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Coexistence and the productivity of white clover-perennial ryegrass mixtures

D. R. Evans, J. Hill, T. A. Williams and I. Rhodes
Institute for Grassland and Animal Production, Welsh Plant Breeding Station, Aberystwyth, Dyfed SY23 3EB, Wales, UK

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Summary. Yield comparisons between five white clover-perennial ryegrass mixtures, whose individual components had previously coexisted, and a corresponding set of ten mixtures based on components that had not coexisted disclosed a yield advantage to the former group of 8.5% over a 4-year period. All five clover populations produced their highest yields when associated with their coexisting grass. The coexisting mixtures also yielded more grass in spring, probably due to the exotic origin of the majority of the companion grasses, reinforced by the nitrogen transfer process between clover and grass. The relative proportions of clover attained by the five populations was apparently unaffected by grass companion. These results are briefly discussed in the context of improving the productivity of white clover-perennial ryegrass mixtures.

Key words: Coexistence – White clover – Perennial ryegrass

Introduction

Natural, temperate grasslands are a source of material for the development of new forage crop varieties. This source could prove especially valuable if the putative varieties are destined for use in mixed pastures, since advantage may then be taken of any benefits conferred upon the individual components by their previous coexistence in the natural pasture. Within such pastures, opportunities for seedling development will be severely restricted. Consequently, the survival and persistency of individuals will depend upon their capacity for vegetative reproduction and spread (Breese and Hayward, 1971). Over a period of time, therefore, coexistence may result in increased vegetative growth of some of the components, which could then be harnessed for agricultural purposes after suitable selection and screening. By the same token, however, the subsequent multiplication of seed of these varieties could prove difficult.

In the context of clover-grass pastures Hill (1977), Breese (1977) and Wilson et al. (1980) have all urged the development of varieties designed specifically for use in mixtures. Moreover, experimental evidence suggests that the productivity of such mixtures may be increased when their individual components have previously coexisted. Thus Turkington and Harper (1979) reported that, when four white clover clones, collected from different areas of the same pasture, were each grown in a series of experimental mixtures with four different grass species, significant increases in clover yield occurred when both the clover clone and grass species had previously coexisted. Likewise Joy and Laitinen (1980) found evidence of a yield advantage for a red clover-timothy mixture based on coexisting components over a comparable mixture composed of bred cultivars. Evans et al. (1985) found that, during a 2-year period, coexistence conferred an average yield advantage of 14% on white clover-perennial ryegrass (*Trifolium repens* – *Lolium perenne*) mixtures compared to their counterparts containing components that had not previously coexisted.

This paper extends the original results presented by Evans et al. (1985) to cover the 4-year duration of the experiment.

Materials and methods

Full experimental details were given by Evans et al. (1985), but briefly the experimental material comprised five different white clover populations, each matched to a perennial ryegrass population collected simultaneously from the same site. Of the five paired populations, four were collected from established natural pastures, with two coming from Switzerland (populations 1 and 3), and one each from Italy and France (populations 2 and 4, respectively). The remaining population (5) was collected in southern England from a sown pasture established 7 years prior to collection. From this latter population the white clover variety Menna was subsequently developed.

Each of these five clover populations was grown with its coexisting grass population and with two other contrasting grass companions, S.23 and Ba 9462, giving 15 clover-ryegrass mixtures in all. The experiment was established in 1980, using a split plot design with four replicates. Main plots were provided by the three grass groups, coexisting, S.23 and Ba 9462, while subplots were supplied by the five clover populations. Each subplot, which measured 3.3 x 1.5 m, was sown with its allotted mixture at a rate equivalent to 3 and 12 kg ha^{-1} of clover and ryegrass, respectively. Annual dressings of potash and phosphate were applied at the rate of 250 kg ha^{-1}, while an initial dressing of 5 t ha^{-1} of ground limestone was applied to the seedbed.

The experiment was topped over at intervals during the establishment year. Each plot was delineated with creosote to prevent ingress of clover stolons from neighbouring plots. Over its 4-year duration the experiment was cut 14 times, using an Allen autoscythe set to a cutting height of 3 cm. Three cuts were taken in the first harvest year (1981), five in the second, four in the third, but only two were possible in 1984 because of a prolonged drought. At each harvest a 0.5 m border was cut from around every subplot and discarded. Each subplot was then cut and the fresh material weighed. A 100 g sample of this material was taken and separated into its clover and grass fractions, which were then dried and weighed. Information was therefore obtained on the clover, grass and combined dry matter yields of the 15 mixtures grown here. In addition, the annual clover dry weight of these mixtures was divided by the corresponding dry weight of the companion grass, to give a relative measure of the amount of clover in each mixture. Values greater than unity indicate that the mixture contains more than 50% clover, and vice versa for values less than unity. This derived character is a modified version of the component yield quotient (CYQ) used by Aarsen and Turkington (1985).

Results

Dry matter production

Annual dry matter yields of the 15 mixtures, partitioned into their clover and ryegrass fractions are presented in Table 1, the CYQ values are given in Table 2 and mean squares from the corresponding analyses of variance in Table 3. Overall, clover yields were significantly higher in the coexisting mixtures. Moreover, within all five populations the average annual yield of clover was highest when they and their coexisting grass were grown together (Table 1). Although this pattern fluctuated between cuts, it was reasonably consistent over years. Particularly noteworthy is the relatively high clover contribution to the

Table 1. Clover (C), Grass (G) and combined (Comb) dry matter yields (kg ha^{-1}) for the 4 harvest years

Clover population	Grass companion	1981			1982			1983			1984			Annual mean		
		C	G	Comb	C	G	Comb	C	G	Comb	C	G	Comb	C	G	Comb
1	Coexisting	410	2,156	2,566	4,639	3,528	8,167	4,495	4,418	8,913	1,176	2,176	3,352	2,680	3,069	5,749
	S.23	80	3,514	3,594	1,208	2,109	3,317	4,311	3,407	7,718	1,093	1,531	2,624	1,673	2,640	4,313
	Ba 9462	214	3,444	3,658	3,439	2,749	6,188	3,185	4,768	7,953	682	1,596	2,278	1,880	3,139	5,019
2	Coexisting	1,402	2,837	4,239	8,401	3,074	11,475	5,828	4,214	10,042	1,616	2,823	4,439	4,312	3,237	7,549
	S.23	361	3,522	3,883	6,360	2,177	8,537	7,091	3,234	10,325	1,600	1,380	2,980	3,853	2,578	6,431
	Ba 9462	732	3,200	3,932	7,926	3,170	11,096	6,236	3,718	9,954	1,171	1,742	2,913	4,016	2,958	6,974
3	Coexisting	635	3,010	3,645	7,493	3,202	10,695	6,508	3,326	9,834	1,803	1,625	3,428	4,110	2,791	6,901
	S.23	282	3,493	3,775	5,959	2,471	8,430	7,363	2,840	10,203	1,674	1,618	3,292	3,820	2,605	6,425
	Ba 9462	470	3,466	3,936	6,746	2,659	9,405	6,179	4,071	10,250	1,110	1,956	3,066	3,626	3,038	6,664
4	Coexisting	784	2,372	3,156	7,042	3,445	10,487	5,224	4,597	9,821	1,409	2,698	4,107	3,615	3,278	6,893
	S.23	335	3,561	3,896	5,502	2,679	8,181	5,414	4,850	10,264	1,371	2,245	3,616	3,156	3,334	6,490
	Ba 9462	704	3,447	4,151	6,438	3,390	9,828	4,566	5,628	10,189	1,392	2,384	3,776	3,275	3,711	6,986
5	Coexisting	924	3,792	4,716	7,870	2,769	10,639	7,029	3,079	10,108	1,648	1,405	3,053	4,368	2,761	7,129
	S.23	331	3,413	3,744	6,451	2,268	8,719	6,684	3,591	10,275	1,835	1,564	3,399	3,825	2,709	6,534
	Ba 9462	782	3,362	4,144	7,554	2,851	10,405	7,132	2,859	9,991	1,796	2,257	4,053	4,316	2,832	7,148
Mean	Coexisting	831	2,834	3,665	7,089	3,204	10,293	5,817	3,926	9,743	1,531	2,145	3,676	3,817	3,027	6,844
	S.23	278	3,501	3,779	5,096	2,341	7,437	6,173	3,584	9,757	1,515	1,668	3,183	3,265	2,773	6,038
	Ba 9462	580	3,384	3,964	6,421	2,964	9,385	5,459	4,208	9,667	1,230	1,987	3,217	3,423	3,136	6,559

Table 2. Component yield quotients (CYQ) for the 4 harvest years

Clover population	Grass companion	1981	1982	1983	1984	Mean	% clover	(Overall %)
1	Coexisting	0.19	1.36	1.10	0.56	0.80	47	
	S.23	0.02	0.57	1.31	0.71	0.65	39	
	Ba 9462	0.06	1.30	0.70	0.43	0.62	37	(41)
2	Coexisting	0.49	2.80	1.39	0.60	1.32	57	
	S.23	0.11	2.98	2.43	1.36	1.72	60	
	Ba 9462	0.23	2.50	1.70	0.66	1.28	58	(58)
3	Coexisting	0.22	2.39	2.14	1.17	1.48	59	
	S.23	0.08	2.42	2.26	0.88	1.41	59	
	Ba 9462	0.14	2.64	1.52	0.58	1.22	54	(58)
4	Coexisting	0.36	2.06	1.16	0.53	1.03	52	
	S.23	0.10	2.06	1.12	0.63	0.98	49	
	Ba 9462	0.21	1.92	0.83	0.59	0.89	47	(49)
5	Coexisting	0.24	2.98	2.38	1.17	1.69	61	
	S.23	0.10	2.80	1.88	1.24	1.51	59	
	Ba 9462	0.25	2.82	2.64	0.82	1.63	60	(60)
Mean	Coexisting	0.30	2.32	1.63	0.81	1.26	56	
	S.23	0.08	2.17	1.80	0.96	1.25	54	
	Ba 9462	0.18	2.24	1.48	0.62	1.13	52	(54)

Table 3. Mean squares from the analysis of clover (C), grass (G) and combined (Comb) dry matter yields ($\times 10^{-3}$), and CYQ over years

Item	d.f.	C M.S.	G M.S.	Comb M.S.	CYQ M.S.
Replicates (R)	3	181.460	408.911	182.197	0.737
Grass groups (G)	2	1,845.239***	790.099	3,812.038***	0.463
Coexist *v* Non coexist	1	3,407.582***	80.805	4,538.602***	0.296
S.23 *v* Ba 9462	1	282.897	1,499.394*	3,085.473**	0.629
R × G	6	308.635	167.756***	227.852	0.469
Clover populations (C)	4	10,052.983***	994.522	9,268.264***	6.786***
C × G	8	158.863	132.414	276.863	0.286
C × R	12	194.860	63.743	88.798	0.324
C × G × R	24	148.230**	77.002	173.995**	0.181
Years (Y)	3	65,172.464	12,989.673	48,683.230	49.254***
Y × R	9	238.711	132.784	474.017	0.141
Y × G	6	1,234.269**	642.993	1,876.187***	0.335
Y × Coexist *v* Non coexist	3	733.339	1,018.239	2,205.735***	0.090
Y × S.23 *v* Ba 9462	3	1,735.199**	267.747	1,546.639**	0.580
Y × R × G	18	120.857**	85.250*	204.473***	0.121
Y × C	12	1,031.439**	467.015**	698.198***	1.391***
Y × C × G	24	109.123*	245.185*	326.032***	0.252**
Cuts within years (CwY)	10	20,408.393***	11,251.208***	26,255.030***	
CwY × R	30	86.724	99.824**	71.943	
CwY × G	20	260.086***	597.721***	809.236***	
CwY × Coexist *v* Non coexist	10	298.390***	1,050.240***	1,329.678***	
CwY × S.23 *v* Ba 9462	10	221.782***	145.201***	288.794***	
CwY × C	40	365.079***	155.644***	595.749***	
CwY × C × G	80	45.992	122.546***	131.866**	
Pooled error (CYQ)	528	58.312	40.419	66.943	(106) 0.110

Throughout $*P=0.05–0.01$, $**P=0.01–0.001$, $***P<0.001$

annual productivity of the coexisting mixtures in the first harvest year. Of these five clover populations, the Swiss Alpine collection (1) was relatively low-yielding, whereas the Italian and indigenous material (2 and 5, respectively) were comparatively high-yielding, though this pattern was not wholly consistent either between cuts or years. There was a decline over the last 2 years in the average clover yields of those mixtures having Ba 9462 as grass companion. This was unexpected because Ba 9462 had been selected for long, rigid leaves and erect tillers, features that should improve its spatial compatibility with white clover (Rhodes and Ngah 1983; Evans et al. 1985). Overall, however, clover yields in mixtures with Ba 9462 were intermediate between S.23 and coexisting mixtures.

Turning to the ryegrass yields, no significant differences exist between the three grass groups, which is surprising since S.23 and Ba 9462 have been consciously selected for increased monoculture yield, whereas the majority of the coexisting populations probably have not. As we shall see later though, a more volatile picture emerges when the seasonal distribution of these yields is considered.

On average the coexisting mixtures significantly outyielded the remaining mixtures. Again, however, significant interactions existed with years and cuts. Thus, a yield advantage for the coexisting mixtures occurred only in the 2nd and 4th harvest years. Within all five clover populations, the mixture with S.23 invariably had the lowest overall yield, though this picture also varied between years and cuts (Table 1).

From the analysis of CYQ values, it is evident that the relative proportion of clover in the mixture depended mainly on the clover population, with population 1 having the lowest (41%) and 5 the highest overall proportion (60%). Grass companion apparently had no significant effect; it merely modified the relative proportion of clover in these mixtures from year to year. Of itself, therefore, coexistence does not affect the relative proportion of clover attained by the five clover populations in mixtures with these perennial ryegrasses.

Seasonal distribution of dry matter

The analyses presented in Table 3 indicate that the productivity of these mixtures and their individual components lacked consistency both within and between seasons. Histograms depicting the seasonal distribution of yields over the 4 harvest years are presented in Fig. 1. These reveal not only the yield superiority of the coexisting mixtures throughout most of the 2nd harvest year, but also the advantage which they apparently enjoy at the beginning of the 2nd, 3rd and 4th harvest years. Appearances can be deceptive, however,

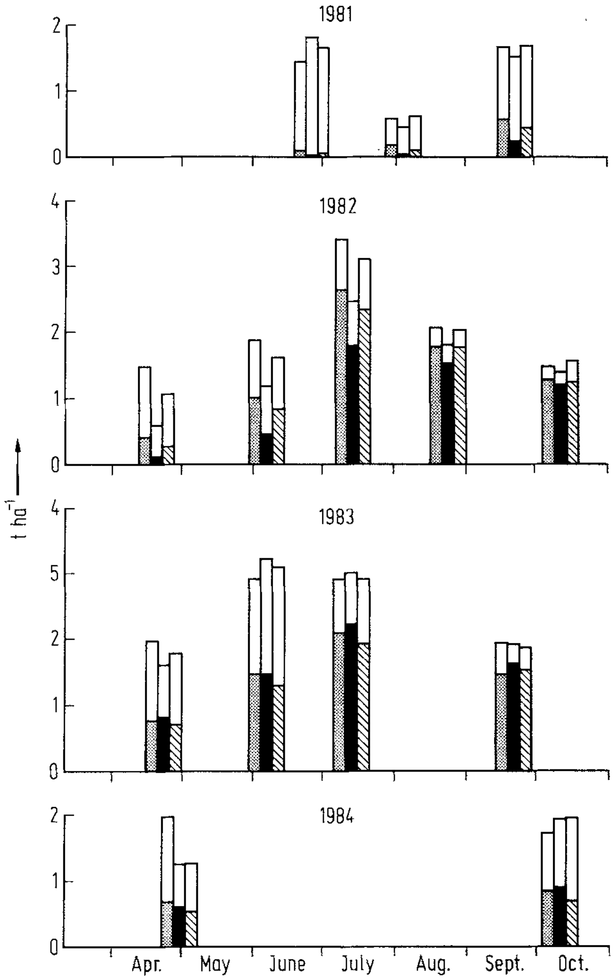

Fig. 1. Seasonal distribution of mixture and component yields (t ha^{-1}) for the duration of the experiment. In each set of three histograms, the left-hand column represents the coexisting mixture, the centre S.23 and the right-hand Ba 9462. Clover yields are represented respectively by the stippled, shaded and cross-hatched portions

as this increased early growth is probably due more to the exotic origin of most of this material rather than coexistence per se, because the only coexisting mixture to be based on indigenous material – (5) – failed to show this early superiority. Since much of this improved early season growth was the result of increased grass productivity, it may be concluded that the coexisting grasses associated with populations 1–4 have an early growth habit.

Discussion

These results suggest that what Harper (1967) calls "ecological combining ability" has increased the overall productivity of those clover-ryegrass mixtures based on components that have previously coexisted by 8.5%, rising to 13% over those mixtures based on S.23. It would be unwise to put a cash value on these increases, if only because of the dangers inherent in extrapolating from the cutting regime imposed in this experiment to a continuous grazing management likely to be encountered in farming practice (Evans and Williams 1987). Nevertheless, it is thought that a 1% increase in the productivity of a clover-grass pasture is worth £ 4.5 million annually to UK agriculture (Rhodes and Webb 1987). The adoption of coexisting mixtures would also stimulate clover usage, so leading to other, less tangible but nonetheless important benefits, particularly in sensitive environmental areas. Thus, a greater reliance upon the nitrogen fixed by clover could reduce the levels of nitrogenous fertilizer applied by farmers to their pastures, thereby lowering nitrate levels in rivers and water courses.

An interesting feature of these results is the finding that grass companion apparently has no overall effect on the relative proportion of clover in the mixture, as measured here by the CYQ values. A similar result was obtained by Hill and Michaelson-Yeates (1987c) with a completely different set of clover-ryegrass mixtures. Thus, where the supply of nitrogen to the pasture is provided mainly by biological fixation, it may be that this proportion is largely determined by the clover variety. However, before any conclusions can be drawn, a more detailed study of this aspect of the results is required.

Coincidentally, the coexisting mixtures have improved early season growth, due primarily to increased grass production. Although the exotic origin of the majority of the coexisting grasses offers a partial explanation for this effect, nitrogen transfer from clover to grass also has to be considered, particularly since recent work indicates that this indirect contribution by the clover to increased grass productivity also reaches its peak in spring (Evans et al. 1988). As a corollary to this, such grasses may afford greater winter protection to the stolon network, so increasing the spring yield of white clover. Indeed this may have happened during the 2nd harvest year of the present experiment, when nearly 60% of the clover produced by the coexisting mixtures had been harvested by the third cut in mid-July (Fig. 1). This is higher both in absolute and percentage terms than the clover yielded by the remaining mixtures over the same period.

If the "ecological combining ability" of mixture components is to be improved, then a different breeding strategy is required from those used in conventional varietal improvement. Ideally these latter techniques should be reserved for those crops that are grown in monocultures, where individuals are exposed only to the effects of intra-genotypic (specific) competition. In mixtures, the additional, though usually lesser pressures exerted by inter-genotypic (specific) competition must also be considered (Hill et al. 1987). Consequently, the development of varieties for use in mixtures requires that the participating components coexist during their evaluation (Evans et al. 1985; Hill and Michaelson-Yeates 1987a, b). This approach could be used to improve not only the clover-ryegrass pastures of temperate grasslands (Evans et al. 1985), but also the intercropping systems of agriculture practised in many developing countries (Chirwa 1985). Here, too, emphasis has generally been placed upon varietal improvement per se without due regard to the agricultural environment in which the material will subsequently be grown. Other areas, such as the improvement of agro-forestry systems of farming, may also benefit from the use of components that have previously coexisted. It may also be possible to improve compatibility in one of the putative components by breeding for specific characters, as happened here with Ba 9462. The increased yields obtained when Ba 9462 replaced S.23 as the companion grass attest to the success of this approach. However, clover yields in those mixtures with Ba 9462 tailed off during the last two harvest years, possibly because the open growth habit of this companion grass afforded less winter protection to the stolon network.

Although these results suggest that the use of components derived from coexisting populations may be one way of increasing the productivity of clover-grass mixtures, the actual mechanics of improving "ecological combining ability" remains obscure. Obviously it would be an advantage to identify those attributes which promote compatibility between specific components, regardless of whether this compatibility is spatial or temporal (Rhodes 1981). But this will be no easy task, because as this experiment shows, the effects lack consistency over cuts and years, and would almost inevitably differ between cutting and grazing managements. However, from a breeding point of view, a more pragmatic approach may be desirable so that the benefits of improved "ecological combining ability" can be exploited whenever possible.

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