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Genetica. — *The inheritance of necrotic lesions in «Zea mays» (blotch leaf) as a single factor linked to «wx».* Nota di ACHILLE GHIDONI, presentata (*) dal Corrisp. C. BARIGOZZI.

RIASSUNTO. — Una anormalità nelle foglie di mais, consistente nella presenza di numerose aberrazioni necrotiche dei tessuti che appaiono come piccole chiazze circondate da un alone giallognolo, è un carattere ereditabile, alla cui base sta una singola coppia di fattori *Bl, bl*.

Negli incroci eseguiti con vari testers normali il carattere descritto si manifesta in molti casi nella F_1. Ciò dimostra che l'allele responsabile delle chiazze necrotiche è parzialmente dominante sul tipo selvatico. I dati raccolti in reincroci e in F_2 indicano che questo gene segrega indipendentemente dal gene *su* (cromosoma 4), e che esso è probabilmente associato a *wx* nel cromosoma 9.

Necrotic lesions occurring in certain stocks of maize mainly in leaf blades and sheets have been described by Emerson (1923) as an inherited character. They usually begin to appear by the time the plants are in the fourth leaf stage in the distal region of the leaf blade as a few yellowish dots rapidly increasing in number and size, soon degenerating into spots of dead tissue. A yellowish halo may spread and persist in the surrounding tissues, giving an unhealthy aspect to the subjects affected by this character. The blotches at first sight seem to be similar to those caused by the infection of *Helminthosporium*, although no pathogen has been isolated in association with this character. Within the same plant the blotches may vary in size from small dots, barely resoluble, to spots of a few millimeters, elliptically shaped lengthwise; the number of blotches is usually high and may be rather uniform, or vary in relation to the younger or older parts of the plant. Greater variations in the expression of the blotch leaf character were found from plant to plant in response to the genetic background as well as to the environmental conditions such as light intensity. Inheritance of the blotch leaf character, according to Emerson (1923), is based on a single pair of alleles of which the recessive was found to be responsible for the abnormal phenotype in the experimental conditions reported. However, Emerson pointed out that some F_1 plants occasionally revealed the blotch leaf character. The gene symbol assigned to it is *Bl, bl* and this gene was not placed on the map by Emerson or by other workers. Inherited traits of similar nature include: a *blotch leaf* linked to chromosome 2 (Neuffer and Coe, 1968); bl_2 (R. G. Wiggams, unpublished, cited by Weijer, 1952): *necrotic leaf spot*, allelic to zn_1 zebra necrotic (Hornbroock and Gardner, 1970; Gardner, 1971), a recessive beginning to be expressed from the 5th leaf stage on; *leaf fleck* lf_1 (Brewba-

(*) Nella seduta del 12 maggio 1973.

ker, 1970), recessive, not placed on the map; *leaf fleck disease*, for which a cytoplasmic inheritance factor and a seed-borne viral agent were proposed by Atanasoff (1955; 1966).

The present paper concerns the inheritance, and provides a preliminary indication of linkage, of a blotch leaf gene whose action on phenotype is very similar in many respects to that described by Emerson.

MATERIAL AND METHODS

Two stocks (A and B) of sweet corn known to carry a clorophyll abnormality in the form of necrotic blotches were given to the Author one by K. V. Rinehart and to other by E. B. Doerschug at the Indiana University in 1967. The *blotch leaf* phenotype appeared very similar in both stocks; and a similar behaviour of this character was observed in the preliminary breeding experiments. The two stocks were not followed separately since they probably carried the same genetic condition.

In the summer of 1969 a chromosome 2 tester (lg_1, gl_2, v_4) was crossed with the blotched plants as the female parent following the report of a *blotch leaf* trait linked with chromosome 2 (Neuffer and Coe, 1968). Many F_1 individuals raised in 1970 were blotched but these could not be backcrossed to the tester which failed to nick. However, plants homozygous for the blotch leaf character were crossed in 1970, as the pollen parent, to a set of translocations all marked *wx*, each involving chromosome 9 and another chromosome, in order to place on the map what was supposed to be a single factor involved in the blotch leaf phenotype. The translocation used in these crosses were the following:

T 1–9 "8389", T 2–9 b, T 3–9 c, T 4–9 "5657", T 4–9 b, T 4–9 g, T 5–9 a, T 5–9 c, T 5–9 d, T 6–9 a, T 6–9 b, T 7–9 a "4363", T 8–9 "6673", T 8–9 d, T 9–10 b.

These translocations came from the Maize Genetics Cooperative and the Author had access to them in the field of Prof. G. Gavazzi.

Many blotched plants appeared in the F_1 (between homozygous blotched and non blotched individuals of the translocation stocks) in all crosses, although the expression varied from family to family. This fact suggested crossing the F_1 *blotched* with *non blotched*, *wx* testers. F_2 progenies of F_1 blotched subjects were also obtained.

After obtaining F_2 progenies and the test cross progenies described in the previous section, classifications were made for the phenotypes *blotched*, *non blotched*, *Ww* , *wx*, and *Su* , *su*.

Classification:

Wx = starchy endosperm, blue staining with Lugol's liquid;
wx = waxy endosperm, brown staining with Lugol's liquid;
Su = starchy, smooth endosperm;

su = sugary, wrinkly endosperm;
Bl = *blotch leaf* = necrotic lesions with yellowish halo (incompletely dominant);
bl = *non blotch leaf* = green leaves with no necrotic lesions.

The classification of blotched plants was done partly in the field, partly in the greenhouse: the different environmental conditions did not seem to greatly affect the results.

RESULTS

The following were the outcome of preliminary crosses:

PARENTS AND CROSSES	PROGENY
Blotched A, selfed	Blotched and non blotched in variable proportions
Blotched B, selfed	Blotched and non blotched in variable proportions
Blotched A × blotched B	Blotched and non blotched in variable proportions
Non blotched A × non blotched B	Blotched and non blotched with an excess of non blotched
Blotched A × non blotched B	Blotched and non blotched with an excess of non blotched
Non blotched A × blotched B	Blotched and non blotched with an excess of non blotched

The appearance of many blotched F_1 individuals, although frequency and intensity of expression varied in different crosses, showed that the *blotch leaf* gene is dominant, though incompletely. Table I reports data obtained from F_2 progenies, while Table II reports data obtained from test cross progenies.

The *Su* : *su* ratio fits the expected 3 : 1 and 1 : 1 ratios for F_2 and test cross progenies respectively in both *blotch* and *non blotch* classes. The defect of the *su* class is mainly due to the lower germination percentage of *su* seeds. The linkage test of *blotch leaf* with *su* is negative since these genes segregate independently, as summarized in Table III and IV.

Blotched and non blotched plants show ratios very different from the 1 : 3 which would be the case if *blotch leaf* were a recessive gene. The excess of the *blotch* class over 1/4 in F_2 indicates the dominance of *blotch* over *non blotch*. The poor expression of *blotch leaf* is obvious in both test cross and F_2 data where non blotched plants often appear with higher frequencies. When analizing the linkage relationship between *blotched* and *waxy* an association was surprisingly found between the two characters in all F_2 progenies and in all test crosses. The $Wx : wx$ ratios differ from 3 : 1, but in opposite ways, in the *blotch* and *non blotch* classes. These results are best seen in Tables V and VI where they are summarized. In the blotched class $Wx : wx > 3 : 1$, while in the *non blotch* class $Wx : wx < 3 : 1$ in the F_2's; in the blotch class $Wx : wx > 1 : 1$, while in the *non blotch* class $Wx : wx < 1 : 1$ in test crosses.

TABLE I

F_2 *results after selfing* F_2 *individuals obtained by crossing* Su, Wx, blotch × su, wx, non blotch.

Genotype and Pedigree number: $\frac{Su}{su}\ \frac{Wx}{wx}\ \frac{blotch}{non\ blotch}\ \otimes$

			Blotch	*Non blotch*		*Blotch*	*Non blotch*
1913	⊗	*Su*	362	306	*Wx*	375	220
		su	102	87	*wx*	89	173
1914	⊗	*Su*	78	78	*Wx*	89	66
		su	20	25	*wx*	9	37
1915	⊗	*Su*	29	26	*Wx*	34	16
		su	8	8	*wx*	3	18
1916	⊗	*Su*	139	175	*Wx*	175	103
		su	46	22	*wx*	10	84
1917	⊗	*Su*	78	99	*Wx*	90	80
		su	16	29	*wx*	4	48
1919	⊗	*Su*	28	34	*Wx*	35	30
		su	8	8	*wx*	1	12
1925	⊗	*Su*	44	86	*Wx*	55	60
		su	12	20	*wx*	1	46
1926	⊗	*Su*	—	—	*Wx*	33	43
		su	—	—	*wx*	0	65
1928	⊗	*Su*	68	68	*Wx*	83	65
		su	15	27	*wx*	0	30

⊗ = This symbol stands for "self pollination".

TABLE II

Test cross results of F_1 *individuals* (*the same as in* Table I) *to testers* wx, Su, non blotch *or* wx, su, non blotch.

Genotype and Pedigree number:

$$\left.\begin{array}{r} \textit{wx, Su non blotch } (2074) \\ \text{or: } \textit{wx, su non blotch } (1912) \end{array}\right\} \text{testers} \times \frac{Wx}{wx}\ \frac{su}{su}\ \frac{N}{T}\ \frac{blotch}{(non\ blotch)}\ (1913\text{–}1924)$$

		Blotch	*Non blotch*		*Blotch*	*Non blotch*
2074×1913	*Su*	—	—	*Wx*	124	106
	su	—	—	*wx*	24	102
1912×1914	*Su*	41	82	*Wx*	71	59
	su	54	84	*wx*	24	107
1912×1915	*Su*	85	71	*Wx*	119	103
	su	67	56	*wx*	33	124
2074×1917	*Su*	—	—	*Wx*	129	329
	su	—	—	*wx*	10	260
2074×1918	*Su*	—	—	*Wx*	64	154
	su	—	—	*wx*	8	160
2074×1920	*Su*	—	—	*Wx*	100	143
	su	—	—	*wx*	14	98
2074×1921	*Su*	—	—	*Wx*	10	22
	su	—	—	*wx*	1	50
2074×1922	*Su*	—	—	*Wx*	42	50
	su	—	—	*wx*	5	82
2074×1923	*Su*	—	—	*Wx*	88	107
	su	—	—	*wx*	9	121
2074×1924	*Su*	—	—	*Wx*	73	91
	su	—	—	*wx*	3	146

TABLE III

Summary of data showing the independent relationship between su *and* blotch leaf *in* F_2 *progenies reported in* Table I.

	Blotch	*Non blotch*	Total	% Germination
Su	826	872	1698	67.7
su	227	226	453	56.2
Total . . .	1053	1098	2151	

class	χ^2 (3 *Su* : 1 *su*)	P (*d.f.* = 1)
blotch	= 6.65	∼ 0.01
non blotch	= 11.42	∼ 0.001
Total . . .	= 17.80	< 0.001

TABLE IV

Summary of data showing the independent relationship between su *and* blotch leaf *in test crosses reported in* Table II.

	Blotch	*Non blotch*	Total	% Germination
Su	126	153	279	92.04
su	121	140	261	89.8
Total . . .	247	293	540	

class	χ^2 (1 *Su* : 1 *su*)	P (*d.f.* = 1)
blotch	= 0.10	0.7–0.8
non blotch	= 0.57	0.4–0.5
Total . . .	= 0.60	0.4–0.5

TABLE V

Summary of data on linkage relationship between wx *and* blotch leaf *in* F_2 *progenies reported in* Table I.

	Blotch	*Non blotch*	Total	% Germination
Wx	969	683	1652	65.4
wx	117	501	618	62.7
Total . . .	1056	1184	2370	

class	χ^2 (3 *Wx* : 1 *wx*)	P (*d.f.* = 1)
blotch	= 117.2	< 0.001
non blotch	= 189.3	< 0.001
Total . . .	= 9.9	∼ 0.001

TABLE VI

Summary of data on linkage relationship between wx *and* blotch leaf *in test crosses reported in* Table II.

	Blotch	*Non blotch*	Total	% Germination
Wx	820	1064	1884	81.6
wx	131	1350	1481	80.4
Total . . .	951	2414	3365	

class :	χ^2 (1 *Wx* : 1 *wx*)	P (*d.f.* = 1)
blotch	= 499.2	< 0.001
non blotch	= 33.8	< 0.001
Total...	= 48.3	< 0.001

DISCUSSION

The differences between the ratios found and the expected ratios support the hypothesis of linkage between *blotch leaf* and *waxy* of chromosome 9, short arm. The data indicate that the intensity of the linkage is around 15 map units, although further tests are needed mainly because the incomplete dominance of the *blotch leaf* gene may have resulted in inaccurate classification.

As an alternative, these data could be interpreted as a result of interaction between the two genes. In other words, the *blotch leaf* gene would be better expressed in the *Wx*/background. However, this hypothesis is not supported by the presence of *wx* and *blotch* plants with a good expression of the latter character.

One of the main points of interest in the present work is the dominant expression of the *blotch leaf* gene, although a considerable variation of the expression is found in F1 progenies of blotched plants of different stocks. The genetic background is believed to be largely responsible for these variations although environmental conditions, such as light intensity and heat, as reported by Emerson (1923), are an important factor.

The aspect of the well localized necrotic lesions recalls that of necrotic spots caused by various agents, although pathogens such as those belonging to Fungi, Bacteria or Viruses have not so far been isolated. The nature of the degeneration of the leaf tissues found in the leaf blotches therefore remains unknown.

A cytoplasmic factor, as hypotesized by Atanasoff (1965), can be excluded in the case of the *blotch leaf* material here described because the inheritance of this character is based upon a typical nuclear condition, as also pointed out by Brewbaker (1970), with male as well as female transmission.

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