JOURNAL OF AGRICULTURAL SCIENCE IN FINLAND
Maataloustieteellinen Aikakauskirja
Vol. 63: 307—20, 1991

Assessment of competition and yield advantage in addition series of barley variety mixtures

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Abstract. In an addition series experiment the competition between three barley varieties (Agneta, Arra and Pomo) and the yield performance of mixtures were evaluated. Also two levels of nitrogen fertilization (50 and 100 kgN/ha) were applied.

Two approaches (the replacement series and the linear regression equation) were used to analyse the competitive relationship based on grain yields in two-component mixtures. In three-component mixtures the replacement series approach was applied. Both methods showed a similar dominance order of the varieties with Arra always being dominant and Agneta subordinate. The relationship between varieties was independent of the number of varieties in the mixture. Increase in available nitrogen strengthened the competitiveness of Arra especially in the dense, two-variety mixtures.

Some mixtures overyielded but the differences were not statistically significant. The yield advantage based on relative yield tótal or on the ratio of actual and expected yield was greatest when the density and nitrogen fertilization were low and especially when one component in the mixture was a rather low yielding variety (Agneta). The land equivalent ratios (LER) (the reference pure culture yield was the maximum yield of each variety) were close to one, suggesting that under optimal growing conditions the yield advantage of barley varietal mixtures is marginal.

Index words: Competition, yield advantage, barley, mixtures, models

INTRODUCTION

Although plant density and mixture composition are different aspects of the same general phenomenon of inter-plant competition, they have generally been treated in isolation (WRIGHT 1981). Competition between species or varieties is often studied by varying the proportions of two components in a mixture in which the total plant density is held constant (de WIT 1960), whereas competition among plants in monoculture is studied by means of systematic variation in plant density as reviewed by WILLEY and HEATH (1969).

In monocultures, intragenotypic competition results in a reciprocal relationship between mean yield per plant and density (WILLEY and HEATH 1969, RADOSEVICH 1987). In two-genotype mixtures, the mean yield of each species is dependent upon the relative frequencies of the two genotypes and upon the overall density (HARPER 1977), as long as there is niche overlap between them (FIRBANK and WATKINSON 1985).

Several methods or approaches have been developed to study plant competition in mixed stands (RADOSEVICH 1987, FIRBANK and WATKINSON 1990). Each method considers density, spatial arrangement and proportion to varying degrees. These methods generally fall into different types of experiments: additive, replacement series and addition series. In each method, total or individual plant yield, plant growth rate or plant mortality can be measured. Each method is a form of bioassay in which the response of one species is used to describe the influence of the other. The methods are thoroughly reviewed by RADOSEVICH (1987) and FIRBANK and WATKINSON (1990).

In addition to breeding purposes (POWELL et al.1985) it is important to separate intra- and intergenotypic competition in order to select varieties for the use of cereal cultivar mixtures. According to previous considerations (de WIT 1960, SPITTERS 1983), the yield advantage of mixtures can be predicted if the intragenotypic competition in the mixture is greater than the intergenotypic competition. Thus any quantitative analysis of competitive interactions must consider both intra- and intergenotypic competition. To achieve a more accurate assessment of the relative strengths of competition in mixtures of spring barley, an experiment was conducted with commercial varieties.

In the present experiment, replacement series (substitutive) (de WIT 1960, HARPER 1977) at three total plant densities of barley variety mixtures and monocultures were used to assess the competitive relationship between varieties and yield advantages of mixtures. The design of the present experiment combines the essential features of additive and replacement series experiments, varying both the total density and the individual component densities. The design is termed addition series by SPITTERS (1983).

Two approaches were used to analyse competition. The first approach was to use measures of competitive abilities and combining abilities of varieties based on the relative yield responses according to the de Wit model (de WIT 1960, de WIT and van den BERG 1965). The other approach used to analyse competition is based upon linear regression with the reciprocal of average plant grain yield as dependent variable and density as the independent variable (WRIGHT 1981, SPITTERS 1983).

MATERIALS AND METHODS

Description of the experiment

The field experiment of the addition series was carried out at the Experimental Farm of the University of Helsinki at Helsinki Viikki (60° 13′N, 25° 00′) in 1983. A split-split-plot design was used where factors were nitrogen fertilization (50 kg N/ha and 100 kg N/ha) in main plots, total density (200, 400 and 600 seeds/m^2) in the subplots and genotypic structure of the stands in subsubplots. The genotypic structure of stands consisted of three barley varieties (Agneta, Arra and Pomo) in all possible combinations of two- (50:50) and three- (33:33:33) component mixtures and monocultures. The number of replicates was three. For the general description of six-row barley varieties used in the experiment, see JOKINEN (1991).

The soil was silty clay of pH 4.9. The plot size was 10 m^2 (1.25 m x 8 m) with rows spaced 12.5 cm apart. The fertilizer was granular NPK (N 2%, P 8%, K 12%) (500 kg/ha) combined with calcium ammonium nitrate (CAN) (N 27%). The fertilizer was placed 8 cm deep in the soil. The mixtures were mixed mechanically before sowing. The sowing date was 16 May. The crops were kept free of weeds by one application of the herbicide Actril S (2—3 liters/ha mixed with 300 liters of water) containing MCPA (235 g/l), dichlorprop (184 g/l), ioxynil (38 g/l) and bromoxynil (24 g/l) at the time of shoot emergence. At maturity an entire area of each plot was harvested (10 August) and grain yields were determined (kg/ha at 15% moisture content).

Sampling and analyses

The number of plants in each plot was determined by counting the number of seedlings in four randomly chosen 1-m-long rows/plot about three weeks after sowing before the start of tillering. Similarly the number of generative shoots was determined after the complete ear emergence of the cultivars (the cultivars were not separated in mixtures).

From each mixture yield samples of 400 seeds were taken for determination of the seed yield of the components. The separated samples of each mixture as well as samples of each pure stand yield were used for determination of 1000 grain weights (g). The grain weight in mixtures was determined by dividing the weight of the fraction by the number of seeds. The grain weight of each monoculture was determined from samples of 3x100 seeds.

The grain yields, 1000 grain weight and number of generative shoots were subjected to analyses of variance for split plot design (Steel and Torrie 1980). Mean separation was accomplished by Tukey's honestly significant difference test (HSD) ($P = 0.05$) (Steel and Torrie 1980).

de Wit model approach. The analysis of the replacement series data was performed qualitatively by visual interpretation of the responses of the relative yields to the initial proportion (de Wit 1960, de Wit and van den Berg 1965, Harper 1977, Trenbath 1978). Relative yield (RY) in mixture for each variety was calculated as grain yield at each density and proportion, divided by the mean monoculture yield at that density. Relative yield total of a mixture (RYT) was calculated by adding up the relative yields of the components in a given mixture. Calculation of land equivalent ratio (LER) was based on the assumption that the sole crop yield of each variety used in the calculation was at its optimum density (= maximum yield) (Trenbath 1976).

The competitiveness of one variety against another is expressed by the competitive ratio (CR) which is the ratio between the relative yields of the varieties (Willey and Rao 1980). Details of the calculations (RY, RYT and CR) are shown elsewhere (Jokinen 1991). No statistical analysis was performed since no single method has been adopted for quantifying interactions in replacement series design (Vandermeer 1989).

Reciprocal yield approach. The significance of hyperbolic yield-density equations in various systems has been described elsewhere (Wright 1981, Spitters 1983, Firbank and Watkinson 1985, 1990, Connolly 1987, Roush et al. 1989). Here is a brief summary based on the review by Vleeshouwers et al. (1989).

With mixed density (N1, N2) of two species, the yield of species 1 (Y1) as a function of those densities is assumed to be

$$Y1 = N1/(b0 + b11N1 + b12N2) \quad (1)$$

where b0 is an intercept term, b11 denotes the effect of intraspecific competition, while b12 measures the effect of interspecific competition on species 1. The yield function for species 2 (Y2) is

$$Y2 = N2/(b0 + b21N1 + b22N2) \quad (2)$$

where b0 is an intercept term, b22 denotes the effect of intraspecific competition, while b21 measures the effect of interspecific competition on species 2. For simplicity of interpretation, equations (1) and (2) are often rearranged to inverse linear models (Spitters 1983, Connolly 1987)

$1/W1 = N1/Y1 = b0 + b11N1 + b12N2$ (3)
and
$1/W2 = N2/Y2 = b0 + b21N1 + b22N2$ (4)

where 1/W1 and 1/W2 are the inverse weight/plant. In this model, the reciprocal of average yield/plant of genotype 1 (1/W1) is described by a theoretical maximum yield/plant (1/b0) by its own density (N1) and by the density of a second genotype (N2). Thus both total density and relative density (proportion) are incorporated in this approach to quantifying competitive interactions. According to equation (3), plants of species 1 can be replaced by plants of species 2 in a certain ratio, b11/b12, without changing the weight/plant of species 1, irrespective of the mixture in which the exchange takes place. The ratio b11/b12 is called the relative competitive ability (RC) or in the terminology of CONNOLLY (1987) the substitution rate S1 and is a measure of how many plants of genotype 2 can substitute one plant of genotype 1 without changing the weight/plant of genotype 1. Similarly, b22/b21 is called the substitution rate S2 in equation (2). For example, a substitution rate of 3 in equation (3) means that substituting 3 plants of species 2 for one plant of species 1 leaves the weight/plant of genotype 1 unchanged.

The niche differentiation of species (NDI) grown in mixture is expressed by the quotient

$NDI = (b11/b12)/(b21/b22)$

If NDI is different from unity, the substitution rates for the genotypes are not reciprocal; a value greater than unity indicates some kind of niche separation between genotypes; a value less than unity indicates some kind of inhibition. If NDI is equal to or less than one, the two species compete for the same resources (SPITTERS 1983, CONNOLLY 1987). WRIGHT (1981) also gave more interpretative properties for the b-parameters than presented here.

The multiple linear regression was carried out with the standard statistical package Stat80 (HP-1000). The yield used in calculations was the grain yield/plant. The number of functional units, i.e. number of plants per area used as independent variables in regression, was that at the beginning of the period over which the competition effects were studied. Thus the number of functional units was independent of the competition effects studied. Although also three-variety mixtures were involved in the experiments only two-variety mixtures were included in the reciprocal model because the data was inadequate for the analysis.

Table 1. Influence of nitrogen fertilization, density and genotypic composition of the stand on the number of generative shoots per plant. Means of shoots in density columns, in the average columns and in the average row, followed by the same letter are not significantly different at the 5% level (HSD test).
Ag = Agneta, Ar = Arra, Po = Pomo.

	Nitrogen fertilization (kg N/ha)											
	50 Density (plants/m²)				100 Density (plants/m²)				Average Density (plants/m²)			
Stand	200	400	600	Average	200	400	600	Average	200	400	600	Average
Ag	1.20a	0.84a	0.76a	0.93a	1.49cd	0.83a	0.65a	0.99a	1.35bc	0.84a	0.71a	0.96ab
Ar	1.27ab	0.81a	0.78a	0.95a	1.65d	0.90a	0.68a	1.08a	1.46cd	0.86a	0.73a	1.02bc
Po	1.22a	0.83a	0.84a	0.96a	1.20a	0.86a	0.65a	0.90a	1.21a	0.85a	0.75a	0.93a
Ag Ar	1.43b	0.82a	0.77a	1.01a	1.57cd	0.89a	0.74a	1.07b	1.50d	0.86a	0.76a	1.04c
Ag Po	1.40b	0.73a	0.74a	0.96a	1.31ab	0.91a	0.72a	0.98ab	1.36bc	0.82a	0.73a	0.97abc
Ar Po	1.32ab	0.82a	0.76a	0.97a	1.13ab	0.81a	0.74a	0.95a	1.32ab	0.82a	0.75a	0.96ab
Ag Ar Po	1.30ab	0.77a	0.73a	0.93a	1.43bc	0.79a	0.73a	0.98a	1.37bc	0.78a	0.73a	0.96ab
Average	1.30a	0.80b	0.77b	0.96a	1.42a	0.86b	0.70c	0.99b	1.36a	0.83b	0.74c	0.98

Table 2. The grain yield (kg/ha) of monocultures and mixtures of barley cultivars. A/E is the ratio of the actual and expected yield of the mixtures. Grain yield means in different nitrogen columns, grain yield means in the average column and grain yield means in the average row, followed by the same letter are not significantly different at the 5% level (HSD test).

Stand	Density (plants/m²)	Nitrogen fertilization (kgN/ha) 50 Grain yield	50 A/E	100 Grain yield	100 A/E	Average Grain yield	Average A/E
Agneta (Ag)	200	3677		3736		3707	
	400	4003		39023		3953	
	600	4276		4152		4214	
	Average	3985 a		3930 a		3958 a	
Arra (Ar)	200	3933		4600		4267	
	400	4436		4790		4613	
	600	4406		4634		4520	
	Average	4257 ab		4675 b		4467 b	
Pomo (Po)	200	4204		4239		4222	
	400	4961		4759		4860	
	600	4698		4684		4691	
	Average	4621 c		4561 b		4591 b	
AgAr	200	4356	114	4466	107	4411	111
	400	4572	108	4711	108	4642	108
	600	4533	104	4540	103	4537	104
	Average	4487 bc	109	4572 b	106	4530 b	108
AgPo	200	4251	108	4263	107	4257	108
	400	4397	98	4376	101	4387	100
	600	4731	105	4476	101	4604	103
	Average	4460 bc	104	4372 b	103	4416 b	104
ArPo	200	4404	108	4386	99	4395	104
	400	4614	98	4698	98	4656	98
	600	4469	98	4786	103	4628	101
	Average	4496 bc	101	4623 b	100	4560 b	101
AgArPo	200	4359	111	4516	108	4438	110
	400	4724	106	4720	105	4722	106
	600	4668	105	4726	105	4697	105
	Average	4585 bc	107	4654 b	106	4619 b	107
	Average	4413 a		4484 a		4449	
Mono	200	3938		4192		4065	
	400	4467		4484		4476	
	600	4459		4490		4475	
	Average	4288		4389		4339	
2-mixture	200	4337	110	4372	104	4354	107
	400	4528	101	4595	103	4562	102
	600	4577	103	4600	102	4589	103
	Average	4481	105	4522	103	4501	104
3-mixture	200	4359	111	4516	108	4438	110
	400	4724	106	4720	105	4722	106
	600	4668	105	4726	105	4697	105
	Average	4585	107	4654	106	4619	107

RESULTS

Development during the growing season

Arra seedlings emerged about three days earlier than Agneta or Pomo. The actual density of stands was approximately equal (0.95—1.05) to the expected sowing density (data not given).

In general an increase of density and decrease of the nitrogen fertilization decreased the number of shoots per plant (Table 1). Differences in the plant shoot number of stands having different genotypic composition were significant ($p<0.05$) only at the lowest density at both levels of nitrogen fertilization. At the lowest density and low level of nitrogen fertilization the shoot number of a mixture exceeded the shoot number of the varieties grown in pure culture.

Table 3. Thousand grain weights (g) of varieties. The analysis of variance is done separately for each variety. Grain weight means in different nitrogen columns, grain weight means in the average column and grain weight means in the average row, followed by the same letter are not significantly different at the 5% level (HSD test).

Variety	Stand	Nitrogen fertilization (kgN/ha)		
		50	100	Average
Arra (Ar)	Mono	34.0 a	33.7 a	33.8 a
	ArAg	33.6 a	36.1 b	34.9 b
	ArPo	35.4 b	35.0 ab	35.2 b
	ArAgPo	36.2 b	36.2 b	36.2 c
	Average	34.8 a	35.2 a	35.0
Pomo (Po)	Mono	37.1 a	36.5 a	36.8 a
	PoAg	38.7 b	37.0 a	37.9 b
	PoAr	36.7 a	36.0 a	36.3 a
	PoAgAr	38.6 b	37.4 a	38.0 b
	Average	37.8 a	36.7 a	37.3
Agneta (Ag)	Mono	33.6 a	32.7 a	33.2 a
	AgAr	31.5 a	31.1 a	31.3 b
	AgPo	32.7 a	31.0 a	31.9 b
	AgArPo	32.3 a	31.4 a	31.9 b
	Average	32.5 a	31.6 a	32.1

Actual and expected grain yields

On an average the monocultures yielded the least and the three-variety mixtures the most (Table 2). The yield differences of the stands having different composition of varieties depended on the level of the nitrogen fertilization (nitrogen fertilization x composition of

Table 4. The influence of nitrogen fertilization, density and the component in the mixture on the relative yields ($x10^{-2}$) of different barley varieties grown in two-variety mixtures.(X = Average).

Variety	Density	Nitrogen fertilization (kgN/ha)											
		50				100				Average			
		Component				Component				Component			
	(plants/m²)	Ag	Ar	Po	X	Ag	Ar	Po	X	Ag	Ar	Po	X
Agneta (Ag)	200		48	46	47		43	51	47		46	49	47
	400		38	41	40		35	45	40		37	43	40
	600		39	45	42		31	42	37		35	44	39
	Average		42	44	43		36	45	41		39	45	42
Arra (Ar)	200	66		60	63	62		52	57	64		56	60
	400	68		59	64	70		56	63	69		58	63
	600	65		56	61	70		63	67	68		60	64
	Average	66		58	62	67		57	62	67		58	62
Pomo (Po)	200	61	49		55	55	47		51	58	48		53
	400	56	40		48	55	42		49	56	41		48
	600	60	43		52	58	40		49	59	42		50
	Average	59	44		52	56	43		50	58	44		50

Table 5. The influence of nitrogen fertilization and density on the relative yields ($x10^{-2}$) of different barley varieties grown in three-variety mixtures.

Variety	Density (plants/m²)	Nitrogen fertilization (kgN/ha) 50	100	Average
Agneta	200	29	28	29
	400	27	28	28
	600	24	25	25
	Average	27	27	27
Arra	200	45	42	44
	400	47	44	46
	600	45	46	46
	Average	46	44	45
Pomo	200	36	36	36
	400	32	31	32
	600	35	33	34
	Average	34	33	34

stand $F(6,72)=2.825$, $p=0.016$). This was mainly due to the strong response of Arra to increasing nitrogen fertilization.

There were no statistically significant differences between the yields of the mixtures. The yield of a given mixture differed significantly only from the yield of a component grown alone when Agneta was in the mixture. Then the mixture yield was higher than the monoculture yield of Agneta.

The average actual yield of the mixture exceeded the expected where the lowest yielding variety Agneta grown in the monoculture was one of the components. When the two high yielding varieties Arra and Pomo were grown in the mixture, the average actual yield was close to expected. It is important to note that the ratio of the actual and expected yield of a given mixture was usually highest when the

Table 6. The influence of nitrogen fertilization, density and the composition of the mixture on the relative yield totals (RYT) and land equivalent ratio (LER) of barley variety mixtures.

Mixture	Density (plants/m²)	RYT Nitrogen (kg N/ha) 50	100	Average	LER Nitrogen (kg N/ha) 50	100	Average
AgAr	200	1.14	1.05	1.10	1.00	0.99	1.00
	400	1.06	1.05	1.06	1.04	1.03	1.04
	600	1.04	1.01	1.03	1.04	0.99	1.02
	Average	1.08	1.04	1.06	1.03	1.00	1.02
AgPo	200	1.07	1.06	1.07	0.92	0.95	0.94
	400	0.97	1.00	0.99	0.94	0.97	0.94
	600	1.05	1.00	1.03	1.02	0.99	1.01
	Average	1.03	1.02	1.03	0.96	0.97	0.97
ArPo	200	1.09	0.97	1.03	0.95	0.92	0.94
	400	0.99	0.98	0.99	0.99	0.98	0.99
	600	0.99	1.03	1.01	0.97	1.00	0.99
	Average	1.02	0.99	1.01	0.97	0.96	0.97
AgArPo	200	1.10	1.06	1.08	0.95	0.97	0.96
	400	1.06	1.03	1.05	1.04	1.01	1.03
	600	1.04	1.03	1.04	1.02	1.00	1.01
	Average	1.07	1.04	1.06	1.00	0.99	1.00
Average	200	1.10	1.04	1.07	0.96	0.96	0.96
	400	1.02	1.02	1.02	1.00	1.00	1.00
	600	1.03	1.02	1.03	1.01	1.00	1.01
	Average	1.05	1.03	1.04	0.99	0.99	0.99

density was low, especially at the low nitrogen fertilization level.

Grain weight

The increasing density decreased linearly the grain weight of each variety (data not given). The grain weight of Agneta was highest ($p<0.05$) when the variety was grown in monoculture (Table 3). The grain weight of Arra was usually higher in mixtures than in monocultures. The grain weight of Pomo was the lowest in monoculture and in the mixture with Arra.

Relative yields (RY), relative yield totals (RYT) and land equivalent ratio (LER)

Arra always yielded more in mixtures than in monoculture (Tables 4 and 5). Arra acquired more space in the mixtures with Agneta than in the mixtures with Pomo. At the high nitrogen fertilization level the relative yields of Arra usually increased with increasing density.

Almost without exception Agneta was a variety in which relative yield was lower than expected. Pomo yielded less in mixture than in monoculture when the component was Arra, whereas when the component was Agneta, it yielded more (Table 4).

The relative yield totals were more frequently greater than one (71%, $n=24$) than equal (8%) to or below (21%) one. The relative yield total correlated well with the ratio of actual and expected yield ($r=0.972$, $p<0.001$, $df=22$). As a rule, the relative yield total of a given mixture was greatest at the lowest density and at the low level of nitrogen fertilization (Table 6). LER-values were close to or below one (Table 6).

Competition — competitive ratio (CR)

Arra was always the dominant component in the mixture ($CR>1$) (Fig.1). In general, Arra was more dominant over Agneta than over Pomo. Pomo was more dominant than Agneta. In two variety mixtures the competitiveness of the dominant component was

Table 7. Multivariety reciprocal yield models ($1/W = B0 + B1N1 + B2N2$) for interactions between different barley varieties grown at two levels of nitrogen fertilization (Ag = Agneta, Ar = Arra, Po = Pomo).*

Variety a (b) b (a)	Nitrogen	BO Ba0 Bb0	B1 Baa Bbb	B2 Bab Bba	R^2	RC Baa/Bab Bbb/Bba	1/RC Bab/Baa Bba/Bbb	NDI	$(Bab \times Bba)^{1/2}$
Ag (Ar)	50	58.71	2.29	3.60	0.99	0.63	1.59	1.28	1.96
Ar (Ag)	50	52.99	2.17	1.07	0.99	2.03	0.49		
Ag (Ar)	100	—71.91	2.63	5.21	0.99	0.50	2.00	1.17	2.16
Ar (Ag)	100	21.98	2.09	0.90	0.99	2.33	0.43		
Ag (Po)	50	138.73	2.11	2.80	0.98	0.75	1.32	1.11	1.95
Po (Ag)	50	51.24	2.00	1.36	0.99	1.47	0.68		
Ag (Po)	100	12.02	2.45	3.19	0.99	0.77	1.30	1.04	2.16
Po (Ag)	100	73.12	1.98	1.47	0.99	1.35	0.74		
Ar (Po)	50	39.37	2.20	1.63	0.99	1.35	0.74	1.00	2.14
Po (Ar)	50	22.19	2.07	2.81	0.99	0.74	1.35		
Ar (Po)	100	57.61	2.16	1.30	0.99	1.55	0.65	1.08	2.00
Po (Ar)	100	—4.10	2.15	3.08	0.99	0.70	1.43		

* b-values x 10^{-3}. NDI (Niche differentiation index) = (Bbb/Bba)/(Bab/Baa). 1/W is the reciprocal yield of an individual plant (grain yield/plant). B0 is the reciprocal of the theoretical maximum yield of an individual, B1 describes influences of intragenotypic competition, B2 describes influences of intergenotypic competition, N is plant density and RC predicts relative competitive ability of each genotype. $p<0.01$ for B1 and B2 in each model.

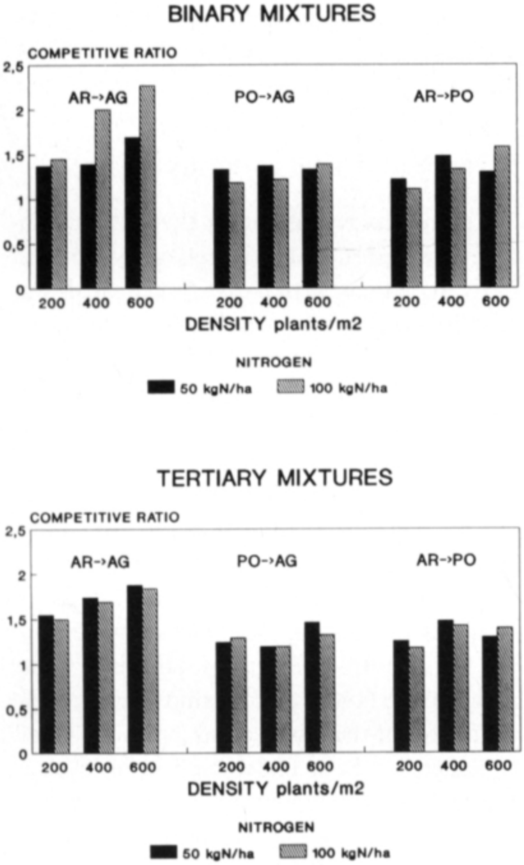

Figure 1. The effect of density and nitrogen fertilization on the competitive relationship between barley cultivars grown in binary and tertiary mixtures. (Ar- > Ag the competitive ratio of Arra over Agneta. Ar = Arra, Ag = Agneta, Po = Pomo).

greatest at the highest density and at the highest level of nitrogen fertilization.

Competition — regression model

Table 7 shows a summary of the regression parameters and the derived indices. The inverse yield/plant of barley variety depended linearly on its own density and on the density of the other component. This result shows the fact that both density and proportion had an influence on the responses of the varieties.

In most cases the intra-genotypic competition of the lower yielding variety was weaker than the inter-genotypic competition. However, there was a Montgomery effect in the mixture of Arra and Pomo. In this case the intra-genotypic competition of the higher yielding Pomo was less severe than inter-genotypic competition and vice versa for Arra. Thus in the mixture the higher yielding Pomo was depressed.

The results of the relative competitive ability (RC) of a variety showed that Arra was a stronger competitor than the other varieties. The relative competitive ability of Arra increased with increasing nitrogen fertilization with Arra being more aggressive against Agneta than Pomo. Pomo was a stronger competitor than Agneta.

In general the niche differentiation index (NDI) was greater than one. NDI was usually greater at the low than at the high level of nitrogen fertilization.

According to the model, the yield of some mixtures exceeded the yield of both monocultures at high density since $(Bab \times Bba)^{1/2}$ was less than both Baa and Bbb. Overyielding according to the model occurred at the low level of nitrogen fertilization in mixtures of Agneta and Arra, and Agneta and Pomo. The mixture of Arra and Pomo overyielded at the high level of nitrogen fertilization.

DISCUSSION

Evaluation of yield advantage

In addition to overyielding, the evaluation of yield advantage can be based on the relative yield total (proportional model) and on the ratio of actual to expected yield (additive model) (Trenbath 1978). In the present experiments both the relative yield total and the ratio of actual to expected yield were usually equal in a given total density of each replacement series. This is because the yield differences between monocultures in most cases were reasonably small and the fundamental difference between approaches based on the expected additivity and proportionality disappeared.

However, the reader should observe that the evaluation of mixture advantage does have its restrictions. When the higher yielding component grown in monoculture is an aggressor, yield difference between monocultures being rather large, as in the mixture of Arra and Agneta at the high level of nitrogen fertilization, it is obvious that the ratio of actual yield and expected yield shows greater yield advantage than relative yield total. TRENBATH (1974) showed that there is the tendency for actual mixture yields to lie above expected combined with the closeness of RYT's to unity.

When the higher yielding component is depressed (Montgomery effect), as in the mixture of Arra and Pomo at the low level of nitrogen fertilization, the results based on the ratio of actual and expected yields can favour the use of monocultures. In the case of the Montgomery effect mixtures will be preferred over monocultures based on the relative yield total.

As a conclusion, the determination of the yield advantage should be based on relative yield total if all the components are to be grown and especially if the yields of the components have different values. Neither method of analysis is preferable if the aim is to maximize production; rather the mixture yield should be compared with the yield of the highest yielding pure culture.

A critical measurement of the yield advantage of mixtures in general involves also a demonstration that the sole crop density used is the optimum. This is because there is an obvious danger of confounding the effects of beneficial interactions between components with simple response to changed density. The results of the present experiment showed how the interpretation of the yield advantage of the mixtures may change only because the mixture yield is compared to the yield of the pure cultures growing in equal density, i.e. constant density (RYT), or to the yield of pure cultures growing at optimum density (LER). Thus without the certainty that the sole crop density is optimal, RYT or LER involving varying densities can be misleading as demonstrated also by TRENBATH (1976) and CONNOLLY (1986).

Occurrence of yield advantage

The results revealed that the yield advantage as determined by the relative yield total or by the ratio of actual to expected yields was usually higher at lower levels of expected yield. This was mainly caused by the low density combined with low nitrogen fertilization, i.e. under suboptimal production conditions. Also AUFHAMMER and STUTZEL (1989) observed that mixture effects tended to be positive with low and negative with high production intensities. Similarly SAGE (1971) and VALENTINE (1982) reported that the yield advantage of mixtures was only apparent at a low density, but not at normal seed rates. However, CLAY and ALLARD (1969) did not find that the yield advantage of the mixture was in general greater under low than under high yield levels.

From a practical point of view there are not very many reasons to use lower than optimum densities except if there is lack of seeds and one tries to prevent lodging. Then it may be more justified to use mixtures than monocultures. This is because the observed yield advantage of certain mixtures (RYT > 1) in agricultural terms means that to obtain the same yields of both varieties (or three varieties), a greater area is needed sowing them separately than sowing them in a mixture.

The results also suggest that when one component like Agneta in the present experiment is an unsuccessful producer in pure culture in a certain environment, the others may overcompensate. Thus the curves of the varieties in the replacement diagram did not compensate each other, giving rise to a relative yield total above one.

Overyielding which occurred in the present experiment was not statistically significant, agreeing with the previous results for barley mixtures in Finland (JOKINEN 1991). In this respect the results are consistent with the findings of PALVAKUL et al. (1973) and LANG et al.

(1975) who stated that the yield advantage from mixtures of high yielding varieties is small or zero.

It should be emphasized that the present and previous results (JOKINEN 1991) suggest that the yield difference between different mixtures is smaller than the yield difference between individual varieties. Thus the probability of selecting a lower yielding mixture is smaller than a lower yielding individual variety. HUHN (1987) also concluded that a mixture will show an increasing phenotypic stability with increasing number of components based on both theoretical and experimental results.

Competitive ability

The reader should observe that Arra was always more competitive than any other variety in the present and in previous experiments (JOKINEN 1991) irrespective of its monoculture yield in relation to the other varieties. If a large number (572) of mixtures including cereals, grasses and legumes is considered, the positive correlation between dominance in mixtures and yield in pure stands is not very strong (0.3) according to the review of TRENBATH (1974). These findings indicate that there are also other characteristics than the pure culture yield of a variety itself, such as differences in juvenile growth, which determine the competitive ability of a variety (SPITTERS 1979, SPITTERS and van den BERG 1982, JOKINEN 1991).

In this experiment, Agneta was not able to use the available space in the mixtures as efficiently as expected. This situation appeared especially at the high level of nitrogen fertilization and at the high density where the competition was usually the most severe and the dominance-suppression relationship prevalent. Also the monoculture yield of Agneta was reduced in respect to other varieties (see JOKINEN 1991). This might be because of its well known sensitivity to low pH of the soil. Thus these results suggest that a genotype which is not well adapted in a certain environment may also be a poor competitor in that environment. It is important to note that then the lower yielding variety is unfavoured in competition. BLIJENBURG and SNEEP (1975) showed that the only barley variety well adapted to local conditions rapidly dominated a mixture.

Competition models

The results of the de Wit analysis concur with the findings of the reciprocal model in describing the competitive ability of a variety. Thus it should be emphasized that the competitive ratio (CR) can give a good estimate on the relative competitive abilities of the components, especially in the mixture of different genotypes of the same species like cereals at constant density. CONNOLLY (1986) showed that the replacement method is particularly prone to difficulties in mixing species of different sizes. However, the approach proposed by WRIGHT (1981) and SPITTERS (1983) provided more detailed and definitive interpretations about the relative magnitudes of the effects of intra- and intergenotypic competition than did the replacement series analysis.

The advantages of fitted models over replacement series analysis are that they deal directly with yield and are not restricted to single total density. The fitted models can be applied to any combination of frequency and density as shown by WRIGHT (1981), SPITTERS (1983) and FIRBANK and WATKINSON (1985).

The fitted models can be used for optimizing the benefits of mixtures under different growing conditions. For example, according to the competition model, a component like Arra which benefitted from mixed culture (Bab < Baa) will not only give a higher yield at any density than in monoculture but is also predicted to respond favorably to higher densities in mixture than in monoculture. The results of the present experiment also indicated that at low nitrogen fertilization levels the niche differentiation index (NDI) might be higher than at high nitrogen fertilization levels. This suggests that certain genotypes might avoid each other more at low than at high levels of nitrogen fertilization.

Although the reciprocal yield approach partitioned the influences of intra- and intergenotypic competition, the coefficients for intra- and inter-genotypic competition provided by the model may simplify the system. It is likely that at the very low density the actual yield of components in the mixture will reach the expected yield, which explicitly means that intra-genotypic competition is equal to inter-genotypic and in the model Baa = Bab and Bbb = Bba. However, the parameters in the regression model are constant for all densities. Thus it is important to note that the parameters of the reciprocal model can be used to characterize the competitive patterns more precisely at higher densities as stated also by WRIGHT (1981). However, the same general pattern of intra- and intergenotypic competition is expected to be retained even at lower densities, as the results of the present experiment also suggest.

Importance of competition

Caution should be exercised when one evaluates the importance of competition in the selection process of barley breeding according to these results, because commercial varieties were used. However, the results indicated that intragenotypic competition might differ from intergenotypic competition even between commercial varieties. The finding differs from the result of BAKER and BRIGGS (1984) who concluded that the performance of commercial barley varieties was similar in competition with other genotypes as in pure stands. The role of competition may not have been fully assessed in their study. POWELL et al. (1985) emphasized that intergenotypic competition is of great importance in barley breeding programs.

CLAY and ALLARD (1969) concluded that varieties selected for high yielding ability in pure stand would not have precisely the biological properties necessary for favourable interaction in heterogeneous populations. Thus it is more likely that genotypes with such properties would be found in populations with a history of mutual selection. It will, however be a rather challenging task for breeders to identify genotypes within species which exploit the environmental supplies of growth factors in different ways in a wide range of environments, i.e. genotypes which do not only compensate but complement each other. The results of the present experiment and also previous studies (e.g. SANDFAER 1970, BLIJENBURG and SNEEP 1975, SPITTERS 1979, JOKINEN 1991) where relative yield totals were calculated, suggest that at least commercial barley varieties seem to compete for the same growth factors at recommended densities and in optimal production conditions.

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SELOSTUS

Ohralajikkeiden välisen kilpailun ja seosten sadontuoton arviointi lisäyssarjakokeesta

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Lisäyssarjamalliin perustuvan kenttäkokeen avulla tutkittiin kolmen ohralajikkeen (Agneta, Arra ja Pomo) välistä kilpailua ja sadontuottoa kahden ja kolmen komponentin seoksissa. Kokeessa käytettiin kahta typpilannoituksen määrää (50 ja 100 kgN/ha).

Kahden lajikkeen seoksista jyväsadon määrään perustuvat kilpailusuhteet analysoitiin kahden kilpailumallin avulla (korvaussarja- ja lineaarinen regressioanalyysi). Kolmen lajikkeen seoksista kilpailusuhteet määritettiin korvaussarja-analyysilla. Molempien mallien tulokset olivat samansuuntaisia. Lajikkeista vallitsevin oli Arra ja väistyvin Agneta. Lajikkeiden keskinäiset vallitsevuussuhteet olivat yhtäläiset kahden ja kolmen lajikkeen seoksissa. Typpilannoituksen lisäys voimisti Arran kilpailukykyä varsinkin tiheissä, kahden lajikkeen seoskasvustoissa.

Jotkut seokset ylituottivat, mutta erot eivät olleet tilastollisesti merkitseviä. Yleensä seoksen satoetu oli suurin, kun kasvutiheys ja typpilannoituksen määrä oli pieni ja varsinkin seoksen yhden komponentin (Agneta) ollessa heikkosatoinen satoedun määrityksen perustuessa suhteelliseen kokonaissatoon (RYT) tai todellisen ja odotetun sadon väliseen suhteeseen. Kun satoedun määritys tehtiin käyttämällä kunkin lajikkeen maksimaalista puhdaskasvustosatoa (maaekvivalenttisuhde, LER) ei satoetua juurikaan esiintynyt. Siten optimaalisissa oloissa lajikeseosten satoetu oli marginaalinen.