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Intergenotypic Competition and Shoot Production in Wheat Plants

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Abstract. In field experiments, the competition among plants of two distinct wheat genotypes in binary mixtures, and among three genotypes being grown in adjacent rows was investigated. The competition greatly affected the over-ground dry weight, weight of stem and grain per plant. This effect was undercompensatory, the depression in poor competitor was higher than the enhancement of strong competitor for all these characteristics. From final components of grain yield per plant, the number of fertile stems and number of grains per ear were more affected than weight per grain. More expressively than weight of grain on the main-stem ear, the weight of grain per average secondary ear-bearing stem was affected by competition in binary mixture. The enhancement in standard height — a strongly competitive genotype — reached in binary mixture about 10% for this last characteristic in comparison with the value from the pure stand. Some morphological characteristics of plants being in relation with competition for grain yield per plant are discussed in these experiments.

In hybrid population where there is a segregation, and in the early screening of lines being grown in adjacent rows, the distinct genetic types of plants may be in neighbourhood. In such situations the interaction between individuals may occur. MATHER (1969) pointed out that individuals may cooperate to their mutual advantage or individuals may be antagonistic to one another. When A and B come together, A is on the average at an advantage by comparison with the situation where A has come together with a second A, and B is on the average at a disadvantage by comparison with the situation where B has come together with a second B. This is the competition in the sense that the term is generally used (SAKAI 1955, DONALD 1963). Plant breeders are concerned with intergenotypic competition since such competition may be a source of bias in evaluation test and impose limitations on the bulk hybrid method of plant breeding (AKIHAMA 1968, JENSEN and FEDERER 1965, JENNINGS and AQUINO 1968, ALLARD and ADAMS 1969).

In this study competition is defined as an interaction between different genotypes and does not include the interaction between plants within

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a genotype. It was conducted to ascertain the effect of the competition among wheat genotypes seeded both in binary mixture and adjacent rows, on breeding valuable characteristics, over-ground dry weight, grain yield per plant and its final components.

Material and Methods

Field Experiments

The study had been conducted for two years (1970 and 1971) at the I.C.C., Kroměříž. Two series of experiments were carried out in which the competition of *Triticum aestivum* L. genotypes in binary mixtures, and in adjacent rows was evaluated.

(i) Binary Mixture Competition

Two cultivars Mironovskaya 808 and Moisson, designated as MI and MO, each of both being contrasted for plant type, were used. Mironovskaya 808 is standard height (about 100 cm), high yielding cultivar with horizontal leaves. On the other hand Moisson is short-stemmed (about 70 cm) with erect leaves. Pure and mixed populations (1 : 1) were made at three nitrogen levels and spacing densities. The nitrogen doses were 60, 120, and 60 + 60 kg N, when in the last case N was applied at the end of tillering. For the different densities the spaces 15 × 12.5 cm, 3.75 × 12.5 cm and 3.75 × 6.25 cm were used, in which the first value designates the distance of seeds within a row. Thus in each treatment three replications of two pure stand plots and one mixed plot were used. In the mixture two cultivars were planted alternatively in both directions. Five row plots were used, rows were 1.5 m long.

The competitive ability (c.a.) per plant was estimated by subtracting the value of a characteristic measured in the pure stand (P) from that of mixed stand (M), and this difference was expressed in % of pure stand performance. Thus c.a. = 100 (M−P)/P.

(ii) Adjacent Row Competition

The three genotypes chosen for testing were the cultivars MI, MO, and Kašticką osinatka, designated as KA. Each of the cultivars was grown separately on pure plots and row-mixed plots. The arrangement of five rows within plots was as follows: XXXXX in pure-, and YYXYY in row-mixed plots, where X and Y represent rows of the test and competitor genotypes, respectively. The distance between rows was 12.5 cm and between plants within row 15 cm and 3.75 cm. The rows were 1·5 m long. All possible pairwise combinations of row-mixed plots including reciprocals, and pure plots were used, thus the total number of variants ($p^2 = 9$) was equivalent to GRIFFING's (1956) diallel method 1. The field design was a randomized complete block with three replications. Original measurements from center row of each plot were used in the analyses. The sum of squares of the competition variants was subdivided into four parts, using the model proposed by EBERHART *et al.* (1964).

Characteristics Evaluated

Careful sampling of five plants free from border effect was made for each genotype from center row on each plot at harvest. After harvest the data measured or computed for each plant were: over-ground dry weight [g], dry weight of stem [g], grain yield per plant [g], number of ear bearing — fertile — stems, average number of grains per ear, average weight per grain (in mg), weight of grain on main stem ear [g], and weight of grain per average secondary stem [g].

Results

Competition in Binary Mixtures

The spacing densities and years markedly influenced the overground dry weight of plants of the both genotypes in pure stands and mixtures. In the mixture with Mironovskaya 808, this characteristic for the Moisson plants in all treatments was lower than in pure stand (Table 1). The enhancing and depressing effects for the both genotypes used were found not to be compensatory, the depressing effect was of greater magnitude. The depression of Moisson cultivar in mixture reached about − 19%. Moisson cultivar is the

TABLE 1

COMPETITIVE ABILITIES of two cultivars expressed as the relative values of the over-ground dry weight per plant in pure stand.

	Competitive ability [%]			Pure stand [g]	
	MI	MO	Dif.	MI	MO
Nitrogen					
60 kg	−0.90	−18.51	17.61	17.77	13.18
120 kg	1.34	−21.33	22.67	18.71	11.58
60 + 60 kg	8.48	−18.52	27.00	19.35	13.66
Space					
15 × 12·5 cm	0.64	−18.65	19.29	31.32	21.07
3·75 × 12·5 cm	10.49	−13.97	24.46	13.25	8.95
3·75 × 6·25 cm	1.24	−27.06	28.30	11.26	8.39
Year					
1970	2.13	−23.75		23.94	14.36
1971	4.82	−13.79		13.28	11.24
Mean	3.12	−19.36		18.61	12.81

Cultivars: MI = Mironovskaya 808, MO = Moisson
Particular values from 90, overall mean from 270 plants
$LSD_{(0.05)}$ for cultivars, nitrogen, space and year = 2.04 g, 1.85 g, 1.31 g and 1.50 g, respectively

relatively poor competitor for over-ground dry weight per plant. The differences between competitive abilities of the both genotypes for this characteristic increased with nitrogen doses and stand density increasing.

The results for dry weight of stem and grain per plant are quite similar (Table 2). In mixture the poorly competitive Moisson plants were −30% for dry stem weight and −16% for grain weight, compared with pure stand characteristics. The poor competitive ability for grain yield per plant in Moisson cultivar was in mixture associated with lower number of fertile

TABLE 2

RELATIVE COMPETITIVE ABILITIES of two cultivars in the binary mixture (1 : 1)

Plant characteristics	Competitive ability [%]	
	Mironovskaya 808	Moisson
Dry weight of stem per plant	0.67	−30.34
Grain yield per plant	7.54	−15.78
Number of fertile stems per plant	−5.14	−16.53
Number of grains per ear	8.27	−2.50
Average weight per grain	3.54	1.64

Single values from 270 measurements

TABLE 3

MEAN SQUARES from the analyses of variance for three complex plant characteristics

Source	df	Over-ground dry weight	Weight of stem	Weight of grain
Replication	2	18.7485	7.2730	6.7911
Space (S)	1	5 663.7075++	1 501.3253++	1 233.4296++
Year (Y)	1	497.9408++	310.9312++	41.5648+
Variants (V)	8	314.2583++	110.3417++	52.0408++
General compet. (GC)	1	261.5408++	79.6358++	41.8034+
Genotypes (G)	2	772.6929++	309.4999++	106.3045++
GC × G	2	44.8086	11.4040	15.6021
Specific compet.	3	205.8409++	53.7599++	43.5699++
V × Y	8	87.1338++	30.6900++	21.2121+
V × S	8	84.9200++	31.2645++	12.3839
S × Y	1	187.4935++	26.1960+	105.2972++
V × S × Y	8	47.8326+	16.8209++	8.5974
Error	70	21.6969	5.8093	7.2593

+ and ++ denote significant at the 5 and 1 % levels, respectively

stems per plant. On the other hand the relatively strong competitor for grain yield per plant, Mironovskaya 808, had in mixture about 8 % higher number of grains per ear than in pure stand, with the number of fertile stems not increasing.

TABLE 4

PERCENTUAL VALUES of the over-ground dry weight per plant for cultivars tested in row-mixed plots in competition with the surrounding cultivars.

Cultivars tested	Surrounded by the cultivar [%] KA	MI	MO	Mean	Value from pure plots [g]
Space: 15 × 12.5 cm					
KA	—	65.45	94.21	79.83	37.13
MI	103.90	—	102.73	103.32	27.45
MO	57.02	67.54	—	62.28	25.20
Mean	80.46	66.50	98.47	81.81	
Space: 3.75 × 12.5 cm					
KA	—	79·25	118.72	98.99	13.25
MI	58.60	—	97.98	78.29	15.87
MO	62.28	60.77	—	61.53	11.93
Mean	60.44	70.01	108.35	79.60	

Cultivars: KA = Kašticá osinatka
MI = Mironovskaya 808
MO = Moisson

This type of competition did not significantly affect the average weight per grain. In both genotypes a small tendency of increasing this characteristic was observed in comparison with the pure stand.

One-year experiment in 1970 did not show significant differences between competitive abilities of wheat genotypes for weight of grain on main stem ear, especially due to compensation of number of grains with weight per grain in this ear. But in the combined analysis from two years, the differences at P 0.05 appeared, especially due to the number of grains. Plants of Mironovskaya 808 have in mixture about 7 % higher weight of grain for main-stem ear, compared with the magnitude of this characteristic from pure stand. More expressively the weight of grain per average secondary ear-bearing stem was affected by competition in binary mixture, it being in this cultivar higher in average about 10% than in pure stand. This competitive effect increased rapidly with increasing density, reaching about 18% of value from pure stand at the narrowest spacing.

TABLE 5

EFFECT OF ADJACENT-ROW COMPETITION on the grain yield per plant

Cultivars tested	Surrounded by the cultivar KA [%]	MI [%]	MO [%]	Mean [%]	Value from pure plots [g]
Space: 15 × 12.5 cm					
KA	—	69.81	95.86	82.84	17.16
MI	104.16	—	105.22	104.69	13.22
MO	58.84	72.44	—	65.64	13.46
Mean	81.50	71.13	100.54	84.39	
Space: 3.75 × 1.25 cm					
KA	—	82.14	123.21	102.68	6.55
MI	74.97	—	107.04	91.01	7.67
MO	63.47	67.73	—	65.60	6.57
Mean	69.22	74.94	115.13	86.43	

Competition in Adjacent Rows

Table 3 gives a part of results of the experiment in which three wheat cultivars were grown in pure plots and in row-mixed plots. From mean squares of this table it may be seen that different distance between plants within a row, and years, influenced all the three complex plant characteristics. To ascertain the effect of each cultivar as a test genotype and that as a neighbour, data in Table 4 and 5 were arranged in a diallel array. Each of the two distances between plants within a row are shown separately.

The individual values in the rows in Table 4 give two-year means for the over-ground dry weight per plant of each cultivar tested, when it was surrounded by rows of a specific other cultivar in percentage of this characteristic of each cultivar, planted in pure plots. Absolute values of the over-ground dry weight in g per plant for each cultivar from pure plots are on the right side of this table. The columns indicate the effect of each cultivar as a competitor for the over-ground dry weight of its neighbours. The overall row and

TABLE 6

MEAN SQUARES FROM THE ANALYSES OF VARIANCE for final components of the grain yield per plant

Source	df	Number of fert. stems	Number of grains per ear	Weight per grain
Replication	2	2.922 3	4.205 5	13.512 7
Space (S)	1	326.911 2++	791.158 7++	16.016 0
Year (Y)	1	21.422 3++	742.770 7++	1 336.403 8++
Variants (V)	8	12.077 0++	380.220 9++	98.007 9++
General compet. (GC)	1	15.778 5++	9.238 2	0.000 1
Genotypes (G)	2	23.493 4++	1 382.714 6++	358.600 2++
GC × G	2	3.256 6	35.605 7	4.897 4
Specific. compet.	3	9.112 6++	65.296 1+	19.022 7
V × Y	8	6.502 3++	31.976 2	17.575 3
V × S	8	2.816 2	22.579 5	7.186 8
S × Y	1	7.002 3+	90.768 3+	172.546 1++
V × S × Y	8	2.271 5	32.887 1	12.776 8
Error	70	1.608 2	19.465 1	17.104 4

+ and ++ denote significant at the 5 and 1 % levels, respectively

column means indicate that Moisson was the poorest competitor among these three individual cultivars, and on the other hand, it was the mixed neighbour, because the over-ground dry weight of plants of other cultivars sometimes benefited and sometimes suffered when surrounded by rows with Moisson. There is an interaction of competition with space. With the increasing distance between plants within a row, the competitive ability of Mironovskaya 808 reversed from strong to poor. The effect of adjacent-row competition on the over-ground dry weight per plant was undercompensatory and in average reached -20%, compared with mean value for this characteristic from the pure plots. This difference was indicated by significant mean square for general competition in Table 3.

As to weight of grain per plant (Table 5) the Moisson cultivar had the poorest competitive ability when surrounded by other genotype rows. In this situation the percentual value of this characteristic for Moisson plants was about -34%, compared with its pure plots.

The effect of adjacent row competition on final components of the grain yield per plant is evident from Table 6. As pointed out by general competition mean squares, the only characteristic in which genotypes in row-mixtures and pure plots were different was the number of fertile stems per plant. In row-mixed plots the value of this characteristic was about 15% lower than in monotypical, pure plots. The poor competitor Moisson produced about −32% fertile stems. The average weight per grain was influenced by this type of competition in the least extent.

Discussion

Experiments with intergenotypic competition have shown that many agronomic and breeding valuable characteristics in wheat plant are affected by this competition. Generally, this effect was high and undercompensatory in these experiments for complex plant characteristics, such as over-ground dry weight, weight of stem and grain per plant. The influence on number of fertile stems and number of grains per ear suggests that the competition among wheat genotypes begins in the earlier stages of plant development.

Many workers have considered the association of competitive ability for yield with specific plant characteristics, especially in rice. JENNINGS and AQUINO (1968) observed in rice that strong competitor had more tillers, longer and more leaves, greater LAI, height and dry weight than poor competitors. In mixtures, the strong competitors intercepted more light at the expense of the poor competitors. In these experiments with wheat the light interception was not measured. But the relation between competitive ability for grain yield per plant with some leaves and stem characteristics of plants from pure stands was investigated. It follows from path coefficient analyses that especially a genotype with more horizontally disposed flag leaf, with greater number of tillers at the beginning of heading, with higher angle of second leaf from the top and greater height of plants at heading in pure stand, may be strong competitor in mixture, when planted in a close neighbourhood with other distinct genotypes. All these observations compared with KAWANO and TANAKA (1967) in rice, SMITH *et al.* (1970) in oat, show that in cereals relatively a close relation between the plant-type and its competitive ability exists.

In these experiments also negative correlation ($r = -0.8744^{++}$) between competitive ability of plants of single genotypes and their influence on distinct neighbours for grain yield per plant was found. In this situation especially genotypes with higher area of the second leaf from the top, with higher sum of lengths of 1 + 2 + 3 leaves from the top at heading, eventually with higher sum of lengths of uppermost two leaves at shooting acted in this way.

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V polních pokusech byla sledována konkurence mezi rostlinami dvou odlišných genotypů pšenice v dvousložkových směsích a mezi třemi genotypy, pěstovanými v sousedních řádcích. Konkurence značně působila na váhu sušiny nadzemní hmoty, váhu stébel a váhu zrna rostliny. Tento vliv byl podkompenzační, snížení u slabého konkurenta bylo vyšší než zvýšení silného konkurenta u všech těchto charakteristik. Z konečných složek výnosu zrna rostliny byly více ovlivněny počet produktivních stébel a počet zrn v klasu než váha jednoho zrna. Výrazněji než váha zrna klasu hlavního stébla byla konkurencí v dvousložkové směsi ovlivněna váha zrna průměrného vedlejšího produktivního stébla. Zvýšení u standardně vysokého — silně konkurujícího genotypu — dosáhlo u posledně jmenovaného znaku ve dvousložkové směsi okolo 10 % ve srovnání s hodnotou z čistého porostu. Jsou diskutovány některé morfologické charakteristiky rostliny, které jsou ve vztahu s konkurencí ve váze zrna rostliny.