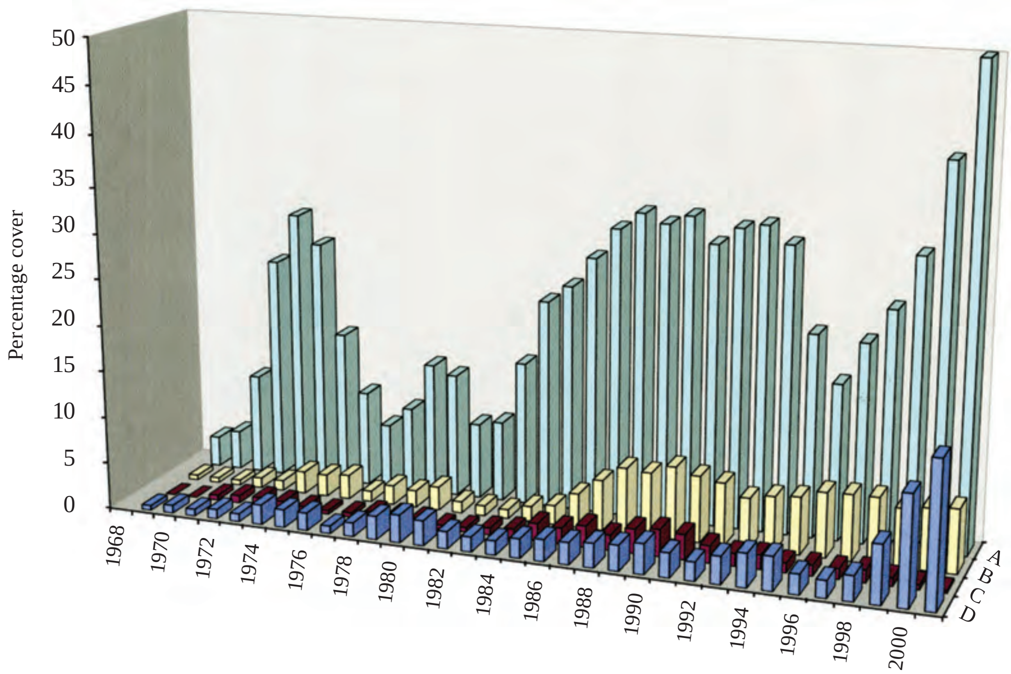

Fig. 20 Fluctuations in the abundance of White Clover (Trifolium repens) *under the four treatments, over time.'D' plot data are in the foreground, with 'C' and 'B' plots behind them leaving 'A' plots at the back*

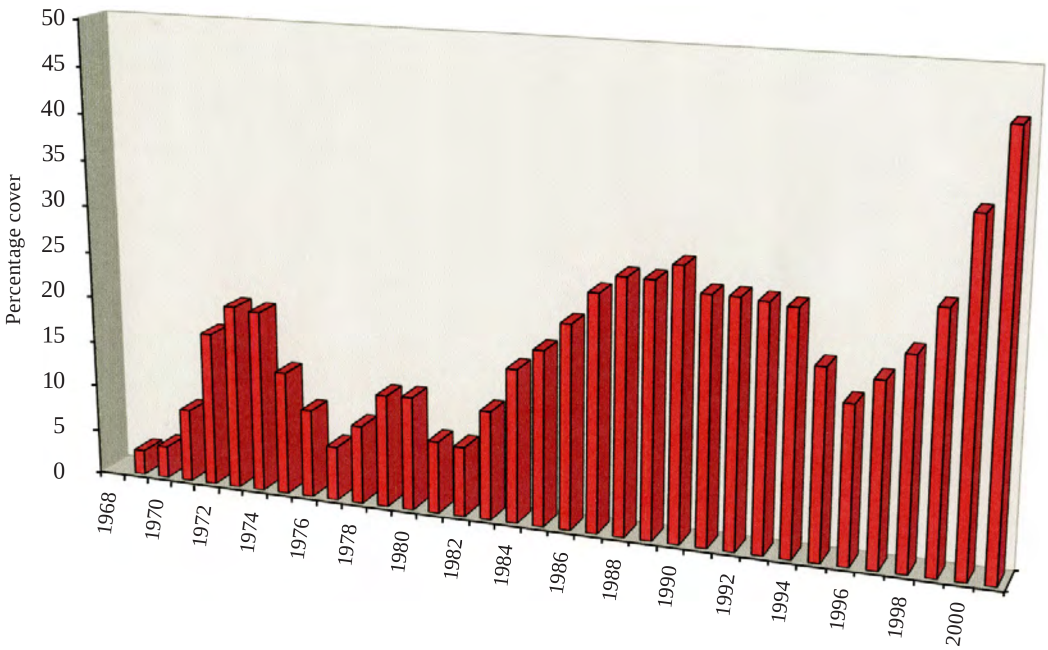

Fig. 21 Overall mean fluctuations in the abundance of White Clover in summer, 1969–2001

cut out the light. The low clover values in the early years must reflect the under-grazing of the sward in Court Field in 1960-1967.

Obviously, the overall impression to be gained from Figs 20 and 21 is of a plant increasing in abundance, showing something of the cyclical pattern displayed by other taxa but maintaining a strange 'stand' from 1987 to 1994. (Note that, as for moss, 'D' plots are displayed in the foreground of Fig. 20 and 'A' at the back.)

A secondary feature seen in Fig. 21 is the rise, in the 'B' plots', from ca 1% to ca 5% cover between 1984 and 1989 and its subsequent continuation at about that level. 1984 was the last year in which the smoothed mean percentage cover of Cock's-foot exceeded 10% (Fig. 8).

More surprising is the rise of this plant in the 'D' plots after 1997. I notice that the equivalent graph for moss (Fig. 13) also shows an increase in the 'D' plots at this time and so there may have been more light available at ground level in those years.

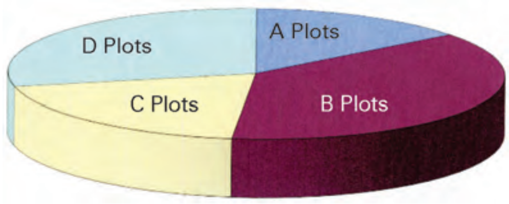

Fig. 22 The overall distribution of Yarrow (Achillea millefolium) *in the grass plots during summer, 1969–2001*

Yarrow (*Achillea millefolium*)

I chose this plant for study because of the ease with which it could be distinguished from everything else growing in the plots in March 1968 by the shape of its leaves. The specific epithet '*millefolium*' translates as 'thousands of leaves' which is not literally true but each leaf is so finely divided that it might give that impression.

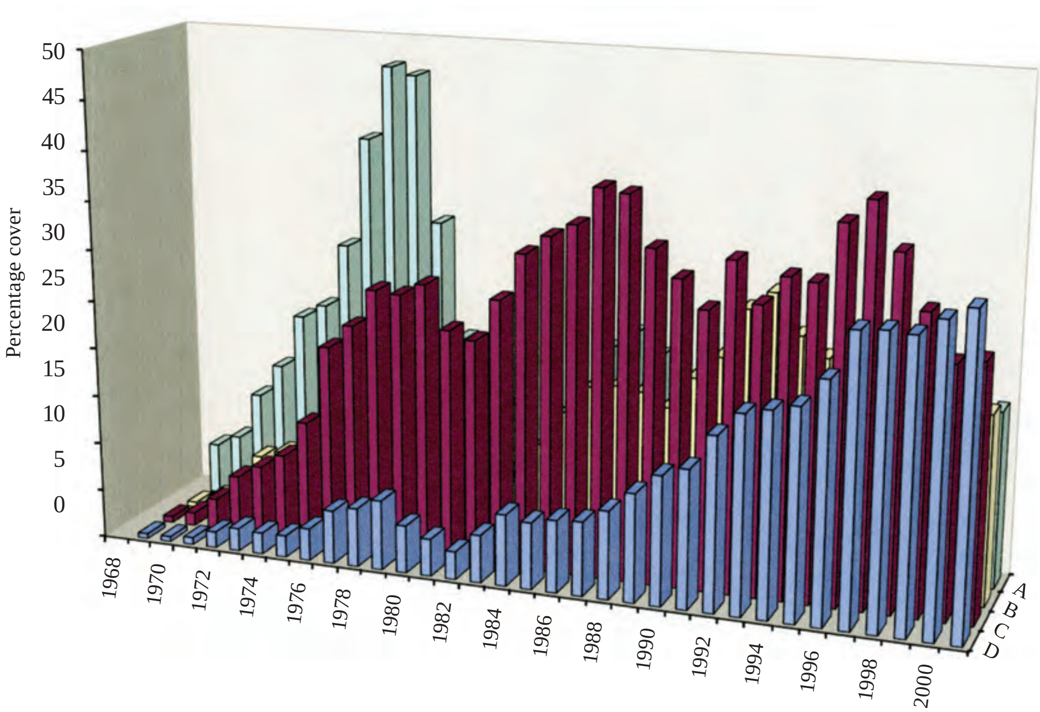

Fig. 23 Fluctuations in the abundance of Yarrow (Achillea millefolium) *under the four treatments, over time. 'A' plot data are in the foreground, with 'B' and 'C' plots behind them leaving 'D' plots at the back*

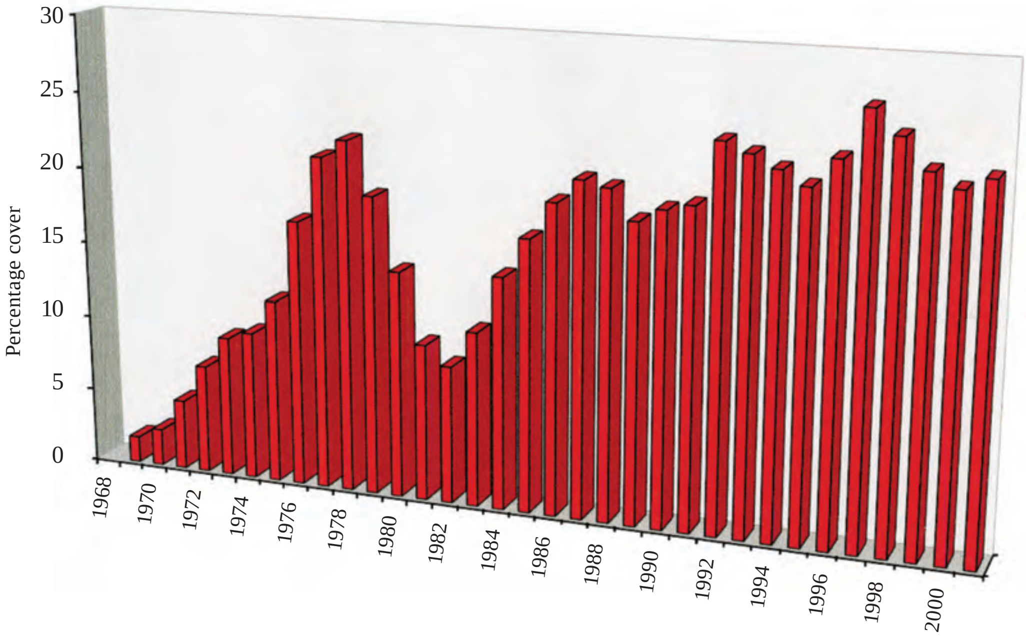

Fig. 24 Overall mean fluctuations in the abundance of Yarrow in summer, 1969–2001

Overall, Yarrow achieved the highest percentage cover in the 'B' plots (Fig. 22) but that was not always the case (Fig. 23).

I had always assumed this to be regarded as a weed in agricultural grassland and was surprised to read that it is sometimes included in seed mixtures (Moore 1966). There is, however, no suggestion that it was sown in Nettlecombe and the percentage cover was low under all treatments in 1968 (Tables 2 and 3). Thereafter it was initially most successful in the unmown 'D' plots but, from the early 1980s it scored most highly in the 'B' plots, although it later became increasingly abundant in the 'A' plots. All in all, the data confirm that this is a plant well suited to the grassland habitat, being able to thrive under a range of conditions (Fig. 24).

Other plants

This 'dustbin' category includes every plant that was not one of the other seven target taxa. It is thus the category most prone to error as any group of students that failed to recognise one of those seven will have included the 'hit' in this category. Thus the group that sampled the plot 'B2' on 13 July 2001 (Table 4) seems to have been reluctant to positively identify more than a few individuals of the named plants in this recently-mown sward – recording 'other grasses' as 72% cover, 'other plants' as 81% and nothing else more than 5%.

None of these 'other plant' species were included in the original seed mix, so it is not surprising that their cover values were low when the experiment started. And, as no attempt was made to discourage their colonisation (no herbicides were applied), it was to be expected that they would increase both in numbers of species and in total cover.

When Charles Sinker made his list (in March 1969) of species that had colonised the 'D' plots in their first year there were ten species of 'other plants'. That number had risen to 37 when Dr D. H. Dalby compiled a flora for all the plots in July 1978.

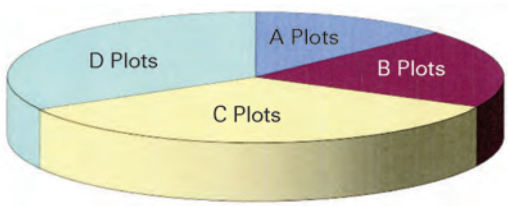

Fig. 25 The overall distribution of 'other plants' in the grass plots during summer, 1969–2001

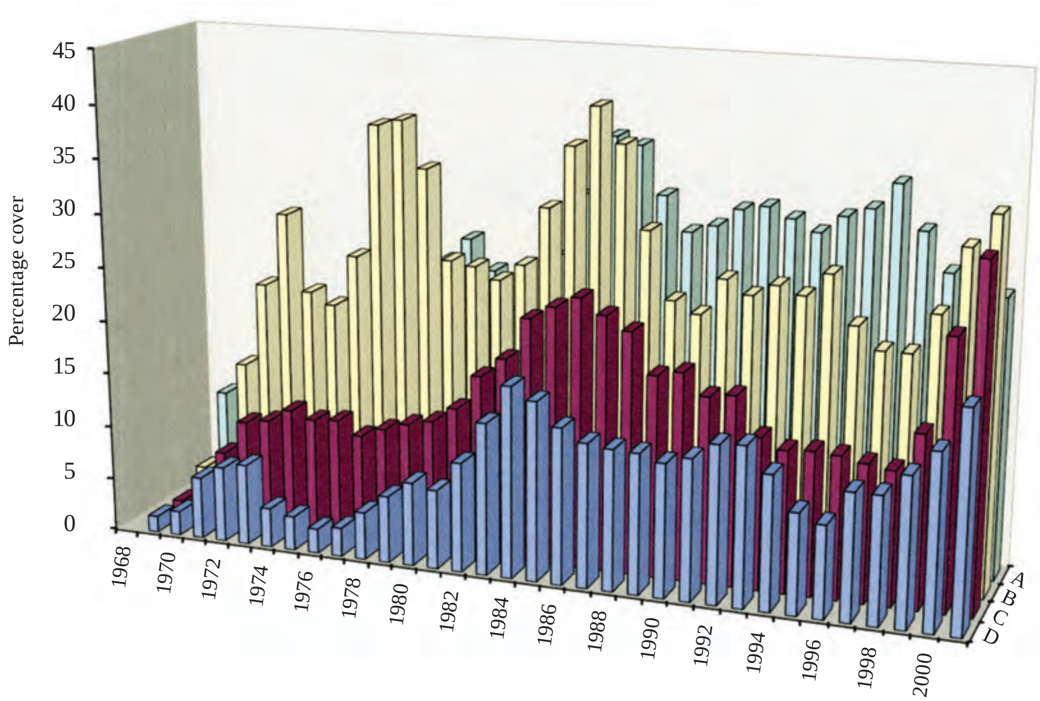

Fig. 26 Fluctuations in the abundance of the 'other plants' under the four treatments, over time. 'A' plot data are in the foreground, with 'B' and 'C' plots behind them leaving 'D' plots in the background. The bars represent smoothed averages of the data collected in summer (May–July)

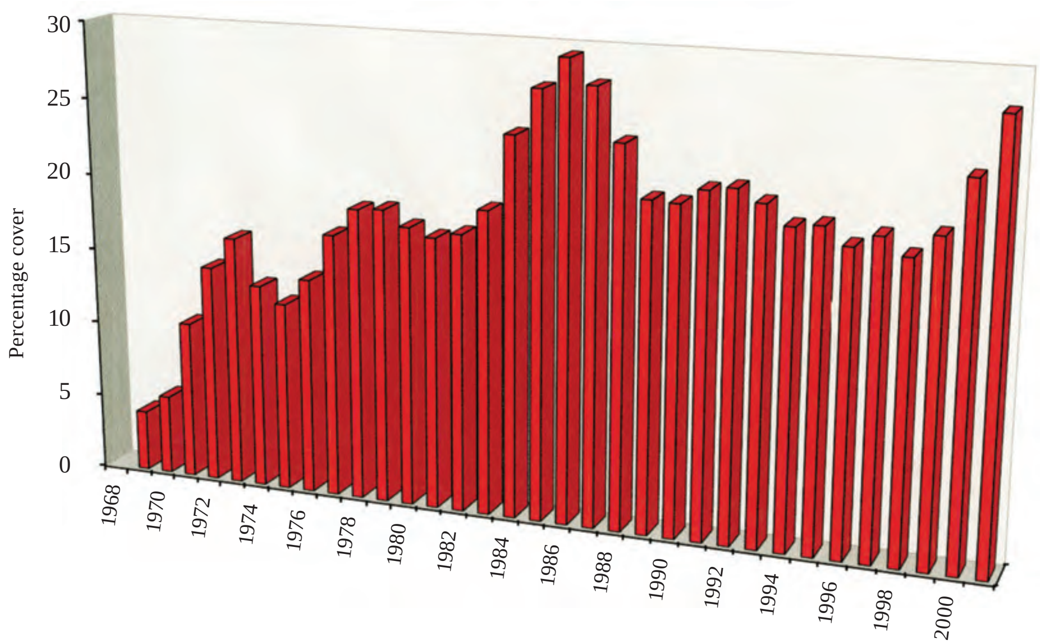

Fig. 27 Overall mean fluctuations in the abundance of the 'other plants' in summer, 1969–2001

And the number remained at that level in 1988 and again in 1998 but they were not exactly the same species.

The summary pie-chart (Fig. 25) shows that these plants are discouraged by mowing (the 'C' and 'D' slices are almost exactly equal). Species richness tells much the same story; the 1998 survey identified 15 'other plants' in the 'A' plots, 18 in 'B', 19 in 'C' and 23 in 'D'. Figure 26 shows that percentage cover was initially highest in 'C' plots with 'D' and 'B' catching up to peak in the mid-1980s. Then after a ten-year period of apparent stasis there was another spike in abundance (see the right-hand end of the graph in Fig. 26). This may be an artefact. I retired at the end of 1999 and the plots were sampled much less frequently thereafter. In other words, there was less human disturbance.

In the other half of Court Field, exclusion of grazing livestock in 1972 had resulted in the development of secondary woodland in the valley floor by 2000 (Crothers 2015). Nothing remotely comparable occurred in the Experimental Plot, despite a regular delivery of acorns. Fifty-two tree seedlings were identified within the Experimental Plot in July 1991, 17 of which were growing in the plots, mostly within 25mm of the plot margin and in plots furthest from the house (Crothers 1991). Rooks and Jackdaws, that harvest acorns from the trees on the slope above the plots, carry their trophies down to the flat valley-floor to feed on them. The close-mown paths between the plots were obviously suitable sites and the acorns that survived to germinate were presumably ones that had shot off sideways into the vegetation when stabbed by a beak.

Few of the oak seedlings survived to their second summer and only one grew to about a metre high. Growing conditions are extreme. The soil is very thin (c. 50 mm) over the levelled Old Red Sandstone 'shillet' and dries out quickly during hot summers. It can also be cold at times; frost having been recorded in every month of the year (Ratsey 1973) and a grass-minimum of -14°C was recorded on one occasion.

DISCUSSION

Compared with the other end of Court Field, which was well on its way to woodland in less time, the grass plots changed very little. Unlike the earlier paper (Crothers 2015) this one is not illustrated with many photographs because they show very little change once the 'D' plots had recolonised, although the paths got narrower. But whilst the vegetation remained grassland, and all of the chosen study species remained present, nobody seeing the data presented in this paper could imagine a stable state over the thirty years.

The underlying transition has been from a

Fig. 28 Students collecting data on the grass plots, 2 May 1985. The weather station occupies the right-hand corner of the Experimental Plot. The drums in the foreground contained North Sea crude destined for an oil-pollution experiment on the Exmoor coast (it had to be stored n metres away from an inhabited building.) The other 'boxes' are snail cages for research on Cepaea *species*

sown pasture, boosted by (moderate) applications of artificial fertiliser, to a much less productive regime. Fertility levels must have been dropping throughout, especially in the mown plots from which the clippings were removed. Plants with high nutrient requirements, including an agriculturally-improved weakly- or in-fertile strain of Cock's-foot, introduced in the seed mix, declined over time. I presume that this is why Creeping Buttercup similarly declined.

Reduced soil fertility allowed wild White Clover to increase thanks to its ability to 'fix' atmospheric Nitrogen. But the overall increase in Yarrow was most probably due to a decrease in competition.

The peaks and troughs, so evident in the various graphs, whilst not obviously related to any of the recorded meteorological data, must reflect the outcomes of intense competition active within this grassland community. I suspect that each was triggered by some external stimulus (meteorological or otherwise), which then affected all the other species.

Tailpiece

It could perhaps, be argued that this paper has no place in these Proceedings as it is not concerned with natural history – based, as it is, on human management of an essentially artificial environment for an educational purpose. Others may argue that a paper based on student data (with all its inherent inaccuracies) has no place in a serious publication. I ask both groups of people to widen their horizons and to think outside the box.

I contend that the changes highlighted here are unlikely to have been confined to these plots. I suggest that most plant communities probably show comparable fluctuations over time – with obvious consequences for the animal, fungal and other communities that depend upon them. The 'Balance of Nature' is far from stable, even in apparently stable communities.

The importance of the history of a site cannot be exaggerated. In this case, knowing that the land had been ploughed and reclaimed for agriculture in 1960 was invaluable. Forty years later, several components of that seed mix still thrived; others, unsuited to this site, have effectively gone. And that single act, on one afternoon in March 1968, when I removed the turf from the 'D' plots remains the reason for the differences still visible between them and the 'C' plots.

Dr J. H. Crothers,

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