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Observations on heterosis in *Zea mays* L.*

Obserwacje nad heterozją u *Zea mays* L.

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Great advances in corn breeding were obtained thanks to the application of scientific methods, based on a knowledge of genetics.

By means of selection and inbreeding it was possible in random mating populations of corn to isolate types, which became facultatively self-fertile. Such types presented the starting point, from which it was possible to bred pure lines.

In some cases hybrids, derived from crosses between two inbred lines, exhibited heterosis, but in the next generations a decline in vigour was observed. Therefore it was assumed, that the vigorous growth of F_1 hybrids is connected with their heterozygous state.

Our experiments were performed in order to establish whether by selection and inbreeding of some of the most vigorous plants in F_2 and in succeeding generations it was possible to isolate lines with fixed vigorous growth. In our preliminary report (from 1960) we presented data concerning the possibility of obtaining such lines, it was stated that the increase in height of such plants was accompanied by a corresponding retardation in time of flowering.

The experimental material was of American origin and included inbred lines from Minnesota, Wisconsin, Connecticut, Indiana and Texas. Numerous crosses were performed between these inbred lines and only those are investigated, which exhibited vigorous growth in F_1 hybrids. The cross between the inbreds WD and W9 is the most investigated, their F_1 exhibited a considerable degree of vigour in comparison with the parental plants. In F_2, there has been observed the occurrence of some plants exceeding the F_1 hybrids in vigour. By means of inbreeding the most vigorous plants in F_2 and succeeding generations, it was possible after several years to isolate lines with a hereditary fixed vigorous growth, exceeding that of F_1 hybrids.

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The problem now was to verify whether the differences between the fixed vigorous line and F_1 hybrids, as well as parental types are significant. In connection with this in 1959 an experiment in randomized blocks in two replications was performed. Inbred lines WD and W9, F_1 hybrids and the fixed vigorous line No 10 were used in the experiment. Each plot was a long rectangle 15.2 m $\times$ 2.4 m in size, with a surface of 36.5 m^2. The plants 20 in each row, grew in 4 rows on the plot. The total number of plants per plot was 80. The seed was sown in pots in a greenhous and after a months time the plants were transferred outdoors to fertile soil. During the growth season a nitrogen fertilizer was applied at the rate of 5 g per plant (the nitrogen being nitrate of soda).

To estimate the earliness of flowering the date of pollen shedding of each plant was noted. Starting with the end of August measurements were taken of the height of plants, length and width of leaves of a whole plant, and the length and the number of internodes on the main stem. The earliness of each plant was defined by the number of days from seeding to pollen shedding. The surface of each leaf was computed according to Montgomery's formula:

$$\frac{3 \times l \times w}{4},$$

where l is the length of leaf and w the width. The total sum of the leaf surfaces of a whole plant was computed, and the sum of the leaf surfaces only of the main stem. For each series of plants growing on one plot the arithmetic mean of each investigated feature was computed. An analysis of variance according to Fisher's method was performed, by calculating the confidence interval and the significance of differences on the level $p = 0.05$.

The results are given in Table 1. The table presents in the first, second, third and fourth column the arithmetic means of parental types, WD and W9, their F_1 and of the fixed vigorous line No. 10. In the fifth column the value of the confidence interval, μt, in the sixth the value F_0, in the seventh the value of theoretical F, in the last column the value of the general accuracy of the experiment, expressed by μt in % of the general mean value. The first row presents data concerning the height of plants in cm., the second — the leaf surfaces sum of the main stem in cm^2, the third — the leaf surfaces sum of the whole plant in cm^2, the fourth — the leaf length in cm, the fifth — the leaf width in cm, the sixth — the number of days from seeding to pollen shedding.

On the basis of the analysis of variance it was stated that for all traits with few exceptions the differences are significant and statistically proved for the parental plants, F_1 and the fixed vigorous line No 10. All the differences exceed the value of the confidence interval.

Table 1

Arithmetic means of the parents, F_1 line No. 10, and the value for: μt, F_o, F_{theor}, and general accuracy of the experiment

Trait	1	2	3	4	5	6	7	8
	WD	Wg	F_1	1N°10	Mt	F_0	F theor.	general accuracy
Height of plants in cm.	105,56±0,99	141,71±0,72	171,12±0,8	231,56±109	13,09	340,28	9,23	7,8%
Leaf surfaces sum of the main stem in cm²	1778±27,96	2624,5±30,41	3178±31,5	6399,5±61,36	418,05	472,8	9,23	11,9%
Leaf surfaces sum of the whole plant in cm²	1827,5±21,17	2624,5±30,41	3427,5±59,9	6418,5±58,3	327,46	759,7	9,23	8,8%
Leaf length in cm²	41,56±0,29	46,3±0,24	49,53±0,27	54,75±0,27	2,33	114,73	9,23	4,0%
Leaf width in cm	6,07±0,7	6,59±0,04	6,86±0,04	10,46±0,06	1,13	64,05	9,23	15%
Number of days from seeding to pollen shedding	74,3±0,18	81,04±0,22	73,21±0,06	91,22±0,18	4,05	85,06	9,23	5%

The height of plants may be considered as being composed of two component traits: the number of internodes and their mean length. Investigating the inheritance of each component trait separately in an experiment, performed in 1960, it was possible to state in F_1 the dominance of a larger number of internodes characterizing the line W9. The arithmetic mean amounts to: for 1. WD = 11.42 ± 0.09 cm., for 1. W9 = = 13.04 ± 0.1 cm., for F_1 = 13.18 ± 0.12 cm. Neither parental form differed significantly in the internode length. The arithmetic mean for 1. WD = 12.15 ± 0.1 cm., for 1. W9 = 12.59 ± 0.09 cm. However in F_1 the internode length exceeds both parental types: x = 14.6 ± 0.13 cm. The increased height of F_1 plants may be explained by the lengthening of internodes caused by a more intensive intercalar growth and the dominance of a greater number of internodes.

For the trait of the leaf surfaces sum of the main stem as of the whole plant the obtained differences between the series were also significant. In connection with a greater number of tillers in line WD and of F_1 hybrids the value of respective arithmetic means for the leaf surfaces sum of the whole plant is somewhat higher, however in spite of this the differences are statistically proved.

On the basis of the obtained results it may be assumed that F_1 hybrids exhibit an increased growth in comparison with the parental types, line No. 10 is significantly more vigorous than the parents as well as F_1 hybrids. The increase of the sum of the leaf surfaces of a whole plant in F_1 hybrids may be explained by the dimension of leaves becoming larger in length and width. On the basis of the analysis of variance it was stated that for the leaf length and leaf width the differences have been proved with the exception for the differences between the parents and F_1, that for the leaf width are not significant.

Concerning plant earliness, significant differences between parental lines and the line No. 10 were obtained. The difference between F_1 and the earlier parent is not significant. The heterosis for earliness in F_1 hybrids although occuring does not prevail significantly over the earlier parental type. The cause of this not too strongly expressed heterosis for earliness is the too great a difference between both parental lines at the time of flowering. In connection with the established dependence of the time of flowering on plant vigour, it was interesting to elucidate to what degree the differences in earliness of crossed lines influence the earliness and vigour of F_1 hybrids.

Breeders are aware that in general F_1 hybrids exhibit heterosis for earliness. Thus it was interesting to verify whether the F_1 hybrids are always earlier than corresponding parental types and to elucidate the relationship between the number of days from seeding to pollen shedding, expressed by the mean value of both parents, and the plant height of their F_1 hybrids. For this purpose 27 crosses are performed between inbreds, differing from each other, to a smaller or greater degree, in earliness. Thus early lines were intercrossed, medium early and late ones, as well as late lines with early ones.

To define the earliness of the parental plants and their F_1 — the date of pollen shedding of each plant was noted. The height of a plant is a characteristic feature of vigour and our investigations on heterosis were based on this trait. Both the parental plants and the F_1 hybrids are sufficiently uniform. To define the parental types and respective F_1 the arithmetic mean was computed for 10 plants in respect to their height and earliness.

From the experimental data it was stated that the heterosis for earliness occured in F_1 only in those cases where both parental types differed slightly from each other in earliness, namely if the difference was not more than 7 days. This concerned both the early inbreds, medium and late ones. In the case when both crossed parents differed by a larger number of days, exceeding 10, in earliness, the F_1 as a rule did not exhibit heterosis for earliness and was later than the earlier parent. The graph (Fig. 1) presents data illustrating the behaviour of several typical crosses. The graph shows the number of days from seeding to pollen shedding, versus the height of plant in cm. (on the ordinate). The numbers of parental lines and their F_1 are given on the top of each vertical line. As is seen in the case of small differences between the parents in earliness — F_1 exhibits heterosis for earliness. In the case of considerable differences, exceeding 10 days, F_1 is located asymmetrically between the parents and is always shifted in the direction of the earlier parent. Heterosis for earliness can be explained by assuming the presence of dominant genes for shortening the number of days from seeding to pollen shedding. Besides, additive genes exhibiting blending inheritance can participate in determining the time of flowering. On the Table 2 are

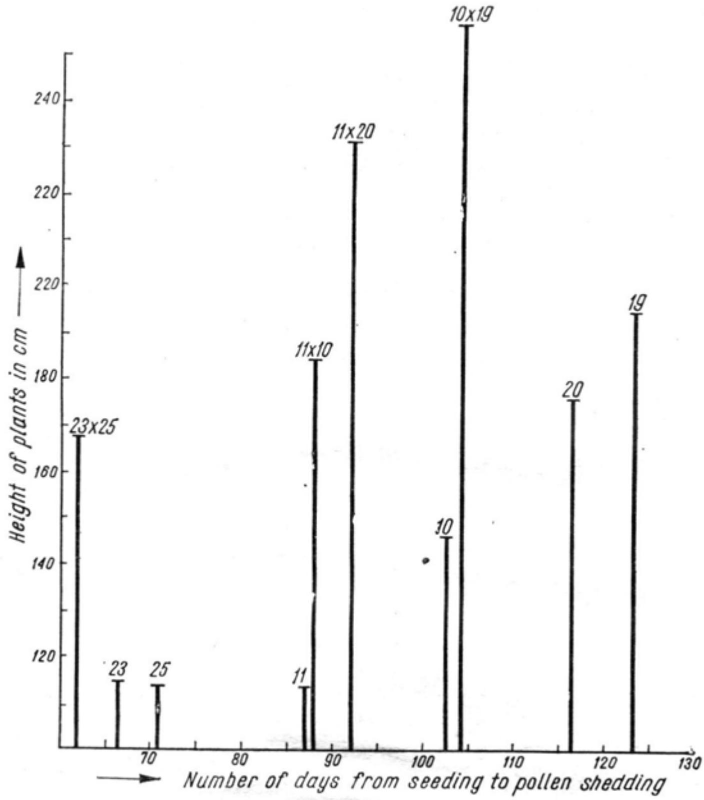

Fig. 1. The graph shows the number of days from seeding to pollen shedding, versus the height of plant in cm. The numbers of parental lines and their F_1 are given on the top of each vertical line

given theoretical and observed values for genotypes of the parents and their F_1 as concerns the action of genes determining the number of days from seeding to pollen shedding.

To estimate the relationship between the difference in earliness between the crossed parents and the degree of heterosis for earliness of their F_1 hybrids the correlation coefficient was computed for the value of difference in earliness between the parents expressed in days and the heterosis for earliness in F_1 hybrids expressed by a shortening of the number of days from seeding to pollen shedding in relation to the earlier parent. If the date of pollen shedding of the earlier parent is defined by zero — then the effect of heterosis for earliness is expressed in negative numbers and the difference between the crossed parent — in positive ones. Only lines exhibiting heterosis for earliness were taken into account when the correlation coefficient was computed. The value of the coefficient of correlation, $r = -0.51 \pm 0.21$ shows a negative correlation between these traits. The smaller is the difference in earliness between the parents the stronger is the heterosis for earliness in corresponding F_1.

Table 2

Theoretical and observed values for genotypes of the parents and their F_1 as concerns the action of genes determining the number of days from seeding to pollen shedding*

DESIGNATION	GENOTYPE	T oreti al value	Observed value
l № 19	aa bb cc dd ee ff gg hh ii	122 days	123 days
l № 10	aa bb C_2C_2 D_2D_2 E_8E_- F_4F_- gg hh ii	102 ″	102 ″
F_1 № 19 x № 10	aa bb C_2c D_2d E_8e_- F_4f_- gg hh ii	106 ″	104 ″
l № 11	aa $B_{16}B_-$ C_2C_2 D_2D_2 E_8E_- F_4F_- gg hh ii	86 ″	87 ″
F_1 № 10 x № 11	aa $B_{16}b_-$ C_2C_2 D_2D_2 E_8E_- F_4F_- gg hh ii	86 ″	87,2 ″
l № 20	aa bb cc dd E_8E_- ff gg hh ii	116 ″	116 ″
F_1 № 20 x № 11	aa $B_{16}b$ C_2c D_2d E_8E_- F_4f_- gg hh ii	90 ″	92 ″
l № 25	$A_{14}A_-$ $B_{16}B_-$ cc D_2D_2 E_8E_- F_4F_- G_4G_- H_1H_- ii	71 ″	70,75 ″
l № 23	$A_{14}A_-$ $B_{16}B_-$ cc D_2D_2 E_8E_- ff G_4G_- hh $I_{10}I_-$	66 ″	66 ″
F_1 № 25 x № 23	$A_{14}A_-$ $B_{16}B_-$ cc D_2D_2 E_8E_- F_4f_- G_4G_- H_1h_- $I_{10}i_-$	61 ″	61,8 ″

* Letters C and D refer to genes exhibiting blending inheritance.

In order to estimate the relationship between the earliness of crossed parents and the vigorous growth of their F_1 hybrids the correlation coefficient was computed for the arithmetic mean of the number of days from seeding to pollen shedding of both parents and the height of their F_1 hybrid. The value of the correlation coefficient, $r = 0.905 \pm 0.03$ shows a strong correlation between these traits. The later the crossed parental types are the more vigorous is the F_1 hybrid. Figure 2 shows from left to right the vigorous line No. 10, the F_1 generation, the parental lines W9 and WD.

In general the phenomenon of vigorous growth of hybrids exhibiting heterosis may be considered from the point of view of the increase of the intensity of metabolic processes. The higher the amount of growth substances present in plants the stronger they will act.

Fig. 2. The vigorous line No. 10, the F_1 generation, the parental lines W9 and WD (shown from left to right)

It may be assumed that after crossing a certain parental form, containing a precursor of a defined growth substance, with a parental form, possessing a complementary factor, which in cooperation with the precursor in their F_1 hybrid gives rise to a specific growth substance, heterosis occurs. This promotes a stronger development of the root system and a more intensive growth of vegetative parts.

The experimental data suggest that in the case of heterosis we have to do with a small number of genes complementing each other in such a manner, that a more intensive growing rate of longer duration assures vigorous growth.

It would be of great interest to examine the effects of factors responsible for the metabolic processes leading to heterosis. This could give an interesting view — point in the interpretation of this phenomenon. A biochemical approach to this problem could bring results of considerable practical use.

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STRESZCZENIE

Przekrzyżowano między sobą 21 linii wsobnych kukurydzy pochodzenia amerykańskiego. Uwzględniono w badaniach tylko takie krzyżówki, które wykazały w F_1 heterozję. Najdalej posunięte są badania nad krzyżówką między liniami wsobnymi WD i W9. Prowadząc selekcję w potomstwie najbujniejszych osobników F_2 wyodrębniono linie przekraczające rozmiarami mieszańce F_1. W oparciu

o przeprowadzone doświadczenia w blokach losowanych stwierdzono, że różnice między linią z dziedzicznie utrwaloną bujnością, między F_1 i formami rodzicielskimi są statystycznie udowodnione. Na podstawie krzyżowania linii wsobnych (27 krzyżówek) różniących się między sobą wczesnością stwierdzono, że przy różnicy przekraczającej 10 dni mieszańce F_1 nie wykazują heterozji wczesności. Heterozję wczesności można wyjaśnić przyjmując występowanie genów dominujących, zmniejszających liczbę dni od siewu do momentu pylenia; obok tego występują geny kumulatywne o dziedziczeniu pośrednim, biorące udział w wyznaczaniu długości tego okresu. W przypadku występowania heterozji, wyrażonej bujnością, wchodzi w grę niewielka liczba dopełniających się czynników dziedzicznych, warunkujących bujność.

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