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J. Mitchley; P. J. Grubb

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CONTROL OF RELATIVE ABUNDANCE OF PERENNIALS IN CHALK GRASSLAND IN SOUTHERN ENGLAND

I. CONSTANCY OF RANK ORDER AND RESULTS OF POT- AND FIELD-EXPERIMENTS ON THE ROLE OF INTERFERENCE

J. MITCHLEY* AND P. J. GRUBB

Botany School, Downing Street, Cambridge CB2 3EA

SUMMARY

(1) A study of the relative abundance of perennial species in chalk grassland in southern England revealed great constancy ($P < 0{\cdot}001$) in rank order: (a) across any one site (twenty stands of 0·48 m^2 in an area of 3480 m^2), (b) from year to year (1980–82) and (c) between two sites 150 km apart. Comparison of these records with transformed data from phytosociological accounts in the literature provides evidence of high constancy of rank order over much larger areas and longer periods. Ancient chalk grassland is thus an ideal community for investigation of the mechanisms determining the relative abundance of species.

(2) Two experiments were carried out to determine the extent to which the order of relative abundance may be explained by short-term (1–2 years) ability to interfere with growth of plants of other species in the vegetative phase.

(3) In an outdoor pot experiment, fourteen dicotyledons were grown in monocultures and in mixtures with one or two standard species (a grass and a dicotyledon). After 18 weeks there was a significant positive correlation between interference ability in the experiment and mean relative abundance in the field. Essentially, the same results were found after 70 weeks.

(4) In a field experiment, six dicotyledons were grown in monocultures, and in all possible mixtures of two species, in plots on an area of chalk grassland cleared of turf. After 62 weeks, the order in interference effects paralleled the order of relative abundance in the grassland. There was also a positive correlation between interference ability and the mean height of rosette leaves of each species. This suggests the importance of above-ground interference.

(5) After 115 weeks, and for 3 years afterwards, additional elements of the perennial life-history became important in determining performance in the plots, especially longevity of adult individuals, degree of lateral spread and the frequency of establishment of seedlings.

(6) We suggest that the control of relative abundance in chalk grassland involves steady-state relationships: (i) between species with taller (and more widely-spreading) and shorter individuals and (ii) between species with longer- and shorter-lived individuals. The balance between species is largely determined by the frequency and timing of grazing and by the frequency of regeneration from seed.

INTRODUCTION

There have been few experimental studies designed to explain the control of relative abundance of different species in herbaceous plant communities (Grubb, Kelly & Mitchley 1982). The rank order of abundance of species in a community may be relatively constant or may fluctuate or may change directionally after a major disturbance such as fire.

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* Present address: Dept. of Biological Sciences, University of Lancaster LA1 4YW.

Explanation of the rank order of abundance should be easier to establish in a community where the order is relatively constant. Experience suggests that chalk grassland might fulfil this requirement.

Several properties of a plant species may be important in determining its relative abundance in a given community: longevity, extent of lateral spread, effectiveness of dispersal in time and distance, ease of establishment from seed, and potential for interference (under appropriate conditions) between plants of the same age and between plants of different age. By 'interference' we mean 'those hardships which are caused by the proximity of neighbours' (Harper 1961), and we measure this effect in terms of cover, yield or seed output. Some studies have shown that the potential for interference can be important in determining relative abundance in spontaneous vegetation (Marshall & Jain 1969; Torssell, Rose & Cunningham 1975; Fowler 1982) but that a high potential does not always lead to high relative abundance (Rabinowitz 1981; Grubb 1982).

Grazed chalk grassland commonly consists of a turf *c.* 2–15 cm tall, and is notable for its intimate mixture of species (often 30 or more in 0·25 m^2). At least some of the perennials appear to be very long-lived, i.e. 10 years or more. There is therefore an *a priori* case that the hierarchy is maintained largely by the repeated effects of interference between adult plants. However, even if the potential for interference is the basic determinant of the hierarchy, it may be that, for some species, the length of life or ease of establishment from seed may affect their position in the rank order (Grubb 1977).

This paper has four parts. In the first, results are presented from a study of the extent of constancy of the hierarchy of chalk grassland perennials at a range of sites. In the second part, results are reported from a pot experiment in which fourteen dicotyledons, spanning the range of relative abundance in the field, were grown in monocultures and in mixtures with two 'standard species' (a grass and a dicotyledon). In the third part, results are reported from a field experiment with six dicotyledons grown in all combinations. Finally, in the Discussion, the results are drawn together and consideration is given to the problem of explaining how the sparser species are not ousted altogether.

Our nomenclature follows *Flora Europaea* (Tutin *et al.* 1964–80).

CONSTANCY OF RELATIVE ABUNDANCE IN CHALK GRASSLAND

The question—how constant is chalk grassland?—touches on three levels: constancy across a site, constancy from year to year and constancy from site to site. A critical study was made of the relative abundance of perennial species in permanent stands at two sites, approximately 150 km apart and both at approximately 150 m altitude, in Sussex (Castle Hill National Nature Reserve, National Grid reference TQ 369069, 50°50′N, 0°4′W) and Wiltshire (Wylye Down National Nature Reserve, National Grid reference SU 002360, 51°7′N, 1°59′W) in southern England. The Sussex site has the steeper slope (15–20° *v.* 5–10°), is south-facing and was winter-grazed by cattle (September–March) during the study period. The Wiltshire site is west-facing and was grazed all the year by both sheep and cattle. In recent years, most of the turf in both study areas has been kept to <10 cm tall (excluding inflorescences). At each site, a plot of 80 m × 48 m was chosen and divided into twenty sub-plots of 16 m × 12 m. In each sub-plot, one stand of 0·48 m^2 was chosen at random and marked permanently with 15-cm long steel tubes driven into the ground at two diagonal corners per stand. The relative abundance of perennial species was estimated in each stand by recording the leaves of plants intercepted by a fine sewing needle (point quadrat) mounted on a frame and lowered vertically through the vegetation at 120 or 240 randomly chosen points. This sampling was carried out nine times between 1980 and 1982 at the Sussex site and seven times at the Wiltshire site. Mitchley (1983) provides further details of the sampling method.

Constancy across a site

Of the thirty-five species found in the stands at the Sussex site, eighteen (51%) occurred in all twenty stands of $0{\cdot}48\ m^2$ and twenty-seven (77%) in more than sixteen of them (Table 1). Of the thirty-nine species at the Wiltshire site, these values were twenty-three (59%) and twenty-seven (69%), respectively. Friedman's test for randomized blocks (Sokal & Rohlf 1981), applied to the rank orders of cover in the twenty stands at a site, showed highly significant constancy of rank ($P < 0{\cdot}001$) between stands on each sampling occasion.

Constancy from year to year

In 1981, the turf at the Sussex site grew about twice as tall as in previous years, because of reduced winter-grazing; in the following year, grazing was increased to remove the tall growth. However, the rank orders of thirty-four species remained remarkably constant for all pair-wise comparisons for equivalent sampling periods between 1980 and 1982 (Kendall's rank correlation test (Sokal & Rohlf 1981), $P < 0{\cdot}001$). The rank orders of thirty-seven species at the Wiltshire site showed even greater constancy for equivalent comparisons.

Constancy from site to site

Of the thirty-five perennial species found in the stands at the Sussex site, twenty-nine (83%) were also found in the stands at the Wiltshire site, plus ten others (Table 1). The rank order was very similar for the species common to the two sites ($P < 0{\cdot}001$).

Wider comparisons

We can relate our ranking obtained in 1981 to those derived from three sets of forty $1\text{-}m^2$ relevées recorded during July–August in chalk grassland in Wiltshire in 1965–68 (Wells 1975). The three sets are for grassland in which the most abundant graminoids were *Carex humilis*, *Festuca ovina* + *rubra* and *Bromus erectus*, respectively. We have transformed Wells' cover-abundance values on the Domin scale, in order to bring them to an approximately linear scale (Bannister 1966), and taken means of the transformed values. Table 2 shows the results of the comparisons between the rank orders from Wells' data and those from our Sussex and Wiltshire sites. All comparisons indicate highly significant constancy in the rank orders for forty-two species in 1982 for all comparisons. The Sussex site is most strongly correlated with Wells' *Bromus erectus* grassland, and the Wiltshire site with his *Carex humilis* type.

Table 3 shows the rank orders of twenty-seven dicotyledonous species derived (after transformation) from various published sources. Despite some obvious variability, there is clear constancy in the rank order of many species in the different rankings. Comparison of these nine rankings with our Sussex site again reveals a high degree of constancy ($P < 0{\cdot}01$ or $<0{\cdot}001$, mostly). There is thus evidence for relatively fixed hierarchies of perennial species in chalk grassland over extensive areas, and through fairly long periods, wherever management is reasonably constant.

Table 1. The perennial species found in the study areas at chalk grassland sites in Sussex and Wiltshire. The first two columns indicate the frequency of each species (numbers out of twenty 0·48-m^2 stands in which present). Mean cover estimates (percentage of total contacts within each stand) for the twenty stands at a site are shown in the remaining columns. Values in 1981 and 1982 are for 'cover-repetition', i.e. repeat hits of the same species at a point quadrat are included. Values for 1980 are for 'non-repetitive cover', i.e. excluding repeat hits. Symbols: –, species absent from the site; (+), species present at the site but not found in any of the stands between 1980 and 1982; +, species found in some of the stands but with a mean cover estimate of <0·5%. Frequency values for additional species (Sussex followed by Wiltshire): ***Bellis perennis***: +, 1; ***Galium verum***: 3, 1; ***Cynosurus cristatus***: +, 1; ***Festuca arundinacea***: +, 3; ***Holcus lanatus***: 1, +.

			Cover estimates (percentage of total contacts per stand)															
	Frequency		Sussex 1980			Sussex 1981			Sussex 1982			Wilts 1980			Wilts 1981			Wilts 1982
Species	Sussex	Wilts	June	Aug.	Nov.	Mar.	June	Sep.	Feb.	June	Sep.	June	Sep.	Nov.	Apr.	June	Sep.	June
Sanguisorba minor	20	20	12	19	11	5	25	23	5	25	23	22	26	19	9	30	28	34
Leontodon hispidus	20	20	6	8	7	2	10	14	+	12	18	6	7	5	2	8	7	9
Hippocrepis comosa	19	(+)	4	10	9	4	10	13	2	8	14	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Thymus praecox	20	20	6	10	8	6	9	9	3	8	9	3	3	3	1	4	4	4
Cirsium acaule	20	20	9	8	1	1	13	12	+	12	11	6	6	1	1	7	7	7
Asperula cynanchica	20	16	5	8	7	2	6	9	+	6	9	1	2	2	+	2	2	2
Plantago lanceolata	20	20	2	5	6	2	6	8	2	6	9	6	11	12	4	11	12	12
Lotus corniculatus	20	20	4	7	4	1	8	9	+	6	7	3	3	3	1	6	6	6
Hieracium pilosella	18	20	3	4	3	3	5	4	1	3	3	5	3	3	2	5	5	4
Succisa pratensis	20	20	2	3	2	1	4	5	1	3	5	10	12	8	4	16	14	15
Filipendula vulgaris	18	9	2	3	3	1	4	4	1	3	3	1	1	1	+	1	1	1
Scabiosa columbaria	20	18	1	2	2	1	2	4	1	3	5	2	2	1	1	2	2	2
Pimpinella saxifraga	19	19	2	3	2	+	3	3	0	3	5	1	1	1	+	1	1	1
Centaurea nigra	19	20	2	3	1	1	4	2	0	3	4	2	2	1	+	3	2	2
Phyteuma orbiculare	20	–	2	3	1	+	4	2	0	3	3	–	–	–	–	–	–	–
Plantago media	20	20	1	3	1	1	2	3	0	2	3	6	7	5	2	9	8	9

Species	Frequency		Cover estimates (percentage of total contacts per stand)															
			Sussex 1980			Sussex 1981			Sussex 1982			Wilts 1980				Wilts 1981		Wilts 1982
	Sussex	Wilts	June	Aug.	Nov.	Mar.	June	Sep.	Feb.	June	Sep.	June	Sep.	Nov.	Apr.	June	Sep.	June
Polygala vulgaris	19	–	2	1	1	1	2	2	1	2	2	–	–	–	–	–	–	–
Ranunculus bulbosus	19	20	1	2	2	2	2	0	1	1	1	1	1	1	1	2	0	2
Prunella vulgaris	19	19	+	1	1	1	1	1	+	+	1	1	1	+	+	1	1	1
Viola hirta	15	7	+	1	1	+	1	1	+	2	2	+	+	+	0	+	+	+
Campanula rotundifolia	5	16	+	+	+	+	+	+	+	+	+	1	1	1	+	1	1	1
Trifolium pratense	1	20	+	0	0	0	+	+	0	+	+	2	3	2	1	2	1	1
Betonica officinalis	(+)	18	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	2	2	3	1	3	3	3
Primula veris	(+)	9	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	+	+	+	+	1	+	1
Serratula tinctoria	–	20	–	–	–	–	–	–	–	–	–	9	9	1	1	13	10	13
Helianthemum nummularium	–	20	–	–	–	–	–	–	–	–	–	6	8	8	2	6	7	6
Campanula glomerata	–	13	–	–	–	–	–	–	–	–	–	1	1	+	+	1	1	1
Polygala calcarea	–	13	–	–	–	–	–	–	–	–	–	1	1	1	+	1	1	1
Brachypodium pinnatum	20	–	12	20	22	8	20	33	8	21	38	–	–	–	–	–	–	–
Festuca ovina + rubra	20	20	11	11	17	13	21	26	20	22	33	22	24	25	22	24	36	30
Bromus erectus	20	–	11	21	18	12	16	15	6	19	31	–	–	–	–	–	–	–
Carex flacca	20	20	2	5	7	5	14	19	16	20	23	12	22	21	10	23	25	26
Briza media	20	20	4	7	9	5	6	9	5	8	15	11	15	13	7	10	9	13
Koeleria macrantha	20	20	3	4	4	3	4	3	2	4	7	7	5	8	5	5	2	8
Avenula pratensis	20	20	2	3	3	1	2	2	2	3	6	7	9	11	3	4	5	7
Danthonia decumbens	11	20	1	2	2	1	2	3	1	3	4	5	6	7	3	4	5	6
Carex caryophyllea	19	20	1	1	1	+	1	1	1	3	4	5	3	4	2	5	5	7
Dactylis glomerata	7	20	+	1	+	+	+	+	+	+	1	1	3	2	1	2	2	3
Avenula pubescens	1	7	0	0	0	+	+	0	+	+	+	0	+	0	+	+	+	+
Carex humilis	–	20	–	–	–	–	–	–	–	–	–	21	24	20	8	14	28	38

TABLE 2. Values of Kendall's *tau* for comparisons of the relative abundance rankings from chalk grassland sites in Sussex and Wiltshire (derived from Table 1) with those of Wells (1975) for three chalk grassland communities in Wiltshire. Probability symbols (two-tailed tests): ***, $P < 0{\cdot}001$; **, $P < 0{\cdot}01$. N.S., not significant. Other symbols: †, June 1981, $n = 13$ (graminoids) and 29 (dicotyledons); ††, June 1982, $n = 42$.

Comparison	Sussex	Wiltshire
Bromus erectus grassland		
† Graminoids	0·540(**)	0·307 (N.S.)
† Dicotyledons	0·397 (***)	0·556 (***)
†† All species	0·406 (***)	0·353 (***)
Carex humilis grassland		
† Graminoids	0·065 (N.S.)	0·755 (***)
† Dicotyledons	0·471 (***)	0·614 (***)
†† All species	0·342 (***)	0·539 (***)
Festuca ovina grassland		
† Graminoids	0·247 (N.S.)	0·461 (**)
† Dicotyledons	0·410 (***)	0·570 (***)
†† All species	0·356 (***)	0·459 (***)

THE POT EXPERIMENT

Materials and methods

Species

The fourteen species used in this experiment are marked with asterisks in Table 3, and their average relative abundance in chalk grassland in England is indicated. The grass (*Bromus erectus*) and the dicotyledon (*Leontodon hispidus*), both species of generally high relative abundance in chalk grassland in England, were the standard species with which the fourteen experimental species were grown. The two standard species will be referred to by their generic names only for the remainder of this section.

Seed

Most seed was collected between August and November 1979 from the Devil's Ditch earthwork in Cambridgeshire (National Grid reference TL 585645). Exceptions were: *Lotus corniculatus* from a chalk cutting in East Sussex (TQ 387093); *Sanguisorba minor* from the Devil's Ditch in July 1979; *Cirsium acaule* from Castle Hill National Nature Reserve, East Sussex (TQ 369069); *Prunella vulgaris* from a scrub–grassland mixture in a chalk quarry in Cambridgeshire (TL 482575).

Soil

This was collected from the site on Aston Rowant National Nature Reserve, Oxfordshire (SU 723959), which was used for the field experiment described in the third part of this paper. The site is just below the brow of a ridge capped with a thin layer of clay-with-flints. The soil is mainly derived from chalk but contains some clay and flints; the pH is *c.* 7·5 in the upper 5 cm. Soil was collected in April 1980 from an area of 20 m × 10 m and from a depth of 0–15 cm, and taken to the University Botanic Garden at Cambridge where it was sieved through a 1-cm wire mesh and stored in galvanized bins until required. For planting, plastic pots of 14 cm diameter and 9 cm deep were filled to within 2 cm of the rim with the soil, each pot containing *c.* 1 litre of soil.

TABLE 3. Relative abundance rankings derived from nine phytosociological surveys of chalk grassland in Great Britain. Bold numbers indicate the particular species of a Biological Flora study and are not included in the mean rank. Key to sources: 1–3 Wells (1975): 1, *Festuca ovina* grassland; 2, *Carex humilis* grassland; 3, *Bromus erectus* grassland; 4–9 Biological Flora of the British Isles: 4, *Cirsium acaulon* (=*acaule*) (Pigott 1968); 5, *Senecio integrifolius* (Smith 1979); 6, *Helianthemum nummularium* (Proctor 1956); 7, *Hippocrepis comosa* (Fearn 1973); 8, *Hypochoeris maculata* (Wells 1976); 9, *Pulsatilla vulgaris* (Wells & Barling 1971). The ranking for our Sussex site is derived from the mean cover estimates for the three June recording periods 1980–82 (Table 1). The mean air-dry weight for seeds of each species is indicated. Species marked with asterisks are included in the pot experiment, and those marked with carets are included in the field experiment.

	Literature source											
	1	2	3	4	5	6	7	8	9	Mean rank	Sussex site rank	Seed weight (mg)
†**Sanguisorba minor*	2	1	4	2	1	2	3	1	1	1·9	1	4·7
†**Leontodon hispidus*	7	2	3	6	4	4	6	9	4	5·0	3	1·1
**Lotus corniculatus*	5	5	1	4	5	6	7	6	10	5·4	6	1·3
†**Cirsium acaule*	6	3	5	**1**	3	5	14=	5	3	5·6	2	3·9
**Plantago lanceolata*	1	4	2	7	8	8	9=	2	11=	5·9	7	2·2
Helanthemum nummularium	12	9	11	5	11	**1**	2	3	2	6·9	–	1·3
Hieracium pilosella	15	14	17	8	2	9	4	11	5	9·4	9	0·18
†**Hippocrepis comosa*	11	11	12	9	6	11	**1**	13=	6	9·9	5	3·7
Succisa pratensis	4	6	6	12	21=	12	24=	7	19	10·9	10=	1·3
Thymus praecox	19	19	25	3	10	3	5	4	11=	11·1	4	0·11
**Scabiosa columbaria*	10	12	10	10=	13	14	9=	18	8	11·7	15	1·6
**Plantago media*	3	8	7	13	15	15=	18	15	14	12·1	16=	0·53
**Centaurea nigra*	14	22	21	15	17=	10	13	8	7	12·8	10=	2·2
Filipendula vulgaris	21	16	15	10=	7	19	12	13=	13	14·1	12=	0·70
**Campanula rotundifolia*	16	18	18=	18	14	13	8	17	9	14·6	21	0·072
†**Pimpinella saxifraga*	17	15	13	16	20	15=	9=	20	15	15·8	14	1·2
**Prunella vulgaris*	9	13	9	21=	19	22	20=	12	18	16·0	20	0·77
Asperula cynanchica	13	10	20	23	17=	7	19	22	20	16·8	8	0·96
Viola hirta	25	17	16	14	23	18	16=	10	17	17·4	19	2·8
Ranunculus bulbosus	18	21	18=	19=	12	24	14=	24	16	18·6	18	2·0
Trifolium pratense	8	7	8	24	25			25	23=	20·1	22	1·4
**Campanula glomerata*	23	20	22	19=	21=	17		21	21	20·1	–	0·18
Primula veris	20	23	14	17	24	25	20=	16	23=	20·3	23=	0·89
Polygala vulgaris	22	24	24	21=	16	20=	16=	19	22	20·6	16=	1·9
†**Achillea millefolium*	24			25	9	20=	20=	23	25	22·1	23=	0·13
**Astragalus danicus*				26		23	20=	26=	26	24·4	–	1·6
Phyteuma orbiculare			23	27	26					25·3	12=	0·22

Experimental design

There were four treatments for each experimental species: (i) monocultures, (ii) two-species mixtures with *Bromus*, (iii) two-species mixtures with *Leontodon*. (v) three-species mixtures with both *Bromus* and *Leontodon*. Each pot was planted with nineteen plants in a hexagonal design with a between-plant spacing of 3 cm (Fig. 1), and there were three replicate pots per treatment. *Bromus* and *Leontodon* were included as experimental species as well, though for these two species the second and third treatments, respectively, were omitted.

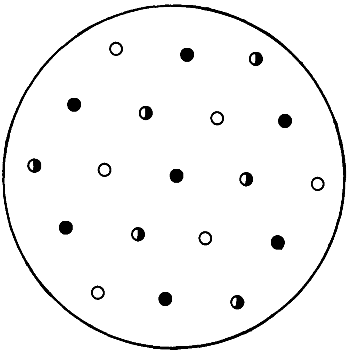

FIG. 1. The planting design in a pot experiment conducted with chalk grassland species; spacing between plants is 3 cm. In the three mixture-treatments, the filled circles represent individuals of the experimental species concerned. In two-species mixtures, the open and half-filled circles represent individuals of the standard species (*Bromus* or *Leontodon*). In the three-species mixtures, the open circles represent one of the standard species and the half-filled circles the other. The six individuals in the outer hexagon (filled circles) are used in the analysis of interference effects.

Planting procedure

Germinated seed was sown between 16 and 20 May 1980 and the pots kept in the glasshouse for one month. On 24 June 1980, the pots were fully randomized on transparent polyethylene sheeting within an open, south-facing sand-based frame. Re-randomization was carried out twice each month. Watering, from overhead irrigation sprays, was carried our every day during summer, reduced in the autumn and omitted in winter.

Analysis

Between 16 and 18 September 1980, leaf number and the length of the longest leaf (shoot number and length in the case of *Lotus corniculatus*) were recorded for the six plants of the experimental species in the outer hexagon in each pot (Fig. 1). The plants were harvested between 16 and 20 September 1981, 70 weeks after planting, when they were clipped at ground level and the above-ground material was dried at 70 °C for 48 h before being weighed to ±1 mg.

The mean performance value was calculated for the six plants in each pot, and the three replicate values for each treatment were used to calculate the mean and its error. In 1980 there were two measures of performance, namely leaf number per plant and length of the longest leaf. To provide a single measure we used the product of these two—the maximum total leaf length per plant. Interference ability was calculated as the difference between performance in the mixture and the monoculture, expressed as a percentage of that in the monoculture. The values for interference ability have been ranked amongst the experimental species to produce hierarchies of interference ability. Two-tailed rank correlation tests were used to assess the relationship between interference ability in the experiment and relative abundance in the field.

Results

Results after one season (18 weeks)

The results are shown in Table 4, where the species are divided arbitrarily into eight 'relatively abundant' species and eight 'sparse' species according to their position in the field abundance hierarchy (Table 3). Of the seven 'relatively abundant' dicotyledons, only *Lotus corniculatus* shows a significant decrease in leaf (=shoot) length in the presence of *Bromus*, when compared with its monoculture. All seven species show no significant decrease in the presence of *Leontodon.* In contrast, five of the eight 'sparse' species show a significant decrease in leaf length in the presence of *Leontodon* (*Campanula glomerata*, *C. rotundifolia*, *Pimpinella saxifraga*, *Achillea millefolium* and *Astragalus danicus*) and four of these also show a significant decrease in the presence of *Bromus*. *Pimpinella saxifraga* suffered significant interference from *Leontodon* but not from *Bromus* at this stage.

TABLE 4. Performance of sixteen chalk grassland species, in a pot experiment, on 16–18 September 1980 (18 weeks after planting) as measured by maximum leaf length (shoot length for *Lotus corniculatus*) per plant (mean of three replicates). Values have also been transformed to percentage difference as a measure of interference ability. These values show the difference between performance in a mixture with *Bromus erectus* or *Leontodon hispidus*, or both, and a monoculture, expressed as a percentage of that in the monoculture. The species are ordered according to their mean rank in the field (Table 3) and divided arbitrarily into eight 'relatively abundant' and eight 'sparse' species. The mean performance values for the 'relatively abundant' species are calculated for the seven dicotyledonous species, excluding *Bromus*. Symbols: M, monocultures; B, with *Bromus erectus*; L, with *Leontodon hispidus*; LSD$_{0\cdot05}$, least significant difference, t = 5%. Bold type indicates that performance in a mixture is significantly different from that in a monoculture ($P < 0{\cdot}05$).

	Mean maximum leaf length per plant (mm)					Percentage difference		
	M	+B	+L	+B + L	LSD$_{0\cdot05}$	+B	+L	+B + L
Bromus erectus	397		339	303	186		−15	−24
Sanguisorba minor	159	96	117	114	68	−40	−26	−28
Leontodon hispidus	162	180		131	37	+11		−19
Lotus corniculatus	166	86	163	120	80	**−48**	−2	−28
Cirsium acaule	79	85	93	143	52	+8	+18	**+82**
Plantago lanceolata	203	220	200	228	42	+8	−2	+12
Hippocrepis comosa	156	148	144	139	73	−5	−8	−11
Scabiosa columbaria	130	122	115	108	30	−6	−12	−17
Mean values (−*Bromus*)	151	134	139	140		−10	−5	−1
Plantago media	79	67	85	84	25	−15	+7	+6
Centaurea nigra	153	159	151	148	47	+4	−1	−3
Campanula rotundifolia	98	35	48	46	32	**−64**	**−51**	**−53**
Pimpinella saxifraga	84	73	47	47	28	−13	**−44**	**−44**
Prunella vulgaris	223	204	248	172	113	−9	+11	−23
Campanula glomerata	53	27	25	18	17	**−49**	**−54**	**−67**
Achillea millefolium	125	69	77	74	41	**−45**	**−38**	**−41**
Astragalus danicus	87	35	28	22	32	**−60**	**−30**	**−38**
Mean values	113	84	89	76		−31	−30	−38

TABLE 5. Performance of sixteen chalk grassland species, in a pot experiment, on 16–20 September 1981 (70 weeks after planting) as measured by above-ground dry weight (mean of three replicates). Values have also been transformed to percentage difference values, as in Table 4. The mean performance values for the 'relatively abundant' species are calculated for the seven dicotyledonous species, excluding *Bromus*. Bold type indicates that performance in a mixture is significantly different from that in a monoculture ($P < 0{\cdot}05$). Symbols as in Table 4.

	Mean above-ground dry weight per plant (mg)					Percentage difference		
	M	+B	+L	+B + L	$LSD_{0{\cdot}05}$	+B	+L	+B + L
Bromus erectus	234		288	203	77		+23	−13
Sanguisorba minor	167	83	188	91	85	**−50**	+12	−46
Leontodon hispidus	105	60		39	53	−43		**−62**
Lotus corniculatus	85	22	144	38	64	**−75**	**+69**	−55
Cirsium acaule	87	98	102	137	70	+12	+17	+57
Plantago lanceolata	232	222	293	272	92	−5	+26	+17
Hippocrepis comosa	59	34	57	35	49	−42	−3	−38
Scabiosa columbaria	91	53	88	56	63	−42	−3	−38
Mean values (−*Bromus*)	118	82	145	95		−35	+20	−24
Plantago media	116	63	78	62	39	**−46**	**−33**	**−47**
Centaurea nigra	116	159	157	160	51	+37	+36	+38
Campanula rotundifolia	48	7	44	9	39	**−85**	−8	**−82**
Pimpinella saxifraga	56	13	33	8	21	**−76**	**−42**	**−86**
Prunella vulgaris	334	294	378	226	50	−12	+13	**−32**
Campanula glomerata	30	3	5	3	7	**−90**	**−84**	**−92**
Achillea millefolium	122	32	64	28	66	**−74**	−47	**−77**
Astragalus danicus	64	4	5	3	21	**−93**	**−93**	**−95**
Mean values	111	72	96	62		−55	−32	−59

Results after two seasons (70 weeks)

The results are shown in Table 5. Two of the seven 'relatively abundant' dicotyledons show a significant decrease in shoot dry weight in the presence of *Bromus* when compared with their monocultures (*Lotus corniculatus* and *Sanguisorba minor*). However, the legume *Lotus corniculatus* shows an *increase* in shoot dry weight in the presence of *Leontodon*. All five other species show no significant difference in shoot dry weight when grown with either *Bromus* or *Leontodon* alone. In contrast, in the presence of *Bromus*, six of the eight 'sparse' species show a significant decrease in shoot dry weight when compared with their monocultures (*Astragalus danicus*, *Campanula glomerata*, *C. rotundifolia*, *Pimpinella saxifraga*, *Achillea millefolium* and *Plantago media*) and four of these show a significant decrease in the presence of *Leontodon*. *Campanula rotundifolia*, which showed significant effects of interference from *Leontodon* after 18 weeks, now shows virtually no difference in shoot dry weight in the presence of *Leontodon* when compared with its monoculture. There is a similar, though less dramatic, result for *Achillea millefolium*. These two species have, to a certain extent, overcome the early negative effects of interference from *Leontodon*. In the presence of both *Bromus* and *Leontodon*, all but one (*Centaurea nigra*) of the eight 'sparse' species show a significant decrease in shoot dry weight when compared with their monocultures. For equivalent treatments, only one of the 'relatively abundant' species (*Leontodon*) shows significant negative effects of interference.

Interference ability and relative abundance

Table 6 shows the hierarchies of interference ability and monoculture performance, and Table 7 gives the values of Kendall's *tau* from rank correlation tests. There is no significant correlation between monoculture performance and relative abundance for both seasons

TABLE 6. Hierarchies of performance in a monoculture and interference ability (percentage difference values, see Table 4) of fifteen chalk grassland dicotyledons in a pot experiment in 1980 and 1981. Results are derived from Tables 4 and 5. Species are ordered by mean rank in the field (Table 3). Bold type indicates that a rank differs by more than four places from the field rank, and asterisks that a rank in 1980 differs by more than four places from the equivalent rank in 1981.

	Monoculture			+*Bromus*			+*Leontodon*			+*Bromus* and *Leontodon*		
	1980		1981	1980		1981	1980		1981	1980		1981
Sanguisorba minor	5		3	**10**		**9**	**10**		6	**9=**		**7**
Leontodon hispidus	4		**7**	1	*	**7**	4		7	7		**10**
Lotus corniculatus	3	*	**10**	**12**		**11**	6=	*	1	**9=**		**9**
Cirsium acaule	**14**		**9**	2=		2	1		4	1		1
Plantago lanceolata	2		2	2=		3	6=		3	2		3
Hippocrepis comosa	6	*	**12**	5		5=	8		8=	5		6
Scabiosa columbaria	8		8	6		5=	9		8=	6		5
Plantago media	**13**	*	6	9		8	**3**	*	11	3	*	8
Centaurea nigra	7		5	**4**		**1**	**5**		2	4		2
Campanula rotundifolia	10	*	14	**15**		13	13		10	13		12
Pimpinella saxifraga	12		13	8		12	12		12	12		13
Prunella vulgaris	**1**		**1**	**7**		**4**	**2**		**5**	**8**		**4**
Campanula glomerata	15		15	13		14	14		14	14		14
Achillea millefolium	**9**	*	**4**	11		10	11		13	11		11
Astragalus danicus	11		11	14		15	15		15	15		15

TABLE 7. Values of Kendall's *tau* for comparisons between the relative abundance ranking of chalk grassland species (Table 3) and hierarchies of performance in a monoculture and interference ability in a pot experiment, 1980 and 1981 (Table 6). Symbols: **, $P < 0{\cdot}01$; *, $P < 0{\cdot}05$; N.S., not significant. Superscripts: [a], all species, $n = 15$; [b], excluding *Lotus corniculatus*, $n = 14$.

	Monoculture	+*Bromus*	+*Leontodon*	+*Bromus* and *Leontodon*
[a]1980	0·293 (N.S.)	0·396 (*)	0·363 (N.S.)	0·402 (*)
[a]1981	0·154 (N.S.)	0·339 (N.S.)	0·567 (**)	0·344 (N.S.)
[b]1981	0·165 (N.S.)	0·416 (*)	0·544 (**)	0·453 (*)

($P = 0{\cdot}1$ and 0·4); we cannot predict relative abundance from performance in the monoculture. However, for the results after one season, there are significant positive correlations between relative abundance and interference ability in both the two-species mixtures with *Bromus* and in the three-species mixtures ($P = 0{\cdot}04$). The 'relatively abundant' species have the greater, and the 'sparse' species the lesser interference ability. Interference ability in the two-species mixtures with *Leontodon* was not correlated with relative abundance ($P = 0{\cdot}06$).

For the results after two seasons, there is a significant positive correlation between interference ability in the two-species mixtures with *Leontodon* and relative abundance ($P = 0{\cdot}003$). The other two correlations do not reach significance ($P = 0{\cdot}08$ and 0·07). However, *Lotus corniculatus* was attacked by an unknown predator in both seasons, and was particularly affected in the mixtures with *Bromus* (Tables 4 and 5). If *Lotus corniculatus* is removed from the analyses, there are significant positive correlations between interference ability and relative abundance for all three mixture treatments ($P < 0{\cdot}05$). There is a clear distinction in timing between the 'abundant' and 'sparse' species in the experiment. The 'sparse' species not only suffer greater interference from the standard species, but they also experience these effects much earlier (Tables 4 and 5). A notable exception is *Centaurea nigra*, a 'sparse' species of high interference ability. This combination of characters, shared to a lesser extent by *Prunella vulgaris*, is considered further below.

THE FIELD EXPERIMENT

Materials and methods

Field site

The site chosen was Bald Hill on the Aston Rowant National Nature Reserve in Oxfordshire (National Grid reference SU 723959, 51°39′N, 0°57′W), from which the soil was taken for the pot experiment. The slope of Bald Hill faces south-west with a gradient of 5–25° and an altitude of *c.* 240 m. The vegetation is a chalk grassland of rather low species-richness with abundant *Carex flacca* and *Festuca ovina* as well as *Asperula cynanchica*, *Cirsium acaule*, *Leontodon hispidus* and *Thymus praecox*. A plot measuring 14 m × 8 m at the top of the slope (gradient 5°) was marked out and cleared of turf by shallow rotavation (5–15 cm deep) on 13 April 1980. The loose turf was sieved and the soil taken to the Botanic Gardens in Cambridge to grow the experimental plants. A rabbit-proof fence was erected around the plot, with a 1-m corridor all round (Fig. 2).

Species, seed collection and seedling preparation

The six species are marked with carets in Table 3, and their average relative abundance in chalk grassland in England is indicated. These species will be referred to by their generic names alone for the remainder of this section.

Most of the seed was collected in 1979 from the Devil's Ditch in Cambridgeshire but some of the *Cirsium* achenes were collected from Castle Hill National Nature Reserve (see above). All *Sanguisorba* fruits were provided by T. C. E. Wells from plants growing on calcareous clay at Monks Wood Experimental Station in Huntingdonshire (National Grid reference TL 201798) in 1979.

Between 21–31 April 1980, freshly germinated seeds were transplanted into trays measuring 85 cm × 25 cm × 7 cm, which had been previously filled to within 1 cm of the rim with chalk topsoil from the experimental area at the field site. The seedlings (100 per tray) were spaced 4 cm apart and kept in a glasshouse for one month to establish. In June 1980, the trays were transferred outside into a south-facing, open frame until required.

Experimental design and planting procedure

The six species were grown in all fifteen two-species mixtures, together with the six monocultures, giving twenty-one treatments. Overall plant density was the same in all treatments and there were equal proportions of the two species in each mixture. The experiment was planted in three randomized blocks each containing the full twenty-one treatment plots (Fig. 2). Each treatment plot measured 70 cm × 70 cm and was planted with thirty individuals in a hexagonal design with a spacing of 12 cm between plants (Fig. 3). When two months old and 1–5 cm in diameter, the experimental plants were transplanted into the treatment plots within a 48-h period on 9–11 July 1980. The plots were weeded prior to planting, and again on 21 August and 16 October 1980 when dead individuals of the experimental species were replaced, as far as possible, from stocks kept on site.

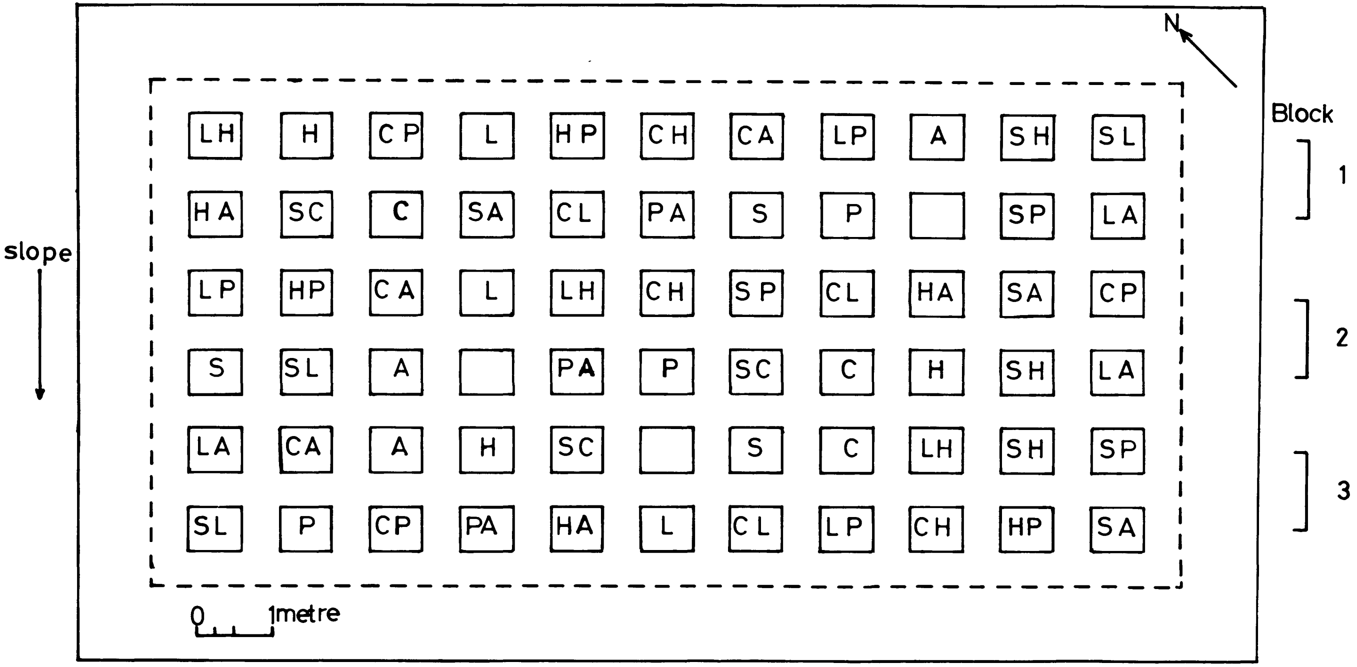

FIG. 2. Plan of a field experiment conducted in chalk grassland. The treatment plots are arranged down the slope in three randomized blocks, each containing the full six monocultures and the fifteen possible mixtures of two species. The unbroken line represents the rabbit-proof fence and the broken line the boundary of turf clearance. Species: A, *Achillea millefolium*; C, *Cirsium acaule*; H, *Hippocrepis comosa*; L, *Leontodon hispidus*; P, *Pimpinella saxifraga*; S, *Sanguisorba minor*. Single letters represent the monocultures and pairs of letters the mixtures. The three plots shown empty were planted with all six species, but the results are not discussed in this paper.

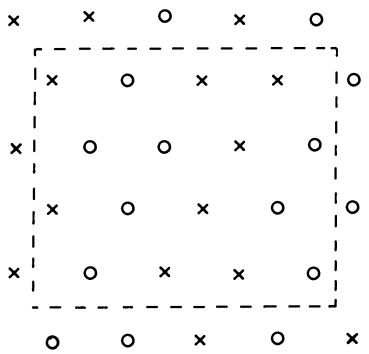

FIG. 3. The planting pattern in a field experiment conducted in chalk grassland. Plot size is 70 cm × 70 cm and the spacing between plants is 12 cm. The circles and crosses represent the positions of two components in mixtures. Recording was restricted to the area within the dotted line, including sixteen individual plants at the beginning of the experiment.

Observations and measurements, 1980–85

On 17–18 October 1980 (14 weeks after planting), the number of leaves per plant and the radius of the rosette was recorded for the sixteen central plants in each treatment plot (those within the broken line in Fig. 3). On 23–29 September 1981 (62 weeks after planting), cover-repetition (parts of the same or another species overlying the same point) of the experimental species was estimated from 160 random point quadrats using a fine sewing needle mounted on a pin of 0·5 cm diameter. This was lowered vertically through the vegetation sampled from within a central square of 40 cm × 40 cm in each treatment plot. Mitchley (1983) provides further details. Repeat contacts were recorded and cover-repetition estimates were calculated as the percentage of total contacts within a treatment plot. The height of the turf, excluding inflorescences and flower-stem leaves, was measured to ±0·5 cm at sixteen random points in each treatment plot. On 24–30 September 1982 (115 weeks after planting), cover-repetition and turf height were estimated as above.

All six experimental species set viable seed in 1981 (and *Leontodon* in 1980) and seedlings appeared in the plots in spring 1982. Thus, each treatment plot was now occupied not only by the species originally planted but also by one or more invading species. On 26–28 April 1982, the density of seedlings in the monoculture plots was estimated in one hundred 2 cm × 2 cm squares selected at random from within a 50 cm × 50 cm quadrat placed in the centre of the plot. The lower limit of density recorded by this method is 25 seedlings m^{-2}.

The onward growth of established individuals was determined in the monocultures from the cover estimates made in September 1982. Because the cover of all the experimental species present within a plot was recorded in 1982, the cover of each invading species in any monoculture plot could be readily assessed. In September or October in 1983–85, the frequency of each experimental species in the monocultures was determined by its presence within the twenty-five 10 cm × 10 cm squares of a 50 cm × 50 cm quadrat placed over the centre of the plot.

Analysis of productivity and aggressiveness

For mixtures of two species, we may define the following variables: y_{ij}, unit performance of species i in the mixture with species j (mean of three replicates); and y_{ii}, unit performance of species i in the monoculture.

The matrix **Y** of yield values, with six rows and six columns for combinations of six species, has elements y_{ij}. The row mean $(y_{i.})$ gives the mean performance of species i in all mixtures and the column mean $(y_{.i})$ gives the mean performance of i species in the presence of j. Yield values can be transformed to the dimensionless relative yield by dividing yield in the mixture by yield in the monoculture. Thus, the matrix **X** of relative yield values has elements:

$$x_{ij} = (y_{ij}/y_{ii})$$

As a measure of apparent mutual stimulation or inhibition, we use the relative yield-total (de Wit & van den Bergh 1965), redefined on a per-plant basis by McGilchrist & Trenbath (1971) as half the sum of the component relative yields:

$$r_{ij} = 0{\cdot}5[(y_{ij}/y_{ii}) + (y_{ji}/y_{jj})]$$

The value of r_{ij} for any pair of species is expected to be ≈ 1 because proportional yield changes in mixtures are usually compensatory (Trenbath 1978).

As a measure of interference we use aggressiveness, defined as half the difference between the component relative yields (McGilchrist & Trenbath 1971):

$$a_{ij} = 0{\cdot}5[(y_{ij}/y_{ii}) + (y_{ji}/y_{jj})]$$

Such measures have been widely adopted by plant ecologists for studying interactions between species. However, this approach has recently been criticized as being of limited value because it does not assess the contribution of between- and within-species interference to the determination of mixture yields (Jolliffe, Minjas & Runeckles 1984). We are unable to use the alternative method that they propose since it relies upon the comparison between monoculture yield and yield projected from the yield:density curve, and no such curves are available from the present experiment.

Results

Mortality of the experimental plants

Table 8 shows the percentage of dead plants observed on 27 March 1981, thirty-seven weeks after planting. These values represent minima for the mortality of plants in the experiment since no replacement of these plants was made. The species most seriously

Table 8. The percentages of dead plants of chalk grassland species (i in mixture with j) in a field experiment on 27 March 1981 (36 weeks after planting). Each value is the mean of three replicate plots and each plot initially contained thirty plants. The diagonal elements (bold type) show the percentage of dead plants in the monocultures and these values are excluded from the mean values. Abbreviations are the initial letters of the species names in the left-hand column.

	Species *j*						
	Am	*Ca*	*Hc*	*Lh*	*Ps*	*Sm*	Mean
Species *i*							
Achillea millefolium	**4**	4	20	13	11	20	13·8
Cirsium acaule	36	**39**	31	40	29	58	38·7
Hippocrepis comosa	4	2	**1**	2	2	4	3·1
Leontodon hispidus	0	2	2	**0**	0	0	0·9
Pimpinella saxifraga	2	4	2	7	**6**	1	3·6
Sanguisorba minor	0	0	4	0	2	**1**	1·3
Mean	8·4	2·4	12·0	12·4	8·9	16·9	

affected was *Cirsium*, due to poor establishment on the bare soil and lack of replacement plants. No correction was made for these missing plants in the results presented below.

Appearance of the plots, 1980–85

Some characteristics of the plants in the monoculture plots are given in Table 9. In October 1980, individual plants were small (<10 cm diameter), there was almost no leaf overlap between neighbours and cover was much less than 50% in most monoculture plots, though *Leontodon* reached 59% and was the only species to flower.

TABLE 9. Some characteristics of the monoculture plots in a field experiment in chalk grassland, 1980–82. Percentage ground cover in 1980 is calculated from the estimates of mean rosette radius (Table 10), and in 1981 and 1982 from the point quadrat data, excluding repeat hits. Turf density is the mean number of leaves contacted by each point quadrat contacting at least one leaf. Mean turf height (excluding flower-stem leaves) is from measurements made at sixteen random points in each plot. The mean number of inflorescences per plant is calculated for all plants in a plot. Symbol: ND, not determined.

	Ground cover (%)			Turf density		Turf height (cm)		Inflorescences per plant		
	1980	1981	1982	1981	1982	1981	1982	1980	1981	1982
Sanguisorba minor	42	98	100	2·8	4·4	10	15	0	ND	37
Leontodon hispidus	59	70	76	2·0	2·6	5	4	1	20	16
Cirsium acaule	17	56	61	1·5	1·6	2	2	0	1	2
Hippocrepis comosa	28	99	100	2·7	2·4	4	5	0	ND	82
Pimpinella saxifraga	18	38	60	1·1	1·3	2	2	0	3	ND
Achillea millefolium	24	30	51	1·0	1·4	2	2	0	3	6

By September 1981, individual plants had grown much larger, neighbouring plants were overlapping above ground and most monoculture plots had >50% ground cover, except for *Achillea* and *Pimpinella* (30 and 38%, respectively). Most individuals of all species flowered. Both *Sanguisorba* and *Hippocrepis* reached 100% ground cover in their monoculture plots.

By September 1982, all species had achieved >50% ground cover in their monoculture plots. The cover of *Pimpinella*, *Achillea* and *Leontodon* increased considerably in many plots through seedling establishment, though some seedlings of all species were observed in most plots.

By September 1983, the individuals originally planted in 1980 no longer dominated in all plots. In *Leontodon*, *Pimpinella* and *Achillea* plots, most of the original individuals had disappeared, and the plots contained seedlings and juvenile individuals (<10 cm diameter) with limited reproductive capacity. In *Sanguisorba*, *Hippocrepis* and *Cirsium* plots, most of the original individuals persisted, the former two showing particularly high ground cover. Recently established juvenile individuals of all six species were present in most plots.

In September 1984 and 1985, the appearance of the plots was similar to that in 1983. Numerous new species, from outside the experiment, had invaded the experimental plots from 1982 onwards. The most invasive of these species (those occurring in twelve or more of the eighteen monoculture plots in September 1985, and occurring in at least one replicate of each of the six experimental species) were the grasses *Dactylis glomerata*, *Brachypodium sylvaticum* and *Briza media*, the perennial dicotyledons *Asperula* *cynanchica*, *Campanula rotundifolia*, *Scabiosa columbaria* and *Plantago lanceolata*, and the short-lived dicotyledons *Linum catharticum* and *Gentianella germanica* (species ordered by decreasing frequency in each group).

Results in 1980

Table 10 shows the matrices of mean leaf number per plant and mean rosette radius in the different treatments, together with the various transformations applied in the analysis. The rank order by row means ($y_{i.}$) for leaf number was: *Leontodon* > *Hippocrepis* > *Sanguisorba* > *Achillea* > *Pimpinella* > *Cirsium*, and for rosette radius was: *Leontodon* > *Sanguisorba* > *Achillea* > *Hippocrepis* > *Pimpinella* > *Cirsium*. These rank orders are virtually the same as those for the monocultures; therefore, performance in the mixture is predictable from that in the monoculture.

The column means ($y_{.i}$) show little variation, suggesting little differential interference between neighbouring plants at this stage. Relative yield and relative yield-total values also indicate little interference, with all values ≈ 1. However, some consistent trends suggest that there is some interference. For example, *Sanguisorba* shows relative yield values of >1 in four out of the five possible cases, and both *Cirsium* and *Hippocrepis* show values of <1 in all five possible cases (Table 10). The aggressiveness values reflect these observations. Any interactions between neighbouring plants would have been below ground at this stage, since most rosettes were much less than 10 cm in diameter and the plants were originally spaced 12 cm apart.

Results in 1981 and 1982: productivity

Tables 11 and 12 show the matrices of cover-repetition per half-plot for the experimental species in the different teatments in both years, together with the three transformations applied in the analysis. In 1981, the rank order by cover in monoculture was: *Sanguisorba* > *Hippocrepis* > *Leontodon* > *Cirsium* > *Pimpinella* > *Achillea*. Predictably, this order is the same as that by row means ($y_{i.}$) and almost the inverse of that by column means ($y_{.i}$): *Cirsium* > *Pimpinella* > *Achillea* > *Hippocrepis* > *Leontodon* > *Sanguisorba*.

Most species perform least well in mixtures with species of higher cover, and best with those of lower cover. The discrepancies between the two orders are caused by species that perform relatively better, or relatively worse, in a mixture compared with a monoculture (i.e. *Cirsium* and *Achillea*, respectively). Performance in a mixture is not wholly predictable from that in a monoculture. The values for relative yield-total are ≥ 1 in most mixtures. The overall mean values are 1·12 in 1981 and 1·22 in 1982, suggesting a limited degree of niche differentiation between species.

In 1982 the rank orders changed markedly, particularly that for relative yield where the order by row means ($y_{i.}$) was: *Hippocrepis* > *Pimpinella* > *Sanguisorba* > *Achillea* > *Leontodon* > *Cirsium*. The differences between the rank orders in 1981 and 1982 suggest that factors other than interference had become important, e.g. differences between species in frequency of seedling establishment, longevity of adult individuals and degree of lateral spread. Individuals of *Leontodon*, *Pimpinella* and *Achillea* appeared relatively short-lived (2–3 years) in the experiment, but all three increased considerably in cover in 1982 through seedling establishment. Conversely, most of the original individuals of *Sanguisorba*, *Hippocrepis* and *Cirsium* were still present in 1985, and individuals of all three species, and especially *Hippocrepis*, increased in 1982 through lateral vegetative spread.

TABLE 10. Results from a field experiment in which six chalk grassland species were grown in all possible pairs, *i* and *j*. (a) Mean leaf number per plant, and (e) mean rosette radius (cm), of species *i* in a mixture with species *j* on 17–18 October 1980 (14 weeks after planting). Each value is the mean of three replicates, each with sixteen plants per plot. Three transformations are applied to the data: (b) and (f) relative yield; (c) and (g) relative yield total; (d) and (h) aggressiveness (see text). The row and column means are calculated, excluding the diagonal elements (bold type). Abbreviations are the initial letters of the species names in the left-hand column.

			Species *j*				Row mean
	Am	*Ca*	*Hc*	*Lh*	*Ps*	*Sm*	$y_{i.}$
Species *i*							
(a) *Achillea millefolium*	**10·1**	11·3	9·6	10·3	13·7	8·3	10·6
Cirsium acaule	6·6	**7·0**	6·9	6·9	6·8	5·3	6·6
Hippocrepis comosa	16·7	19·2	**21·4**	19·4	14·5	17·0	18·0
Leontodon hispidus	35·7	28·8	28·5	**28·3**	25·5	30·6	29·6
Pimpinella saxifraga	7·1	8·7	8·6	7·6	**7·9**	7·8	8·0
Sanguisorba minor	12·4	15·6	19·7	15·2	14·9	**12·9**	15·1
Column mean $y_{.i}$	14·8	15·1	15·8	14·6	13·9	13·7	
(b) *Achillea millefolium*	**1·00**	1·12	0·95	1·02	1·36	0·82	1·05
Cirsium acaule	0·94	**1·00**	0·99	0·99	0·97	0·76	0·94
Hippocrepis comosa	0·78	0·90	**1·00**	0·91	0·68	0·79	0·84
Leontodon hispidus	1·26	1·02	1·01	**1·00**	0·90	1·08	1·05
Pimpinella saxifraga	0·90	1·10	1·09	0·96	**1·00**	0·99	1·01
Sanguisorba minor	0·96	1·21	1·53	1·18	1·16	**1·00**	1·17
Column mean $y_{.i}$	0·97	1·06	1·10	1·01	1·01	0·91	
(c) *Achillea millefolium*	**1·00**	1·03	0·87	1·14	1·13	0·89	1·01
Cirsium acaule	1·03	**1·00**	0·94	1·00	1·04	0·98	1·00
Hippocrepis comosa	0·87	0·94	**1·00**	0·96	0·88	1·16	0·97
Leontodon hispidus	1·14	1·00	0·96	**1·00**	0·93	1·13	1·03
Pimpinella saxifraga	1·13	1·04	0·88	0·93	**1·00**	1·07	1·01
Sanguisorba minor	0·89	0·98	1·16	1·13	1·07	**1·00**	1·04
(d) *Achillea millefolium*	**0·00**	0·09	0·09	–0·12	0·23	–0·07	0·044
Cirsium acaule	–0·09	**0·00**	0·04	–0·02	–0·06	–0·23	–0·072
Hippocrepis comosa	–0·09	–0·04	**0·00**	–0·05	–0·21	–0·37	–0·15
Leontodon hispidus	0·12	0·02	0·05	**0·00**	–0·03	–0·05	0·022
Pimpinella saxifraga	–0·23	0·06	0·21	0·03	**0·00**	–0·08	–0·002
Sanguisorba minor	0·07	0·23	0·37	0·05	0·08	**0·00**	0·16
(e) *Achillea millefolium*	**3·3**	3·5	2·9	3·0	3·5	2·9	3·2
Cirsium acaule	2·2	**2·7**	2·4	2·6	2·3	1·8	2·3
Hippocrepis comosa	3·0	3·0	**3·6**	3·2	2·8	3·0	3·1
Leontodon hispidus	5·6	5·5	4·9	**5·2**	5·2	5·6	5·3
Pimpinella saxifraga	2·9	3·6	2·9	2·7	**2·9**	2·9	3·0
Sanguisorba minor	4·1	4·9	5·3	4·9	5·2	**4·4**	4·8
Column mean $y_{.i}$	3·5	3·9	3·7	3·6	3·7	3·4	
(f) *Achillea millefolium*	**1·00**	1·07	0·90	0·93	1·07	0·89	0·98
Cirsium acaule	0·82	**1·00**	0·87	0·96	0·85	0·66	0·86
Hippocrepis comosa	0·82	0·83	**1·00**	0·88	0·78	0·83	0·86
Leontodon hispidus	1·08	1·06	0·94	**1·00**	1·01	1·09	1·03
Pimpinella saxifraga	0·99	1·23	0·99	0·93	**1·00**	0·98	1·02
Sanguisorba minor	0·92	1·11	1·19	1·10	1·16	**1·00**	1·08
Column mean $y_{.i}$	0·94	1·05	0·98	0·97	0·98	0·90	
(g) *Achillea millefolium*	**1·00**	0·94	0·86	1·01	1·03	0·90	0·96
Cirsium acaule	0·94	**1·00**	0·85	1·01	1·04	0·89	0·96
Hippocrepis comosa	0·86	0·85	**1·00**	0·91	0·89	1·01	0·92
Leontodon hispidus	1·01	1·01	0·91	**1·00**	0·97	1·09	1·00
Pimpinella saxifraga	1·03	1·04	0·89	0·97	**1·00**	1·07	1·00
Sanguisorba minor	0·90	0·89	1·01	1·09	1·07	**1·00**	0·99

Table 10—*continued*

	Species *j*						Row mean
	Am	*Ca*	*Hc*	*Lh*	*Ps*	*Sm*	$y_{i.}$
Species *i*							
(h) *Achillea millefolium*	**0·00**	0·13	0·04	–0·08	0·04	–0·02	0·022
Cirsium acaule	–0·13	**0·00**	0·02	–0·05	–0·19	–0·22	–0·11
Hippocrepis comosa	–0·04	–0·02	**0·00**	–0·03	–0·10	–0·18	–0·068
Leontodon hispidus	0·08	0·05	0·03	**0·00**	0·04	–0·01	0·038
Pimpinella saxifraga	–0·04	0·19	0·10	–0·04	**0·00**	–0·09	0·024
Sanguisorba minor	0·02	0·22	0·18	0·01	0·09	**0·00**	0·10

Table 11. Results from a field experiment in which six chalk grassland species were grown in all possible pairs, *i* and *j*. (a) Cover-repetition per half-plot (mean of three replicates) of species *i* in a mixture with species *j* on 23–29 September 1981 (62 weeks after planting). Three transformations are applied to the data: (b) relative yield; (c) relative yield total; (d) aggressiveness (see text). The row and column means are calculated, excluding the diagonal elements (bold type). Abbreviations are the initial letters of the species names in the left-hand column.

	Species *j*						Row mean
	Am	*Ca*	*Hc*	*Lh*	*Ps*	*Sm*	$y_{i.}$
Species *i*							
(a) *Achillea millefolium*	**14**	32	8	13	18	11	16·0
Cirsium acaule	26	**42**	21	10	30	7	22·7
Hippocrepis comosa	174	184	**131**	117	116	75	132·8
Leontodon hispidus	100	163	92	**72**	122	74	103·8
Pimpinella saxifraga	20	36	18	12	**21**	7	19·0
Sanguisorba minor	222	285	218	153	256	**138**	212·0
Column mean $y_{.i}$	92·7	123·7	81·3	62·8	93·8	52·0	
(b) *Achillea millefolium*	**1·00**	2·29	0·57	0·93	1·29	0·79	1·15
Cirsium acaule	0·62	**1·00**	0·50	0·24	0·71	0·17	0·54
Hippocrepis comosa	1·33	1·40	**1·00**	0·89	0·89	0·57	1·01
Leontodon hispidus	1·39	2·26	1·28	**1·00**	1·69	1·03	1·44
Pimpinella saxifraga	0·95	1·71	0·86	0·57	**1·00**	0·33	0·90
Sanguisorba minor	1·61	2·07	1·58	1·11	1·86	**1·00**	1·54
Column mean $y_{.i}$	1·15	1·79	0·97	0·79	1·24	0·65	
(c) *Achillea millefolium*	**1·00**	1·45	0·95	1·16	1·12	1·20	1·15
Cirsium acaule	1·45	**1·00**	0·95	1·25	1·21	1·12	1·16
Hippocrepis comosa	0·95	0·95	**1·00**	1·09	0·87	1·08	0·99
Leontodon hispidus	1·16	1·25	1·09	**1·00**	1·13	1·07	1·12
Pimpinella saxifraga	1·12	1·21	0·87	1·13	**1·00**	1·09	1·07
Sanguisorba minor	1·20	1·12	1·08	1·07	1·09	**1·00**	1·09
(d) *Achillea millefolium*	**0·00**	0·83	–0·38	–0·23	0·17	–0·41	–0·004
Cirsium acaule	–0·83	**0·00**	–0·45	–1·01	–0·50	–0·95	–0·75
Hippocrepis comosa	0·38	0·45	**0·00**	–0·19	0·01	–0·50	0·030
Leontodon hispidus	0·23	1·01	0·19	**0·00**	0·56	–0·04	0·39
Pimpinella saxifraga	–0·17	0·50	–0·01	–0·56	**0·00**	–0·76	–0·20
Sanguisorba minor	0·41	0·95	0·50	0·04	0·76	**0·00**	0·53

Results in 1981 and 1982: aggressiveness

The values for aggressiveness show a wide range in both years, with maximum values of 1·01 in 1981 and 0·68 in 1982 (Tables 11 and 12). The generally higher values in 1981 indicate greater interference in the primary establishment phase of the experiment. The rank order by aggressiveness in 1981 was: *Sanguisorba* > *Leontodon* > *Hippocrepis* >

TABLE 12. Results from a field experiment in which six chalk grassland species were grown in all possible pairs, i and j. (a) Cover-repetition per half-plot (mean of three replicates) of species i in a mixture with species j on 24–30 September 1982 (115 weeks after planting). Three transformations were applied to the data: (b) relative yield; (c) relative yield total; (d) aggressiveness (see text). The row and column means are calculated excluding the diagonal elements (bold type). Abbreviations are the initial letters of the species names in the left-hand column.

	Species j						Row mean $y_{i.}$
	Am	*Ca*	*Hc*	*Lh*	*Ps*	*Sm*	
Species i							
(a) *Achillea millefolium*	**36**	71	28	46	47	35	43·8
Cirsium acaule	42	**49**	25	25	45	14	33·3
Hippocrepis comosa	198	222	**120**	169	205	115	171·5
Leontodon hispidus	87	185	104	**99**	140	75	115·0
Pimpinella saxifraga	48	75	23	68	**39**	55	51·3
Sanguisorba minor	320	335	262	305	269	**221**	285·3
Column mean $y_{.i}$	121·8	156·2	93·7	118·7	124·2	85·8	
(b) *Achillea millefolium*	**1·00**	1·97	0·78	1·28	1·31	0·97	1·22
Cirsium acaule	0·86	**1·00**	0·51	0·51	0·92	0·29	0·68
Hippocrepis comosa	1·65	1·85	**1·00**	1·41	1·71	0·96	1·43
Leontodon hispidus	0·88	1·87	1·05	**1·00**	1·41	0·76	1·16
Pimpinella saxifraga	1·23	1·92	0·59	1·74	**1·00**	1·41	1·32
Sanguisorba minor	1·45	1·52	1·19	1·38	1·22	**1·00**	1·29
Column mean $y_{.i}$	1·18	1·69	0·85	1·22	1·26	0·90	
(c) *Achillea millefolium*	**1·00**	1·41	1·21	1·08	1·27	1·21	1·20
Cirsium acaule	1·41	**1·00**	1·18	1·19	1·42	0·90	1·18
Hippocrepis comosa	1·21	1·18	**1·00**	1·23	1·15	1·07	1·14
Leontodon hispidus	1·08	1·19	1·23	**1·00**	1·58	1·07	1·19
Pimpinella saxifraga	1·27	1·42	1·15	1·58	**1·00**	1·31	1·29
Sanguisorba minor	1·21	0·90	1·07	1·07	1·31	**1·00**	1·09
(d) *Achillea millefolium*	**0·00**	0·56	−0·44	0·20	0·04	−0·24	0·024
Cirsium acaule	−0·56	**0·00**	−0·67	−0·68	−0·50	−0·62	−0·61
Hippocrepis comosa	0·44	0·67	**0·00**	0·18	0·56	−0·11	0·35
Leontodon hispidus	−0·20	0·68	−0·18	**0·00**	−0·16	−0·31	−0·034
Pimpinella saxifraga	−0·04	0·50	−0·56	0·16	**0·00**	0·10	0·032
Sanguisorba minor	0·24	0·62	0·11	0·31	−0·10	**0·00**	0·24

Achillea > *Pimpinella* > *Cirsium*, and in 1982: *Hippocrepis* > *Sanguisorba* > *Pimpinella* > *Achillea* > *Leontodon* > *Cirsium*. These rank orders are in close agreement with those derived from the productivity measures.

For the 1981 results, there was a significant positive correlation between mean turf height in the monocultures and mean aggressiveness ($P < 0{\cdot}05$, Fig. 4a). This result suggests that the plants with the tallest leaves suppressed others and the leaf height of individuals determines the performance in mixtures. The relationship between canopy structure and relative abundance will be examined in a subsequent paper.

Interference and relative abundance

The hypothesis that interference ability may determine relative abundance in the field is reinforced by the similarity between relative aggressiveness in the experiment and relative abundance of the six species. The rank order by mean aggressiveness in 1981 (Table 11) was: *Sanguisorba* > *Leontodon* > *Hippocrepis* > *Achillea* > *Pimpinella* > *Cirsium*, and by relative abundance (Table 3): *Sanguisorba* > *Leontodon* > *Cirsium* > *Hippocrepis* > *Pimpinella* > *Achillea*. The higher position of *Achillea* for aggressiveness may be due to

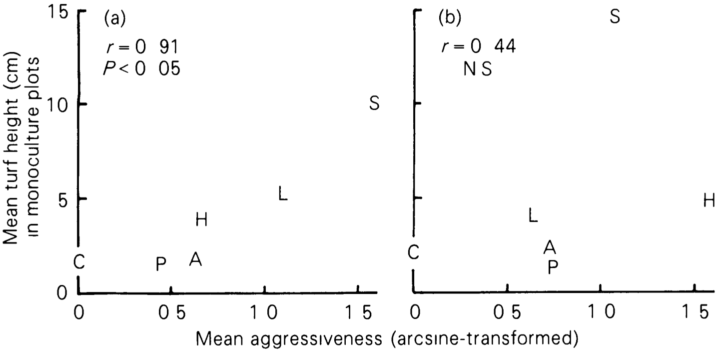

FIG. 4. The relationship between mean turf height (excluding flower-stem leaves) and mean aggressiveness (Tables 11 and 12, values are arcsine-transformed) for the six species in a field experiment conducted in chalk grassland. (a), 23–29 September 1981: (b), 24–30 September 1982. The value of the correlation coefficient *r* is indicated. Symbol: NS, not significant. Species codes as in Fig. 2.

its expansion by stolons in the relatively open ground of the experiment, a situation not usually encountered in chalk grassland turf. *Cirsium* has a low position because many plants died in the experiment (Table 8) and there was no grazing. The spiny leaves of *Cirsium* protect it from severe grazing, which may explain its generally greater abundance in closely-grazed chalk grassland.

For the 1982 results, the correlation between turf height and aggressiveness disappears (Fig. 4b). This suggests that height is less important and other factors more so; some possibilities are discussed below.

Seedling invasion in 1982

Seedling densities in April

Table 13 shows the estimates of seedling densities in the monoculture plots. The row totals indicate the overall invasiveness of each species into alien plots, and the column totals indicate the resistance to invasion shown by the different monocultures.

Another measure of invasiveness is the percentage of the total seedlings of a species that occurs in alien plots; these values are given in Table 13. *Achillea* and *Leontodon* are the most invasive species, with 70–80% of their seedlings occurring in alien plots. *Achillea* has the lightest seeds (0·13 mg, Table 3) and whilst those of *Leontodon* are much heavier (1·1 mg), the achenes have a fixed pappus enhancing dispersal. The apparent invasiveness of *Pimpinella*, which has a large row total in Table 13, reflects the huge number of seedlings that were found. The relative invasiveness of *Pimpinella* is somewhat lower since most seedlings (70%) were in its own monoculture plots. *Hippocrepis* and *Sanguisorba* are the least invasive species, with the heaviest seeds (3·7 and 4·7 mg, respectively), and 97% of their seedlings occur in their monocultures. *Cirsium* has heavy seeds (3·9 mg) but is apparently very invasive (Table 13), being found in all plots except those planted with *Leontodon*. However, the densities of *Cirsium* are much lower than those recorded for the other invasive species. No doubt the pappus plays a role in the dispersal of *Cirsium* achenes, though unlike that of *Leontodon* it is not fixed and sometimes becomes detached from the achene prior to dispersal. Invasiveness appears closely related to apparent dispersibility (Table 13).

TABLE 13. The density of seedlings (m^{-2} on 26–28 April 1982; each value being the mean of three replicate plots) invading the monocultures in a field experiment in chalk grassland. The row and column totals are calculated excluding diagonal elements (bold type). Species are ordered by mean rank in the field (Table 3). Symbols: +, seedlings present in a plot but at a mean density of <8 m^{-2} and not detectable by the sampling method used: ND, not determinable. The final column shows the percentage of the total seedlings of a species, which occur in alien plots. Abbreviations are the initial letters of the species names in the left-hand column.

			Species planted					
	Sm	*Lh*	*Ca*	*Hc*	*Ps*	*Am*	Row total	Proportion in alien plots (%)
Species invading								
Sanguisorba minor	**1050**	+	+	33	+	+	33	3·1
Leontodon hispidus	125	**192**	117	92	83	75	492	72
Cirsium acaule	25	0	**+**	+	17	17	59	ND
Hippocrepis comosa	0	8	0	**292**	0	0	8	2·7
Pimpinella saxifraga	250	325	508	750	**7983**	1517	3350	130
Achillea millefolium	167	950	325	892	658	**725**	2992	80
Column total	567	1283	950	1767	758	1609		

Results for resistance to invasion of monoculture plots are less straightforward (Table 13, column totals). Some of the most resistant plots are those with potentially the harshest microclimate (Table 9)—either a tall, dense vegetation as with *Sanguisorba* (*c.* 15 cm) or a short turf with much bare ground as with *Cirsium* (*c.* 2 cm and 44% bare ground in 1981, when most seed was dispersed). *Achillea* plots are amongst the least resistant, though they also have much bare ground (70% in 1981). However, *Achillea* has tall inflorescences (*c.* 40 cm), which possibly ameliorated the microclimate.

Leontodon plots are amongst the least resistant, though the number of *Pimpinella* seedlings in these plots is quite low. *Pimpinella* plots appear very resistant to invasion but contain many *Pimpinella* seedlings, which are not included in the marginal totals. *Hippocrepis* plots are the least resistant of all, despite a dense cover of vegetation (Table 9). However, the *Hippocrepis* turf is quite short (*c.* 5 cm) and seems to provide the ideal 'seed bed', with many seedlings establishing amongst the pinnate leaves of adult *Hippocrepis* individuals.

Invasiveness and relative abundance

The three most invasive species in Table 13 are *Achillea*, *Leontodon* and *Pimpinella*. Of these, *Leontodon* (one of the 'relatively abundant' species) invades all monoculture plots to a density of *c.* 100 seedlings m^{-2}. In contrast, the two 'sparse' species, *Achillea* and *Pimpinella*, show differential invasiveness, with the least invasion into plots containing the 'relatively abundant' species *Sanguisorba*. The three least invasive species, *Hippocrepis*, *Sanguisorba* and *Cirsium*, are all 'relatively abundant' in chalk grassland and may be analogous to the classic 'climax' species of forest tree with large and poorly dispersed propagules. In general, the occasional occurrence of seedlings of the three least invasive species in alien plots depends upon the close proximity of such plots to a seed source (cf. Table 13 with Fig. 2).

Onward growth of established individuals in 1982

Cover-repetition in September

The cover-repetition estimates in Table 14, excluding diagonal elements, indicate the onward growth of the seedling populations in the monoculture plots. Row means measure

TABLE 14. The onward growth of seedlings invading the monoculture plots in a field experiment in chalk grassland as estimated by cover-repetition per plot (mean of three replicates) of seedling and juvenile individuals on 24–30 September 1982 (20 weeks after estimation of the seedling densities in Table 13). Row and column means are calculated excluding the diagonal elements (bold type) which show the mean cover-repetition of all individuals of a species (including those originally planted in 1980) in its monoculture plots. Species are ordered by mean rank in the field (Table 3). Abbreviations are the initial letters of the species names in the left-hand column.

	Species planted						Row
	Sm	*Lh*	*Ca*	*Hc*	*Ps*	*Am*	mean
Species invading							
Sanguisorba minor	**442**	0	0	1	2	2	1·0
Leontodon hispidus	14	**197**	15	7	36	30	20·4
Cirsium acaule	0	0	**97**	1	0	0	0·4
Hippocrepis comosa	0	0	0	**239**	0	0	0·0
Pimpinella saxifraga	7	8	24	11	**78**	33	16·6
Achillea millefolium	1	11	8	3	25	**73**	9·6
Column mean	4·6	3·8	9·4	4·6	12·6	13·0	

onward growth of seedlings in alien plots, and column means measure the resistance to the growth of seedlings shown by monoculture plots. The three species with the most rapid increases in cover, *Leontodon*, *Pimpinella* and *Achillea*, are those that showed the greatest invasiveness in April (Table 13). However, *Leontodon* now leads in terms of absolute cover, whereas *Achillea* and *Pimpinella* led in terms of seedling densities. This shift probably results from the higher growth rates of *Leontodon* seedlings and the larger size of individuals. The three species increasing in cover most slowly, *Hippocrepis*, *Cirsium* and *Sanguisorba*, are those that showed the least invasiveness in April (Table 13).

Of the three monoculture plots that appear most resistant to seedling growth in Table 14, those of *Sanguisorba* also showed resistance to seedling invasion in April (Table 13). However, *Hippocrepis* plots were amongst the least resistant to invasion in April, and so the slow increase in the cover of seedlings in these plots is surprising. The short, but dense, *Hippocrepis* turf may restrict seedling growth. The slow increase in cover of *Pimpinella* seedlings in *Leontodon* plots follows from the low numbers of seedlings established earlier in the year.

Onward growth of seedlings and relative abundance

The two 'sparse' species, *Achillea* and *Pimpinella*, show the slowest increase in cover in plots containing the 'relatively abundant' species *Sanguisorba* and fairly slow increase in plots of the other three 'relatively abundant' species, *Cirsium*, *Hippocrepis* and *Leontodon*. These two 'sparse' species grow best in each other's plots. The 'relatively abundant' species *Leontodon* increases steadily in all plots, including those with *Sanguisorba*, but most rapidly in plots with the sparse species, *Achillea* or *Pimpinella*. The 'relatively abundant' species, *Cirsium*, *Hippocrepis* and *Sanguisorba*, all show very slow increase in cover in all plots except their respective monocultures, due to the low numbers of their seedlings in April (Table 13).

Longer-term trends, 1983–85

Frequency of the species in the monoculture plots

The results are shown in Table 15 and five points may be noted. First, the three 'relatively abundant' species, *Sanguisorba*, *Hippocrepis* and *Cirsium*, are always most

TABLE 15. Invasion of the monoculture plots in a field experiment in chalk grassland as measured by mean frequency (numbers out of twenty-five 10 cm × 10 cm squares in which present; mean of three replicates) of each of the six species in each of the monocultures. (a) 10–11 October 1983; (b) 12–13 September 1984; (c) 3 October 1985. Row and column means are calculated, excluding the diagonal elements (bold type), which show the mean frequency of a species in its monoculture plots. Abbreviations are the initial letters of the species names in the left-hand column.

		Species planted						Row
		Sm	*Lh*	*Ca*	*Hc*	*Ps*	*Am*	mean
Species invading								
(a)	*Sanguisorba minor*	**25**	3	2	2	1	4	2·4
	Leontodon hispidus	16	**19**	19	20	25	19	19·8
	Cirsium acaule	0	0	**23**	2	1	0	0·6
	Hippocrepis comosa	0	1	1	**25**	3	1	1·2
	Pimpinella saxifraga	14	18	22	16	**25**	24	18·8
	Achillea millefolium	4	14	15	9	24	**17**	13·2
	Column mean	6·8	7·2	11·8	9·8	10·8	9·6	
(b)	*Sanguisorba minor*	**25**	6	4	6	5	6	5·4
	Leontodon hispidus	18	**15**	20	22	25	22	21·4
	Cirsium acaule	1	0	**21**	3	2	0	1·2
	Hippocrepis comosa	0	5	2	**25**	10	10	5·4
	Pimpinella saxifraga	12	20	23	22	**25**	24	20·0
	Achillea millefolium	8	10	14	7	22	**11**	12·2
	Column mean	7·8	8·2	12·6	11·8	12·8	12·4	
(c)	*Sanguisorba minor*	**25**	15	11	10	7	18	12·2
	Leontodon hispidus	23	**19**	23	21	25	24	23·1
	Cirsium acaule	13	1	**21**	5	4	5	5·7
	Hippocrepis comosa	1	8	10	**25**	14	17	10·0
	Pimpinella saxifraga	21	16	22	22	**25**	23	20·7
	Achillea millefolium	10	10	16	11	23	**8**	14·2
	Column mean	13·6	10·2	16·5	13·7	14·8	17·2	

abundant in their original plots. In general, the other species are either equally abundant or more abundant in alien plots. Secondly, species invade at different times. Three rapid invaders, *Leontodon*, *Pimpinella* and *Achillea*, had invaded all other monoculture plots by September 1982, whilst *Sanguisorba* had not invaded *Cirsium* and *Leontodon* plots until 1983; *Cirsium* had not invaded *Leontodon* and *Achillea* plots until 1985 and *Hippocrepis* had not invaded *Sanguisorba* plots until 1985. Thirdly, there is a similar result for resistance to invasion shown by the different monoculture plots. *Hippocrepis* plots had been invaded by all five other species by 1982, whilst *Sanguisorba* plots had not been completely invaded until 1985. Fourthly, the below-average frequency of alien species in *Sanguisorba* and *Leontodon* plots is obvious in all three years. *Sanguisorba* plots were the most resistant to seedling invasion, but *Leontodon* plots were much less resistant (Table 13). Fifthly, most species increased in frequency in alien plots; invasion is continual. However, *Achillea* declines in its monoculture plots and is certainly the least persistent of the three originally most invasive species.

Frequency trends and relative abundance

The two 'sparse' species, *Achillea* and *Pimpinella*, persist through regeneration from seed, though *Pimpinella* is always more abundant than *Achillea*. The 'relatively abundant' species *Leontodon* behaves similarly, though its relative cover is higher than the two 'sparse' species in all plots. The 'relatively abundant' species *Sanguisorba*, *Hippocrepsis* and *Cirsium* continue so through lateral vegetative spread and persistence of long-lived individuals. These three species invade alien plots from seed, but the rate of invasion is relatively low; the order of invasiveness is generally: *Sanguisorba* > *Hippocrepis* > *Cirsium* (Table 15).

DISCUSSION

Criticisms and limitations of the experiments

Interpretation is limited by the artificiality of even-aged, evenly-spaced systems. However, the long duration of the field experiment precludes some of these objections. Analysis of the shoot fraction alone ignores the potential role of roots and rhizomes (cf. Hall 1978).

Specific criticisms of the pot experiment include the differential effects of the limited rooting volume in the shallow pots. The naturally deeper-rooting species, e.g. *Sanguisorba minor* and *Hippocrepis comosa*, may be adversely affected compared with shallower-rooting species, e.g. *Plantago lanceolata*. Nutrients probably limited growth in the experiment, and the dramatic increase of the legume *Lotus corniculatus* with *Leontodon hispidus* in the second season (Table 5) perhaps depended on nitrogen fixation. Specific criticisms of the field experiment include the absence of grazing, which is important in chalk grassland, the wide spacing between plants (12 cm, Fig. 3) and the differential establishment of the experimental plants (Table 8). Again, these objections are reduced by the length of the experiment.

An important effect of the wide spacing of the plants in the field experiment was an increased nutrient supply relative to that available to an individual plant in closed turf. It is also likely that the nutrient supply was increased by decomposition of the roots of the plants removed by rotavation before the experiment. The plants grew vigorously in the first 2 years, and individuals of the same species establishing in later years were always much smaller. The increased nutrient supply and growth rate almost certainly shortened the life-cycle of the inherently shorter-lived perennials. The disappearance of virtually all the original *Pimpinella saxifraga* plants after less than 3 years may be contrasted with what was found by J. B. Dickie and P. J. Grubb (unpublished) for plants in undisturbed tussocky grassland dominated by *Bromus erectus* in Cambridgeshire (TL 582647); of 100 flowering adults mapped in 1974, fifty-one were still present 4 years later. We have evidence of an analagous effect in *Ranunculus bulbosus*. Sarukhán & Harper (1973) found the half-life for established adults in a pasture on relatively fertile soil to be within the range 19–87 weeks; in contrast, at our chalk grassland site in Sussex, of 106 adults mapped in 1983, ninety-five remained after three years (P. J. Grubb, unpublished). The enhanced nutrient supply in our field experiment probably brought out, more quickly than would otherwise have been seen, an inherent difference in longevity between species, but the artificial conditions perhaps exaggerated the difference relative to that found in spontaneous turf.

Interference and relative abundance

The positive correlation found between interference ability and relative abundance is a major finding. The relative abundance of chalk grassland perennials can be explained qualitatively by the interference effects observed in the pot experiment. Five out of the seven 'relatively abundant' dicotyledons are relatively resistant to interference from *Bromus erectus* (Table 5). Conversely, six of the eight 'sparse' dicotyledons are very susceptible to interference. The two remaining 'sparse' species, *Prunella vulgaris* and especially *Centaurea nigra*, are relatively resistant to interference. Interference ability must not be viewed solely as a mechanism leading to high relative abundance, but in some cases as a mechanism that offsets the disadvantage of local small population size (Rabinowitz 1981).

In the field experiment, we suggest that above-ground morphology (expressed crudely through leaf height) is a component of interference ability. This requires further study, for we do not understand exactly how interference occurs. The present experiments, in shallow pots with restricted rooting volume and nutrient limitation, and in field plots with much leaf overlap between neighbouring plants, would suggest a *prima-facie* case for the role of both effects. The high relative yield values for *Hippocrepis comosa* in the field experiment in 1982 (Table 12) may be due to nitrogen fixation. There is a need for more experimental evidence, e.g. new experimental designs (Jolliffe, Minjas & Runeckles 1984), field manipulations (Pigott 1982; Berendse 1983) and long-term experiments (van Andel & Nelissen 1981; Grubb 1982). It would be particularly interesting to study interference between a suite of grasses where the differences in morphology between species are more subtle.

We suggest that interference, both above and below ground, between adults, reinforced by longevity and vegetative spread, determines high relative abundance. Further, we suggest that the sparser species remain sparse through their lower interference potential. A major question for a species-rich turf like chalk grassland is whether the abundance of 'sparse' species is determined only by the effects of the one or two most abundant species, or by their relationship with other sparse species (cf. Grubb 1986). A recent study of limestone grassland (A. Mahdi & R. Law, unpublished) suggests the former.

In general, we expect species with longer-lived taller individuals to be favoured in chalk grassland with periodic grazing (or mowing), and those with longer-lived laterally spreading individuals where grazing is continual. *Leontodon hispidus*, an abundant but relatively short-lived species, at least in the field experiment, is an interesting exception. Persistence of *Leontodon hispidus* at high relative abundance is probably determined by its relatively high short-term interference ability (Table 11) and frequency of seedling establishment (Table 13).

The persistence of sparse species

If abundance is determined largely by interference, expressed in part through height, what prevents the lower-growing sparse species from being excluded? We suggest two possibilities. First, grazing causes more damage to the taller species and gives at least a temporary advantage to the shorter. Secondly, the dicotyledons in chalk grassland differ greatly in longevity, with a continuum from annuals (all hemiparasitic) via biennials and pauciennials to short-lived and then long-lived perennials. The population sizes of annuals and biennials fluctuate greatly from year to year (During *et al.* 1985; Grubb 1986), whilst the population sizes of paucennials (Grubb 1986, Fig. 12.2) and relative vegetative cover of the shorter-lived perennials (e.g. *Pimpinella saxifraga* and *Ranunculus bulbosus*, Table 5), are much less variable. It may be that the shorter-lived perennials become established more frequently from seedlings. Many of the 'sparse' dicotyledons, e.g. *Pimpinella saxifraga* and *Ranunculus bulbosus*, are more common as juveniles in chalk grassland turf than are some of the more abundant species, e.g. *Cirsium acaule*, *Hippocrepis comosa* and *Sanguisorba minor* (A. Martinez-Yrizar, unpublished), though seedlings of most of these species appear more or less equally common in the turf. Whether this phenomenon extends to dispersal is unknown, though the eight 'sparse' species from the pot experiment have lighter propagules than the seven 'relatively abundant' species (mean value 0·83 mg *v.* 2·63 mg, Table 3). Rabinowitz (1978) (see also Rabinowitz & Rapp 1981) also found this result for sparse and abundant prairie grasses.

The relative decline of *Achillea millefolium* in the field experiment (Table 15) is compatible with its greater abundance in other communities, such as roadside verges or meadows. The persistence and relative abundance of *Achillea millefolium* in chalk grassland is probably determined by the degree of seed immigration from outside the chalk grassland community (cf. Warwick & Briggs 1980).

Little is known about the different grass species with respect to longevity and seedling establishment in chalk grassland. Large numbers of both seedlings and juveniles of some species, e.g. *Briza media*, are found in late summer and autumn. Harberd (1961) has shown, in his study of the longevity of *Festuca rubra* clones, that despite practical difficulties, such work can be very fruitful.

Conclusion

Chalk grassland is a community in which the hierarchy of relative abundance is remarkably constant from year to year and from place to place, provided that the soil and grazing régimes are also constant. We suggest that control of the relative abundance of perennials involves a balance between taller and shorter species and between longer- and shorter-lived species. Relative abundance is largely determined by the frequency and timing of grazing and by the frequency of establishment of different species from seed. This work emphasizes the particular importance of: (i) interference between adults, (ii) longevity of adults, and (iii) ability to establish seedlings at a distance from the parent.

In other plant communities, the relative importance of the species characteristics considered here may be quite different, but it must be stressed that for no plant community have we sufficient information on these aspects.

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