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Genetic Analysis of Seed-Weight in Reciprocal Crosses of Flax (*Linum usitatissimum* L.)

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Summary. Materials used in this study consisted of small and large seeded flax varieties Redwing and Beta 210, and of their reciprocal crosses and backcrosses. The seed weight means (mg's/seed) of reciprocal crosses were the same in F_1 but significantly different in F_2 and F_3 generations indicating thus their nonequivalence with respect to this character. This nonequivalence was detectable also in the backcross reciprocals. On the assumption that Redwing and Beta 210. have different plasmatypes and the hybrid has the same plasmatype as its female parent, the available 24 families, including the parents as selfs, were grouped into two genomically the same but plasmatically supposedly different sets. A detailed analysis of the family means in these two sets led to the conclusion that the inheritance of the character considered was rather complicated. In F_1 generation the Beta 210 set of genes was partially dominant over its allelic Redwing set ($[h] < [d]$). In the subsequent generations the Beta 210 set of genes has sustained a certain degree of loss of expressivity. This loss was 73% in the plasmatypically Redwing set of families and 20% in the plasmatypically Beta 210 set of families. This difference in the loss of expressivity and the gene-dosis effects, detected mainly in the plasmatypically Beta 210 set of families, indicated that the nature of the reciprocal cross nonequivalence observed in this study was both cytoplasmic and nuclear.

Introduction

The mode of the inheritance of seed weight in reciprocal crosses of flax (*Linum usitatissimum* L.) dealt with in this study, has been briefly reported by Smith and Fitzsimmons (1964, 1965). In their 1965 paper the authors have pointed out that the seed weight in the reciprocal flax crosses they were dealing with, was inherited in a manner similar to that reported by Chandraratna and Sakai (1960) for reciprocal rice crosses. As in rice, the seed weight differences between the reciprocals appeared to be controlled both plasmatypically and genotypically. However, in contrast with rice, the nonequivalence of reciprocals with respect to seed size, expressed itself beginning with the second and not the first filial generation. This failure of expression of reciprocal differences in the F_1 generation was not explained satisfactorily at that time.

Materials and Methods

At the time when the typescript of the previous paper (1965) was submitted for publication, the compilation of data on seed-weight was not complete. For the present paper all the seed-weight data obtained for flax varieties Redwing and Beta 210, and for their reciprocal crosses and backcrosses were used. All the family means, including those for which there were no additional data, were calculated anew. The standard errors of the generation, or family, means were obtained from the corresponding "within family – between plot" variances. It was assumed that the parents Redwing and Beta 210 were different for seed-weight both plasmatypically and genotypically, and that the hybrid and its female parent had the same plasmatype. Therefore, the families were grouped into two supposedly plasmatypically different sets, as given in Table 1, where "set of $\pi(R)$ families" and "set of $\pi(B)$ families" refer, respectively, to families assumed to have the same plasmatype as Redwing (R) and to those assumed to have the same plasmatype as Beta 210 (B). The formulation of the genetic models and the analysis of family means followed the patterns discussed theoretically by Aksel (1974), where the two sets of reciprocal families were expressed idiotypically in a generalized form, as $\{\pi(A), \cup_k \{a, b\}_k\}$ and $\{\pi(B), \cup_k \{a, b\}_k\}$. In these expressions π stands for plasmatype, $\cup_k\{a\}_k$ = set of alleles contributed by parent A and $\cup_k\{b\}_k$ = set of alleles contributed by parent B. In the present case $A = R$ (Redwing) and $B = B$ (Beta 210). Consequently, we shall write $\cup_k\{r\}_k$ instead of $\cup_k\{a\}_k$.

Experimental Results

From the data in Table 1 it is obvious that the seed-weight means of the varieties Redwing and Beta 210, referred to hereafter as R and B, are different, and that the means of reciprocal crosses (RB) and (BR) in the first filial generation are the same, viz., $\bar{x}(RB)\ F_1 - \bar{x}(BR)\ F_1 = 0.12 \pm 0.13^{ns}$. With this information alone one would be inclined to conclude that the parents R and B were genotypically different but plasmatypically the same with respect to seed-weight. Such a conclusion would be valid if the equality of the seed-weight means of reciprocals were preserved in the subsequent generations of selfing. The differences $\bar{x}(RB)\ F_2 - \bar{x}(BR)\ F_2 = -1.60 \pm 0.29^{***}$ [1] and $\bar{x}(RB)\ F_3 - \bar{x}(BR)\ F_3 = -1.11 \pm \pm 0.15^{**}$ calculated from the data (Table 1) show this not to be so. This quantitative genetic nonequivalence of the reciprocals, which in the present case

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[1] In the text: $*** = P < 0.01$; $** = 0.01 < P < < 0.02$; $* = 0.02 < P < 0.05$ and $ns = P > 0.05$ (usually).

Table 1. *Mean Seed-Weights of Redwing (R) and Beta 210 (B) and of their Reciprocal Crosses and Backcrosses*

$\pi(R)$ Set of Families	No. of Plots[1]	Mean Seed-Weight (mg)	$\pi(B)$ Set of Families	No. of Plots	Mean Seed-Weight (mg)
R (self)	30	4.91 ± 0.04	B (self)	23	9.51 ± 0.23
(RB) F_1	6	8.13 ± 0.08	(BR) F_1	6	8.01 ± 0.08
(RB) F_2	3	6.09 ± 0.28	(BR) F_2	2	7.69 ± 0.07
(RB) F_3	18	5.84 ± 0.10	(BR) F_3	20	6.95 ± 0.11
$[R(RB)]$ F_1	11	5.74 ± 0.15	$[B(BR)]$ F_1	6	9.35 ± 0.16
$[R(RB)]$ F_2	5	5.20 ± 0.15	$[B(BR)]$ F_2	5	8.88 ± 0.28
$[R(BR)]$ F_1	4	5.88 ± 0.12	$[B(RB)]$ F_1	12	9.00 ± 0.13
$[R(BR)]$ F_2	5	5.27 ± 0.19	$[(B(RB)]$ F_2	5	7.92 ± 0.30
$[(RB)\ R]$ F_1	10	5.77 ± 0.18	$[(BR)\ B]$ F_1	6	9.10 ± 0.14
$[(RB)\ R]$ F_2	5	5.73 ± 0.19	$[(BR)\ B]$ F_2	5	8.67 ± 0.25
$[(RB)]$ F_1	12	8.79 ± 0.13	$[(BR)\ R]$ F_1	6	5.99 ± 0.06
$[(RB)]$ F_2	5	7.83 ± 0.18	$[(BR)\ R]$ F_2	5	5.71 ± 0.11

[1] The parental, F_2 and F_3 plots were considerably larger than those of F_1's ($\neq 40-100$ plants as compared to $7-9$ plants, respectively). The entire experiment consisted of 6438 plants.

manifested itself beginning with the F_2 generation, implies that the parents R and B probably differ with respect to seed weight both genotypically and plasmatypically. Furthermore,

$$\bar{x}(RB)\ F_2 - \left(\frac{1}{4}\right)[\bar{x}(R) + 2\bar{x}(RB)\ F_1 + \bar{x}(B)] = = -1.58 \pm 0.29^{***} \tag{1}$$

but

$$\bar{x}(BR)\ F_2 - \left(\frac{1}{4}\right)[\bar{x}(R) + 2\bar{x}(BR)\ F_1 + \bar{x}(B)] = = 0.08 \pm 0.10^{nx}\,. \tag{2}$$

Since the reciprocal crosses $R \times B$ and $B \times R$ involve the same set of differential loci, the disagreement between the differences (1) and (2) confirms the plasmatypic inequality of the parents R and B [$\pi(R) \neq \pi(B)$ in Aksel's (1974) notation]. It also indicates that the set of genes contributed by B to $R \times B$ hybrids has been affected by $\pi(R)$ but its allelic set contributed by R to $B \times R$ hybrids has not been affected by $\pi(B)$. In other words, since $\bar{x}(RB)\ F_1 - \bar{x}(BR)\ F_1 = 0.12 \pm 0.13^{ns}$ and the difference (2) $= 0.08 \pm 0.10^{ns}$, the difference (1) $= = -1.58 \pm 0.29^{***}$ has to be attributed to both $\pi(R) \neq \pi(B)$ and the $\{\pi(R),\ \upsilon_k\{r\}_k\}$ — sensitivity of the set of genes contributed by B to the $R \times B$ hybrids, and not to epistasis. Let us consider the two sets of families individually.

Set of $\pi(R)$ families. In regard to this set it is assumed that the differential genes of B were affected in $\pi(R)$ when contributed either by (RB) F_1 or $(BR)F_1$, and were not affected when contributed directly by B itself (Aksel 1974, assumption 6c). Consequently, the system of linear equations for this set will be as given in Table 2, where the parameters m, $[d]$ and $[h]$ have the usual meaning (see, e.g., Mather and Jinks 1971), the parameters $\Delta_{[d]}$ refer to the effect of $\pi(R)$ on differential genes of B when heterozygous and homozygous respectively, the weights are reciprocals of the squares of standard errors of the respective family means and the ε's are the differences between the expected and the observed family means. The weighted least square solution of the system of equations given in Table 2 gives:

$$m = 7.20 \pm 0.11^{***}\,,$$
$$[d] = 2.30 \pm 0.11^{***}\,,$$
$$[h] = 0.93 \pm 0.15^{***}\,,$$
$$([h] - \Delta_{[h]}) = -0.54 \pm 0.21^{*}\,,$$
$$\Delta_{[d]} = 3.37 \pm 0.37^{***}\,.$$

The expected family means were obtained by substituting the estimates of the parameters m, $[d]$, $j = ([h] - \Delta_{[h]})$ and $\Delta_{[d]}$ in the corresponding equation in Table 2. The observed mean of the ith family ($i = 1, 2, \ldots, 12$) deviates from its expected value by ε_i. The adequacy of the genetical model was tested by $\chi^2 = \sum_i w_i\, \varepsilon_i^2$ with $n - k$ degrees of freedom ($n =$ no. of equations, $k =$ np. of parameters to be fitted to them). The data in this particular case fits the model: $\chi^2 = 7.8393$; $DF = 7$; $0.30 < P < 0.50$.

Set of $\pi(B)$ families. It was shown that

$$\bar{x}(BR)\ F_1 - \bar{x}(RB)\ F_1 \simeq 0$$

and

$$\bar{x}(BR)\ F_2 - \left(\frac{1}{2}\right)\bar{x}(BR)\ F_1 - \left(\frac{1}{4}\right)[\bar{x}(R) + \bar{x}(B)] \simeq 0\,,$$

i.e., as far as the F_1 and F_2 generations of the $B \times R$ cross are concerned, there was no indication of $\pi(B)$ effect on $U_k\{r\}_k$ or of non-allelic interaction. Consequently, $\bar{x}(BR)\ F_3$ and its expected value

$$\left(\frac{1}{4}\right)[\bar{x}(R) + 2\bar{x}(BR)\ F_2 + \bar{x}(B)]\,,$$

or

$$\left(\frac{1}{8}\right)[3\bar{x}(R) + 2\ (BR)\ F_1 + 3\bar{x}(B)]\,,$$

would be the same. However, this happens not to be the case, since the pertinent data from Table 1

Table 2. *The System of Linear Equations for the Set $\pi(R)$ Families*

i	Family	Weight (w_i)	Equations of Differences
1	R (self)	625	$m - [d] - 4.91 = \varepsilon_1$
2	(RB) F_1	156	$m + [h] - 8.13 = \varepsilon_2$
3	(RB) F_2	13	$m + \left(\frac{1}{2}\right)([h] - \Delta_{[h]}) - \left(\frac{1}{4}\right)\Delta_{[d]} - 6.09 = \varepsilon_3$
4	(RB) F_3	100	$m + \left(\frac{1}{4}\right)([h] - \Delta_{[h]}) - \left(\frac{3}{8}\right)\Delta_{[d]} - 5.84 = \varepsilon_4$
5	$[(RB)\ R]$ F_1	31	$m - \left(\frac{1}{2}\right)[d] + \left(\frac{1}{2}\right)([h] - \Delta_{[h]}) - 5.77 = \varepsilon_5$
6	$[(RB)\ R]$ F_2	28	$m - \left(\frac{1}{2}\right)[d] + \left(\frac{1}{4}\right)([h] - \Delta_{[h]}) - \left(\frac{1}{8}\right)\Delta_{[d]} - 5.73 = \varepsilon_6$
7	$[R(RB)]$ F_1	45	$m - \left(\frac{1}{2}\right)[d] + \left(\frac{1}{2}\right)([h] - \Delta_{[h]}) - 5.74 = \varepsilon_7$
8	$[R(RB)]$ F_2	45	$m - \left(\frac{1}{2}\right)[d] + \left(\frac{1}{4}\right)([h] - \Delta_{[h]}) - \left(\frac{1}{8}\right)\Delta_{[d]} - 5.20 = \varepsilon_8$
9	$[R(BR)]$ F_1	59	$m - \left(\frac{1}{2}\right)[d] + \left(\frac{1}{2}\right)([h] - \Delta_{[h]}) - 5.88 = \varepsilon_9$
10	$[R(BR)]$ F_2	28	$m - \left(\frac{1}{2}\right)[d] + \left(\frac{1}{4}\right)([h] - \Delta_{[h]}) - \left(\frac{1}{8}\right)\Delta_{[d]} - 5.27 = \varepsilon_{10}$
11	$[(RB)\ B]$ F_1	51	$m + \left(\frac{1}{2}\right)[d] + \left(\frac{1}{2}\right)[h] - 8.79 = \varepsilon_{11}$
12	$[(RB)\ B]$ F_2	31	$m + \left(\frac{1}{2}\right)[d] + \left(\frac{1}{4}\right)([h] - \Delta_{[h]}) - \left(\frac{1}{8}\right)\Delta_{[d]} - 7.83 = \varepsilon_{12}$

gives:

$$\bar{x}(BR)\ F_3 - \left(\frac{1}{4}\right)[\bar{x}(R) + 2\bar{x}(BR)\ F_2 + \bar{x}(B)] = \\ = -0.50 \pm 0.13^{***}$$

and, similarly,

$$\bar{x}(BR)\ F_3 - \left(\frac{1}{8}\right)[3\bar{x}(R) + 2\bar{x}(BR)\ F_1 + 3\bar{x}(B)] = \\ = -0.46 \pm 0.14^{***}\,.$$

This result is similar to that observed in F_2 generations of the $R \times B$ cross, with the difference that there is no $\pi(R)$ effect to supplement the effect of $\upsilon_k\{r\}_k$ on $\upsilon_k\{b\}_k$, that the onset of the $\upsilon_k\{r\}_k$ effect is delayed for one more generation (F_3 instead of F_2) and that this effect is less pronounced, viz., $-0{,}46 \pm 0.14$ ($P < 0.01$) for (BR) F_3 as compared to

$$\bar{x}(RB)\ F_3 - \left(\frac{1}{8}\right)[3\bar{x}(R) + 2\bar{x}(RB)\ F_1 + 3\bar{x}(B)] = \\ = -1.60 \pm 0.13^{***}\,.$$

The genetic situation in the backcrosses appears to be complicated by gene-dosis effects and by the effects of paternal plasmatype. The effects of the dosis of $\upsilon_k\{r\}_k$ on the expressivity of its allelic set $\upsilon_k\{b\}_k$ in the $[(BR)\ R]$ backcross are:

$$\bar{x}[(BR)\ R]\ F_1 - \left(\frac{1}{2}\right)[\bar{x}(R) + \bar{x}(BR)\ F_1] = \\ = -0.47 \pm 0.07^{***}$$

and

$$\bar{x}\ [(BR)\ R]\ F_2 - \left(\frac{1}{2}\right)[\bar{x}(R) + \bar{x}(BR)\ F_2] = \\ = -0.59 \pm 0.12^{***}\,.$$

The backcrosses $[B(BR)]$ and $[(BR)\ B]$ both obtain $\upsilon_k\{r\}_k$ from a male parent having $\pi(B)$, whereas the backcross $[B(RB)]$ obtains $\upsilon_k\{r\}_k$ from a (RB) F_1 male which has $\pi(R)$. Assuming $\upsilon_k\{b\}_k$ contributed by (RB) F_1 to have been affected by $\upsilon_k\{r\}_k$, the latter backcross would be expected to differ from the former two, which because of their idiotypic equality have to be the same. The means of $[B(BR)]$ F_1 and $[(BR)\ B]$ F_1, and of $[B(BR)]$ F_2 and $[(BR)\ B]$ F_2 are respectively, 9.22 ± 0.11 and 8.77 ± 0.15. The effects of the doses of $\upsilon_k\{b\}_k$ on its allelic set $\upsilon_k\{r\}_k$ in these backcrosses are:

$$(9.22 \pm 0.11) - \left(\frac{1}{2}\right)[(9.51 \pm 0.23) + (8.01 \pm 0.08) = \\ = 0.46 \pm 0.16^{***}$$

and

$$(8.77 \pm 0.15) - \left(\frac{1}{2}\right)[(9.51 \pm 0.23) + (7.69 \pm 0.07) = \\ = 0.17 \pm 0.19^{ns}$$

in the F_1 and the F_2 generations, respectively. Consequently, in the F_1 generation the effects of the doses of $\upsilon_k\{r\}_k$ and $\upsilon_k\{b\}_k$ are $(-0.47 \pm 0.07^{***}) \simeq \simeq (-1)\ (0.46 \pm 0.16^{***})$, whereas in F_2 generation they are $(-0.59 \pm 0.12^{***}) \neq (-1)$ (0.17 ± 0.19^{ns}). The tests for gene-dosis effect in the $[B(RB)]$ backcross obtains 0.24 ± 0.19^{ns} and $-0.68 \pm 0.32^{*}$ in the F_1 and the F_2 generations respectively. This fairly detailed analysis of the set of $\pi(B)$ families shows that it is reasonable to postulate the following: when acting under $\pi(B)$ conditions the gene set $\cup_k\{r\}_k$ affects its allelic set $\cup_k\{b\}_k$ in the $B \times R$ cross beginning with the F_3 generation and in the backcrosses beginning with the F_2 generation, except for the backcross $[B(RB)]$ where it acts beginning with the F_1 generation. Consequently, the equations for the expected observed family mean differences can be formulated as given in Table 3, where the parameters $\delta_{[h]}$ and $\delta_{[d]}$ pertain to gene-dosis effects.

A weighted least square solution of the system of linear equations given in Table 3 gives:

$$m = 7.21 \pm 0.11^{***}$$
$$[d] = 2.30 \pm 0.25^{***}$$
$$[h] = 0.82 \pm 0.17^{***}$$
$$\Delta_{[h]} = 0.66 \pm 0.31 \quad (0.05 < P < 0.10)$$
$$\Delta_{[d]} = 0.94 \pm 0.37 \quad (P \simeq 0.05)$$
$$\delta_{[h]} = 0.97 \pm 0.29^{**}$$
$$\delta_{[d]} = -0.33 \pm 0.95 \quad (P > 0.50)$$

It was found that $\chi^2 = \sum_i w_i\varepsilon_i^2 = 7.386$ $(DF = 5;$ $0.10 < P < 0.20)$ which shows that there is a fairly good agreement between the expected and the observed values of family means. Both $\Delta_{[h]}$ and $\Delta_{[d]}$ are different from zero with a reasonable degree of reliability $(0.05 < P < 0.10)$. Consequently, it may be said that the gene-set $\cup_k\{r\}_k$ of Redwing has affected the expressivity of the allelic set $\cup_k\{b\}_k$ contributed by Beta 210 even when acting under the $\pi(B)$ conditions, but its effect is delayed for one generation and is considerably less pronounced than that of the $\{\pi(R), \cup_k\{r\}_k\}$ complex in the set of $\pi(R)$ families where $([h] - \Delta_{[h]}) - [h] = \Delta_{[h]} = 1.47$ and $\Delta_{[d]} = 3.37 \pm 0.37^{***}$. The parameters $\delta_{[h]} = 0.97 \pm 0.29^{*}$ and $\delta_{[d]} = -0.33 \pm 0.95$ $(P > 0.5)$ show that in the $\pi(B)$ families the expressivities of the allelic sets $\cup_k\{r\}_k$ and $\cup_k\{b\}_k$ were affected by gene-dosis when heterozygous only.

Discussion of the Results and Conclusions

The analysis of the experimental data has shown that the reciprocal crosses between the flax varieties Redwing (R) and Beta 210 (B) were not equivalent with respect to seed weight. This nonequivalence expressed itself phenotypically in the reciprocal crosses beginning with the F_2 generation, and in the backcrosses and their reciprocals beginning with the F_1 or the F_2 generation. As expected, the estimated values of the parameters m, $[d]$ and $[h]$ in the $\pi(R)$ set of families were not significantly different from those in the $\pi(B)$ set of families, the corresponding

Table 3. *The System of Linear Equations for the Set of $\pi(B)$ Families*

i	Family	Weight (w_i)	Equations of Differences
1	B (self)	19	$m + [d] - 9.51 = \varepsilon_1$
2	(BR) F_1	156	$m + [h] - 8.01 = \varepsilon_2$
3	(BR) F_2	204	$m + \left(\frac{1}{2}\right)[h] - 7.69 = \varepsilon_3$
4	(BR) F_3	83	$m + \Big(\frac{1}{4}[h] - \left(\frac{1}{4}\right)\Delta_{[h]} - \left(\frac{3}{8}\right)\Delta_{[d]} - 6.95 = \varepsilon_4$
5	$[(BR)\ B]$ F_1	51	$m + \left(\frac{1}{2}\right)[d] + \left(\frac{1}{2}\right)[h] + \left(\frac{1}{2}\right)\delta_{[h]} - 9.10 = \varepsilon_5$
6	$[(BR)\ B]$ F_2	16	$m + \left(\frac{1}{2}\right)[d] + \left(\frac{1}{4}\right)[h] + \left(\frac{1}{4}\right)\delta_{[h]} + \left(\frac{1}{8}\right)\delta_{[d]} - 8.67 = \varepsilon_6$
7	$[B(BR)]$ F_1	39	$m + \left(\frac{1}{2}\right)[d] + \left(\frac{1}{2}\right)[h] + \left(\frac{1}{2}\right)\delta_{[h]} - 9.35 = \varepsilon_7$
8	$[B(BR)]$ F_2	13	$m + \left(\frac{1}{2}\right)[d] + \left(\frac{1}{4}\right)[h] + \left(\frac{1}{4}\right)\delta_{[h]} + \left(\frac{1}{8}\right)\delta_{[d]} - 8.88 = \varepsilon_8$
9	$[B(RB)]$ F_1	59	$m + \left(\frac{1}{2}\right)[d] + \left(\frac{1}{2}\right)[h] - \left(\frac{1}{2}\right)\Delta_{[h]} + \left(\frac{1}{2}\right)\delta_{[h]} - 9.00 = \varepsilon_9$
10	$[B(RB)]$ F_2	11	$m + \left(\frac{1}{2}\right)[d] + \left(\frac{1}{4}\right)[h] - \left(\frac{1}{4}\right)\Delta_{[h]} - \left(\frac{1}{8}\right)\Delta_{[d]} + \left(\frac{1}{4}\right)\delta_{[h]} + \left(\frac{1}{8}\right)\delta_{[d]} - 7.92 = \varepsilon_{10}$
11	$[(BR)\ R]$ F_1	278	$m - \left(\frac{1}{2}\right)[d] + \left(\frac{1}{2}\right)[h] - \left(\frac{1}{2}\right)\delta_{[h]} - 5.99 = \varepsilon_{11}$
12	$[(BR)\ R]$ F_2	83	$m - \left(\frac{1}{2}\right)[d] + \left(\frac{1}{4}\right)[h] - \left(\frac{1}{4}\right)\Delta_{[h]} - \left(\frac{1}{8}\right)\Delta_{[d]} - \left(\frac{1}{4}\right)\delta_{[h]} - \left(\frac{1}{8}\right)\delta_{[d]} - 5.71 = \varepsilon_{12}$

differences being -0.01 ± 0.06, 0.00 ± 0.27 and 0.21 ± 0.23.

The difference $(1/2)\ \Delta_{[d]} - \Delta_{[h]}$ tests the effect of the state of zygosity of the paternal set of alleles on the degree of its loss of expressivity. Since in the analysis of the $\pi(R)$ set of families the parameter $\Delta_{[h]}$ appears as a component of the parameter $([h] - \Delta_{[h]})$ this test was made by calculating the value and the standard error of the function $y = (1/2)\ \Delta_{[d]} + ([h] - \Delta_{[h]}) - [h]$ (Re. standard error of a function, see, e.g., Chebotareff 1958). Obviously y and $(1/2)\ \Delta_{[d]} - \Delta_{[h]}$ are equivalent. In this particular case $y = 0.22 \pm 0.30^{ns}$, and it can be said that the loss of expressivity by the paternal set of alleles in the $\pi(R)$ set of families was the same whether homozygous or heterozygous.

In the $\pi(B)$ set of families the paternal set of genes i.e., the set contributed by Redwing, has not been affected in its expressivity. On the contrary in (BR) F_3, in $[B(RB)]$ F_1 and F_2, and in $[(BR)\ R]$ F_2 it has adversely affected the expressivity of its allelic (maternal) set ($\Delta_{[d]} = 0.97$ and $\Delta_{[h]} = 0.66$; $0.05 < P < 0.10$) and this without being supplemented by $\pi(R)$ as in the case of $\pi(R)$ set of families. The difference $(1/2)\ \Delta_{[d]} - \Delta_{[h]} = -0.19 \pm 0.38^{ns}$ shows that the state of zygosity of the maternal set of alleles has not influenced the degree of its loss of expressivity.

The difference between $\Delta_{[h]}$ and $(1/2)\ \Delta_{[d]}$ is not significant statistically in either set of families; hence $\Delta_{[d]}$ may be used alone to derive the conclusion that $100\ [(\Delta_{[d]}/\pi(R)) - (\Delta_{[d]}/\pi(B)) \div (\Delta_{[d]}/\pi(R))] = 72\%$ of the loss of expressivity by the set of differential genes of Beta 210 in the $\pi(R)$ set of families can be attributed to the influence of Redwing cytoplasm and the remaining 28% to that of the set of Redwing alleles. Consequently, the source of the nonequivalence of the reciprocal Redwing — Beta 210 crosses can be considered as being both cytoplasmic and nuclear.

The relative effects of loss of expressivity by Beta 210 genes in the $\pi(R)$ and $\pi(B)$ sets of families are $\Delta_{[d]} \div 2[d] = 0.73$ and $\Delta_{[d]} \div 2[d] = 0.20$ respectively, i.e., the effect of $\{\pi(R), \cup_k\{r\}_k\} \subset \{\pi(R)\ \cup_k\{r, b\}_k\}$ on $\cup_k\{b\}_k$ is nearly four times that of $\cup_k\{r\}_k \subset \{\pi(B)\ \cup_k\{r, b\}_k\}$. By postulating the assumption of equality of gene effects, one could say that in the $\pi(R)$ set of families $\simeq 75\%$ of the Beta 210 genes have completely lost their expressivity. The respective figure for the $\pi(B)$ set of families is 20%. Provided that the, possibly unlikely, case of equality of gene-effects is true, the number of genes controlling the seed-weight difference between Redwing and Beta 210 must be either four or five or a multiple of either number. (Note that $75\% = 100\% \times 3/4$ and, $20\% = 100\% \times 1/5$.)

The presence of gene doses effects was revealed both by direct comparisons of the Mather's (1949) scaling test type and by the weighted least square solution of the system of linear equations implied by the $\pi(B)$ set of families.

Zusammenfassung

Als Material für die vorstehenden Untersuchungen wurden die kleinkörnige Leinsorte Redwing, die großkörnige Beta 210 und ihre reziproken Kreuzungen und Rückkreuzungen verwendet. Die Mittelwerte des Samengewichtes (in mg/Samen) der reziproken Kreuzungen waren in der F_1 gleich, unterschieden sich jedoch in der F_2 und F_3, ebenso wie in den reziproken Rückkreuzungen, signifikant voneinander und zeigten damit eine Ungleichwertigkeit hinsichtlich dieses Merkmals auf.

Ausgehend von der Annahme, daß Redwing und Beta 210 unterschiedliche Plasmotypen besitzen und der Bastard im Plasmotyp dem mütterlichen Elter entspricht, wurden die verfügbaren 24 Familien einschließlich der Selbstungen der Eltern in zwei genomatisch gleiche, jedoch plasmatisch unterschiedliche Gruppen klassifiziert. Eine detaillierte Analyse der Familienmittel innerhalb der Gruppen führt zu dem Schluß, daß die Vererbung des betrachteten Merkmals verhältnismäßig kompliziert ist. In der F_1 war die Menge der Beta 210-Gene über die allele Menge der Redwing-Gene partiell dominant ($[h] < [d]$). In den folgenden Generationen erleidet die Menge der Beta 210-Gene eine gewisse Einbuße an Expressivität. Dieser Verlust beträgt 73% in den Familien des Plasmotyps Redwing und 20% in den Familien des Plasmotyps Beta 210. Dieser Unterschied im Verlust der Expressivität und die Dosiseffekte, die vornehmlich in den Familien mit dem Plasmotyp Beta 210 nachgewiesen werden, zeigen, daß die Ursache der Ungleichwertigkeit der reziproken Kreuzungen sowohl plasmatisch als auch kernbedingt ist.

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