J. agric. Sci., Camb. (1967), 71, 223–231
With 1 text-figure
Printed in Great Britain

Diallel analysis of competition between grass species

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(*Received 20 May 1968*)

SUMMARY

Timothy [S. 50], meadow fescue [S. 53], perennial ryegrass [S. 23], Italian ryegrass [S. 22] and cocksfoot [S. 143] were grown together in all possible pair combinations at two levels of fertility, in a pot experiment. Dry weight of herbage and tiller counts were determined at 136 and 198 days from sowing. The data were analysed for competitive effects by the application of the diallel analysis technique of Durrant (1965). The competitive effects were largely compensatory in type with dominant species such as Italian ryegrass and perennial ryegrass increasing in mixtures, relative to their pure stand values, more than species such as timothy and meadow fescue declined. This resulted in a tendency for the mixture means to exceed their mid-constituent values.

The competitive effects on the reciprocal differences were seen to be predominantly of the alpha type; that is, there was a constant increase or decrease in one or more species when grown with others. The alpha values were found to be correlated with the unmixed species values so that $\bar{b}$, the mean effect, was appropriately calculated from alpha. The over-all value of $\bar{b}$ was $-1{\cdot}216$, which means that for each gram difference in weight between the species when grown by themselves there was 2·452 g increase in difference between the species when grown in mixtures, the larger species increasing and/or the smaller species decreasing. There were significant differences in $\bar{b}$ values between harvests, the $\bar{b}$ competitive effects being approximately twice as large in the more mature plants. Although the alpha competitive effects increased in magnitude with time the species order remained relatively constant, and in terms of competitive ability the species could be placed in the ascending order, meadow fescue, timothy, cocksfoot, perennial ryegrass and Italian ryegrass.

Tiller number showed a similar pattern, but the $\bar{b}$ values were smaller, and not significant. Nevertheless competition had differential effects upon the plant weight/tillering relationship and it is possible that the resultant morphological changes would influence the re-growth quality of the species.

The conclusions derived from the analysis of reciprocal differences in this work is compared with earlier examples.

INTRODUCTION

The grass breeder is in the difficult position of having to select his material from spaced plants knowing that under pure sward conditions not only will differences between varieties be minimized, but also that competitive interactions between varieties and species will occur when they are subsequently grown together in mixtures (Lazenby, 1957). There is some evidence to suggest that the relative performance of varieties when grown in monoculture swards may be predicted from their growth attributes as single-spaced plants, provided that the population density is such that there is a complete ground cover of herbage and that no interactions occur between density and growth rhythm (Lazenby & Rogers, 1964). The relative performance of varieties when grown in mixed swards is less predictable, the growth potential of the sward components being modified under stress of competition. Selection pressures may be such that only a small proportion of the viable seed sown survives the early establishment phase, and furthermore, marked variability in survival is found between varieties of the same species (Charles, 1961). Attempts have been made to select high-yielding genotypes under sward conditions by controlling the level of competition and defoliation in a simulated sward (Cooper, 1960). Further advances by the breeder in the selection of genotypes displaying those characters which determine yield under sward conditions, and the grouping of compatible genotypes, may be achieved by selecting from a simulated sward. A convenient method is to grow the genotypes under consideration, in all possible pair combinations; that is to say, in a diallel arrangement. It is then of interest to compare the mean yields of given genotypes in pure stand to the mean yields of their mixtures. The manner in which they compete can be analysed by methods given by Durrant (1965), which permit comparisons to be made between mixtures and, as well, the mixtures in different environments.

Five well-known varieties, one from each of the five principal British grassland species, were grown in a competition diallel to examine their competitive relationships with regard to yield and tiller number.

MATERIALS AND METHODS

The varieties selected for the study were as follows: *Phleum bertolonii*, S. 50; *Festuca pratensis* Huds, S. 53; *Lolium perenne* L., S. 23; *Lolium multiflorum* Lam., S. 22; *Dactylis glomerata* L., S. 143. Seed of each was sown in earthenware pots of 8-in diameter. Sowing at a uniform spacing was achieved by means of a hardboard template which was so constructed as to give an inner and an outer circle of holes, the radius of the inner circle being 1 in and of the outer circle 3 in. Radii were drawn at 45° angles so that sixteen sites were available. The mixtures had seed of each species alternated within rows and within radii. Two seeds per site were sown on 10 December 1962, and later singled. There were two levels of soil fertility: a standard John Innes potting compost and a field soil of low fertility. The competition 'diallel' was replicated twice to give a total of sixty pots.

The pots were randomized and remained in a heated greenhouse until the first harvest on 24 April 1963, when the inner row was harvested to obtain tiller numbers and dry weight at 136 days. The pots were then removed from the greenhouse and placed outside until the second harvest on 25 June, 198 days from sowing.

As a preliminary to the main analysis, which is concerned with reciprocal differences, a graphical interpretation of the competitive effects was obtained from the covariance analysis of the basic data. This enabled a summary of the situation to be made with regard to both reciprocal differences and means.

Expressed in the simplest terms, the analysis of reciprocal differences to be used permits a separation of competitive effects into three components:

(i) Alpha competition, which is characterized by either a constant increase or decrease in one or more species when grown with others.

(ii) Beta competition, in which the competitive

Table 1. *Mean plant dry weight in grams* (× 100)

Values for first and second replicates given in each cell of the table.

Varieties	Associates: S. 50	S. 53	S. 23	S. 22	S. 143
	First harvest, low fertility				
S. 50	32 33	12 18	17 15	9 10	21 20
S. 53	28 22	25 26	21 18	11 8	45 30
S. 23	53 64	58 47	38 40	17 23	85 39
S. 22	90 107	85 107	84 78	52 67	90 66
S. 143	43 24	47 26	42 25	9 26	28 19
	First harvest, high fertility				
S. 50	62 55	49 43	58 42	15 13	49 41
S. 53	28 33	48 34	25 31	18 8	29 55
S. 23	82 72	58 60	54 72	26 26	75 72
S. 22	135 147	187 208	209 165	112 98	177 182
S. 143	45 66	42 57	41 36	17 15	49 51
	Second harvest, low fertility				
S. 50	137 156	250 201	129 51	46 33	194 157
S. 53	135 113	121 134	87 68	22 19	100 111
S. 23	245 276	323 237	132 127	62 89	276 232
S. 22	359 462	387 364	303 261	186 178	410 396
S. 143	155 213	136 156	86 81	55 56	149 140
	Second harvest, high fertility				
S. 50	454 463	465 499	324 177	64 87	384 336
S. 53	278 248	326 312	130 166	40 42	249 314
S. 23	502 654	634 620	398 367	164 160	612 433
S. 22	1002 921	939 758	1071 955	559 483	690 870
S. 143	437 335	425 439	270 182	76 59	374 400

effect of one species upon another is a function of the difference between the species grown by themselves. Where small species are suppressed by large species we would therefore expect the beta component to be relatively large.

(iii) $\bar{b}$, which gives the average beta value over all species and is a measure of the extent to which large species suppress small species and/or are themselves increased in size when grown with small species. There is some ambiguity here, for alpha effects correlated with the values of the species grown by themselves also contribute to $\bar{b}$.

The meaning and derivation of these terms are given by Durrant (1965) and have been illustrated by Norrington-Davies (1967).

RESULTS

The analysis of dry weight

The data recorded for dry weight are given in Table 1. The W_r/W_s graphs (Fig. 1) for the summed replicates show that all points occur in the area $ZXQT$, where for the most part they are clustered about the line ZQ. From this, one concludes that the competition is largely compensatory where the larger species is increased in size and/or the smaller species is decreased in size in mixtures. In so far as there is a spread at right angles to ZQ parallel with NM and also a negative correlation between the $(W_r + W_s)$ and the species values when grown alone (i.e. the larger species are to the left of ZQ

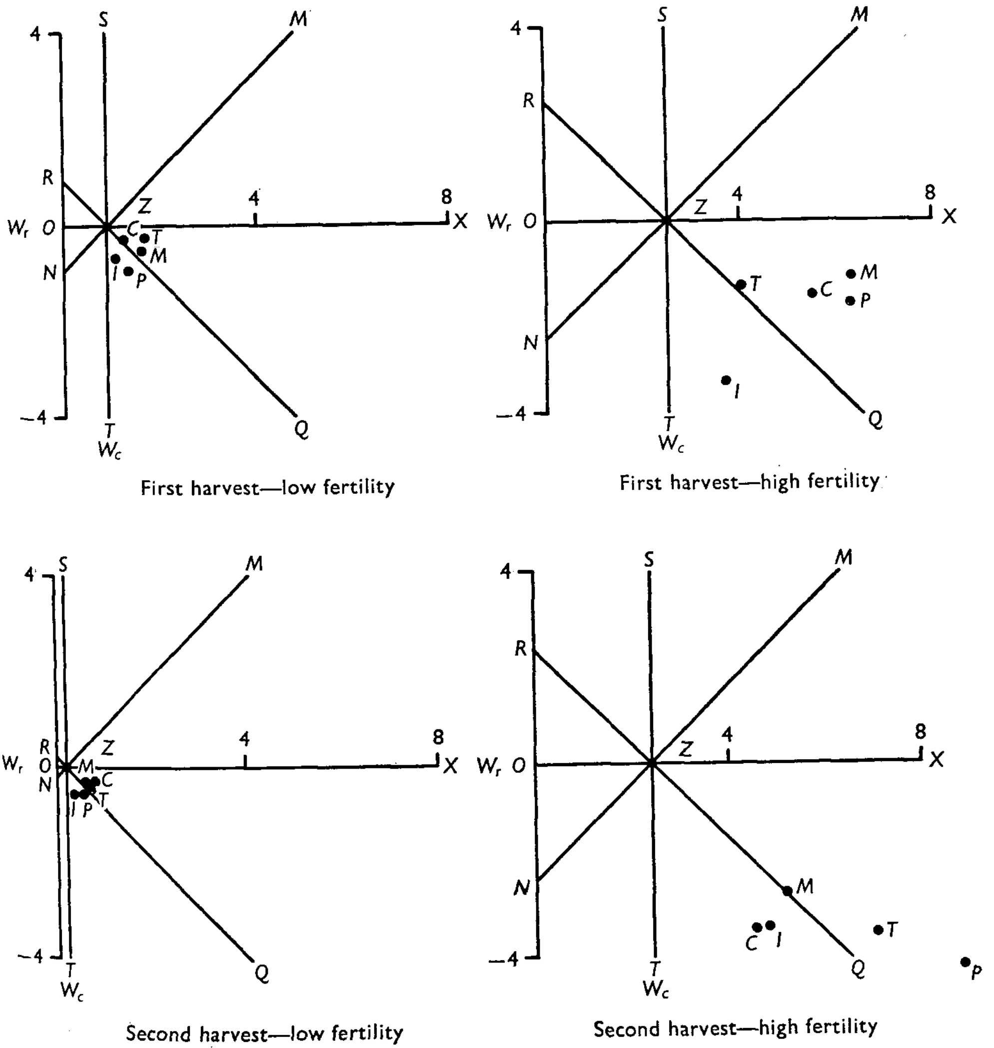

Fig. 1. Array covariances for the summed replicates: first harvest (× 10)

Table 2. *Estimated values for dry weight*

The two entries are for the first and second replicates.

Variety	P'	a	b	Joint a'	Joint b'
		First harvest, low fertility			
S. 50	−3	−28·0	−0·185	−22·69	0·692
	−4	−26·8	−0·846	−21·05	−0·432
S. 53	−10	−9·4	0·862	13·38	0·183
	−11	−13·0	−0·437	4·46	−0·580
S. 23	3	6·8	−2·448	−3·42	−0·946
	3	4·4	−0·577	1·23	−0·049
S. 22	17	43·6	−2·496	6·88	0·302
	30	28·2	−0·908	4·95	0·232
S. 143	−7	−13·0	0·124	5·88	−0·231
	−18	7·2	1·116	10·40	0·829
Total	0	0	−4·143	0·002	0
			−1·652		
$\bar{b}$		−1·130	−0·829	−1·231	
		−0·358	−0·330	−0·503	
		First harvest, high fertility			
S. 50	−3	−20·8	0·213	−17·97	0·629
	−7	−28·8	0·576	−22·11	0·587
S. 53	−17	−30·2	−0·196	−5·21	0·104
	−28	−20·2	0·799	33·59	−0·379
S. 23	−11	−7·4	−0·644	18·19	−0·752
	10	−18·8	−0·926	−33·86	0·036
S. 22	47	79·4	−1·505	2·23	−0·068
	36	92·0	−2·906	29·17	−0·203
S. 143	−16	−21·0	−0·048	2·78	0·088
	−11	−24·2	0·339	−6·79	−0·041
Total	0	0	−2·180	0·02	0·001
			−2·118		
$\bar{b}$		−0·819	−0·436	−0·787	
		−0·885	−0·424	−0·771	
		Second harvest, low fertility			
S. 50	−8	−47·0	−0·023	−8·88	−0·261
	9	−133·4	−4·176	−180·49	−1·181
S. 53	−24	−126·4	−0·096	−38·93	0·860
	−13	−116·4	5·008	−62·16	−0·122
S. 23	−13	73·2	2·304	144·40	−0·973
	−20	94·6	11·070	163·22	0·620
S. 22	41	213·8	−5·506	34·01	0·119
	31	226·2	−12·882	122·02	0·690
S. 143	4	−113·6	−0·351	−130·60	0·255
	−7	−71·0	4·826	−42·60	−0·007
Total	0	0	−3·672	0·01	0
			3·846		
		−2·149	−0·735	−2·252	
		−1·786	0·769	−2·025	

Table 2 (*cont.*)

Variety	p'	a	b	Joint a'	Joint b'
		Second harvest, high fertility			
S. 50	32	−228·4	−0·975	−352·62	−0·419
	58	−269·8	0·495	−438·64	−0·336
S. 53	−97	−256·2	0·095	25·93	0·555
	−93	−216·2	0·216	−29·81	0·571
S. 23	−24	47·4	−1·607	173·51	−1·791
	−38	115·4	1·114	240·68	−0·722
S. 22	137	534·6	−3·391	136·86	0·560
	78	553·2	−5·280	397·06	0·573
S. 143	−48	−97·4	0·927	16·31	1·095
	−5	−182·6	−0·960	−169·29	−0·087
Total	0	0	−4·951	−0·01	−0·001
			−4·415		
$\bar{b}$		−1·470	−0·990	−1·732	
		−1·128	−0·883	−1·288	

and the smaller to the right) this indicates that deviations from a compensatory type of competition give mixture means tending towards the larger of the two species involved in the respective mixtures. The strong displacement of the points from Z along ZQ should give a high negative $\bar{b}$ value and/or a strong positive correlation of the alpha values with the values of their respective species grown alone. Individual species themselves should not differ very much in beta competition, unless beta competition is correlated with the values of the species grown alone, since the scatter of the points from the mean displacement from Z is mainly towards a line of unit slope rather than along ZQ. The graphs give no information on differences between the species in alpha competition. The magnitude of the competitive effect increases with time, and is shown by the increased displacement of the points from Z along ZQ.

Assuming the presence of alpha competition only, the alpha values, estimated from the reciprocal differences, are given in Table 2, and the analysis of variance in Table 3 (a) shows them to be significant. Positive alpha values indicate that species either suppress their associates by a constant amount and/or are themselves enhanced in growth by a constant amount, the converse being true for those varieties with negative alpha values. The correlation coefficients of the alpha values with the unmixed values, $r_{a/P}$, are generally high, ranging from 0·46 to 0·97. This means that the larger species are increased in mixtures more than the smaller, and/or the smaller species are decreased, more than the larger. This may be alternatively interpreted as $2\bar{b}$ with negative sign since it is equivalent to the amount by which large species suppress smaller species and/or are themselves increased when grown with smaller species.

The analysis of beta competition, Tables 2 and 3 (b), shows that this type of competition has lower significance, and in many cases is not significant. Furthermore, the $\bar{b}$ values calculated from beta are of considerably lower magnitude than the $\bar{b}$ values calculated from alpha.

In the joint analyses for alpha and beta where alpha correlated with its unmixed species value is included with $\bar{b}$, it is clear that most of the reciprocal differences are due to alpha and $\bar{b}$ in Table 3 (c). Applying a more critical test; when the alpha sum of squares of the alpha analysis, Table 3 (a), is subtracted from the joint sum of squares (alpha + beta) the remainder in most cases is not significant. When the beta sum of squares taken from the beta analysis, Table 3 (b), is subtracted from the joint sum of squares, a highly significant remainder sum of squares is obtained. Competition therefore is of predominantly the alpha type.

The differences between the alpha values may themselves be tested more critically by using an error mean square, $Ve_M + (n/2)Ve_P$ (McGilchrist, 1965), where Ve_M and Ve_P are the error mean squares of mixed and unmixed species respectively. Keeping the replicates separate, and taking the residual mean squares in Table 3 (a) for both Ve_M and Ve_P, alpha remains highly significant.

The variability of the alpha values for the five species between the two harvest times showed a significant increase ($P < 0·01$); that is, the alpha competitive effects increased in magnitude with time, but the relative order of the species remained

Table 3. *Analysis of variance of estimates for dry weight*

		Low fertility				High fertility			
		Replicate 1		Replicate 2		Replicate 1		Replicate 2	
Component	D.F.	M.S.	V.R.	M.S.	V.R.	M.S.	V.R.	M.S.	V.R.
Total	10								
				First harvest					
(*a*) Alpha competition									
Alpha	4	1868	36**	1095	3	5090	19**	6650	33**
Residual	6	51		276		258		200	
(*b*) Beta competition	5	1410	8*	886	3	4115	15**	5411	36**
Residual	5	166		261		267		149	
(*c*) Alpha and beta competition	7	1118	62**	750	4	3112	71**	3764	23*
a'	3	656	36**	497	3	578	13*	3053	19*
b'	3	155	8	552	3	546	12*	352	2
$\bar{b}$	1	6908	383**	3472	21*	17864	406**	13973	88**
Residual	3	18		159		44		159	
				Second harvest					
(*a*) Alpha competition									
Alpha	4	50254	42**	60313	55***	259585	18**	295140	20**
Residual	6	1195		1087		14701		14410	
(*b*) Beta competition	5	28486	2	46236	14**	165920	3	130556	1
Residual	5	13151		3318		59629		122848	
(*c*) Alpha and beta competition	7	29671	182**	34733	22*	160257	81**	170463	7
a'	3	33883	208**	66486	43**	145097	73**	364614	15*
b'	3	1277	8	1234	—	39129	20*	9186	—
$\bar{b}$	1	127104	780**	68097	44**	962075	485**	324385	13*
Residual	3	163		1545		1982		24594	

Significance levels are indicated as follows: * significant at 5 %, ** at 1 %, *** at 0·1 % levels of probability.

virtually constant, so that, judged from the alpha values, the competitive ability of the five species may be expressed in the ascending rank order, meadow fescue, timothy, cocksfoot, perennial ryegrass, Italian ryegrass.

It may be that characters of growth associated with competitive vigour are more likely to be revealed as beta competition, and although in general there are no highly significant differences between the species in this respect their average beta competition, $\bar{b}$, is worth further study. As stated, this is related to correlated alpha, and since alpha is highly significant and gives much greater uniformity over replicates, $\bar{b}$ values calculated from alpha rather than beta have been used. In a joint regression analysis $\bar{b}$ calculated from the regression of a on P from all eight sets of data is highly significant when tested against the residual variation about the regression lines ($P = 0{\cdot}01$). The $\bar{b}$ values for the eight diallels are analysed in Table 4. The two errors, which are not significantly different, have been combined to give an over-all significant $\bar{b}$ value of $-1{\cdot}216$, which means that larger species increase and/or smaller species decrease to give an over-all increase in difference of 2·432 g for each gram difference in weight between the respective species grown by themselves. There is also a significant difference between harvests. The average values for the first and second harvests are $-0{\cdot}798$ and $-1{\cdot}633$, so that on average the $\bar{b}$ competitive effects are twice as large among the more mature plants as among the younger plants.

Table 4. *Analysis of variance of $\bar{b}$ values calculated from alpha*

	S.S.	D.F.	M.S.	V.R.	P
Total	14·100	8			
$\bar{b}$	11·822	1	11·822	99·34	< 0·001
Plots	0·498	3	—	—	—
Treatments	0·157	1	0·157	1·32	—
Replicates	0·249	1	0·249	2·09	—
Error (*a*)	0·092	1	0·092	—	—
Harvests	1·395	1	1·395	11·72	< 0·05
Error (*b*)	0·385	3	0·128	—	—
Error (*a*)+(*b*)	0·477	4	0·119	—	—

The analysis of tiller number

The analysis of tiller number in Table 5 gave essentially the same result in that alpha was highly significant, but not beta. Consequently no further

Table 5. *Mean number of tillers at harvest* (× 10) *for the two replicates*

Varieties	Associates: S. 50	S. 53	S. 23	S. 22	S. 143
	First harvest, low fertility				
S. 50	118	90	78	60	110
	126	108	73	48	93
S. 53	115	109	105	73	100
	103	116	83	50	123
S. 23	198	215	155	105	205
	218	178	158	120	173
S. 22	150	115	140	106	185
	155	148	120	114	183
S. 143	128	105	68	43	111
	125	103	95	115	96
	First harvest, high fertility				
S. 50	191	188	213	58	173
	182	173	138	63	158
S. 53	125	156	83	68	160
	123	135	123	50	108
S. 23	303	238	236	95	268
	238	228	238	113	228
S. 22	235	283	223	155	188
	268	275	185	171	265
S. 143	105	168	125	55	146
	160	133	100	53	124
	Second harvest, low fertility				
S. 50	154	148	155	50	205
	173	180	105	55	145
S. 53	115	124	115	55	135
	138	151	85	35	130
S. 23	220	250	203	130	250
	273	248	174	133	255
S. 22	143	195	138	110	153
	153	168	110	103	150
S. 143	130	120	100	70	143
	140	150	78	70	143
	Second harvest, high fertility				
S. 50	261	263	215	80	235
	290	220	178	88	280
S. 53	158	173	118	65	170
	145	138	128	60	183
S. 23	388	423	326	120	278
	423	378	283	138	258
S. 22	275	253	188	204	198
	173	385	275	165	258
S. 143	198	168	148	65	166
	145	188	130	53	139

details are given other than the levels of significance in Table 6. It is noteworthy, however, that the difference between alpha and beta is more pronounced than with plant weight, only one of the sixteen beta mean squares being significant. Furthermore, the $\bar{b}$ values are smaller, and none is significant. One might therefore expect that the correlation between tiller number and plant weight is not complete and that, although competition increases the plant weight of the larger species and/or decreases that of the smaller species, tiller weight is not similarly affected. Since tiller number is an important agronomic character its relationship to plant weight in the species grown alone was compared with that in the mixtures by calculating plant weight/tiller number correlation coefficients.

The correlation of tillering and dry weight

Although there was an over-all positive correlation at both levels of fertility for the whole diallel (Table 7) when the pure stand values and mixture values were examined separately, the pure stand values showed a negative correlation at the low level of fertility, and no correlation at the higher level of fertility. The mixture values in contrast showed a highly significant positive correlation throughout. To examine the mixtures correlation in more detail, pure stand values estimated from the mixture values were substituted in the diallel tables by using Yates's (1947) method of estimating parental values in genetic diallels.

The row means of the revised diallels are now the means of each of the five species when grown with all their associates, and the column means are the means of all five associates when grown with each of the species in turn.

If competition has no effect on the plant weight/tiller number relationship then the correlation coefficients given by the row means should either be negligible or negative as in the pure stands and that of the column means should be zero. The actual correlation coefficients for the column means are about 0·95, which means that in competition, on average, over all species, plant yield and tiller number increase or decrease together when grown with each of the other species in turn. The correlation coefficients of row means are also consistently positive, although they are not so large because of the depressing effect of the intrinsic negative, or low correlation of the species themselves exhibited in the pure stands. Analysis of variance of the r values transformed to Z give significant differences between pure stands and rows, pure stands and columns, and also between rows and columns. It seems therefore that the growth characteristics of the species are changed when competing with each other.

Table 6. *Probability levels of the estimates of tillering and values of* $\bar{b}$

Component	Low fertility		High fertility	
	Replicate 1	Replicate 2	Replicate 1	Replicate 2
	First harvest			
Alpha SS	< 0·01	< 0·001	< 0·001	< 0·001
Beta SS	N.S.	N.S.	N.S.	N.S.
Alpha and beta competition	N.S.	< 0·05	< 0·01	< 0·01
a'	< 0·05	< 0·01	< 0·01	< 0·01
b'	N.S.	N.S.	N.S.	N.S.
$\bar{b}$	N.S.	N.S.	N.S.	N.S.
$\bar{b}$	−0·269	−0·226	0·173	−0·570
	Second harvest			
Alpha SS	< 0·001	< 0·001	< 0·01	< 0·05
Beta SS	N.S.	N.S.	N.S.	N.S.
Alpha and beta competition	< 0·05	< 0·01	< 0·01	N.S.
a'	< 0·01	< 0·001	< 0·01	< 0·05
b'	N.S.	N.S.	< 0·01	N.S.
$\bar{b}$	N.S.	< 0·01	N.S.	N.S.
$\bar{b}$	0·188	0·553	0·068	0·207

Table 7. *Correlation coefficients* (r) *for tillering/dry weight at second harvest*

	Low fertility		High fertility	
	Replicate 1	Replicate 2	Replicate 1	Replicate 2
Complete diallel	0·63**	0·55**	0·58**	0·67***
Pure stands	−0·48	−0·71	0·15	0·25
Mixtures	0·68***	0·59**	0·61**	0·71***
Species (row totals)	0·42	0·20	0·35	0·65
Associates (column totals)	0·95*	0·95*	0·99**	0·96*

Significance levels are indicated as follows: * significant at 5 %, ** at 1 %, *** at 0·1 % levels of probability.

DISCUSSION

The tendency within binary mixtures of the five species considered is for one component of the mixture to increase in dry weight relative to its pure stand value, whilst the other falls. However, this compensatory change is not complete. If it were, all points would lie on the line ZQ in the W_r/W_s graphs. The change is such that the higher yielding pure stand component tends to increase more than its associate decreases, with the result that the mixture means, in general, exceed the mid-constituent values of their components when grown alone. Thus Italian ryegrass, the strongest competitor, is seen to lie consistently to the left of ZQ, whilst meadow fescue and timothy lie consistently to the right. By and large the competitive effects are of the alpha type—that is, additive—but the alpha values are correlated with the parental values, thus giving rise to high $\bar{b}$ values. With the exception of an interchange in position of timothy and meadow fescue between the two levels of fertility at first harvest, the five species retain their rank order in magnitude of alpha values over both harvests and at the two levels of fertility. The rank order indicates the relative competitive ability of the five species, and the individual alpha values measure this relationship quantitatively.

It is evident from the changed relationship of dry weight to tillering between pure stand values and mixture values that the morphology of the five species alters when they are grown together in binary mixtures. The change is such that the number of tillers per unit dry weight of the weaker competitor increases, whilst that of the stronger competitor decreases. Two basic situations may be described: one in which the number of tillers per unit dry weight of the stronger competitor is lower than that of the weaker competitor in pure stand, and the other in which the situation in pure stands is reversed. Thus, for example, in taking replicate one of the high fertility treatment at final harvest, Italian ryegrass has a value of 3·62 tillers per unit dry weight in pure stand, which decreases to 2·69 tillers per unit dry weight in competition with meadow fescue, whereas meadow fescue has a value of 5·30 tillers per unit dry weight in pure stand, increasing to 16·25 tillers per unit dry weight in competition with Italian ryegrass. This represents the first situation. An example of the second situation is the interaction between perennial ryegrass and meadow fescue, where perennial ryegrass in pure stand has a value of 8·19 tillers per unit dry weight as compared with a value of 5·30 tillers per unit dry weight in meadow fescue. In competition between them, perennial ryegrass falls to 6·67 tillers per unit dry weight whilst meadow fescue increases to 9·07. It is the marked change in morphology that is of agronomic interest. Theoretically at least, such morphological changes should in turn lead to different patterns of re-growth after harvesting and, as a consequence, may well alter the digestibility levels of the mixture components.

In an earlier paper (Norrington-Davies, 1967) an analysis of data presented by Williams showed both alpha and beta competition but there was a high $\bar{b}$ value of $-0{\cdot}505$, which suggested an interpretation in terms of beta. The mixture means tended to the value of the smaller species. Williams's results were compared with an experiment carried out in this department with barley, where here again there was a high $\bar{b}$ value calculated from the alpha values, but in this case there was no evidence of beta competition from the analysis of variance. The mixture means tended to the values of the larger species. The interpretation in the case of the five grass species is intermediate between that given for Williams's data and that of the barley experiment. Here competition is predominantly (but not exclusively) alpha, the alpha values being correlated with their pure stand means. The mixture means, as in the case of the barley experiment, tend to the values of the larger species. The overall $\bar{b}$ value for the grass species of $-1{\cdot}216$ is considerably higher than the $\bar{b}$ values of the previous experiments discussed and shows the competitive effects between the grass species to be of greater magnitude, under the conditions in which the three experiments were carried out.

I thank Dr Alan Durrant for his assistance and interest in this work.

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