

The measurement and analysis of competitive ability among populations of white clover and perennial ryegrass

J. Hill and T. P. T. Michaelson-Yeates

Welsh Plant Breeding Station, Plas Gogerddan, Aberystwyth, Wales, UK

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Summary. Analysis of the competitive interactions among a set of white clover and perennial ryegrass populations indicated that the intra-specific pressures exerted by the white clover plants upon themselves were significantly greater than the inter-specific pressures they exerted upon the perennial ryegrass. This partitioning of competitive effects could not be carried out on the ryegrass populations, however, because the data required the fitting of separate models to monocultures and duocultures. Although not significant at this stage of the experiment, trends were detected among some of the clover-ryegrass duocultures that could be related to their previous coexistence. The results are briefly discussed in relation to the problems surrounding the measurement of competitive effects among species that ideally require very different managements.

Key words: Inter-specific competition – Intra-specific competition – Co-existence – White clover – Perennial ryegrass

Introduction

Individuals living within a mixed community will be exposed to competition from like and unlike individuals whenever and wherever the demand for an essential resource exceeds its immediate supply. Experimental evidence indicates that the impact of competition between similar individuals is generally the greater (Connell 1983; Hill et al. 1987b), if only because such individuals will make comparable demands upon these resources. Clearly, the development of crop varieties destined for use in mixtures will require alternative

breeding strategies, with the emphasis being placed upon mixture productivity rather than varietal performance per se. Putative mixture components should be brought together at an early stage of the breeding programme so that their “ecological combining ability” may be improved (Harper 1967; Hill and Michaelson-Yeates 1987b). It is in this context that co-adapted components may play a role. Indeed, the use of such components has been advocated as one way of improving the performance of the grass/legume pastures that are a feature of temperate grasslands (Evans et al. 1985), and as a means of increasing the productivity of the inter-cropping systems of agriculture practiced in many developing countries (Chirwa 1985).

The study of competition between two such contrasting competitors as white clover (*Trifolium repens*) and perennial ryegrass (*Lolium perenne*) over a period of time poses certain problems, however, because the former can fix atmospheric nitrogen symbiotically and convert it to plant protein. Moreover, within 2 years of establishment white clover changes from a tap root to a shallow fibrous rooting system (Burdon 1983), and releases the atmospheric nitrogen that it has fixed to the companion grass, following the decay of plant parts (Ball 1977). Ideally, therefore, experiments designed to study competition between white clover and perennial ryegrass should cover these events. The longer such experiments last, however, the greater the management problems are likely to be, particularly in relation to the application of nitrogenous fertilizer. Withholding nitrogenous fertilizer inevitably reduces the long term performance of ryegrass plants in monocultures compared to their performance in duocultures. To apply nitrogen, however, immediately places the clover populations at a competitive disadvantage, because ryegrass utilizes this source of nitrogen more efficiently (Frame and

Newbould 1984; Chestnutt and Lowe 1970), even though white clover will preferentially use mineral nitrogen rather than fix atmospheric nitrogen (Rys and Mytton 1985; Mytton and Rys 1985). Additional problems are created by the defoliation regime, with a cutting-only management expected to favour clover, whereas continuous grazing by sheep drastically reduces the white clover content of a pasture (Evans and Williams 1987). In view of these difficulties, it was decided to adopt a compromise and apply some nitrogenous fertilizer to the ryegrass monocultures, even though this will probably lead to a disparity in ryegrass performance between mono- and duocultures, and hence reduce the amount of information supplied by the experiment.

The present paper analyses the effects of competition upon white clover and perennial ryegrass populations, some of which have previously coexisted.

Materials and methods

Three white clover populations – Menna, Ac 3160 and S.100 – and three perennial ryegrass populations – Ajax, Ba 8625 and S.23 – supplied the experimental material. Of these the Menna/Ajax and Ac 3160/Ba 8625 combinations have a history of coexistence, the latter in Northern Italy, while the former is of indigenous origin. The experiment, which was based on the modified substitution design described by Mather et al. (1982), contained the six populations grown as monocultures and all nine clover-grass duocultures. Its structure is illustrated below with reference to the Menna/Ajax combination, though the same densities and proportions obviously apply to all nine clover-ryegrass combinations.

	Proportion				
Menna	1.00	0.75	0.50	0.25	
Menna/Ajax		0.75:0.25	0.50:0.50	0.25:0.75	
Ajax		0.25	0.50	0.75	1.00

A randomized complete block design with two replicates was used for this experiment, which was sown in May, 1985. In each replicate there were 51 experimental plots, of which 24 (6 × 4) were monocultures and 27 (9 × 3) were duocultures. Each plot measured 1.5 m square. The reference density, N (1.00) was 4.5 kg ha⁻¹ (0.45 g m⁻²) for clover and 15 kg ha⁻¹ (1.5 g m⁻²) for perennial ryegrass, subject to adjustment for germination differences. These seed rates were higher than those commonly used in agricultural practice. Manurial dressings were applied to the seedbed as follows: 5 t ha⁻¹ of ground limestone and 250 kg ha⁻¹ of both muriate of potash (60% K₂O) and superphosphate (21% P₂O₅). The potash and phosphate dressings were repeated annually. In addition, the ryegrass monocultures received 200 kg ha⁻¹ of nitrogen per annum, at which rate the annual yield of the ryegrass monocultures and the clover-ryegrass duocultures were expected to be comparable (Morrison et al. 1985). In this respect, therefore, the ryegrass monoculture plots were treated differently from the remaining experimental plots.

The experiment was established during the summer of 1985, with a clearing cut taken in August. Although some recordings were made during the autumn of 1985, the data presented here relate to 1986, the first full harvest year. During 1986 the experiment was cut five times between May and October, using an Allen autoseythe set to a cutting height of 3 cm. Before each harvest a 0.5 m border was cut from around each plot and discarded. After cutting a 100 g sub-sample of fresh material was collected from each plot and separated into its clover and grass fractions where necessary. These sub-samples were dried and weighed. Other characters were also recorded. Prior to each cut a longitudinal transect was placed down the middle of each plot and the height of the clover and/or grass canopy measured at 60 cm intervals along this transect. After each cut a diagonal transect was placed across all plots containing clover and the number of stolons crossing the transect was recorded. Approximately 10 days after each cut clover leaf number and/or ryegrass tiller number were recorded within four random quadrats per plot. Each quadrat covered 80 cm⁻². Information was therefore obtained on clover dry weight, stolon number, leaf number and canopy height, and on ryegrass dry weight, tiller number and canopy height.

These data were analysed by the techniques devised by Mather and Caligari (1981), with the reference density (N) being 1.00 for this experiment, while x , the proportion of plants in an indicator population omitted from monocultures or substituted by an associate competitor in duocultures, had values of -0.25, -0.50 and -0.75. Full details of the analytical techniques employed here are given by Mather and Caligari (1981) and by Hill et al. (1987a). Briefly, however, regression analysis is used to quantify the relative strengths of intra- and inter-genotypic (specific) competition. If a single indicator genotype or species (A) is grown in a density series of monocultures and the character is defined in such a way that its mean expression shows a linear regression on density, the regression coefficient, b_m , provides a measure of the strength of intra-genotypic (specific) competition. Replacing those individuals omitted from the monocultures of A by the same number of individuals from a second or associate competitor (B) enables a further regression to be calculated, whose slope, b_d , measures the inter-genotypic (specific) competitive effect of B upon A in addition to the intra-genotypic (specific) competitive effect of A upon itself. Subtraction of b_m from b_d will therefore estimate the strength of the inter-genotypic (specific) competitive effect of the associate competitor B upon the indicator population A. The roles of the indicator and associate competitor (A and B) are, of course, reversible.

Analyses and results

Preliminary analyses revealed that, although the clover and grass canopies were taller in duocultures than in monocultures (see also Hill and Michaelson-Yeates 1987a), there were no further differences arising from the omission of plants in monocultures or the substitution by an associate competitor in duocultures. Attention was therefore focussed on the remaining three clover and two ryegrass characters in the ensuing analyses. Prior to these analyses, however, the data were converted to a 'per plant' basis. For this purpose the 25% point ($x = -0.75$) was used as the baseline.

Table 1. Mean dry weight (i), and tiller number (ii) of the three perennial ryegrass populations Ajax, Ba 8625 and S.23 in monocultures and duocultures. The proportion of ryegrass plants omitted in monoculture or substituted by the appropriate white clover associate in duoculture is denoted by x

Associate	x	Indicator					
		Ajax (Aj)		Ba 8625 (Ba)		S.23 (23)	
		(i)	(ii)	(i)	(ii)	(i)	(ii)
Monoculture	0	209.50	31.10	211.15	32.10	231.65	34.15
	-0.25	247.95	42.20	345.30	44.95	257.10	37.55
	-0.50	373.45	66.05	381.45	62.40	408.25	60.35
	-0.75	957.35	124.80	631.75	121.00	898.45	127.50
Menna (Me)	-0.25	71.95	13.70	85.80	12.60	77.65	15.10
	-0.50	103.05	21.25	171.40	22.80	71.25	12.80
	-0.75	163.70	31.30	260.95	29.60	212.10	39.30
AC 3160 (Ac)	-0.25	68.25	12.60	95.30	8.90	100.75	20.60
	-0.50	142.50	20.50	112.25	20.50	85.00	14.95
	-0.75	182.85	25.90	212.90	23.50	198.40	37.00
S.100 (100)	-0.25	87.65	16.90	92.30	17.15	60.40	12.55
	-0.50	87.00	16.30	124.30	14.25	93.40	22.10
	-0.75	272.20	27.40	252.15	30.70	270.35	28.30

Table 2. Mean dry weight (i), leaf number (ii) and stolon number (iii) of the three white clover populations Menna, Ac 3160 and S.100 in monocultures and duocultures. The proportion of clover plants omitted in monoculture or substituted by the appropriate perennial ryegrass associate in duoculture is denoted by x

Associate	x	Indicator								
		Menna (Me)			Ac 3160 (Ac)			S.100 (100)		
		(i)	(ii)	(iii)	(i)	(ii)	(iii)	(i)	(ii)	(iii)
Monoculture	0	161.25	25.10	21.15	184.00	25.00	21.10	208.25	26.35	22.80
	-0.25	242.10	29.40	24.80	269.75	34.35	29.65	274.15	34.85	30.10
	-0.50	401.55	44.65	35.30	414.05	41.65	42.05	371.30	46.10	42.65
	-0.75	879.25	101.90	70.80	769.80	98.00	89.40	821.90	108.60	94.60
Ajax (Aj)	-0.25	257.60	28.80	29.05	243.75	27.85	28.70	275.30	27.20	30.75
	-0.50	325.25	37.90	38.60	382.20	38.90	44.00	399.00	43.95	44.35
	-0.75	756.20	80.40	88.10	767.05	83.30	83.60	722.80	76.10	75.10
Ba 8625 (Ba)	-0.25	256.00	27.00	27.10	255.40	28.65	31.60	267.10	27.30	28.40
	-0.50	347.65	36.60	38.95	379.60	39.55	39.40	396.35	42.55	44.75
	-0.75	733.80	73.80	82.30	696.95	74.40	83.60	550.45	70.30	73.00
S.23 (23)	-0.25	256.75	28.10	28.75	261.85	27.45	27.10	254.45	27.75	27.25
	-0.50	366.30	42.25	44.30	430.25	42.75	47.95	349.60	37.75	44.65
	-0.75	760.05	72.20	65.30	686.80	57.60	75.80	770.95	79.60	90.30

Consequently, the 100% monoculture values ($x = 0$), the 75% mono- and duoculture values ($x = -0.25$) and the 50% mono- and duoculture values ($x = -0.50$) were divided by four, three and two, respectively. The dry weight data were summed over cuts to give an annual figure expressed as g m^{-2} , while the remaining characters were averaged over cuts. These results are presented in Tables 1 and 2. As expected, very little overlap exists between the mono- and duoculture values for either of the ryegrass characters (Table 1).

Thus, the co-linear model originally proposed by Mather and Caligari (1981), which constrains the mono- and duoculture regressions of a given indicator to pass through a common point (e) at the reference density (N), is clearly not appropriate to the ryegrass data. Separate models were therefore fitted to the ryegrass mono- and duoculture data. Two parameters were estimated for the monocultures, namely e_m , the expression of the character at the reference density N , and b_m , which relates the character to change in density

Table 3. The \mathbf{J} and \mathbf{J}^{-1} matrices used to estimate the parameters for the complete clover data (i), the ryegrass monocultures (ii) and the clover and ryegrass duocultures (iii)

	\mathbf{J}					\mathbf{J}^{-1}				
(i)	13.000	-1.500	-1.500	-1.500	-1.500	0.368421	0.631579	0.631579	0.631579	0.631579
	-1.500	0.875	0	0	0	0.631579	2.225564	1.082707	1.082707	1.082707
	-1.500	0	0.875	0	0	0.631579	1.082707	2.225564	1.082707	1.082707
	-1.500	0	0	0.875	0	0.631579	1.082707	1.082707	2.225564	1.082707
	-1.500	0	0	0	0.875	0.631579	1.082707	1.082707	1.082707	2.225564
(ii)				4.000	-1.500	0.699999	1.199999			
				-1.500	0.875	1.199999	3.199999			
(iii)		9.000	-1.500	-1.500	-1.500	0.777778	1.333333	1.333333	1.333333	
		-1.500	0.875	0	0	1.333333	3.428571	2.285714	2.285714	
		-1.500	0	0.875	0	1.333333	2.285714	3.428571	2.285714	
		-1.500	0	0	0.875	1.333333	2.285714	2.285714	3.428571	

Table 4. Estimates of the parameters using \log_{10} transformed data as the dependent variate. Clover (i) includes monocultures whereas clover (ii) relates solely to the duocultures

Character	Dry weight			Tiller no.					
	Aj	Ba	23	Aj	Ba	23			
Ryegrass									
e_m	2.2433	2.3405	2.2900	1.4568	1.4781	1.4591			
e_d	1.6387	1.7219	1.5898	0.9907	0.9203	0.9700			
b_m	-0.8623	-0.5832	-0.7801	-0.8030	-0.7474	-0.7680			
b_{Me}	-0.7267	-0.9187	-0.8577	-0.6533	-0.7479	-0.6678			
b_{Ac}	-0.8783	-0.7760	-0.9155	-0.5634	-0.6053	-0.7249			
b_{100}	-0.9122	-0.8586	-0.9850	-0.5710	-0.7039	-0.6546			
Character	Dry weight			Leaf no.			Stolon no.		
	Me	Ac	100	Me	Ac	100	Me	Ac	100
Clover (i)									
e	2.1555	2.2075	2.2411	1.2704	1.2962	1.2904	1.2413	1.2586	1.2714
b_m	-0.9944	-0.8794	-0.8210	-0.9050	-0.8481	-0.9213	-0.7404	-0.8629	-0.8672
b_{Aj}	-0.8950	-0.8458	-0.7894	-0.7705	-0.7431	-0.7460	-0.8620	-0.8443	-0.7913
b_{Ba}	-0.8988	-0.8138	-0.6822	-0.7242	-0.7099	-0.7106	-0.8297	-0.8296	-0.7728
b_{23}	-0.9267	-0.8366	-0.7725	-0.7574	-0.6290	-0.7307	-0.7791	-0.8232	-0.8487
Clover (ii)									
e_d	2.1409	2.1699	2.2074	1.2047	1.2293	1.2023	1.2094	1.2262	1.2309
b_{Aj}	-0.9200	-0.9104	-0.8461	-0.8831	-0.8578	-0.8969	-0.9168	-0.8998	-0.8609
b_{Ba}	-0.9238	-0.8783	-0.7400	-0.8368	-0.8247	-0.8615	-0.8845	-0.8851	-0.8424
b_{23}	-0.9517	-0.9012	-0.8302	-0.8700	-0.7437	-0.8816	-0.8328	-0.8787	-0.9183

(x), while for duocultures estimates of e_d and b_{di} were obtained within each indicator population. For the clover data the model devised by Mather and Caligari (1981) was fitted initially, though the duoculture data were subsequently analysed separately. Estimates of the various parameters were obtained using the appropriate \mathbf{J} and \mathbf{J}^{-1} matrices presented in Table 3.

For all three ryegrass indicator populations the expression of both characters at the reference density is

significantly higher in monocultures than duocultures, i.e. $e_m > e_d$ (Table 4). Given these different starting points, there are no significant differences thereafter between the mono- and duocultures in the rate at which either character changes with x . Other differences become apparent, however, when the goodness of fit of these models is tested by comparing the mean square deviation (MSD) around the fitted regression lines against the duplicate error variance (MSE). Three

Table 5. Mean square deviations from the regression lines (MSD) and the mean square for duplicate error variance (MSE) for the ryegrass and clover characters (all entries $\times 10^3$). Ryegrass (i) and (ii) refer to mono- and duocultures, respectively. Clover (i) includes both mono- and duocultures whereas (ii) is monocultures only and (iii) is duocultures only. Figures in *parenthesis* indicate the degrees of freedom attached to particular mean squares

Character	Dry weight				Tiller no.			
	Aj	Ba	23	Pooled	Aj	Ba	23	Pooled
Ryegrass (i)								
MSD (2)	14.586*	3.028*	10.665	(6) 9.426***	2.681	3.220	10.375*	5.425**
MSE (3)	0.578	0.154	1.184	(9) 0.639	0.610	0.947	0.857	0.804
Ryegrass (ii)								
MSD (5)	9.748	2.925	22.633*	(15) 11.768	3.521	12.300	23.090**	12.970*
MSE (8)	14.070	6.936	3.965	(24) 8.324	6.999	6.962	3.123	5.694
Character	Dry weight				Stolon no.			
Indicator	Me	Ac	100	Pooled	Me	Ac	100	Pooled
Clover (i)								
MSD (8)	3.818*	1.461	3.860**	(24) 3.046***	4.306*	2.911***	2.954*	3.390***
MSE (12)	1.145	0.587	0.632	(36) 0.788	1.219	0.249	0.873	0.780
Clover (ii)								
MSD (2)	3.345	1.437	7.312*	(6) 4.331***	6.879**	4.831*	6.990	6.233***
MSE (3)	2.091	0.222	0.484	(9) 0.311	0.119	0.217	0.975	0.437
Clover (iii)								
MSD (5)	4.667*	1.070	2.698*	(15) 2.812**	3.639	2.212**	1.126	2.326*
MSE (8)	0.891	0.796	0.718	(24) 0.802	1.749	0.286	0.935	0.990

* $p = 0.05 - 0.01$

** $p = 0.01 - 0.001$

*** $p < 0.001$

Table 6. Bartlett's test for homogeneity of variances within the two ryegrass characters, where the four groups refer to the MSDs and MSEs for mono- and duocultures

Item	Dry weight		Tiller no.
	df	χ^2	χ^2
Between groups	3	15.235**	15.068**
MSE monos v rest	1	14.718***	11.520***
Among remaining groups	2	0.517	3.548
Within groups accumulated over groups	8	9.395	5.240
Total	11	24.630**	20.308*

* $P=0.05-0.01$

** $P=0.01-0.001$

*** $P<0.001$

of the six models do not fit the ryegrass monoculture data, even though the tests are based on only two and three *df*. (Table 5). Pooling these variances over indicator populations confirms that the linear regressions do not provide a satisfactory fit to the monoculture data for either character. Turning to the duocultures, only those models having S.23 as indicator are inadequate, this inadequacy stemming from the aberrant behaviour of the 50:50 duocultures ($x = -0.50$) between S.23 and Menna and S.23 and Ba 8625 (Table 1). Combining these variances over indicator populations indicates that the linear models fit the dry weight data and are of borderline significance for tiller number, even if the S.23 data are retained. A Bartlett's test for homogeneity of variances reveals that the difference in the goodness of fit of these models stems from significantly lower duplicate error variances in the monocultures (Table 6). Although qualitative and quantitative differences apparently exist between these ryegrass populations in the way they react to the competitive pressures exerted upon them in monocultures and duocultures, the different sources of nitrogenous fertilizer available to them must be borne in mind. Because of these disparities it would be unwise to pursue the analysis of the ryegrass data as far as would have otherwise been possible. However, the b_{di} values within Ajax and Ba 8625 can be compared to determine whether any differences in slope arise as a result of previous coexistence. Thus within Ajax b_{Me} may be tested against the mean of b_{Ac} and b_{100} , that is whether $[2b_{Me} - (b_{Ac} + b_{100})] = 0$, and within Ba 8625 whether $[2b_{Ac} - (b_{Me} + b_{100})] = 0$. Following Mather and Caligari (1981), it can be shown that the standard error of this difference equals $\sqrt{6(3.428571 - 2.285714)V}$, where V is the appropriate estimate of error variance. None of these comparisons are formally significant. Nevertheless, it is worth noting that for ryegrass dry weight the b values for the two mixtures that have previously coexisted are lower

than the remaining values within those indicator populations (Table 4).

Turning to the clover data, the model fitted initially encompassed both mono- and duocultures as envisaged by Mather and Caligari (1981). Estimates of e , b_m and b_{di} are presented in Table 4 and the corresponding tests for the goodness of fit of the models are given in Table 5 [clover (i) in both tables]. Generally speaking the models do not fit the data satisfactorily. However, omission of the monocultures reduces the residual deviations around the fitted regression lines and hence improves the goodness of fit for the two vegetative characters, leaf and stolon number [Table 5, clover (iii)]. But, unlike the ryegrass data, the estimates of e_m and e_d within an indicator population are not significantly different from each other for any of the recorded clover characters. Consequently, in this experiment the regressions for mono- and duocultures within a particular indicator population have similar origins. Furthermore, although it is evident from Table 5 [clover (ii)] that the linear models provide an unsatisfactory fit to the monocultures for all three characters, this arises from a combination of increased MSDs and reduced MSEs compared to the corresponding duoculture models. Clearly, differences exist between mono- and duocultures for these clover characters also. Finally, as with Ajax and Ba 8625, so for Menna and Ac 3160 there is no significant effect of coexistence on their performance in duocultures. However, certain patterns can again be detected among the b_{di} values (Table 4). Thus, for the dry weight data those for the coexisting mixtures are the lowest within that indicator population, while for stolon and leaf number the Menna/Ajax combination has the highest slope of the six duocultures having either Menna or Ac 3160 as indicator.

Because of the marked differences in performance of these ryegrass populations between mono- and duocultures, the intra- and inter-specific competition effects (c values) cannot be obtained. They have been calculated for the three clover characters, however, and these values are presented in Table 7 and analysed in Table 8. Caution is required in interpreting these competition effects though, because, as already mentioned, the co-linear models upon which they are based do not always fit the data adequately. Consequently, the error mean squares for these analyses have been calculated in the manner described by Mather et al. (1982) using the pooled MSD for each character, given in Table 5 [clover (i)]. Thus, for clover dry weight the pooled MSD based on 24 *df* is 0.003046. The intra-specific c values ($c_{Me/Me}$, $c_{Ac/Ac}$ and $c_{100/100}$) are calculated directly as $-b_m$, and so are subject to an error variance of $2.225564 V = 0.006779$. The remaining nine c values are all of the form $b_{di} - b_m$ and so have an error variance of $2(2.225564 - 1.082707) V = 2.285714 V$ or

Table 7. Estimates of the intra- and inter-specific competition effects, after \log_{10} transformation, for the three clover characters

Indicator	Dry weight	Leaf no.	Stolon no.
Menna			
$c_{Me/Me}$	0.9944	0.9050	0.7404
$c_{Me/Aj}$	0.0994	0.1345	-0.1217
$c_{Me/Ba}$	0.0956	0.1808	-0.0894
$c_{Me/23}$	0.0676	0.1476	-0.0377
Ac 3160			
$c_{Ac/Ac}$	0.8794	0.8481	0.8629
$c_{Ac/Aj}$	0.0366	0.1050	0.0186
$c_{Ac/Ba}$	0.0656	0.1382	0.0333
$c_{Ac/23}$	0.0427	0.2191	0.0397
S.100			
$c_{100/100}$	0.8210	0.9213	0.8672
$c_{100/Aj}$	0.0327	0.1753	0.0759
$c_{100/Ba}$	0.1388	0.2107	0.0944
$c_{100/23}$	0.0486	0.1906	0.0185

Table 8. Mean squares ($\times 10$) from the analysis of c values given in Table 7

Item		Dry weight	Leaf no.	Stolon no.
Indicators (I)	2	0.043	0.023	0.227
Associates (A)	3	5.167***	3.950***	5.045***
A_1	1	15.458***	11.813***	15.129***
A_2	2	0.021	0.019	0.004
I \times A	6	0.022	0.010	0.010
Error	24	0.069	0.126	0.077

*** $P < 0.001$

0.006962. As these two variance are comparable they have been combined in the proportions $\frac{1}{4}, \frac{3}{4}$ ($=0.006916$) to reflect the proportion of intra- to inter-specific c values within each character. Although highly significant differences exist between associates for all three characters, they invariably arise from the comparison between intra- and inter-specific c values (item A_1 , Table 8). Thus, the behaviour of these clover populations differs markedly between monocultures and duocultures, with the inter-specific pressures they exert upon the ryegrass populations being significantly lower than the intra-specific pressures they exert upon themselves.

Discussion

Although the different nitrogenous fertilizer regimes imposed in this experiment require the fitting of separate models to the ryegrass mono- and duocultures,

this procedure nevertheless enables the differences observed between them to be quantified. Thus, within a particular indicator population the lower performance of the duocultures is due to a significant reduction in both dry weight and tiller number at the reference density, rather than to any differences in the rate at which these characters change with x . Interestingly, the models provide a less satisfactory fit to the monoculture data, due to significantly lower error variances (Table 5). It may well be that in monoculture the ryegrass plants can tap a source of applied nitrogen that is both more plentiful and reliable than the biological source available to their counterparts in duocultures. Although this disadvantage is expected to be short lived, the mean difference between ryegrass mono- and duocultures is nonetheless large. Perhaps more surprising is the effect that applied nitrogen apparently has on stabilizing the performance of these ryegrass populations (Table 6). White clover-perennial ryegrass swards are generally considered to be less productive and reliable than grass swards receiving nitrogen (Morrison et al. 1985). The present results support this view. However, the need to reduce levels of applied nitrogen, particularly in sensitive environmental areas, should encourage the development and use of clover-grass mixtures that take full advantage of clover's ability to fix atmospheric nitrogen.

Although the effects of coexistence are not formally significant, certain trends can be detected. For both clover and ryegrass dry weight those duocultures based upon populations that have previously coexisted (Me/Aj, and Ac 3160/Ba 8625) possess the lowest b_{di} values within that indicator population. This in turn would suggest higher levels of inter-specific competition. By contrast for clover leaf and stolon number the Menna/Ajax combination has the highest b_{di} value of the six duocultures having either Menna or Ac 3160 as indicator, suggesting lower levels of inter-specific competition in this particular combination.

Previous published applications of this model have concentrated on analysing those competitive interactions that occur within a species, such as inbred lines of *Drosophila melanogaster* (Mather and Caligari 1981), genotypes of perennial ryegrass (Mather et al. 1982; Hill et al. 1987a, b), or genotypes of barley (Caligari and Powell 1986). Although there were sound agronomic and environmental reasons for choosing white clover and perennial ryegrass to study the effects of competition between species, it might have been more desirable in the first instance to have used two components that could have been managed alike. This may have avoided the problems encountered here with the analysis of the ryegrass data. Even then difficulties may remain, because the results from the clover data suggest that the combined effects of intra- and inter-

specific competition could create disparities between mono- and duocultures that require different models to be fitted. Thus, a \log_{10} linear model that fitted the clover duoculture data adequately proved unsatisfactory for the corresponding monocultures (Table 5). If the two competing species can be treated alike, the co-linear model originally proposed by Mather and Caligari (1981) may be applied to the data. When, however, such treatment either prejudices the outcome of competition or creates significant disparities between mono- and duocultures, it may prove necessary to fit separate models to the mono- and duoculture data, or otherwise adapt the model.

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