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Studies of Inheritance of Reaction to Common Smut in Corn

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Summary. Reaction to *Ustilago maydis* was studied in resistant and susceptible corn inbreds, their F_1 hybrids and F_2 and F_3 segregants. Marked differences among inbreds in genetic prepotency were found. Segregation was polygenic. The concept of combining ability was applied and estimates of σ_G^2 and σ_S^2 were calculated. Both additive and non-additive gene action was found. Breeding for resistance based on crossing to special susceptible testers was suggested.

The common smut occurs wherever corn has been grown, and it was formerly believed to be one of the most destructive diseases of this crop. For example, estimated losses in the United States were on the average about 1.8% (Plant Disease Reporter 1924, 1925 and 1926), but often up to 15% (SMITH, 1936). No varieties were satisfactorily resistant (POTTER and MELCHERS, 1925). Many investigations carried out during the first four decades of the 20th century showed that the host-pathogen relationship is very complex and, therefore, polygenically controlled. Selection for smut resistance among inbreds turned out to be highly effective and hybrids were developed whose resistance, although not complete, was satisfactory (STRINGFIELD and BOWMAN, 1942). The interest of research workers in the problem of smut control decreased after 1940, although the inheritance of reaction of corn to smut has not yet been explained.

In Poland, as in some other northern areas of corn culture, smut remains an important factor because early flint varieties, which constitute a source of inbreds for production of flint-dent hybrids, are extremely susceptible (RIEGEROWA and SŁABOŃSKI, 1957). They give such a low proportion of acceptably resistant inbreds that little opportunity is left to select for other characters (RIEGEROWA, 1959; RALSKI and RIEGEROWA, 1963; and BOJANOWSKI, 1967a).

The reaction of the corn plant to attacks of the smut fungus is conditioned by variability of the pathogen, variability of the host and the mechanism of infection.

Differences in pathogenicity among physiologic forms and collections of *U. maydis* were reported by several authors (CHRISTENSEN and STAKMAN, 1926; TISDALE and JOHNSTON, 1926; GRIFFITHS, 1928; and EDDINS, 1929). STAKMAN et al. (1933) demonstrated, however, that such differences exist even among combinations of pure monosporidial lines. Consequently, collections and "physiologic forms" may comprise many different biotypes. IMMER and CHRISTENSEN (1931) and CHRISTENSEN and JOHNSON (1935) found no significant differences in the reaction of varieties and inbreds of corn to different collections of the smut fungus. ROWELL and DEVAY (1954), ROWELL (1955) and HOLLIDAY (1961) demonstrated that brandspore production is conditioned by two loci: *a*, with two alleles controlling mating type, and *b*, with multiple alleles controlling pathogenicity. The virulent phase is a dicarion heterozygous at both loci. Owing to constant reassortment of genes between successive infections there are no established races of the pathogen. *U. maydis* is a panmictic population in which various combinations of genes controlling pathogenicity arise as compatible sporidia fuse to form pathogenic dicarions. Plants grown under epiphytotic are exposed to attacks of many different biotypes of the pathogen.

Heritable differences in reaction to smut among inbreds were first reported by JONES (1918) and then by many authors. GARBER and QUISENBERRY (1925), GARBER and HOOVER (1928), IMMER and CHRISTENSEN (1931), HOOVER (1932), CHRISTENSEN and JOHNSON (1935), RALSKI and RIEGEROWA (1963), NEMLJENKO and KULIK (1965) and VOŽDOVA and PRUDEK (1967) found marked differences among inbreds and varieties in amount and location of smut galls and rather high consistency of these characters in different seasons. Nevertheless, reaction of corn to smut is subject to considerable variation due to environmental factors, i.e. climatic conditions, soil fertility, population density, mechanical injuries etc. KYLE (1930) believed that any factors stimulating vigorous growth of meristems are conductive for smut prevalence.

Several techniques of inducing epiphytotic and of inoculation were developed (PIEMEISEL, 1917; TISDALE and JOHNSTON, 1926; PLATZ, 1929; IMMER and CHRISTENSEN, 1928a; EDDINS, 1929; DAVIS, 1936; RIEGEROWA, 1959; and MOLOT, 1962). It was found that inocula with reduced surface tension were more effective than water suspensions (PLATZ, 1929; and DAVIS, 1936). Hypodermal inoculation resulted in still more severe infection. Young seedlings were susceptible when inoculated, but at 3-leaf stage differences — probably physiological — among inbreds were noted by TISDALE and JOHNSTON (1926). RANKER (1930) observed inhibition of growth of the smut fungus by filtrates of some resistant inbreds. PETHŐ (1964) found a relationship between susceptibility to smut and the rate of amino acid synthesis in infected tissues. An interrelation was found between the intensity of infection and the covering of apical buds (EDDINS, 1929) and between ear infection and thickness of husk covering (KYLE, 1929). WALTER (1934) concluded from his study of penetration of hyphae that the mode of entrance of the pathogen is probably of no significance to differential reaction of corn strains to smut. DAVIS (1936) found that the amount of infection was greater than that of its visible symptoms and that artificial stimulation of growth of axillary buds resulted in a doubled percentage of nodal infections. He concluded that infection of buds takes place at early stages of growth but is expressed by gall formation only if the buds grow. A considerable proportion of infected buds may never develop galls. The amount of smut infections depends, therefore, not only upon resistance (in either a morphological or physiological sense), but also upon the growth pattern of the host plant. Since tillers are often smutted, this may account for the increase in the amount of smut resulting from a reduction of population density in highly tillering strains (VOHL, 1938; RIEGEROWA and SŁABOŃSKI, 1957; and unpublished data of DZIEGIELEWSKI and of BOJANOWSKI).

It can be concluded from the literature that reaction of corn to smut, as observed under natural epiphytotic, is a very complex characteristic.

Materials and Methods

The experiments were carried out on the Ursynów Experimental Farm of the Agricultural University in Warsaw in the years 1959 to 1965, and in the smut nursery of the Plant Breeding Station Kobierzyce near Wrocław in 1966 and 1967.

The inheritance of reaction to smut was studied in several inbreds and their progenies. Experimental material was planted in fields heavily infested with brandspores of *U. maydis* collected in several localities in Poland. Additional infestation was also applied at 4—5 leaf stage and again prior to tasseling. Plants were either dusted with brandspores (in 1959 to 1965) or sprayed with water suspension of brandspores (in 1966) or sporidia (in 1967), with a .01% emulsifying agent added to reduce the surface tension (MOLOT, 1962). Inoculation was not applied because no inoculation technique is fully satisfactory. The author shares the opinion of PLATZ (1929) that artificial inoculation eliminates the morphological component of smut resistance. RIEGEROWA (1959) found a marked discrepancy in the intensity of infection between plants exposed to field infection and seedlings inoculated in a greenhouse. Therefore, the most reliable information is obtained if uninjured plants are exposed to epiphytotic.

Table 1. *Percentages of smutted plants in a susceptible open pollinated variety Stanowicka in the years 1961 to 1967*

Year	Locality	Per cent of smutted plants	
		with galls on ears and/or on stalks above ears	total
1961	Ursynów	45	72
1962	Ursynów	13	35
1963	Ursynów	31	70
1964	Ursynów	7	21
1965	Ursynów	7	12
1966	Kobierzyce	20	53
1967	Kobierzyce	31	76

Plants were spaced either 80 × 50 cm (in Ursynów in 1959 to 1965) or 70 × 35 cm (in Kobierzyce in 1966 and 1967), thus making a population density of 25,000 and 40,800 plants per hectare, respectively. Low population density was applied because, according to unpublished Polish data (see BOJANOWSKI, 1967a) it provided for smut infection. These data are in accordance with those of VOHL (1938), RIEGEROWA and SŁABOŃSKI (1957) and WILCOXON and COVEY (1960), but somewhat contradictory to those of PIEMEISEL (1917), KORNFELD (1937) and RUTGER and RISIUS (1966). DAVIS (1936) found that infection increased both ways from the planting rate of 2 or 3 plants per hill.

The intensity of smut damage was determined in percentage of smutted plants. The location of galls was also recorded because, according to IMMER and CHRISTENSEN (1928b) and JOHNSON and CHRISTENSEN (1935), galls located on ears and on stalks above ears are the most destructive.

The prevalence of smut during the period in which the experiments were carried out is illustrated by the percentage of smutted plants in a susceptible open pollinated flint variety Stanowicka, which was used as a check (Table 1). An arbitrary scoring system was developed by the author in order to take into account the number and size of galls. This system was abandoned because a close positive correlation was found between the score and the percentage data (BOJANOWSKI, 1967a). All calculations based on percentages were performed on data transformed to angles according to BLISS (after SNEDECOR, 1956). If there were no smutted plants on a plot, 1/4 n was substituted for 0%, n being the actual number of plants on the plot (BARTLETT, 1947).

An attempt was made to obtain a series of inbreds representing the widest possible range of reaction to smut. Nearly 500 inbreds developed by the author from Polish local strains, as well as from American, French, Dutch, Canadian, Hungarian and Austrian varieties and

Table 2. *Analysis of variance of the percentage (transformed to angles) of smutted plants in 70 inbreds tested in single, 20-plant rows in Ursynów in 1959, 1960, 1961 and 1963*

Source	*DF*	Plants smutted on ears and/or on stalks above ears		Smutted plants (total)	
		S^2	*F*	S^2	*F*
Years	3	2536	21.49***	3771	19.14***
Inbreds	69	1099	9.31***	1854	9.41***
Interaction (taken as the error term)	207	118		197	

*** Significant at .1% level.

Table 3. *Information on inbreds involved in the experiments*

Designation of inbreds	Country of origin	Source	Percentages of plants smutted on ears and/or on stalks above ears in					Percentages of smutted plants in				
			1959	1960	1961	1963	1967	1959	1960	1961	1963	1967
U4	Poland	C.I.V.1	0	0	0	0	3	0	6	0	21	4
U10	Poland	Polish local strain G, flint	6	0	5	—	—	28	0	9	—	—
U12	Poland	Polish local strain B, flint	100	100	100	—	100	100	100	100	—	100
U19	Poland	Prior	95	54	59	36	64	100	100	100	85	86
U123	Poland	Amo	0	0	0	0	0	0	0	0	0	0
U165	Poland	CB	5	0	28	0	—	5	0	41	0	—
U204	Poland	Kingscrost KF	0	0	0	0	—	0	15	0	12	—
U221	Poland	Pioneer 396	18	0	8	26	—	47	29	59	53	—
U231	Poland	Caspersmayers Silozahnmais	84	100	43	—	—	100	100	100	—	—
U240	Poland	Iowa 4417	0	0	0	—	—	0	0	0	—	—
U248	Poland	Polish local strain P, white late microsperm	50	14	8	0	—	100	78	87	31	—
WM13R	U.S.A.		5	0	8	6	10	5	0	36	12	22
W37A	U.S.A.		5	0	0	0	—	5	0	9	0	—
Mt42	U.S.A.		100	39	57	5	42	100	52	72	5	45
CO151	Canada		9	21	0	0	—	9	21	17	0	—
F7	France		—	0	15	0	—	—	0	75	11	—
F115	France		—	15	0	—	—	—	15	0	—	—
72-75-6-1	Canada[1]		—	—	—	—	11	—	—	—	—	18
F2	France		—	0	—	—	—	—	0	—	—	—
W85	U.S.A.		0	19	—	—	—	38	40	—	—	—
W15	U.S.A.		0	12	10	—	—	0	28	19	—	—
WD	U.S.A.		0	41	—	—	—	80	54	—	—	—
EP1	Spain											
W33	U.S.A.											
W374	U.S.A.											
PLS48	Poland	Wigor, o.p. dent										
PLS43	Poland	Oksonska, o.p. early microsperm.										

[1] Inbred obtained from Canada under designation of dash pedigree 72-75-6-1; in other tables referred to as Can.72.

hybrids were tested. Inbreeding was started in 1954 and 1955. Many inbreds were discarded in the course of inbreeding, as poorly adapted. At the same time many established foreign inbreds were tested for adaptability.

Preliminary testing for reaction to smut of 261 of the author's own inbreds (designated by U followed by a number) and of 36 foreign inbreds was carried out from 1959 to 1963. No data were obtained in 1962 because of very poor stands due to unfavorable weather in May. The percentage of smutted plants was determined on 1-row, 20-plants plots without replications. Data for many inbreds are not complete partly because of elimination in the course of inbreeding and testing, and partly because of accidental losses or poor stands. Nevertheless, a series of 70 inbreds was selected which were tested in four seasons, i.e. 1959, 1960, 1961 and 1963. The analysis of variance of these data is given in Table 2. Inbreds involved in experiments are listed in Table 3.

Experimental

Based on the first year of preliminary testing, several resistant (R) and susceptible (S) inbreds were selected in 1960 and intercrossed in $R \times R$ and $R \times S$ combinations. Many crossings were unsuccessful because of differences in flowering time or destruction of susceptible plants by smut.

In 1961, the percentage of smutted plants in 19 F_1 hybrids and 14 parental inbreds was determined in 10-plant rows in 3 replicates. No attempt was made to distinguish between reciprocals because, according to IMMER (1927), HOOVER (1932) and NEMLJENKO and KULIK (1956) no maternal effect was observed in reaction to smut. The results are given in Table 4.

Twenty inbreds were outcrossed in 1960 to a rather smut-susceptible double cross tester (W85 × W15) (Mt42 × WD). The percentage of smutted plants in parental inbreds and in their test-cross progenies was recorded in 1961. Parent-progeny correlation is shown in Table 5.

Segregation of reaction to smut was studied in 1964, 1965 and 1966.

In 1964, the percentage of smutted F_2 plants was recorded in 6 crosses (Table 6). Since, however, data

Table 4. *Percentages (transformed to angles) of plants smutted on ears and/or on stalks above ears (E + S) and of smutted plants (T) in 14 inbreds and their 19 F_1 progenies in Ursynów, 1961*

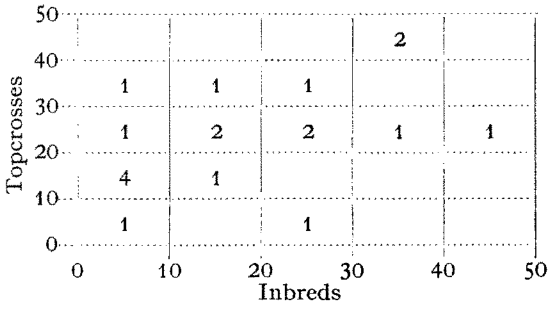
Inbred	Smutted plants		Parents	Smutted plants			
				E + S		T	
	E + S	T		F_1	$F_1 - \overline{P}$	F_1	$F_1 - \overline{P}$
U123	5	5	U123 ×WM13R	10	+ 2.0	20	− 1.0
U240	7	7	U123 ×W37A	7	− .5	37	+28.5**
U204	8	8	U123 ×U204	6	− .5	35	+28.5**
U4	9	9	U123 ×U240	7	+ 1.0	29	+23.0**
W37A	10	12	U123 ×U19	8	−19.5**	39	− 8.5
U10	13	17	U123 ×U248	6	− 4.5	31	− 6.0
CO151	10	24	U123 ×U4	12	+ 5.0	44	+37.0**
WM13R	16	37	U4 ×U10	24	+13.0*	56	+43.0**
U165	32	40	U4 ×U12	45	+ .5	90	+40.5**
Mt42	49	58	U4 ×U19	35	+ 5.5	90	+40.5**
U248	16	69	U4 ×U165	25	+ 4.5	47	+22.5**
U231	41	90	U231 ×WM13R	20	− 8.5	49	−14.5
U19	50	90	U248 ×WM13R	7	− 9.0	57	+ 4.0
U12	80	90	CO151×WM13R	18	+5.0	48	+17.5*
			CO151×W37A	10	0	23	+ 5.0
			U248 ×W37A	8	− 5.0	56	+15.5*
			U248 ×U240	13	+ 1.5	52	+14.0
			CO151×U240	8	− .5	26	+10.5
			Mt42 ×W37A	11	−18.5**	27	− 8.0

Differences are significant * at 5% level
** at 1% level

based on individuals are not dependable, more detailed analyses were performed in 1964, 1965 and 1966 in F_3 progeny rows of 25, 25 and 20 plants, respectively. Eight crosses among 5 resistant and 2 susceptible inbreds were chosen for this study. They represented four $R \times R$ and four $R \times S$ combinations. The distribution of F_3 progenies in classes of percentage (transformed to angles) of smutted plants, with class intervals = 10, are given in Table 7.

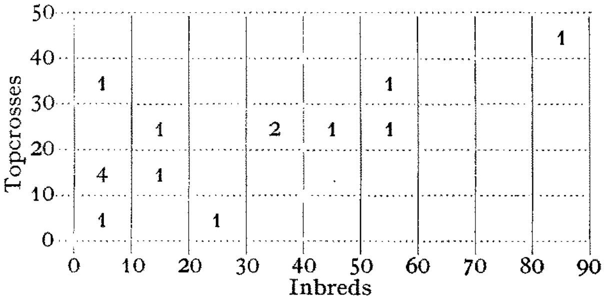
Table 5. *Inbred-topcross correlation in percentages (transformed to angles) of smutted plants in Ursynów in 1961. Tester: (W85 × W15) (Mt42 × WD)*

A. Smut on ears and/or on stalks above ears



Correlation coefficient $r = +.52$ (significant at 5% level)

B. Smutted plants (total)



Correlation coefficient $r = +.20$ (non significant)

The reaction of inbreds and their F_1 progenies to smut was studied again in 1967 in the trial No. XVI in Kobierzyce. The trial was located in a smut nursery and consisted of 36 entries set in 6×6 lattice in 4 replicates of 40-plant, 2-row plots. Since the effectiveness of lattice design was very low, the analysis of variance was performed according to randomized blocks design. The number of smutted plants was so recorded as to enable determining total percentage of smutted plants and also percentages of plants smutted a) on ears, b) on stalks above ears, c) on ears and/or on stalks above ears. The yield of grain at 15.5% moisture level was also determined. The analyses of variance are shown on Table 8. Data concerning 6 inbreds and their 13 F_1 progenies are shown in Table 9.

Table 6. *Percentage of smutted plants in F_2 of six crosses in Ursynów, 1962*

Parental inbreds	Number of plants	Per cent of smutted plants
U123×U4	270	18.1
U4 ×U10	168	18.5
U123×U19	250	19.6
U10 ×U12	187	30.0
U4 ×U19	229	33.6
U4 ×U12	220	37.7

Table 7. *Distributions of F_3 progenies of 8 crosses in classes of percentages (transformed to angles) of smutted plants in the years 1964, 1965 and 1966. Class interval = 10. The arrows mark the mean values of the check variety Stanowicka (see Tab. 1)*

Pedigree	Type of the cross	Frequency in classes of transformed percentages of smutted plants class marks 0	10	20	30	40	50	60	70	80 90	No. of F_3 tested
Year 1964				↓							
U123×WM13R	$R\times R$	48	3	2							53
U123×W37A	$R\times R$	29	3								32
U123×U19	$R\times S$	6	4	2							12
Year 1965				↓							
U123×WM13R	$R\times R$	39	4								43
U123×W37A	$R\times R$	33	1								34
U123×U4	$R\times R$	64	9								74
U10 ×U4	$R\times R$	28	1	1							30
U123×U19	$R\times S$	66	10	3							79
U4 ×U19	$R\times S$	40	34	26							100
U10 ×U12	$R\times S$	12	13	8	3						36
U4 ×U12	$R\times S$	5	12	19	13	8	4	2			63
Year 1966						↓					
U123×WM13R	$R\times R$	20	9								29
U123×W37A	$R\times R$	7	9	1							17
U123×U4	$R\times R2$	23	8	8	2						41
U10 ×U4	$R\times R$		4	6	3	4					17
U123×U19	$R\times S$	8	7	13	8	2	1				39
U4 ×U19	$R\times S$			8	8	15	4	2	1		38
U10 ×U12	$R\times S$		1	1	5	7	6	3	1		24
U4 ×U12	$R\times S$		1	2	6	7	12	5	5	5	43

Table 8. *Analysis of variance in the trial No. XVI in Kobierzyce, 1967*

Character	Source	*DF*	S^2	*F*
Per cent of plants smutted on ears and/or on stalks above ears	blocks	3	42.64	
	entries	35	622.31	32.14**
	error	105	19.36	
Per cent of plants smutted on ears	blocks	3	30.24	
	entries	35	150.99	9.13**
	error	105	16.53	
Per cent of plants smutted on stalks above ears	blocks	3	94.62	
	entries	35	551.59	26.39**
	error	105	20.90	
Total per cent of smutted plants	blocks	3	14.65	
	entries	35	938.28	22.51**
	error	105	41.69	
Per cent of barren plants	blocks	3	32.83	
	entries	35	345.09	13.69**
	error	105	25.20	
Yield of grain at 15.5% moisture level in *q* per hectare	blocks	3	67.10	
	entries	33	1618.04	62.10**
	error	99	26.20	

** Significant at 1% level

The total percentage of smutted plants was also recorded in the yield trial No. VIII in Kobierzyce in 1967. This trial was located in the field and constituted a part of the program of testing inbreds for combining ability in diallel and restricted diallel crosses. It consisted of 90 entries set in 10×9 rectangular lattice in 3 replicates of 2-row plots, 10 m² each. Population density was about 61,300 plants per hectare. Although no artificial infestation was applied, the intensity of smut was rather high. One modified diallel series of 5 lines and one restricted diallel series of 7×4 lines were singled out of this trial for discussion of inheritance of reaction to smut. The results are given in Tables 11 and 12.

Table 9. *Percentages (transformed to angles) of smutted plants, barren plants, and yield of grain of 6 inbreds and 13 F_1 in the trial No. XVI in Kobierzyce, 1967*

Designation of parental inbreds	Plants smutted on: ears		stalks above ears		ears and/or stalks above ears		Smutted plants (total)		Barren plants		Yield of grain q/ha
		$F_1 - \overline{P}$		$F_1 - \overline{P}$		$F_1 - \overline{P}$		$F_1 - \overline{P}$		$F_1 - \overline{P}$	
U123	5.3		5.3		5.3		5.3		5.3		7.4
U4	5.6		11.0		11.0		11.9		9.6		9.6
U19	10.6		51.3		52.9		68.0		52.5		7.3
Mt42	6.6		40.0		40.0		42.5		19.7		16.6
WM13R	10.3		23.6		25.3		31.8		17.4		11.0
Can.72	10.3		14.7		18.8		25.0		12.1		33.5
U123 × WM13R	5.0	− 2.8	5.0	− 9.5**	5.0	−10.3**	34.0	+15.4**	15.0	− 6.3*	68.1
U123 × U4	13.5	+ 8.0**	7.9	− .3	15.9	+ 7.7**	31.8	+23.2**	5.6	− 1.8	52.4
U123 × U19	4.9	− 3.1	4.9	−23.4**	4.9	−24.2**	35.0	− 1.7	4.9	−24.0**	62.8
U123 × Mt42	5.9	− .1	7.1	−15.6**	8.1	−14.6**	21.1	− 2.8	6.0	− 6.5*	56.0
U5 × U19	17.1	+ 9.0**	38.5	+ 7.3*	42.4	+10.4**	59.2	+19.2**	20.5	−10.5**	55.5
U4 × Mt42	5.8	− .3	25.6	+ .1	26.1	+ .6	35.2	+ 8.0**	12.1	− 2.5	45.3
Mt42 × WM13R	6.3	− 2.2	18.2	−13.6**	18.9	−13.7**	31.8	− 5.3	10.0	− 8.5**	60.5
U19 × WM13R	12.8	+ 2.3	30.2	− 7.2*	32.9	− 6.2*	50.4	+ .5	13.3	−21.6**	58.0
Mt42 × U19	10.4	+ 1.8	37.7	− 7.9**	39.1	− 7.4**	48.7	− 6.5	14.8	−21.3**	62.2
Can.72 × U123	4.7	− 3.2	9.2	− .9	9.1	− 2.9	16.1	+ 1.0	4.7	− 4.0	64.2
Can.72 × U4	22.8	+14.8**	12.4	− .4	26.9	+12.0**	35.8	+17.3**	5.7	− 5.1	67.6
Can.72 × U19	7.0	− 3.4	22.8	−10.2**	23.4	−12.5**	39.3	− 7.2	16.7	−15.6**	65.3
Can.72 × Mt42	4.7	− 3.7	18.6	− 8.7**	17.7	−11.7**	18.9	−14.8**	8.1	− 7.8*	71.0

Differences are significant at * 5% level — ** 1% level

Table 10. *Average cross performances and estimates of general (σ^2_G) and specific (σ^2_S) combining ability in respect to the percentage of smutted plants and to yield of 5 inbred lines in a modified diallel series singled out of the trial No. XVI in Kobierzyce, 1967*

Inbred line	Percentages (transformed to angles) of plants smutted on: ears			stalks above ears			ears and/or stalks above the ears			smutted plants			barren plants			Yield of grain in q/ha		
	$\overline{x}$	σ^2_S	σ^2_G	$\overline{x}$	σ^2_S	σ^2_G	$\overline{x}$	σ^2_S	σ^2_G	$\overline{x}$	σ^2_S	σ^2_G	$\overline{x}$	σ^2_S	σ^2_G	$\overline{x}$	σ^2_S	σ^2_G
U123	7.2	5.3	7.5	7.3	50.1	196.1	9.5	37.0	229.6	26.0	0	113.5	5.3	6.0	32.9	58.9	1.9	.3
Can.72	9.8	21.9	0	15.8	38.7		19.3	16.5	0	27.5	0	74.6	8.8	5.8	0	67.0	22.8	68.3
Mt42	6.7	35.2	2.7	22.3	4.4	21.6	22.7	30.5	0	31.0	3.7	12.2	10.3	0	0	58.6	14.7	0
U4	14.8	37.6	32.6	21.1	23.2	0	28.4	14.9	65.1	40.5	0	69.7	11.0	5.6	0	55.2	16.5	34.8
U19	9.0	12.1	0	26.0	42.8	77.1	27.4	52.4	38.1	45.5	2.6	227.5	14.2	9.5	26.8	61.5	10.7	0
Average	7.1	38.1	27.0	18.5	48.0	75.8	21.4	50.2	83.5	34.1	.4	125.3	9.9	7.3	14.4	60.1	20.3	25.4
σ^2_S/σ^2_G		1.41			.63			.60			.0035			.51			.80	

Analysis of variance

Source	DF	S^2	F	S^2	F	S^2	F	S^2	F	S^2	F	S^2	F
Hybrids	9	156.4	9.46**	617.5	29.55*	646.1	33.37**	711.5	17.07**	131.2	5.21**	242.1	9.23**
Parents	4	219.1	2.06	1123.2	5.27*	1202.6	5.99*	1546.6	37.10**	227.1	4.16	411.5	3.85
Interaction	5	106.2	6.42**	213.1	10.19**	200.9	10.38**	43.5	1.04	54.5	2.16	106.8	4.07**
Error	105	16.5		20.9		19.4		41.7		25.2		26.2	

* Significant at 5% level — ** Significant at 1% level

Table 11. *Percentage (transformed to angles) of smutted plants in a modified diallel series singled out of the trial No. VIII in Kobierzyce, 1967*

Parental inbreds	F115	W33	Can.72	EP1	$\bar{x}$	σ_S^2	σ_G^2
F7	25.3	22.3	19.6	22.0	22.3	39.4	45.8
F115		24.0	18.3	38.3	26.5	0	33.3
W33			27.0	37.3	27.7	0	0
Can.72				50.0	28.7	0	46.1
EP1					36.9	95.9	56.4
Average					28.4	53.3	28.8

Analysis of variance

Source	*DF*	S^2	*F*
Hybrids	9	310.4	8.99**
Inbreds	4	454.3	2.33
Interaction	5	195.2	5.59**
Error	176	34.9	

$$\frac{\sigma_S^2}{\sigma_G^2} = 1.85$$

** Significant at 1% level

Table 12. *Percentages (transformed to angles) of smutted plants in a 4×7 restricted diallel series singled out of the trial No. VIII in Kobierzyce, 1967*

Parental inbreds A/B	W375	W33	U221	F115	PLS48	PLS43	EP1	$\bar{x}$	σ_S^2	σ_G^2
Can. 72	25.0	27.0	22.0	18.3	27.7	26.7	50.0	28.1	45.9	0
F2	26.0	35.3	35.7	24.7	29.7	28.0	35.0	30.6	0	11.7
F7	25.0	22.3	40.7	25.3	25.0	37.0	22.0	28.2	46.0	0
U50	23.7	20.3	19.7	12.7	21.3	23.7	25.3	21.0	0	35.1
$\bar{x}$	24.9	26.2	29.5	20.2	25.9	28.8	33.1	27.0		
σ_S^2	0	7.0	53.1	0	0	15.0	123.9		33.0	
σ_G^2	1.5	0	0	42.8	0	0	3.5			7.3

Analysis of variance

Source	*DF*	S^2	*F*
Hybrids	27	173.6	4.98**
Inbreds A	3	366.0	2.73
Inbreds B	6	196.5	1.47
Interaction	18	133.8	3.84**
Error	176	34.9	

$$\frac{\sigma_S^2}{\sigma_G^2} = 3.69$$

** Significant at 1% level

Discussion

The results of preliminary testing (Tab. 2) together with the information presented in Tab. 3 show that inbreds chosen for genetic experiments represented a wide range of variability, both in origin and in reaction to smut. The most resistant inbred U123 was smut-free throughout all tests made by the author. It was also the only strain which was absolutely smut-free in a field test and in a greenhouse test (with inoculation by the technique of ROWELL and DEVAY), which were performed at La Grande Ferrade, France, in 1962[1]). The most susceptible inbred U12 was smutted 100% in most seasons and could be propagated with difficulty.

In the 1961 trial (Tab. 4) the total percentage of smutted plants in F_1 was mostly intermediate, i.e. within the limits set by parental values, but in 4 cases it was equal and in 6 cases higher than that of more smutted parent. If only the most destructive infections (i.e. on ears and/or on stalks above ears) were taken into account, the percentage of smutted plants was intermediate in all cases except two, in which it was lower than that of the less smutted parent; and one, in which F_1 exceeded the more smutted parent. Generally, no regularity of behavior of F_1 was observed. There was some indication of differences among parental inbreds in cross performance in respect to smut reaction, but no conclusions could be drawn because of non-orthogonality of the crosses and low accuracy of the trial.

The results of topcross test (Tab. 5) showed that parent-progeny correlation in reaction to smut was rather low. It amounted to +.20 for the total percentage of smutted plants and +.52 (significant at 5% level) for the percentage of plants smutted on ears and/or on stalks above the ears. As can be seen from the correlation tables, "high smut" inbreds gave mostly "high smut" progeny, while the progenies of "low smut" inbreds showed a great variation. It means that the reaction of an inbred line to smut gives only tentative information on its cross-performance. This is in accordance with observations of BERZSENYI (1962) who found that correlation in reaction to smut was low between inbreds and their topcross progenies, but sufficiently high between different topcrosses of the same inbreds. Susceptible testers offered greater possibility of selecting for resistance.

Data concerning smut percentage in F_2 (Tab. 6) are generally in accordance with what could be expected based on F_1, but they are not critical because the reaction of individual plants to smut is subject to a great variation. Segregation data based on F_3 progenies (Tab. 7) are much more reliable.

Progenies of 3 crosses were tested in three seasons, while those of remaining 5 crosses in two seasons. It can be seen from Tab. 7 that, considering seasonal differences in smut prevalence as measured by the percentage of smutted plants in the check variety,

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[1] The information was kindly provided by Dr. P. MOLOT, Station de la Pathologie Végétale, Pont-de-la-Maye, Gironde, France.

distribution in each of the crosses was essentially the same in all seasons. Small discrepancies might be due to environmental variation, to sampling error and to the fact that not exactly the same sets of F_3 progenies were tested in different seasons.

In $R \times R$ crosses distributions were asymmetrical (except U10 × U4 in 1966) because F_3 progenies were mostly grouped in "low smut" classes. In spite of this fact, differences among crosses were quite apparent. In $R \times S$ crosses distributions were either symmetrical or slightly asymmetrical, depending upon the pedigree of the cross and seasonal prevalence of smut. Intensity of the disease was higher in 1966 than in 1964 and 1965, and some "shift" of distribution is apparent in all crosses. Some progenies classified as "low smut" in 1964 and 1965 occurred in "medium smut" classes in 1966. Similarly, "medium smut" progenies from 1964 and 1965 occurred in "high smut" classes in 1966. It means that the asymmetry of distribution of progenies of most $R \times R$ and some $R \times S$ crosses, particularly in seasons of low smut prevalence, was due to the fact that resistant and medium resistant progenies were grouped together in "low smut" classes. It is possible that F_3 progenies of a cross between two very susceptible lines, if tested under epiphytotic, would be mostly grouped in "high smut" classes, thus making the distribution asymmetrical, but in the opposite way.

Distributions presented in Tab. 7 indicate, therefore, that reaction to smut is a polygenic character and segregates according to a quantitative model. The same type of segregation was observed by IMMER (1927). The resistance of all resistant strains tested by this author seemed to be conditioned generally by the same factors. This is not the case with the data presented in this paper. It is quite apparent that even within groups of inbreds classified as resistant or susceptible, marked differences occur in respect to the number of factors determining the reaction to smut. These numbers, however, can not be determined exactly, although a relatively simple additive model could be constructed to account for the observed distributions, as shown by the author (BOJANOWSKI, 1967b). Reaction to smut is a very complex phenomenon and there is no reason to assume that the effects of all factors involved are additive and of the same magnitude.

Attempts were made to locate factors controlling smut resistance. HOOVER (1932), in studies involving 9 linkage groups, found that at least four groups, corresponding to chromosomes 1, 2, 3 and 5, contained genes associated with the reaction to smut, but each of these groups was represented by plants which carried genes conditioning morphological characters faciliating the infection (e.g. *tassel-seed 4* or *brachytic*). BURNHAM and CARTLEDGE (1939), in crosses between a smut resistant inbred and a series of susceptible translocation stocks, observed association between smut reaction and 13 different points of interchange. SABOE and HAYES (1941) studied backcross progenies of two resistant inbreds with stocks representing translocations in 15 arms of 10 chromosomes. At least 3 factors were found in each inbred. They were located in chromosomes 6, 7 and 8 in one inbred, and in chromosomes 4 and presumably 3 and 5 in the other. These results proved that smut resistance in corn is polygenic and may be conditioned by different factors.

If the reaction to smut were a typically quantitative, cumulative character, the F_1 would be always intermediate to the parents, which apparently is not the case. According to JONES (1918) resistance was dominant. HAYES et al. (1924) found that F_1 progenies of resistant × resistant were more resistant than either parent, while those of resistant × susceptible were intermediate. IMMER and CHRISTENSEN (1928b), IMMER (1927) and IMMER and CHRISTENSEN (1931) found that F_1 was mostly intermediate, but in some cases susceptibility was dominant. F_1 progenies of resistant × resistant were as resistant as parents or slightly more smutted. KYLE (1930) found negative correlation between growth vigor of inbreds and their smut resistance, and also higher amounts of smut in F_1 than in either parent. He attributed increased susceptibility of hybrids to their increased vigor, and he even pointed out the danger of eliminating the most productive strains by selection for smut resistance. On the other hand, no correlation between smut resistance and plant height (taken as a measure of vigor) was found by IMMER and CHRISTENSEN (1931) in 300 F_3 progenies. In experiments of HOOVER (1932), F_1 was intermediate. ČEKALIN (1964) found F_1 to be intermediate, with deviations towards either more resistant or more susceptible parent.

The results presented in this paper are in accordance with literature in that there is no general rule as to the reaction of F_1 to smut. Progenies shown in Tables 4 and 9 represent a range of parent-progeny relationship apparently wider than that found in any other single experiment. This may be attributed to the fact that all investigations referred to in literature were performed on inbreds developed in the course of breeding programs, while in experiments referred to in this paper, a special attempt was made to isolate extremely resistant and susceptible inbreds, with little concern of other characteristics. This is, perhaps, why instances may be found here in which the percentage of smutted plants in F_1 is 1) higher than in either parent ("negative heterosis"), 2) of the same order as in the more susceptible parent ("dominance of susceptibility"), 3) intermediate ("incomplete dominance"), 4) of the same order as in the more resistant parent ("dominance of resistance"), and 5) lower than in either parent ("positive heterosis"). It seems that such a situation can be best expressed in terms of differences between F_1

and the parental mean ($F_1 - \overline{P}$). As can be seen from Tab. 4 and 9, the sign and magnitude of these differences varied not only for different crosses, but also for different locations of smut galls within crosses. In 1961 (Tab. 4), 16 out of 19 F_1 progenies did not differ significantly from parental means in respect to the percentage of plants smutted on ears and/or on stalks above the ears, while in respect to the total percentage of smutted plants, F_1 significantly exceeded the parental mean in 10 cases. This may be possibly attributed to hybrid vigor which stimulated the growth of lower axillary buds, thus increasing the number of galls on lower nodes and suckers. More detailed and accurate data from 1967 (Tab. 9) seem to confirm this assumption. Total percentage of smutted plants in 13 F_1 progenies was in 5 cases higher and in 1 case lower than the parental mean, while in respect to smut galls located on ears and/or on stalks above ears the percentage of smutted plants in F_1 was in 8 cases lower and only in 3 cases higher than the parental mean. The percentage of F_1 plants smutted on ears significantly exceeded the parental mean only in 3 cases. In all these three crosses the line U4 was involved.

The percentage of barren plants in F_1 was in all cases lower than the parental mean, which may be certainly attributed to hybrid vigor. The percentage of barren plants was closely correlated with the percentage of plants smutted on stalks above ears ($r = +.90$ for inbreds and $+.71$ for hybrids, both highly significant). No significant correlation was found in F_1 between the percentage of smutted plants and the yield of grain ($r = -.25$, N.S.), which indicates that smut resistance was not a major component of yield.

The results presented in this paper show that the concept of complete or incomplete dominance is evidently not applicable to the reaction of corn to smut. Neither is this character typically cumulative because F_1 is not always strictly intermediate. Low correlation between inbreds and their cross progenies indicates that inbreds showing the same level of resistance may differ markedly in prepotency. It seems, therefore, that cross-performance of inbreds in respect to smut reaction can be best determined by application of the concept of combining ability. This situation is somewhat analogous to that found by Fergason (1965) in inheritance of resistance to Diplodia stalk and ear rot in corn, where both additive and nonadditive gene action was involved and hybrid progenies gave better estimates of inherent response to the parasite than inbreds themselves.

The combining ability of inbreds in respect to smut reaction was calculated for a modified (without parents and reciprocals) diallel series of F_1 crosses among 5 inbreds, singled out of the trial No. XVI, as well as for a modified diallel series of 5 inbreds and a restricted diallel series of 4×7 inbreds, singled out of the trial No. VIII in Kobierzyce in 1967. Estimates of variance due to general (σ^2_G) and specific (σ^2_S) combining ability for individual inbreds in modified diallel series were calculated according to the formulas given by Sprague and Tatum (1942) and Rojas and Sprague (1952). The only difference being that estimates of σ^2_G were freed not only from error but also from interaction components. Estimates of average σ^2_G and σ^2_S in modified diallel series were calculated after Rojas (1951), and in restricted diallel series after Scheffé (1959). Average σ^2_G and σ^2_S for the whole restricted diallel series were calculated by weighing average values obtained for the two groups, A and B. The σ^2_S/σ^2_G ratio was calculated for each series in order to measure the relative importance of general and specific combining ability.

Average performance of individual inbreds, as well as data concerning combining ability are given in Tab. 10 for the trial No. XVI, and in Tables 11 and 12 for the trial No. VIII.

It can be seen from Tab. 10 that the line U4, although apparently resistant to smut, behaved in crosses as if it were susceptible. On the contrary, a very susceptible inbred Mt42 gave a not very heavily smutted offspring. Estimates of σ^2_G and σ^2_S for total percentage of smutted plants in this series seem to indicate that the character is entirely additive. If, however, the location of smut galls is taken into account, then differences among lines, as well as specific, non-additive effects in some hybrid combinations become apparent. It can be seen that high amount of smut in the offspring of U19 is mostly due to infections on stalks, while in respect to ear infections the offspring of U4 exceeds that of all other lines. The relative importance of the specific combining ability is highest for the latter character. Inbred U123 is definitely the best combiner in respect to all kinds of smut resistance, which can be seen from its average performances and relatively high estimates of general combining ability; particularly if the two most destructive kinds of infections (ears and stalks above ears) are brought together. Combining ability of inbreds in this series in respect to the yield of grain is not related to their reaction to smut.

Data on smut in the trial No. VIII are much less detailed because only the total percentage of smutted plants was recorded. The amount of smut and the range of variability were slightly lower in the trial No. VIII than in No. XVI, but of the same order. There is, however, a striking difference in the magnitude of σ^2_G, which is much greater in No. XVI. The relative importance of specific combining ability for the total percentage of smutted plants in the trial No. VIII amounts to 1.85 for the modified diallel and 3.69 for the restricted diallel series, being, therefore, definitely greater than in the trial No. XVI.

A high percentage of smutted plants in the cross Can. 72×EP1 certainly contributed to the increase of average σ^2_S (Tab. 11 and 12). This cross provides a striking example of interaction because it was the only combination with Can. 72 so heavily smutted. All smut galls in this cross were located at the base of the stalks. Such location is characteristic of EP1, but it was not manifested so strikingly in any other cross involving this line. Both Can.72 and EP1 are excellent combiners under Polish conditions. The occurrence of such interactions should be taken into account in working out pedigrees of commercial hybrids.

The situation found here in respect to combining ability in smut resistance seems analogous to that found by SPRAGUE and TATUM (1942) in respect to combining ability in yields of grain. These authors found that in series of previously tested inbreds, variance due to specific combining ability was usually greater than the corresponding variance due to general combining ability; while in series of untested lines the situation was reversed. This was due to the elimination of low combiners in the course of selection. Similarly, the trial No. VIII consisted of inbreds which were subject to previous selection for desirable phenotypic characters, as well as for productivity in crosses; while some lines involved in the trial No. XVI represented deliberately chosen extremals in respect to reaction to smut.

Conclusions

The reaction of corn plants to the attack of *Ustilago maydis*, being conditioned by several morphological and physiological characters of the host plant, is a complex phenomenon. The inheritance of smut reaction is certainly polygenic and does not fit any single genetic scheme. Segregation seems to be quantitative as far as the total percentage of smutted plants is concerned, but biotypes of corn may differ in their inherent properties concerning the location of smut galls. The performance of F_1 may be specific as to intensity and location of infections. Both additive and non-additive gene action may be involved.

Inbreds of apparently the same level of phenotypic resistance to smut may differ in genetic prepotency in respect to this character. It seems, therefore, that in breeding programs aimed at developing smut resistant biotypes phenotypic screening should be followed by progeny tests. Combining ability in smut resistance can be best determined by crossing with a susceptible tester, preferably heterogeneous, to reduce specific effects. Perhaps a single cross of two inbreds of high prepotency in transmitting susceptibility would constitute an appropriate tester. For example, U4×U19 would be good as such a tester because progenies of the former inbred are smutted on ears, while those of the latter on stalks.

Since testing of prepotency in smut resistance alone would be uneconomic in most practical breeding programs, it might as well constitute a part of testing of combining ability in yield and other important characters.

The author recommended a simultaneous use of 3 single crosses as testers (BOJANOWSKI, 1964). Such systems of testing are applied by several breeders. In special cases one of the single crosses could play the role of a special "smut resistance" tester. It would have to be used as the pollen parent because of an expectedly high incidence of smut galls reducing its productivity.

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Zusammenfassung

An resistenten und anfälligen Mais-Inzuchtlinien, deren F_1-Hybriden und deren F_2- und F_3-Generationen wurde die Reaktion auf *Ustilago maydis* untersucht. Bezüglich der genetischen Präpotenz zeigten sich bei den Inzuchtlinien deutliche Unterschiede. Die Spaltung war polygen. Es wurde die Methode der Prüfung der Kombinationsfähigkeit angewandt und die allgemeine (σ_G^2) und spezielle (σ_S^2) Kombinationsfähigkeit geschätzt. Sowohl additive wie nicht-additive Genwirkung wurde gefunden. Für die Resistenzzüchtung werden Kreuzungen mit besonders anfälligen Testern vorgeschlagen.

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