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INTRA AND INTER-SPECIFIC COMPLEMENTATION BETWEEN *TRITICUM AESTIVUM* L. AND *VICIA FABA* L.

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Mixtures and monocultures of wheat and broad beans were compared using indices such as substitution rates and relative resource totals. The substitution rates indicated a greater competitive effect of broad beans in mixture. However, the product of the substitution rates suggested that the component species were not competing exactly for the same resource pool. The relative resource totals, being more than 1, showed better capture and efficient utilization of available resources by component species in mixture than in monoculture. R^2 values exhibited a good fit to yield-density relationship in both the component species.

Key words: Competition, Resource use, Substitution rates, Relative resource totals.

Introduction

The most commonly suggested reason for higher yields in mixture than monoculture is that the component crops are in some way able to utilize growth resources rather differently; they complement each other by using the total resources more efficiently than when grown separately [1, 2]. However, other more complex factors and relationships might be involved [3-5]. The success of any species in mixture depends upon the associated species [6]. The yield of a mixture might be less than higher yielding pure stands and greater than those of the lower yielding monoculture [4, 5,7] emphasized that when the species in a mixture are able to utilize the environmental resources more efficiently in comparison with their pure stands, they may tend to yield more than the mean of the components. There are also cases in which the mixture yielded more than the higher yielding components [8].

The effect of intra- and inter-specific competition; resource capture and utilization by the component crops in a mixture over their respective pure stands may well be understood using relative resource totals (RRT). An attempt is, therefore, made to evaluate the performance of wheat and broad bean genotypes in pure stand and in mixture; to assess the possibility of better and more effective utilization of available resources by the component species resulting in higher yields per individual in mixture over their respective pure stands by using inverse polynomials as suggested by Connolly [9-10].

Materials and Methods

The experiment was conducted at the Pen-y-Ffridd field station of the University College of North Wales, U.K. Two genotypes of spring wheat (*Triticum aestivum* L.), *viz.*, Minaret and Timmo and 2 genotypes of broad beans (*Vicia faba* L.), *viz.*, Dreadnought and Acme were tested in the experiment. The genotypes were grown at four densities of 100, 200, 400, 800 plants m^{-2} of wheat and 12, 25, 50 and 100 plants m^{-2} of beans in pure stands as well as intercropped in 1:1 proportion in alternate rows at three planting densities. No intercropping was made at low density (D1). The objective of putting in this extra pure stand density was to compare the performance of components' individuals in pure stand at D1 with a similar number of individuals of the components in mixture at density 2 and so on. The experiment was laid out in a randomized complete block design with three replicates. Each block contained 28 plots of 2 x 2m each which were randomly assigned to 16 pure stands and 12 mixture treatments in each block. The sowing was done on 24th April, 1985. The mixture of cereals and legumes were sown in alternate rows in equal proportions. Thus the number of plants of each genotype in pure stands were twice that of mixtures. The spacing within rows was kept constant at 2.5 cm for wheat and 20 cm for beans genotypes whereas the distance between rows was varied from 40, 20, 10 and 5 cm to accommodate different densities. Regularity of spacing and uniformity of sowing depth were achieved by sowing with templates. Seeds of wheat were sown at a depth of 3-4 cm and those of beans at 5-6 cm using a hand dibber. Two seeds per hill were sown to ensure the crop stand which were thinned to one plant per hill after germination. To avoid edge effects, the central 1 x 1m area in each plot was marked and 10 plants each of wheat and beans from this marked area were labelled at random for data recording. Wheat in pure stand took 138 days later to mature whereas wheat in intercropped plots matured 10 days later than its pure culture. Beans in pure stand as well as in intercropped plots were harvested 152 days after sowing. The plants after harvest were dried in an oven at 70° for 72 hrs and

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weighed for total plant dry weight, and then threshed with hand for grain yield per plant.

In addition to an analysis of variance, yield-density relationships were examined for biomass and grain yield per plant by fitting inverse polynomials because of the wide applicability in plant competition studies [9]. Models of the following forms were fitted:

$$W_1^{-1} = a_{10} + a_{11} d_1 + a_{12} d_2 + a_{13} d_3$$

where, W_1^{-1} is inverse of yield per plant of species 1; a_{10} is the constant term; a_{11} is intra-specific coefficient of species 1; a_{12} and a_{13} are inter-specific coefficients with species 2 and 3; d_1, d_2, d_3 are the densities of species 1, 2 and 3 in mixture.

The Substitution Rates (SR) were calculated to evaluate the relative influence of species in mixture. SR for species 1 with species 2 and 3 were calculated as:

$$SR_{1,2} = a_{12} / a_{11} \text{ and } SR_{1,3} = a_{13} / a_{11}$$

To assess the yield advantages/disadvantages of mixture over pure stands, the relative resource totals (RRT) were calculated as:

$$RRT = (d_1/d_{10}) + (d_2/d_{20})$$

and the component d_1/d_{10} for the species 1 with species 2, and 3 was estimated as:

$$d_1/d_{10} = a_{11}\, d_1 / (a_{11}\, d_1 + a_{12}\, d_2) \quad \text{or}$$
$$d_1/d_{10} = a_{11}\, d_1 / (a_{11}\, d_1 + a_{13}\, d_3)$$

The second component d_2/d_{20} of the RRT was estimated similarly.

Results and Discussion

The results (Table 1) showed that the density had a significant effect on grain yield and biomass production per plant in both wheat and bean genotypes. Grain yield and dry matter per plant decreased with increase in density and the highest density (D4) resulted in a significantly lower yield than the other densities. The coefficients of determination (R^2) ranging from 0.876-0.942 indicate a good fit of the inverse linear model for the grain and biomass production per plant in both species.

The regression coefficients (Table 2) reflect a higher level of intra- as well as inter-specific competition in wheat. How-

TABLE 1. RESULTS FOR THE BIOMASS AND GRAIN YIELD PER PLANT FOR BOTH SPECIES OF WHEAT-BEANS MIXTURES.

Genotype combination	Grain yield per plant (gm)				Biomass per plant (gm)			
	Minaret	Timmo	Dread-nought	Acme	Minaret	Timmo	Dread-nought	Acme
100W + 0B	3.98	2.84	–	–	9.01	6.48	–	–
200W + 0B	2.85	2.07	–	–	6.40	4.65	–	–
400W + 0B	1.72	1.27	–	–	3.70	2.72	–	–
800W + 0B	0.47	0.39	–	–	1.00	0.81	–	–
$100W_1 + 12.5B_1$	2.99	–	27.03	–	6.97	–	71.98	–
$100W_1 + 12.5B_2$	3.34	–	–	32.89	7.77	–	–	88.42
$100W_2 + 12.5B_1$	–	2.27	28.46	–	–	5.29	76.59	–
$100W_2 + 12.5B_2$	–	2.41	–	31.46	–	5.62	–	85.83
$200W_1 + 25.0B_1$	1.74	–	20.19	–	3.96	–	59.16	–
$200W_1 + 25.0B_2$	2.07	–	–	28.50	4.69	–	–	79.73
$200W_2 + 25.0B_1$	–	1.29	21.62	–	–	2.95	62.65	–
$200W_2 + 25.0B_2$	–	1.60	–	27.48	–	3.64	–	76.81
$400W_1 + 50.0B_1$	0.38	–	10.54	–	0.82	–	36.23	–
$400W_1 + 50.0B_2$	0.43	–	–	15.20	0.93	–	–	48.71
$400W_2 + 50.0B_1$	–	0.34	13.47	–	–	0.72	44.47	–
$400W_2 + 50.0B_2$	–	0.33	–	16.10	–	0.69	–	53.74
0W + 12.5B	–	–	32.46	36.38	–	–	80.73	91.61
0W + 25.0B	–	–	24.13	26.14	–	–	65.91	74.13
0W + 50.0B	–	–	19.12	20.10	–	–	55.21	61.04
0W + 100.0B	–	–	10.75	12.73	–	–	37.25	41.09
Mean	2.00	1.48	20.78	24.70	4.53	3.36	59.02	70.11
CV%	13.00	13.80	10.20	11.10	16.70	18.00	9.00	10.80
Cd_1 (P<0.05)	0.40	0.32	3.45	4.50	1.17	0.94	8.87	12.67
Cd_2 (P<0.05)	0.55	0.44	4.76	6.20	1.61	1.29	12.10	17.45

W_1 = Minaret; W_2 = Timmo; B_1 = Dreadnought; B_2 = Acme.

ever, the inter-specific competition is more severe than the intra- specific one and the inter-specific is of a higher level when wheat is grown with Dreadnought (B1). For beans the non-significant competition between the members of different species and significant competitive interactions between the members of the same species are reflected through the regression coefficients. These are in quite inconsistent with the results presented in the Table 1.

Higher substitution rates for wheat and lower than for beans (Table 3) reflected the suppression of wheat and the influential behaviour of beans in mixtures. Wheat genotypes perceived the companion beans as about 4 times more influential than a wheat plant. However, the ratio of beans to wheat dry matter per plant in mixture ranges from 10-80. This suggests that the lower perception by wheat of the beans influence may be due to a buffering by resource zone overlap. However, the product of substitution rates, being less than 1, reflects that the component species of the wheat-broad bean intercrops were not competing exactly for the same environmental resources [10].

Intercropping of wheat and beans showed some beneficial effect for grain yield and dry matter production per plant in the bean component over its pure culture. For example, 25 plants of Acme beans were grown with 200 plants of wheat produced higher grain yield and dry matter per plant as compared to 25 plants of beans grown in pure stand. Higher yields of beans in mixture may be attributed to more efficient use of environmental resources [2, 11]. The present results are in accordance with those of Aziz [12] who reported that pea cultivars gave higher grain yield in mixture with barley as compared to their pure cultivation.

The values of RRT ranged from 1.14-1.51 for grain yield and 1.19-1.58 for dry matter production per plant in various genotype combinations (Table 3). RRT values higher than 1 indicate better exploitation of the resource zone by the component species in a mixture through above as well as below-ground interactions. Above-ground effects may be due to larger leaf area in mixture and below-ground because of different rooting systems of the component species since the cereals are comparatively shallow rooted while legumes have a deep root system [13]. Studies by Bakhuis and Kleter [14] indicated that the intercropping advantages are largely due to interactions below-ground.

Yield per unit area is of far more importance to the agriculturist than is yield per plant. The general pattern is asymptotic, in that the final constant yield probably represents the 'maximum fixation energy' that a crop can achieve from the time of sowing to harvest [15, 16].

TABLE 2. ESTIMATES (SE IN PARENTHESIS) OF THE VARIOUS PARAMETERS.

Wheat

Coefficient	Grain yield per plant		Biomass per plant	
	Minaret	Timmo	Minaret	Timmo
Constant	9.97	11.46	3.78	3.93
	(3.36)	(3.03)	(2.61)	(2.15)
d_W	14.95	19.79	7.15	9.53
	(7.33)	(7.10)	(6.84)	(6.80)
d_{B1}	89.40	107.20	35.84	42.50
	(4.68)	(4.27)	(4.02)	(3.68)
d_{B2}	58.10	73.50	22.62	28.70
	(3.73)	(3.45)	(3.09)	(2.88)
R^2	0.920	0.914	0.909	0.905

Beans

Coefficient	Dread-nought	Acme	Dread-nought	Acme
Constant	2.287	1.953	0.9996	0.9419
	(14.60)	(12.70)	(20.51)	(17.00)
d_B	6.803	6.083	1.721	1.578
	(11.20)	(9.22)	(10.74)	(8.67)
d_{W1}	0.6450	0.1455	0.1624	0.0378
	(5.88)	(1.53)	(5.23)	(1.32)
d_{W2}	0.3994	0.1874	0.0801	0.0345
	(4.22)	(1.92)	(3.03)	(1.21)
R^2	0.942	0.904	0.924	0.876

All the coefficients are multiplied by 100 for presentation. d_{B1} and d_{B2} are the coefficients for the beans genotypes grown in association with wheat, d_{W1} and d_{W2} are the coefficients for the wheat genotypes grown with beans.

TABLE 3. SUBSTITUTION RATES (SR) AND RELATIVE RESOURCE TOTALS (RRT) FOR GRAIN YIELD AND BIOMASS PER PLANT FOR BOTH SPECIES OF WHEAT-BEANS INTERCROPS.

Genotype combination	Substitution rates: Wheat	Beans	Product	Relative resource totals (RRT)
Grain yield per plant				
Minaret + Dreadnought	5.98	0.095	0.568	1.14
Minaret + Acme	3.89	0.024	0.093	1.51
Timmo + Dreadnought	5.42	0.059	0.320	1.28
Timmo + Acme	3.71	0.031	0.115	1.48
Total dry weight per plant				
Minaret + Dreadnought	5.01	0.094	0.471	1.19
Minaret + Acme	3.16	0.024	0.076	1.56
Timmo + Dreadnought	4.46	0.046	0.205	1.37
Timmo + Acme	3.01	0.022	0.066	1.58

The crop yield of grain and dry matter appeared to decline very sharply in wheat whereas the bean crop grain yield and dry matter were still increasing at higher densities (Table 4 and 5) For mixtures of Minaret and Acme the RRT for the simple inverse linear model exceeds 1.5 for both grain yield and dry weight per plant. This suggest that there may be considerable overlap in resource zones for the two species. However, this overlap does not translate into a strong crop yield advantage for mixture.

The 'law of final constant yield' [17], is not obeyed in this experiment by the wheat varieties for either grain or dry matter yield. For the bean varieties yields were rising at the highest

TABLE 4. CROP YIELD OF GRAIN FOR PURE STANDS AND MIXTURES OF WHEAT AND BEAN CULTIVARS.

Yield of mixture components (gm/m²)

	Minaret + Dread-nought		Minaret + Acme		Timmo + Dread-nought		Timmo + Acme	
Density	Minaret	Dread-nought	Minaret	Acme	Timmo	Dread-nought	Timmo	Acme
D1	–	–	–	–	–	–	–	–
D2	299	338	334	411	227	356	241	393
D3	348	505	414	713	259	540	319	687
D4	151	527	172	760	136	673	131	805

Total yield (gm/m²)

	Pure wheat		Mixtures				Pure beans	
Density	Minaret	Timmo	Minaret + Dread-nought	Minaret + Acme	Timmo + Dread-nought	Timmo + Acme	Dread-nought	Acme
D1	398	284	–	–	–	–	406	455
D2	571	414	637	745	583	634	603	653
D3	687	507	853	1127	799	1006	856	1005
D4	379	309	678	932	809	936	1075	1273

TABLE 5. CROP YIELD OF DRY MATTER FOR PURE STANDS AND MIXTURES OF WHEAT AND BEAN CULTIVARS.

Yield of mixture components (gm/m²)

	Minaret + Dread-nought		Minaret + Acme		Timmo + Dread-nought		Timmo + Acme	
Density	Minaret	Dread-nought	Minaret	Acme	Timmo	Dread-nought	Timmo	Acme
D1	–	–	–	–	–	–	–	–
D2	697	900	777	1105	529	957	562	1073
D3	792	1479	939	1993	591	1566	728	1920
D4	328	1811	373	2435	288	2223	276	2687

Total yield (gm/m²)

	Pure wheat		Mixtures				Pure beans	
Density	Minaret	Timmo	Minaret + Dread-nought	Minaret + Acme	Timmo + Dread-nought	Timmo + Acme	Dread-nought	Acme
D1	901	648	–	–	–	–	1009	1145
D2	1281	930	1597	1882	1486	1635	1648	1853
D3	1480	1088	2271	2932	2157	2648	2760	3052
D4	803	648	2139	2808	2511	2963	3725	4109

densities, so it is not possible to check whether the law applied for beans.

An inverse yield-density relationship for dry matter and grain yield per plant in various crop species has been reported by many research workers [12, 17-20].

The depressed grain yield and dry matter production of the wheat genotypes at higher densities may be attributed to lodging in most of the intercropped plots because of rain and wind during the reproductive phase of the crop. However, the product of the substitution rates for grain and biomass production, being less than 1 and RRT greater than 1, indicate a better utilization of environmental resources and suggest that wheat and broad beans can successfully be grown in an intercropping system by using appropriate mixture combinations.

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