Theor. Appl. Genet. 58, 247-252 (1980)

THEORETICAL AND APPLIED GENETICS

Genotypic Effects of the Maternal Tissues of Wheat on its Grain Weight*

E. Millet
Division of Field Crops, A.R.O., The Volcani Center, Bet Dagan (Israel)

M.J. Pinthus
The Hebrew University of Jerusalem, Faculty of Agriculture, Rehovot (Israel)

Summary. Reciprocal crosses were made between semi dwarf spring wheat cultivars (*Triticum aestivum* L.) differing in grain weight. The weights of the F_1 grains (on maternal spikes), from intact as well as from defoliated plants, and those of the F_2 grains (on F_1 spikes), were examined. Grain weight was controlled primarily by the genotype of the maternal tissues (pericarp, testa or other floret or spikelet organs, including the vascular system), with complete dominance of heaviness. No indications suggesting maternal inheritance were obtained. The frequency distribution of the weights of the F_2 grains indicated the presence of genotypic effects exerted by the endosperm or embryo. The embryo or endosperm factors for heaviness also seemed to be dominant.

Key words: Maternal tissues – Grain weight – Wheat – *Triticum aestivum* – Caryopsis – Pericarp – Endosperm – Embryo

Introduction

The grain of wheat (*Triticum aestivum* L.), similar to the caryopsis in all the species of the grass family, is composed of diploid maternal tissues (pericarp and testa); diploid hybrid tissues (embryo), and triploid hybrid tissues (endosperm). However, studies of the inheritance of grain weight or grain size in wheat (Sun et al. 1972), have generally not taken into consideration the different genetic composition of these three groups of tissues. Some information on paternal effects on grain weight of common wheat has been presented by Bingham (1966). Paternal effects on grain development of interspecific diploid *Triticum* hybrids have been reported by Gill and Waines (1978). Both studies, while considering the hybrid tissues, seem to neglect the effects of the maternal tissues.

In the present study an attempt was made to differentiate between the effects exerted on individual grain weight by the genotype of the hybrid tissues and those which may be ascribed to the genotype of the maternal tissues. This was done by analysing the weights of F_1 grains (obtained on maternal plants) and of F_2 grains (obtained on F_1 plants) from reciprocal crosses between parents differing in grain weight (these crosses will be referred to hereafter as heavy × light or light × heavy).

Material and Methods

The parentage and origin of each cultivar used in this study are listed in Table 1. All these cultivars are semi dwarf spring types and, with the exception of 'B.L.24' (a breeding line), have been grown commercially in Israel (cv. 'Lakhish' is still a leading cultivar). The plants were grown at the Bet Dagan Experiment Station in 1977 and 1978. Main shoot spikes with 16-20 spikelets were used in this study. At the time of spike emergence (shortly before anthesis) the two basal florets of 10-14 central spikelets were emasculated following the removal of the upper and lower spikelets and the apical florets in the remaining spikelets. The spikes were covered with translucent paper bags which were removed for pollination, replaced thereafter, and kept for about two weeks until complete wilting of the stigmas of all the florets.

In the case of open pollination, plants were grown in pots and their tillers were removed. The pots with the emasculated spikes were transferred into isolated 100-m^2 plots of the cultivar used as pollinator and were kept there until after complete wilting of the stigmas. The plots of the pollinators were sown at low seed rates in order to promote tillering, and on several dates, and thus a rather long period of flowering and pollen shedding was obtained.

In the case of hand pollination, the plants for emasculation were randomly selected from the central rows of 4-6 replicated nursery plots sown at 5 × 25 cm spaces. Either all the emasculated

* This study is based on data obtained by the senior author in his Ph. D. research at The Hebrew University of Jerusalem. The research was financed in part by 'The Fund for the Encouragement of Research' – Histadrut – The General Federation of Labor in Israel. Contribution from the Agricultural Research Organization, Bet Dagan, Israel. No. 173-E, 1980 series

Table 1. Parentage and origin of five spring wheat cultivars

Cultivar	Parentage	Origin
'Lakhish'[a]	('Yaktana' x 'Norin 10-Brevor') x ('Florence' x 'Aurore')	Bred by the late J. Ephrat, A.R.O., The Volcani Center, Bet Dagan
'B.L. 24'[a]	'Bluebird' x ('Ciano-Chris' x 'Olesen')	Selected from CIMMYT material by Y. Atsmon, Hazera Seed Co.
'Mivhor'	'Penjamo' sib x 'Gabo 55'	"
'H-18'	'Sonora 64A' x 'Tz PP-Nainari 60'	"
'Yafit'	('21931/Chapingo 53-Andes' x 'Gabo 56') x 'Andes 64'	"

[a] Cultivar with heavy grains

Table 2. Mean weight of parental grains of the wheat cultivars 'B.L. 24' and 'Mivhor' (regular type) and of the F_1 grains (bold type) from the reciprocal crosses between these cultivars (hand pollination, 1977)

Maternal parent	Sowing date	Selfing and crossing on different spikes					Selfing and crossing on two sides of the same spike			
		No. of spikes	Grainweight, mg		S.E.		No. of spikes	Grainweight, mg		S.E.
'B.L. 24'[a]	20 Dec. 76	17	46.3	**49.1**	1.92	**0.99**	18	49.0	**51.9**[c]	0.69
	29 Dec. 76	16	45.2	**46.3**	1.83	**1.70**	19	48.2	**50.8**[c]	0.96
	4 Jan. 77	8	51.1	**46.9**	2.30	**3.12**	13	47.2	**48.8**[b]	0.68
'Mivhor'	20 Dec. 76	10	40.6	**43.2**	0.63	**1.51**	15	40.8	**40.4**	0.72
	29 Dec. 76	6	41.1	**42.2**	3.26	**1.65**	7	39.1	**39.4**	1.51
	4 Jan. 77	4	39.4	**42.2**	3.08	**2.23**	6	38.2	**41.1**	2.09

[a] Cultivar with heavy grains
[b], [c] Significantly ($P < 0.05$ and $P < 0.01$, respectively) exceeding the value of the immediately comparable treatment

florets of the spike were pollinated with pollen of a single cultivar (the maternal cultivar for selfing), or the florets in the spikelets on one side of the spike were pollinated with the pollen of the maternal cultivar (selfing) and the florets on the other side were pollinated with pollen from a different cultivar (crossing).

The different methods of pollination had no significant effect on seed set and in all cases averages of about 15 grains per spike were obtained. F_1 plants were checked and no more than 1% progenies of selfed florets were found (and discarded). All the grains examined in this study (parental, F_1 and F_2) were normally developed and no shriveled grains were encountered. F_2 grains, obtained from F_1 plants, were examined in 1978. The F_1 plants and plants of the parental cultivars were grown in the field in randomly distributed hills, 40 cm apart, with 2 or 3 plants per hill. After ripening, a single main shoot spike was sampled from each hill and the grains from the second and fourth florets of the eighth and ninth spikelets were examined. The frequency distributions of the weights of these grains were analysed. Normality was tested according to Shapiro and Wilk (1965) and skewness according to Barr et al. (1976).

Results

In most cases, including defoliated plants, the weight of the F_1 grains did not differ significantly from that of the grains from selfed florets of the maternal parent (Tables 2-4). The F_1 Grains and the selfed grains were always taken from similarly treated spikes and in certain cases even from two sides of the same spike (Tables 2, 4). No consistent differences were found between the S.E. of the means of the parental grains and the F_1 grains. In some cases of heavy × light crosses, the F_1 grains were significantly heavier than the grains of the maternal parent, whereas no significantly lighter F_1 grains were found in these crosses. Moreover, with a single exception [intact plants of 'H-18' × 'B.L.24' (Table 4)], no significant differences were found between the weights of the F_1 grains and those of the maternal parent in the light × heavy crosses.

Defoliation at anthesis resulted in significant reductions in grain weight, amounting to 8-18% (Table 4). In the defoliated plants grain weight was presumably restricted due to source limitations and inter-grain competition for supplies could have occurred within their spikes. Indeed, the advantage in weight of the F_1 grains, in certain crosses, over the grains from selfed florets on the same spike, was usually greater on the defoliated plants than on the intact plants (Table 4).

Table 3. Mean grain weight (mg) ± S.E. of self pollinated and cross pollinated spikes of three wheat cultivars tested at three sowing dates (open pollination, 1977)[a]

Maternal parent	Pollinator	Sowing date (1976)		
		16 November	29 November	14 December
'Lakhish'[b]	'Lakhish'[b]	51.2 ± 1.16	52.0 ± 0.86	48.1 ± 1.67
	'Mivhor'	54.8 ± 1.86	53.9 ± 2.98	50.1 ± 2.41
	'Yafit'	55.7 ± 2.71	52.7 ± 0.79	58.0[c] ± 1.00
'Yafit'	'Yafit'	40.2 ± 1.14	42.5 ± 0.81	45.7 ± 1.53
	'Lakhish'[b]	40.1 ± 1.18	41.8 ± 0.80	46.1 ± 2.08
'Mivhor'	'Mivhor'	44.1 ± 1.09	43.3 ± 0.69	37.3 ± 1.89
	'Lakhish'[b]	43.5 ± 1.26	42.9 ± 0.64	39.8 ± 2.48

[a] the number of spikes tested from each combination was 10-20 at the first sowing, 20-40 at the second sowing (in the case of 'Lakhish' x 'Mivhor' only 4 spikes), and 5-10 at the third sowing
[b] cultivar with heavy grains
[c] significantly exceeding grain weight of selfed maternal parent

The mean weights of the examined F_2 grains, from F_1 plants of both heavy × light and light × heavy crosses, amounted to 92-106% of the mean weights of the comparable grains of the respective heavy parent and never differed significantly from the weights of these parental grains (Table 5). The differences in grain weight between the reciprocal crosses were negligible, excluding the possibility of maternal inheritance of this character.

The frequency distributions of the grain weights of the parental cultivars were normal with no significant skewness (except for 'Yafit', spikelet 8, grain 4 and 'Mivhor', spikelet 9, grain 4). The distributions of the weights of the F_2 grains deviated from normal, in most cases, and exhibited significant skewness. The skewness was always negative, i.e., the frequency of the grains heavier than the mean exceeded that of the grains lighter than it. However, the maximal deviation from the mean was always greater below the mean than above it (Table 5). Typical frequency distributions of the grain weights of two parental cultivars and of their reciprocal F_2 populations are presented in Figure 1. It is obvious from this Figure and from Table 5 that the range of weights of the F_2 grains included all the range which was found in the heavy parent as well as the greater part, or all, of the range found in the light parent. Moreover, in most F_2 populations there occurred heavier grains than the heaviest ones of the heavy parent and in the F_2 populations from crosses with 'Mivhor', there also occurred lighter grains than the lightest ones found in this cultivar.

Table 4. Mean weight (mg) of grains from florets pollinated by the maternal cultivar on one side of the spike (regular type) and F_1 **grains** (bold type) from cross pollinated florets on the other side of the same spike, tested on intact plants and on plants defoliated at anthesis (1978)[a]

Maternal parent	Pollinator	Intact plants		Defoliated plants		S.E.[c]
'B.L. 24'[b]	'Mivhor'	60.7	**61.0**	52.6	**52.1**	1.34
	'H-18'	58.2	**58.6**	50.9	**52.2**	"
'Lakhish'[b]	'Mivhor'	61.7	**64.4**[d]	51.5	**55.5**[e]	1.08
	'H-18'	58.7	**60.8**	51.7	**55.2**[e]	"
'Mivhor'	'B.L. 24'[b]	47.0	**47.8**	40.6	**42.3**	1.23
	'Lakhish'[b]	47.3	**46.6**	42.2	**42.6**	"
'H-18'	'B.L. 24'[b]	40.3	**42.4**[d]	34.6	**35.3**	0.96
	'Mivhor'	41.0	**41.7**	34.9	**37.3**[d]	"
'Yafit'	'Lakhish'[b]	43.2	**42.8**	35.9	**35.0**	0.64

[a] the means presented are averages of 12 spikes
[b] cultivar with heavy grains
[c] S.E. of the difference between parental grains and F_1 grains on the same spike
[d,e] significantly ($P < 0.05$ and $P < 0.01$, respectively) exceeding grain weight of selfed florets on the same spike

Discussion

The data presented in Tables 2-4 indicate that the weights of the F_1 grains from heavy × light and light × heavy parents were determined primarily by the maternal parent. This might be attributed to the genotype of the triploid endosperm, assuming that at least two doses of the factors determining heaviness are necessary to obtain a heavy grain, whereas a single dose has no effect on grain weight, and that the effect of three doses is equal to the effect of two doses. Under these assumptions, the mean weight of the F_2 grains should equal the average of the grain weights of the two parents. However, the mean weights of the F_2

Table 5. Weight (mg) of specific parental grains and F_2 grains from F_1 spikes of reciprocal crosses of wheat cultivars differing in grain weight (1978)

		Eight spikelet						Ninth spikelet						
	No. of	Second floret			Fourth floret			Second floret			Fourth floret			SD
	spikes	Mean	Range	SD[b]	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD	Dif.[c]
Parental cultivars														
'B.L. 24'[a]	22	60.3	51-67	4.07	48.5	36-62	7.33	60.7	53-71	4.80	48.3	36-60	7.06	5.28
'Lakhish'[a]	16	63.3	59-69	2.97	50.1	41-59	5.56	61.3	52-71	4.62	51.8	41-60	5.54	4.68
'Mivhor'	20	52.4	43-62	4.23	42.8	34-51	4.65	54.3	46-60	3.94	44.3	32-51	4.18	5.63
'Yafit'	22	44,9	35-53	4.48	33.8	14-43	8.05	47.0	40-55	3.90	36.5	23-47	5.68	2.82
Crosses														
'B.L. 24' x 'Mivhor'	241	59.1	42-75	4.95	48.8	22-61	6.64	60.0	40-72	5.53	51.1	30-68	6.60	6.13
'Mivhor' x 'B.L. 24'	105	58.4	38-72	5.85	48.5	24-62	6.80	59.7	39-79	6.69	51.1	31-68	7.06	5.81
'Lakhish' x 'Mivhor'	77	62.2	43-73	6.28	50.1	29-62	6.32	62.7	45-74	5.73	52.8	37-66	6.01	6.63
'Mivhor' x 'Lakhish'	194	63.3	47-78	5.26	50.1	24-68	6.28	63.5	38-77	5.67	52.4	36-67	5.82	6.50
'Lakhish' x 'Yafit'	68	59.5	39-74	6.07	47.2	34-59	5.93	61.7	47-72	5.00	48.5	31-58	5.71	6.90
'Yafit' x 'Lakhish'	169	60.5	38-73	5.28	45.8	23-64	6.90	61.6	43-71	4.92	47.3	26-62	6.58	5.76

[a] cultivar with heavy grains
[b] standard deviation = $\sqrt{\text{variance}}$
[c] SD of the difference between the weights of the second grains of the eighth and ninth spikelets

grains of all the crosses were similar to the mean grain weight of the respective heavy parent (Table 5). Consequently, the control of grain weight, in the material handled in the present study, should be ascribed primarily to the genotype of the maternal tissues, rather than to the genotypic constitution of the endosperm and the embryo. The similarity between the mean weights of the F_2 grains and the grains of the heavy parent suggests complete dominance of the maternal factors determining heaviness.

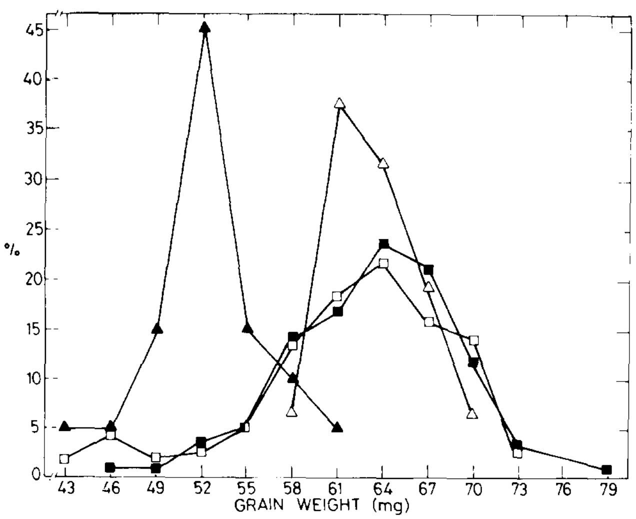

Fig. 1. Frequency distribution of the weights of the grains from the second floret of the eighth spikelet of two parental cultivars ('Lakhish' △; 'Mivhor' ▲) and their reciprocal F_2 populations (F_2 grains on F_1 spikes, 'Lakhish' × 'Mivhor' □; 'Mivhor' × 'Lakhish' ■)

Since the weights of the parental and F_1 grains were determined on spikes from which a considerable number of florets had been removed before anthesis, it may be assumed that in the nondefoliated plants of this study, source limitations did not affect grain weight considerably (Fisher and Hille Ris Lambers 1978). Moreover, for cv. 'Mivhor' and 'H-18' the rather low effect of source limitations on grain weight had been demonstrated in earlier work (Pinthus and Millet 1978). Therefore, it seems improbable that the maternal control of grain weight, demonstrated in this study, is operating, to a great extent, via the supply of nutrients or growth substances to the spike. However, the present information does not enable us to determine whether the maternal tissues, which have a decisive influence on grain weight are those of the grain itself, i.e., the pericarp and testa, or those comprising other floret organs or spikelet organs, including the vascular system, which may affect transport of materials to the grain.

The weights of the F_2 grains have to be evaluated with reference to the weights of the respective parental grains which were grown under similar conditions. Any comparison between them and the F_1 grains, which developed on treated spikes, is not valid. The deviation from normality of the frequency distributions of the weights of the F_2 grains (Fig. 1), the wide range of these weights (Table 5), and the values of their variances which, for grains of the second florets, exceeded those of the parents, demonstrate segregation for grain weight within the F_2 populations. Further indications for this segregation are evident from the variances of the difference between the F_2 grains of the eighth and ninth spikelets (second floret), which in all cases exceeded those for the respective parental grains (Table 5). Assuming that the values of these variances in the parental cultivars are an estimate of environmental variance, any additional portion should indicate genetic variance. Comparisons between the variances of F_2 populations and parental cultivars for the grains of the fourth florets do not seem valid. The development of these grains is more vulnerable to source limitations than that of the basal grains (Pinthus and Millet 1978), and such limitations seem more probable in the parental plants than in the F_1 plants. Indeed, in the eighth spikelet as well as in the ninth spikelet of all the cultivars, the variances for the fourth grain markedly exceeded those for the second grain, whereas the differences between these variances in the F_2 populations were less conspicuous (Table 5).

The segregation within the F_2 populations must be due to the genotypes of the endosperm or embryo (or both), which belong to the F_2 generation, whereas the maternal tissues belong to the non-segregating F_1 generation. The data under consideration do not enable us to discriminate between the genotypic effects of the endosperm and the embryo. These genotypic effects where most obviously expressed in the occurrence of light grains (comprising the whole range of the light parents) within the F_2 populations, although the means of these populations were similar to those of the heavy parent. The smaller deviations from the mean towards the heavy weights than towards the light weights, found in the F_2 populations (Table 5), may be ascribed to the restriction of the expression of high genotypic values of grain weight by the limits set by the maternal tissues. The negative skewness of the frequency distribution of F_2 grains may indicate recessiveness of endosperm or embryo factors for light grains. The occurrence of F_2 grains heavier than the heaviest grains of the heavy parent (Table 5), as well as the cases in which the mean weights of the F_1 grains exceeded significantly those of the heavy maternal parent (Tables 2, 3, 4), can be ascribed either to overdominance of the endosperm or embryo factors for heavy grains, or to the presence of such factors in the light parent, beyond those carried by the heavy parent. Similarly, the occurrence of grains lighter than the lightest grains of 'Mivhor' in the F_2 populations of crosses with this cultivar, may be attributed to recessive endosperm or embryo factors for lightness, carried by the heavy parent and absent in 'Mivhor'.

Information on the mean weights of F_2 grains, from F_1 plants (unfortunately referred to as F_1 means) is presented by Bhatt (1971, 1972), Halloran (1975), and Sun et al. (1972). However, in the absence of data regarding the F_1 grains, only speculative assumptions can be made about the genotypic composition of the maternal tissues and that of the endosperm or embryo of the parental cultivars. In most cases, reported in these studies, the mean weights of the F_2 grains were close to those of the heavier parent whereas they were never close to the lighter parent, which is in agreement with our results. Small deviations from the heavy parent, of similar magnitude to those found by us, may be attributed to genotypic differences between the parents in endosperm or embryo factors.

In certain cases the means of the F_2 grains exceeded those of the heavier parent considerably [up to 39% in a case reported by Bhatt (1971)]. We would attribute this to the combination of different factors for heaviness (maternal as well as endosperm or embryo factors), carried by the parents. In five crosses reported by Bhatt (1971), the parental cultivars did not differ significantly in grain weight, whereas the means of their F_2 grains surpassed those of their parents by 20-38%. This might be explained by assuming that in each cross the grain weight of one parent was restricted by embryo or endosperm factors, although it carried maternal factors for heaviness, whereas in the other parent it was restricted by maternal factors, although it carried endosperm or embryo factors for heaviness. Data on F_3 grains are not presented in this study but are reported by Halloran (1975). In one of his crosses, between two cultivars which apparently did not differ in grain weight, a 12% increase was obtained in F_2, whereas the F_3 mean dropped to that of the parental cultivars. This would have been expected according to the above mentioned assumptions on the genotypes of the parents.

The cases in which the mean weights of the F_2 grains were intermediate between the parents (occurring in all these studies) can be explained assuming that the parents, while carrying similar maternal factors for heaviness, differed in two or three complementary factors of the endosperm or embryo, one parent carrying the dominant alleles for heaviness and the other one carrying the recessive alleles.

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Received June 2, 1980
Communicated by J. MacKey

Dr. E. Millet
Division of Field Crops
A.R.O. The Volcani Center
Bet Dagan (Israel)

Dr. M.J. Pinthus
The Hebrew University of Jerusalem
Faculty of Agriculture
Rehovot (Israel)