THE INHERITANCE OF REACTION TO SMUT, STEM RUST AND CROWN RUST IN SEVERAL COMPOUND OAT CROSSES

by

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INTRODUCTION

The four major diseases of oats in the United States are crown rust, *Puccinia coronata avenae* Corda; stem rust, *Puccinia graminis avenae* Erikss. and Henn.; covered smut, *Ustilago levis* (Kell. and Sw.) Magn.; and loose smut, *Ustilago avenae* (Pers.) Jens. The most effective way of controlling these diseases is the use of resistant varieties. Plant breeders are hybridizing disease resistant oat varieties with varieties of known agronomic value and are producing new disease resistant strains with high yielding ability and other desirable agronomic characters. These breeders can work more efficiently, using valuable short-cut methods, if they understand the manner in which disease resistance is inherited.

The purpose of this investigation was to determine the manner in which resistance to these diseases is inherited in several compound oat crosses.

REVIEW OF LITERATURE

An attempt has been made to review most of the literature on the subject of the inheritance of the reaction of oat hybrids to crown rust, stem rust, covered smut, and loose smut. This review has been summarized in tabular form to show the relationship of the inheritance of disease reaction in the many varieties and crosses that have been studied. Two hundred and eleven crosses have been grouped according to their genetic reaction to each disease. The disease reaction of each parent is indicated as resistant (R), intermediate (I), or susceptible (S). The physiologic race of the disease-producing organism, used in each study, has been shown in the tables as it was designated by the investigator. The genetic reactions of each cross to the various diseases were determined by studies of the disease reactions of the progeny. In most cases F_1, F_2, and F_3 generations were studied; in some instances, however, the F_4 and F_5 generations also were observed.

A summary of crown rust inheritance studies is presented in Table 1. Resistance was dominant and due to one factor in eight crosses while in eight other crosses the reaction was explained on a two-factor basis. Multiple factors were thought to be operating in one cross in which susceptibility was apparently dominant. Two dominant complementary genes for resistance were observed in six crosses.

Dominant inhibitors of resistance were reported in two crosses. In 1939, Torrie observed the action of a gene which partly inhibited the expression of a dominant factor for crown rust resistance in a cross between Iowa 444 and Bond. The inhibitor appeared to be more effective in the mature plant stage in the field than in the seedling stage in the greenhouse.

Weetman (1942) reported that the crown rust resistance of the varieties, Bond and Mutica Ukrania, was due to two dominant complementary genes while that of Victoria was due to one dominant factor. His studies were not included in Table 1 because he failed to mention the crosses involved.

In the crown rust studies, two factors seemed to govern the inheritance as often as one but this was not true in the stem rust studies. The genetical explanations for the inheritance of stem rust reaction in

Table 1.--Summary of literature on studies of inheritance of resistance to crown rust in oat crosses.

Cross	Physiologic race	Investigator
F_2 ratio of three resistant to one susceptible - resistance dominant - one factor		
Red Rustproof (R) x Scotch Potato (S)	unidentified	Davies and Jones (1926, 1927)
Sunrise 23 (R) x Fulghum 47 (S)	3	Dietz and Murphy (1930)
Guyra 51 (S) x Sunrise 23 (R)	3	" " " "
Golden 84 (S) x Red Rustproof 11 (R)	3	" " " "
(Algerian x Calcutta) 89 (R) x Golden 84 (S)	3	" " " "
Lee (S) x Victoria (R)	1	Murphy et al. (1937)
Hairy Culberson (S) x Victoria (R)	1	" " "
Bond (R) x Rainbow (S)	several	Hayes et al. (1939)
F_2 ratio of nine resistant to seven susceptible - resistance dominant - two complementary factors		
Bond (R) x Double Cross A (S)	several	Hayes et al. (1939); Hayes (1941)
Double Cross A (S) x Bond (R)	"	" " " " " "
Bond (R) x Double Cross B (S)	"	" " " " " "
Bond (R) x Anthony (S)	"	" " " " " "
Anthony (S) x Bond (R)	"	" " " " " "
Bond (R) x Iogold (S)	"	" " " " " "
F_2 ratio of three resistant to thirteen susceptible - dominant inhibitor - two factors		
Sunrise 23 (R) x Fulghum 41 (S)	3	Dietz and Murphy (1930)
F_2 ratio of five resistant to eleven susceptible in the mature plant stage - nine resistant to seven susceptible in the seedling stage - partial inhibitor - two factors		
Iowa 444 (S) x Bond (R)	1, 7, 46, and composite	Torrie (1939)
F_2 progeny showing varying degrees of resistance - susceptibility dominant - multiple factors		
Burt (R) x Sixty Day (S)	unidentified	Parker (1920)
Crown rust reaction studied but not explained on a factor basis		
Victoria (R) x Double Cross II-22-220 (S)	1, 2, 3, 4, 6, 7, 17, 24	Smith (1934)
Double Cross II-22-220 (S) x Victoria (R)	"	" "
Victoria (R) x Anthony (S)	"	" "
Anthony (S) x Victoria (R)	"	" "
Victoria (R) x Minrus (S)	"	" "
Minrus (S) x Victoria (R)	"	" "
Victoria (R) x Rainbow (S)	"	" "

41 crosses are presented in Table 2. Resistance was dominant and due to one factor in 37 crosses and susceptibility was dominant and due to one factor in one cross. The stem rust reaction was controlled by two factors in the other three crosses. Two dominant complementary genes for resistance were operating in one of these crosses while dominant inhibitors were masking the expression of dominant genes for resistance in the two other crosses. Resistance was dominant and controlled by one factor in most of the stem rust studies.

Investigators who have studied the inheritance of reaction to the smut diseases of oats have not been able to be as specific in describing the inheritance as the workers in the rust studies have been. This is mainly due to the fact that susceptible plants often escape smut infection and thus appear to be resistant. Such escapes do not occur very frequently in rust studies. Most investigators have merely stated the condition of dominance and the number of factors concerned in the smut reaction of the cross which they observed.

The genetical analyses for the inheritance of reaction to covered smut in 37 crosses are presented in Table 3. Resistance was dominant and due to one factor in 23 crosses; susceptibility was dominant and governed by one factor in one cross. Resistance was dominant and controlled by two factors in seven crosses and dominant and governed by three factors in six crosses. Forty-six crosses analyzed for genetic reaction to loose smut are presented in Table 4. Resistance was dominant and due to a single factor difference in 34 crosses. Resistance was dominant and governed by two factors in five crosses and in seven crosses it was reported to be dominant and controlled by three factors.

Some investigators observed the reaction of crosses to mixtures

Table 2.--Summary of literature on studies of inheritance of resistance to stem rust in oat crosses.

Cross	Physiologic race	Investigator
F_2 ratio of three resistant to one susceptible - resistance dominant - one factor		
White Russian (R) x Victory (S)	unidentified	Garber (1921, 1922), Griffee (1922)
Minota (S) x White Russian (R)	"	" " " " "
White Russian (R) x Minota (S)	"	" " " " "
White Tartar (R) x National (S)	2	Dietz (1925, 1928)
White Tartar (R) x Lincoln (S)	2	" " "
White Russian (R) x Burt (S)	2	" " "
Green Russian (R) x Early Ripe (S)	2	" " "
Green Russian (R) x Burt (S)	2	" " "
(White Russian x Victory) II-18-2 (R) x Black Mesdag (S)	several	Hayes et al. (1928)
(Minota x White Russian) II-18-37 (R) x Black Mesdag (S)	"	" " " "
(Minota x White Russian) II-18-4 (R) x Black Mesdag (S)	"	" " " "
Belar (S) x Reid (R)	1	Waterhouse (1930)
Ruakura (S) x Richland (R)	1	" "
Algerian (S) x White Tartar (R)	1	" "
Algerian (S) x Joanette (R)	1	" "
Markton (S) x Heigira Strain (R)	1, 2, 3, 5, 7	Welsh (1931)
Heigira Strain (R) x Banner (S)	1, 2, 3, 5, 7	Welsh (1931), Gordon and Welsh(1932)
Joanette Strain (R) x (Minota-White Russian x Black Mesdag) (S)	4	" " " " " "
Heigira Strain (R) x Joanette Strain (S)	1, 2, 3, 5, 7	" " " " " "
Richland (R) x (Minota-White Russian x Black Mesdag) (S)	1, 2, 3, 5, 7	" " " " " "
Victory (S) x Green Russian (R)	1, 2, 3, 5, 7	" " " " " "
Gopher (S) x Rainbow (R)	1, 2, 3, 5, 7, 8, 9	Smith (1934)
Bond (S) x Double Cross A (R)	1	Hayes et al. (1939), Hayes (1941)
Double Cross A (R) x Bond (S)	1	" " " " " "
Bond (S) x Double Cross B (R)	1	" " " " " "
Bond (S) x Anthony (R)	1	" " " " " "
Anthony (R) x Bond (S)	1	" " " " " "
Bond (S) x Iogold (R)	1	" " " " " "
Bond (S) x Rainbow (R)	1	" " " " " "
Iowa 444 (R) x Bond (S)	2, 5, 7	Torrie (1939)
Carleton (S) x (Victoria x Richland) (R)	2, 5, 7	" "
Victoria (S) x Richland (R)	2, 5, 7	" "
Bond (S) x C.I. 2884 (S.D. 334) (R)	2, 5, 7	" "
(Victoria x Richland, Sel. 5544-3) (R) x State Pride (S)	2, 5, 7	" "
Nidar (S) x (Victoria x Richland, Sel. 5544-3)(R)	2, 5, 7	" "
Anthony (R) x Victoria (S)	2, 5, 7	" "
Bond (S) x Hawkeye (R)	2, 5, 7	" "
F_2 ratio of one resistant to three susceptible - susceptibility dominant - one factor		
White Russian (R) x Burt (S)	2	Dietz (1925, 1928)
F_2 ratio of nine resistant to seven susceptible - resistance dominant - two complementary factors		
Heigira Strain (S) x Joanette Strain (R)	4	Welsh (1931)
F_2 ratio of three resistant to thirteen susceptible - dominant inhibitor - two factors		
Burt (S) x White Russian (R)	2	Dietz (1925, 1928)
Green Russian (R) x Burt (S)	2	" " "
Stem rust reaction studied but not explained on a factor basis		
Green Russian (R) x Richland (R)	2	Dietz (1925, 1928)
White Russian (R) x Ruakura (R)	2	" " "

Table 3.--Summary of literature on studies of inheritance of resistance to covered smut in oat crosses.

Cross	Physiologic race	Investigator
Smut reaction determined by one factor - resistance dominant		
Hull-less (S) x Black Mesdag (R)	unidentified	Reed (1928)
Early Gothland (R) x Victor (S)	"	" "
Early Gothland (R) x Hull-less (S)	"	" "
Markton (R) x Ligowa (S)	"	Coffman et al. (1931)
Markton (R) x Early Champion (S)	"	" " " "
Markton (R) x Swedish Select (S)	"	" " " "
Hull-less (S) x Black Mesdag (R)	"	Reed (1928, 1934)
Silvermine (S) x Black Mesdag (R)	"	" " "
Early Champion (S) x Black Mesdag (R)	"	Reed (1934)
Seizure (R) x Victor (S)	"	Reed and Stanton (1937)
Scottish Chief (R) x Victor (S)	"	" " " "
Gothland (R) x Monarch (S)	"	" " " "
Rossman (R) x Monarch (S)	"	" " " "
Danish (R) x Monarch (S)	"	" " " "
Seizure (R) x Monarch (S)	"	" " " "
Monarch (S) x Scottish Chief (R)	"	" " " "
Canadian (S) x Markton (R)	"	Reed and Stanton (1938)
Early Champion (S) x Markton (R)	"	" " " "
Markton (R) x Early Champion (S)	"	" " " "
Victor (S) x Markton (R)	"	" " " "
Monarch (S) x Markton (R)	"	" " " "
Canadian (S) x Monarch (R)	1	Reed (1941)
Green Mountain (R) x Monarch (S)	3	" "
Smut reaction determined by one factor - susceptibility dominant		
Danish Island (R) x Monarch (S)	unidentified	Reed and Stanton (1937)
Smut reaction determined by two factors - resistance dominant		
Markton (R) x Large Hulless (S)	unidentified	Gaines and Smith (1929)
Markton (R) x Banner (S)	"	" " " "
Markton (R) x Scottish Chief (S)	"	Coffman et al. (1931)
Victory (S) x (Minota-White Russian x Black Mesdag) (R)	"	Welsh (1931)
Black Mesdag (R) x Victory (S)	"	Johnson (1933)
Colorado 37 (S) x Markton (R)	"	Austin and Robertson (1936)
Markton (R) x Colorado 37 (S)	"	" " " "
Smut reaction determined by three factors - resistance dominant		
Red Rustproof (R) x Black Tartarian (S)	unidentified	Wakabayashi (1921)
Red Rustproof (R) x Black Tartarian (S)	"	Gaines (1925a, 1925b)
Red Rustproof (R) x Abundance (S)	"	" " "
Red Rustproof (R) x Large Hulless (S)	"	" " "
Red Rustproof (R) x Chinese Hulless (S)	"	" " "
Gothland (R) x Black Mesdag (R)	1	Reed (1941)
Smut reaction studied but not explained on a factor basis		
Fulghum (R) x Swedish Select (S)	unidentified	Reed and Stanton (1925)
Iogren (S) x Markton (R)	"	Coffman et al. (1931)
Aurora (S) x Markton (R)	"	" " " "
Markton (R) x Victory (S)	"	" " " "
Markton (R) x Idamine (S)	"	" " " "
Silvermine (S) x Markton (R)	"	" " " "
Early Gothland (R) x Monarch (S)	"	Reed (1931)
Monarch (S) x Early Gothland (R)	"	" "
Early Gothland (R) x Victor (S)	"	Reed (1932a)
Early Gothland (R) x Hull-less (S)	"	Reed (1932b)
Richland (S) x Fulghum (S)	Missouri	Stanton et al. (1934)
Richland (S) x Markton (R)	Missouri	Stanton et al. (1934)
Cornellian (R) x Markton (R)	"	" " " "
Gothland (R) x Markton (R)	unidentified	Reed and Stanton (1938)
Both parents resistant - progeny resistant		
Markton (R) x Black Mesdag (R)	Missouri	Stanton et al. (1934)
Monarch Sel. (R) x Black Mesdag (R)	"	" " " "
Markton (R) x Iogold (R)	"	" " " "
Monarch Sel. (R) x Gothland (R)	1	Reed (1941)
Both parents susceptible - progeny susceptible		
Canadian (S) x Victor (S)	unidentified	Reed (1928)
Silvermine (S) x Hull-less (S)	"	" "
Monarch (S) x Hull-less (S)	"	Reed (1928, 1932b)
Hull-less (S) x Monarch (S)	"	" " "

Table 4.--Summary of literature on studies of inheritance of resistance to loose smut in several oat crosses.

Cross	Physiologic race	Investigator
Smut reaction determined by one factor - resistance dominant		
Turkish Rustproof (S) x Gold Rain (I)	unidentified	Barney (1924)
Early Ripe (I) x Black Mesdag (R)	"	" "
Sixty Day (S) x Black Mesdag (R)	"	" "
Avena nuda var. inermis (S) x Black Mesdag (R)	"	Reed (1925)
Hull-less (S) x Black Mesdag (R)	"	Reed (1928)
Monarch (R) x Hull-less (S)	"	" "
Hull-less (S) x Monarch (R)	"	" "
Hull-less (S) x Black Mesdag (R)	"	Reed (1928, 1934)
Silvermine (S) x Black Mesdag (R)	"	" " "
Early Champion (S) x Black Mesdag (R)	"	Reed (1934)
Dippes Überwinder (S) x Black Mesdag (R)	"	Rosenstiel (1930)
Peragis (S) x Black Mesdag (R)	"	" "
Stamm 01108 (S) x Black Mesdag (R)	"	" "
Carsten III (S) x Black Mesdag (R)	"	" "
Red Rustproof (R) x Carsten III (S)	"	Schattenberg (1934)
Monarch (R) x Dippes Überwinder (S)	"	" "
Gopher (I) x Eckendorfer Frühhafer (S)	"	" "
v. Lochows Gelbhafer (R) x Eckendorfer Frühhafer (S)	"	" "
Echendorfer Frühhafer (S) x Lischower Frühhafer (R)	"	" "
Monarch Sel. (S) x Black Mesdag (R)	Missouri	Stanton et al. (1934)
Fulghum (S) x Black Mesdag (R)	Fulghum	Reed (1935)
Gothland (S) x Monarch (R)	unidentified	Reed and Stanton (1937)
Rossman (S) x Monarch (R)	"	" " " "
Danish (S) x Monarch (R)	"	" " " "
Seizure (S) x Monarch (R)	"	" " " "
Monarch (R) x Scottish Chief (S)	"	" " " "
Danish Island (S) x Monarch (R)	"	" " " "
Early Champion (S) x Markton (R)	"	Reed and Stanton (1938)
Markton (R) x Early Champion (S)	"	" " " "
Victor (S) x Markton (R)	unidentified	Reed and Stanton (1938)
Gothland (S) x Markton (R)	"	" " " "
Gothland (S) x Black Mesdag (R)	1	Reed (1941)
Danish Island (S) x Black Mesdag (R)	1	" "
Green Mountain (S) x Monarch (R)	1	" "
Smut reaction determined by two factors - resistance dominant		
Swedish Select (S) x Burt (R)	unidentified	Barney (1924)
Victory (S) x (Minota-White Russian x Black Mesdag) (R)	"	Welsh (1931)
Red Rustproof (R) x Stamm 01108 (S)	"	Nicolaisen (1931)
Dippes Überwinder (S) x Lischower Frühhafer (R)	"	Schattenberg (1934)
Canadian (S) x Markton (R)	"	Reed and Stanton (1938)
Smut reaction determined by three factors - resistance dominant		
Fulghum (R) x Black Mesdag (R)	unidentified	Barney (1924)
v. Lochow's Gelbhafer (R) x Black Mesdag (R)	"	Nicolaisen (1931)
v. Lochow's Gelbhafer (R) x Red Rustproof (R)	"	" "
(Dippes Überwinder x v. Lochow's Gelbhafer) (R) x Markton (R)	"	Schattenberg (1934)
Carsten III (S) x Markton (R)	"	" "
v. Lochow's Gelbhafer (R) x Markton (R)	"	" "
Monarch (R) x Markton (R)	"	Reed and Stanton (1938)
Smut reaction studied but not explained on a factor basis		
Fulghum (R) x Swedish Select (S)	unidentified	Reed and Stanton (1925)
v. Lochow's Gelbhafer (R) x Fulghum (S)	"	Nicolaisen (1931)
Early Gothland (S) x Monarch (R)	"	Reed (1931)
Monarch (R) x Early Gothland (S)	"	" "
Monarch (R) x Hull-less (S)	"	Reed (1932b)
Hull-less (S) x Monarch (R)	"	" "
Markton (R) x Black Mesdag (R)	Missouri	Stanton et al. (1934)
Monarch Sel. (S) x Black Mesdag (R)	Fulghum	" " " "
Markton (R) x Iogold (S)	Missouri	" " " "
Cornellian (S) x Markton (R)	"	" " " "
Richland (S) x Markton (R)	"	" " " "
Richland (S) x Fulghum (S)	"	" " " "
Richland (R) x Fulghum (S)	Fulghum	" " " "
Lee (S) x Victoria (R)	Similar or identical	Murphy et al. (1937)
Hairy Culberson (S) x Victoria (R)	to Missouri	" " " "
Both parents resistant - progeny resistant		
Markton (R) x Black Mesdag (R)	Fulghum	Stanton et al. (1934)
Markton (R) x Iogold (R)	"	" " " "
Cornellian (R) x Markton (R)	"	" " " "
Richland (R) x Markton (R)	"	" " " "
Both parents susceptible - progeny susceptible		
Canadian (S) x Victor (S)	unidentified	Reed (1928)
Silvermine (S) x Hull-less (S)	"	" "
Early Gothland (S) x Victor (S)	"	Reed (1928, 1932a)
Early Gothland (S) x Hull-less (S)	"	Reed (1928, 1932b)
Seizure (S) x Victor (S)	"	Reed and Stanton (1937)
Scottish Chief (S) x Victor (S)	"	" " " "
Canadian (S) x Monarch (S)	1	Reed (1941)
Monarch Sel. (S) x Gothland (S)	1	" "

of loose and covered smut. These observations are summarized in Table 5. Resistance was dominant and controlled by a single factor difference in two crosses and it was dominant and governed by two factors in eight other crosses. In two crosses resistance was reported to be dominant and due to the action of three factor pairs.

All of the smut studies may be summarized as follows: Explanations of inheritance were offered for 95 crosses. Resistance was dominant and governed by one factor in 59 crosses while in one cross susceptibility was dominant and controlled by one factor. Resistance was dominant and due to two factors in 20 crosses while it was dominant and due to three factors in only 15 crosses.

In summarizing all of the studies on the inheritance of resistance to the four diseases, the reactions of 153 crosses were explained on a factor basis. A single factor difference was shown by 106 crosses, two factors were operating in 31 crosses, three factors were involved in 15 crosses, and multiple factors were reported as governing the reaction of one cross. Resistance was dominant in 150 of the crosses.

Humphrey and Coffman (1937) reported on studies of the disease reaction of F_1 oat hybrids. They reached no conclusions as to the number of factors involved since their study was only with F_1 hybrids. They reported that resistance to stem rust was dominant and resistance to crown rust was either dominant or intermediate. The smut reaction of nine crosses between resistant and susceptible varieties was studied. Resistance to smut appeared to be dominant since none of the inoculated F_1 plants were smutted. These studies of F_1 plants tended to confirm the studies which were presented in Tables 1 to 5. In most cases

Table 5.--Summary of literature on studies of inheritance of resistance to mixtures of loose and covered smuts in oat crosses.		
Cross	**Physiologic race**	**Investigator**
Smut reaction determined by one factor - resistance dominant		
Bond (R) x Anthony (S)	unidentified	Hayes et al. (1939), Hays (1941)
Bond (R) x Iogold (S)	"	" " " " " "
Smut reaction determined by two factors - resistance dominant		
(White Russian x Victory) II-18-2 (S) x Black Mesdag (R)	half and half	Hayes et al. (1928)
(Minota x White Russian) II-18-37 (S) x Black Mesdag (R)	" " "	" " " "
(Minota x White Russian) II-18-4 (S) x Black Mesdag (R)	" " "	" " " "
Iowa 444 (S) x Bond (R)	mostly loose smut	Torrie (1939)
Victoria (R) x Richland (S)	" " "	" "
(Victoria x Richland, Sel. 5544-3) (R) x State Pride (S)	" " "	" "
Smut reaction determined by one main factor and one modifying factor - reistance dominant		
Gopher (S) x Black Mesdag (R)	mostly loose smut	Garber et al. (1928, 1929, 1934)
Black Mesdag (R) x Gopher (S)	" " "	" " " " " "
Smut reaction determined by three factors - resistance dominant		
Bond (R) x Double Cross A (R)	unidentified	Hayes et al. (1939), Hayes (1941)
Bond (R) x Double Cross B (R)	"	" " " " " "

resistance to these diseases was dominant and in many cases it was governed by a single factor difference.

MATERIALS

The four compound crosses used in the studies on the inheritance of rust and smut reaction were made by Mr. Elmer G. Heyne, Division of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture, in the greenhouse at Manhattan, Kansas, during the winter of 1939-40. A Richland-Fulghum selection was used as one of the parents in each of the crosses. The other parents were Anthony-Bond, Fulghum-Victoria, and Fultex. Fultex is a selection from a Fulghum-Victoria cross. These parents were advanced hybrid lines that were presumably homozygous. The crosses studied were Richland-Fulghum x Fulghum-Victoria, Fulghum-Victoria x Richland-Fulghum, Fultex x Richland-Fulghum, and Anthony-Bond x Richland-Fulghum.

Richland-Fulghum is resistant to race 2 of stem rust and to the Fulton, Kanota, and Richland races of loose and covered smut that have been collected in Kansas. This selection is susceptible to race 8 of stem rust and to race 1 of crown rust. Fulghum-Victoria and Fultex carry the resistance of Victoria to the Fulton, Kanota, and Richland races of loose and covered smut in Kansas and to race 1 of crown rust. Fulghum-Victoria and Fultex are susceptible to race 2 of stem rust. Anthony-Bond is resistant to race 8 and race 2 of stem rust. This selection carries the high resistance of Bond to race 1 of crown rust, but it is slightly susceptible to the smut used in this study showing about five percent infection. The disease reactions of the parents are shown

Table 6.--Reaction of hybrid lines, used as parents, to the physiologic races of crown rust, stem rust and smut used as inoculum in studies on the inheritance of disease resistance. Manhattan, Kans., 1941-1942.

Variety	Identification No.	Crown rust* p.r. 1	Stem rust* P.r. 2	Stem rust* P.r. 8	Loose and covered smut* composite of Kanota, Richland and Fulton races
Richland-Fulghum	Kans. 6155	S	R	S	R
Fulghum-Victoria	C.I. 3485	R	S	-	R
Fultex	C.I. 3531	R	S	-	R
Anthony-Bond	Ames 1826	R	S	R	Sl. S

*R = resistant; S = susceptible; Sl. S = slightly susceptible.

in Table 6.

Race 1 of crown rust, the most common race attacking oats in Kansas and adjacent states, was used in these studies. In the stem rust studies, race 2 was used in the field and in some of the greenhouse studies while race 8 was used in other greenhouse studies. The culture of race 8 was obtained from Dr. E. C. Stakman, Minnesota Agricultural Experiment Station. All of the other rust cultures were obtained from Mr. C. O. Johnston, Pathologist, United States Department of Agriculture. A composite of Fulton, Kanota, and Richland races of loose and covered smut was dusted on the seed which was used in the field studies. This smut was obtained from Dr. E. D. Hansing, Department of Botany and Plant Pathology, Kansas State College. The composite used for inoculating the seed planted in the F_2 studies consisted of equal parts of Kanota and Richland races and a smaller proportion of the Fulton race. The smut composite used in the F_3 studies contained equal parts of the races attacking Kanota, Richland and Fulton.

An inexpensive and efficient moist chamber for the greenhouse inoculations was constructed from a large packing box which was waterproofed with a roofing paint. The front of the box was hinged to swing upward providing an opening into the chamber. A three-inch layer of moist sand in the bottom of the box maintained a high humidity which was favorable for spore germination and infection.

Seedling plants growing in two-inch flowerpots were used for all of the greenhouse rust studies. Each pot contained the progeny of a single hybrid plant or parental strain. There were 30 or more plants per pot in most cases. Pots of seedlings were handled and inoculated while they were in shallow, galvanized metal pans. After inoculation, the pots of seedlings were kept in shallow pans of water or in a large trough containing about one-half inch of water. This trough was constructed on a table in the greenhouse and was lined with a heavy roofing material making it water tight.

METHODS

The crosses were made during the winter of 1939-40. The F_1 plants were grown during the next winter in the greenhouse and were tested for reaction to stem rust and crown rust. Half of the seed from each plant was sent to Aberdeen, Idaho, to be grown under irrigation for seed increase purposes. The remainder was innoculated by dusting the seed with a composite of spores of loose and covered smut, then space planted three inches apart in the rust nursery at Manhattan. The parental oat varieties were planted at intervals among the hybrids for comparison.

For the studies made in the field, artificial epiphytotics of crown rust and stem rust were produced in the nursery. Rust spreader rows, border rows and susceptible check rows were inoculated with the rusts by means of hypodermic injections of spore suspensions into the curled leaves of the developing plants. Spores were disseminated from these centers of infection by wind to the parents and the hybrids. In addition spore suspensions were sprayed on the plants in the nursery during periods of damp, rainy weather. The moisture necessary for spore germination and infection was supplied naturally by heavy spring dews and artificially by an overhead sprinkling system. Crown rust inoculations were begun two weeks ahead of the stem rust inoculations in order that crown rust notes could be taken before the stem rust developed.

Crown rust infection was very heavy by June 13, 1941, and notes were taken on parent and F_2 hybrid reaction. The crown rust reaction was recorded on a tag and tied to each plant when it was examined in the field. A severe epiphytotic of stem rust followed the crown rust epiphytotic. When the plants had matured the progeny of a single F_1 plant was pulled and tied into a bundle. Late in the summer the heads from each F_2 plant were removed and placed in an envelope. The stem rust reaction of each plant was noted when the seed was harvested and the stem rust, crown rust, and smut reaction of each F_2 plant was recorded on the envelope containing the seed. The seed of each F_2 plant was threshed, cleaned, and given a number consisting of the F_1 plant number and the F_2 progeny number separated by a dash. The F_2 plants which were grown at Aberdeen, Idaho, were pulled, bundled by F_1 families, and shipped to Manhattan. The seed from these plants was threshed, cleaned, and numbered in the same manner as the Manhattan seed was handled.

Crown rust and stem rust cultures, for the greenhouse studies during the winter, were started on September 30, 1941. The crown rust culture was increased rapidly on Fulton seedlings while the stem rust cultures were grown on Bond to prevent mixtures of crown rust. Rust inoculation consisted of placing the plants in a moist chamber, spraying them with water, and then dusting them with spores. A 24-hour period in the moist chamber at ordinary greenhouse temperatures of 70 to 75 degrees was found to be sufficiently long for infection by either rust. The seedlings were usually inoculated seven days after planting when they were in the primary leaf stage.

The greenhouse plantings were started when the crown rust culture was providing an abundant supply of inoculum. An F_3 family, consisting of approximately 30 seeds from a single F_2 plant, was planted in a sterilized mixture of soil and sand in each pot. Each F_3 family was labeled with a pot label bearing the F_2 plant number. In all of the greenhouse work of planting, inoculating, and note taking the F_3 families were handled in numerical order to simplify note taking and to lessen the chance of mistakes. Plantings of 225 pots, the capacity of the moist chamber, were made every second day. Infected hybrids were used for inoculation purposes after notes on them had been recorded. This gave a continuous supply of inoculum from the hybrids themselves. Readings on the rust reaction could be made 10 to 12 days after inoculation. Approximately 7,000 pots of seedlings were inoculated and observed during the winter. Three pots of each parent were planted and inoculated with the hybrids in each planting giving a constant check on the intensity of inoculation and the purity of the rust cultures.

The stem rust inoculations were started after the last crown rust notes had been taken. Planting, inoculation, and note taking were done in the same manner as for the crown rust studies. Race 2 of stem rust was used for the studies on the Fulghum-Victoria and Fultex hybrids. Race 8 was increased last and was ready for inoculating the Anthony-Bond hybrids when the studies with race 2 were completed. Extreme care was used to prevent a contamination of race 8 by race 2. These races were always kept in different greenhouses. Studies with race 8 were started only after the equipment was sterilized and several days had elapsed after the last culture of race 2 was used.

When the stem rust studies were finished the crown rust resistant F_3 families of the Anthony-Bond x Richland-Fulghum cross were planted again and given a second inoculation with crown rust. This was done to obtain a check on their resistance.

Extreme care was used in keeping all of the rust cultures pure. Differential varieties were inoculated with them at regular periods during the studies to check their purity. The parents which were planted with each group of pots also gave an accurate check on the purity of the cultures.

It was observed in the F_2 and F_3 generations that the inheritance of crown rust reaction in the Anthony-Bond x Richland-Fulghum cross was somewhat complicated. In order to study this reaction more fully, certain F_3 lines were selected and planted in large pots in the greenhouse and were allowed to produce seed during the winter. This seed was smutted and planted in the rust nursery in 1942 in order that the F_4 crown rust reaction of a few selected lines could be observed. Approximately 30 seeds of each F_3 family were smutted and planted in the rust nursery in 1942. Stem rust and crown rust epiphytotics were produced in the same manner as described for the F_2 field tests in 1941. Crown rust and smut notes were taken in the field. Stem rust infection was not heavy enough in the field in 1942 for satisfactory note taking.

DISCUSSION OF RESULTS

The three crosses, Richland-Fulghum x Fulghum-Victoria, Fulghum-Victoria x Richland-Fulghum, and Fultex x Richland-Fulghum are of the same parentage and apparently carry the same genes for disease resistance and susceptibility. These crosses will be designated as the Fulghum-Victoria and Fultex crosses with Richland-Fulghum in this discussion. The other cross, Anthony-Bond x Richland-Fulghum, is distinctly different in its genetic constitution because of Anthony-Bond; it will be treated separately in the discussion.

Smut Studies

Inheritance of Reaction to Smut in Fulghum-Victoria and Fultex Crosses with Richland-Fulghum. The parents of these crosses were highly resistant (0.0 percent) to all of the races of smut used in the inoculations. The smut reactions of the hybrids are shown in Table 7. In the F_2 generation of the Richland-Fulghum x Fulghum-Victoria cross, 9.6 percent of the hybrids were smutted. In the reciprocal cross 3.6 percent of the hybrids were smutted; while 10.5 percent of the F_2 hybrids of the Fultex x Richland-Fulghum cross were smutted.

The F_3 generation was composed of lines coming from F_2 plants grown at Manhattan in the rust nursery and lines from F_2 plants grown at Aberdeen, Idaho, under irrigation. The seed from the irrigated Aberdeen plants was much plumper. The F_3 seedlings in the field were more vigorous as a result of this plumpness, and some of the plants may have escaped smut infection because of their seedling vigor. The F_3 seedlings coming from F_2 plants grown at Manhattan were less vigorous and were probably more susceptible to infection at germination than the Aberdeen seedlings. In addition the seed planted at Aberdeen was not inoculated while that planted at Manhattan was inoculated with the smut composite.

Table 7.--Smut reactions of hybrids. Manhattan, Kans., 1941-1942.

Cross	F_2 reaction: Number of plants observed	F_2 reaction: Number of plants smutted	F_2 reaction: Percent of plants smutted	F_2 plants grown at	F_3 reaction: Number of lines observed	F_3 reaction: Number of lines smutted	F_3 reaction: Percent of lines smutted
Richland-Fulghum x Fulghum-Victoria	104	10	9.6	Manhattan	104	58	55.8
				Aberdeen	20	6	30.0
				Total	124	64	51.6
Fulghum-Victoria x Richland-Fulghum	338	12	3.6	Manhattan	337	141	41.8
				Aberdeen	390	121	31.0
				Total	727	262	36.0
Fultex x Richland-Fulghum	133	14	10.5	Manhattan	133	64	48.1
				Aberdeen	225	79	35.1
				Total	358	143	39.9
Summary of three R-F x F-V crosses	575	36	6.26	Manhattan	574	263	45.8
				Aberdeen	635	206	32.4
				Total	1209	469	38.8
Anthony-Bond x Richland-Fulghum	940	10	1.1	Manhattan	938	406	43.3
				Aberdeen	1094	191	17.5
				Total	2032	597	29.4

At Manhattan, a heavy smut infection in susceptible check rows probably resulted in considerable infection of F_3 seed on F_2 plants at flowering time. Since a significantly higher percentage of the F_3 lines from the Manhattan grown seed were smutted, it may be postulated that this higher infection may be accounted for on a basis of seedling vigor, floral infection or a combination of both of these factors. The Manhattan F_3 lines probably give a truer picture of the actual smut inheritance because there was less escape from infection in these lines. The data obtained from the Manhattan lines were used in determining the inheritance. An F_3 line was considered as smutted if it contained one or more smutted heads. In Richland-Fulghum x Fulghum-Victoria, 55.8 percent of the lines from Manhattan seed were smutted while only 30 percent of the lines from Aberdeen seed were smutted. In the reciprocal cross, 41.8 percent of the Manhattan lines were smutted and 31 percent of the Aberdeen lines were smutted. In the cross, Fultex x Richland-Fulghum, 48.1 percent of the Manhattan F_3 lines were smutted and 35.1 percent of the Aberdeen lines showed smut. The parents of these crosses all showed high resistance (0.0 percent infection) to the races of smut in the composite inoculum. Transgressive segregation for smut susceptibility therefore occurred in these hybrids. If both parents carried complementary recessive factor pairs for smut susceptibility, an F_2 ratio of 15 resistant to one susceptible would be expected. Any hybrid plants carrying both of these recessive factor pairs would be susceptible to smut; while the parents, carrying only one pair of recessive factors, would be resistant. If this were true, one-sixteenth or 6.25 percent of the F_2 hybrids would be expected to be smutted while 6.26 percent were actually observed to be smutted. Theoretically, if there were no escape from infection in the F_3 lines, nine-sixteenths or 56.25 percent of the lines would be expected to be smutted. Actually 55.8 percent of the Manhattan lines in the Richland-Fulghum x Fulghum-Victoria cross were smutted. Slightly lower percentages of infection of the Manhattan lines of the two other crosses can probably be accounted for by escape from smut infection. Smut resistance has been reported to be dominant in nearly all of the crosses which have been studied; thus susceptibility is generally due to a recessive factor pair. However, in these three crosses recessive factor pairs are carried by each of the parents and the parents are resistant. The expression of these pairs is evidently not strong enough in the parents, where only one pair is acting, to make the plants susceptible. Transgressive segregation occurs when both recessive factor pairs come together in the hybrids. Transgressive segregation for smut infection has been reported by Coffman et al. (1931), Garber and Hoover (1934), and Stanton et al. (1934).

Inheritance of Reaction to Smut in the Anthony-Bond x Richland-Fulghum Cross. Richland-Fulghum was highly resistant showing no smut while Anthony-Bond showed about five percent infection, being slightly susceptible. Only 10 plants or 1.1 percent of the 940 F_2 hybrids of this cross were smutted. In the F_3 generation, 43.3 percent of the Manhattan lines were smutted, and 17.5 percent of the Aberdeen lines were smutted. If resistance in this cross were dominant and due to three independently inherited dominant factors one sixty-fourth of the F_2 plants would be expected to be recessive for the three factors and thus be susceptible to smut. This would be 1.56 percent of the 940 F_2 plants or

14.7 plants. Since 10 smutted plants were observed, this is very close to the expected number. In the F_3 generation, 396 (twenty-seven sixty-fourths or 42.2 percent) of the F_3 lines would be expected to show some smutted plants. Actually 406 of the 938 Manhattan lines showed smutted plants; this was 43.3 percent of the lines, very close to the 42.2 percent expected. It is possible that resistance to smut in this cross is dominant and due to three independently inherited factors. Similar inheritance has been reported by eight investigators, see Tables 3, 4 and 5.

Stem Rust Studies

Inheritance of Reaction to Stem Rust in Fulghum-Victoria and Fultex Crosses with Richland-Fulghum. Fulghum-Victoria and Fultex were quite susceptible to race 2 of stem rust. The pustules on these susceptible parents were large, linear, and erumpant, producing many spores. Richland-Fulghum, resistant to this race, had pustules that were small, circular, and inconspicuous. The F_1 plants were almost as resistant as the Richland-Fulghum parent. Two types of rust reaction were observed in the F_2 hybrids. One phenotype resembled the resistant Richland-Fulghum parent and the other was as susceptible as the Fulghum-Victoria and Fultex parents. In the progeny of Richland-Fulghum x Fulghum-Victoria, 65 resistant and 39 susceptible F_2 plants were observed. Two hundred fifty-eight resistant and 80 susceptible plants were observed in the reciprocal of this cross and a ratio of 100 resistant to 33 susceptible plants was observed in the Fultex x Richland-Fulghum cross. The F_2 data seemed to fit a ratio of three resistant to 1 susceptible and resistance appeared to be completely dominant. The stem rust reactions of the hybrids are shown in Table 8.

The F_3 data in general supported the F_2 observations. A comparison of F_2 classification with F_3 breeding behavior is shown in Table 9. The progeny from the susceptible F_2 plants bred true for susceptibility in the F_3 generation while one-third of the resistant F_2 plants bred true for resistance and two-thirds of these plants segregated like the F_2 generation (3 resistant to 1 susceptible). Thirty-three segregating F_3 lines in Fulghum-Victoria x Richland-Fulghum and 14 segregating lines in Fultex x Richland-Fulghum were counted. The counts made in these segregating lines, which were very close to the expected 3:1 ratio, are shown in Table 10. The greenhouse seedling F_3 reactions of these crosses are shown in Table 8. There appeared to be a slight deficiency of lines breeding true for resistance for some unaccountable reason. This lack of resistant lines gives some of the F_3 ratios a highly significant Chi square with a probability of less than .01. However, all other observations indicate that resistance to stem rust in these crosses is dominant and due to one factor. Parent and F_3 hybrid seedling reaction of the Richland-Fulghum x Fulghum-Victoria cross to race 2 of stem rust are shown in Plate I.

Inheritance of Reaction to Stem Rust in the Anthony-Bond x Richland-Fulghum Cross. Both parents were resistant to race 2 of stem rust. The hybrids were as resistant as the parents and did not segregate for reaction to this rust. Anthony-Bond was also resistant to race 8. This resistance was characterized by very small circular pustules surrounded by "green islands" of chlorophyll. Richland-Fulghum was susceptible to this race of stem rust and had large, linear pustules. Race 8 was not

Table 8.--Crown and stem rust reactions of hybrids and goodness of fit. Manhattan, Kans., 1941-1942.

Cross	Observed or expected	F2 generation in field					F3 generation in greenhouse					
		Number of plants					Number of lines					
		R*	S*	Total	X^2	Range of P	R	Seg*	S	Total	X^2	Range of P
Crown rust												
Richland-Fulghum x	O	65	39	104	8.667	less than .01	31	45	44	120	10.317	less than .01
Fulghum-Victoria	E	78	26				30	60	30			
Fulghum-Victoria x	O	258	80	338	0.393	.50-.95	178	368	178	724	0.199	.50-.95
Richland-Fulghum	E	253	85				181	362	181			
Fultex x	O	100	33	133	0.000	100	76	173	104	353	4.636	.05-.10
Richland-Fulghum	E	100	33				88	177	88			
Summary of R-F x	O	423	152	575	0.593	.30-.50	285	586	326	1197	3.376	.10-.20
F-V crosses	E	431	144				299	599	299			
Anthony-Bond x	O	310	630	940	0.121	.50-.95	50	989	952	1991	0.474	.50-.95
Richland-Fulghum	E	305	635				54	996	941			
Stem rust												
Richland-Fulghum x	O	73	31	104	1.282	.20-.30	22	65	33	120	2.850	.20-.30
Fulghum-Victoria	E	78	26				30	60	30			
Fulghum-Victoria x	O	237	101	338	4.024	.01-.05	151	346	227	724	17.370	less than .01
Richland-Fulghum	E	253	85				181	362	181			
Fultex x	O	97	36	133	0.363	.50-.95	66	186	101	353	7.878	.01-.05
Richland-Fulghum	E	100	33				88	177	88			
Summary of R-F x	O	407	168	575	5.336	.01-.05	239	597	361	1197	24.903	less than .01
F-V crosses	E	431	144				299	599	299			
Anthony-Bond x	O						324	632	316	1272	0.151	.50-.95
Richland-Fulghum	E						318	636	318			

*R = resistant; Seg = segregating; S = susceptible.

Table 9.--Comparison of F_2 classification with F_3 breeding behavior to stem rust. Manhattan, Kans., 1941-1942.

Cross	F_2 classification*	F_3 breeding behavior**			
		R	Seg	S	Total
Richland-Fulghum	R	14	55	2	71
x					
Fulghum-Victoria	S	1	4	24	29
	Total	15	59	26	100
Fulghum-Victoria	R	75	154	6	235
x					
Richland-Fulghum	S	--	1	98	99
	Total	75	155	104	334
Fultex	R	17	77	--	94
x					
Richland-Fulghum	S	--	2	32	34
	Total	17	79	32	128
Summary of three	R	106	286	8	400
R-F x F-V crosses	S	1	7	154	162
	Total	107	293	162	562

* F_2 classification -
R = resistant plants.
S = susceptible plants.

**F_3 breeding behavior -
R = breeding true for resistance.
Seg = segregating.
S = breeding true for susceptibility.

Table 10.--Segregation observed in segregating F_3 lines in the greenhouse and goodness of fit. Manhattan, Kans., 1941-1942.

		Crown rust*						Stem rust*					
		Number of lines	Number of plants					Number of lines	Number of plants				
Cross	Observed or expected		R	S	Total	X^2	Range of P		R	S	Total	X^2	Range of P
Richland-Fulghum	O	37	900	271	1171	2.203	.10-.20						
x													
Fulghum-Victoria	E		878	293									
Fulghum-Victoria	O	13	347	101	448	1.440	.20-.30	33	1104	385	1489	0.606	.30-.50
x													
Richland-Fulghum	E		336	112					1117	372			
Fultex	O							14	482	163	645	0.033	.50-.95
x													
Richland-Fulghum	E								484	161			
Summary of R-F x	O	50	1247	372	1619	3.586	.05-.10	47	1586	548	2134	0.490	.30-.50
F-V crosses	E		1214	405					1600	534			
Anthony-Bond	O	440	6137	6836	12973	5.905	.01-.05	52	1811	579	2390	0.723	.30-.50
x													
Richland-Fulghum	E		5999	6974					1793	597			

*R = resistant; S = susceptible.

used in any of the field studies because it has not been generally prevalent in natural infections in this region. It was used only in a greenhouse study of the F_3 generation during the winter. In this study, 324 F_3 families were observed to be breeding true for resistance, 632 families were segregating, and 316 families were breeding true for susceptibility. Counts which were made in 52 of the segregating families showed a ratio of 1811 resistant plants to 579 susceptible plants. It appeared that resistance to race 8 of stem rust was dominant and controlled by one factor in this cross. Plate II shows the seedling reaction of the parents and hybrids and Tables 8, 10, and 11 show the observed and expected ratios and their goodness of fit.

Crown Rust Studies

Inheritance of Reaction to Crown Rust in Fulghum-Victoria and Fultex Crosses with Richland-Fulghum. Fulghum-Victoria and Fultex, resistant to crown rust, had small, nearly circular pustules surrounded by necrotic areas. Severe seedling infection caused a complete drying of the infected leaves of resistant plants giving the seedlings a blighted appearance. The seedling reactions of the parents and the F_3 hybrids to crown rust are shown in Plate III. The F_1 plants were nearly as resistant as the Fulghum-Victoria and Fultex parents. Three different types of rust reaction were observed in the F_2 generation. One phenotype resembled the resistant parent, another resembled the susceptible parent, and a third type was intermediate duplicating the F_1 reaction. The intermediate types and resistant types were grouped together and compared with the

Table 11.--F_3 segregation for reaction to race 8 of stem rust in Anthony-Bond x Richland-Fulghum and tests of goodness of fit. Manhattan, Kans., 1941-1942.

F_1 family	Observed or expected	Number of F_3 lines R*	Seg*	S*	Total	X^2	Range of P
1033	O	48	84	48	180	0.800	.50-.95
	E	45	90	45			
1034	O	47	105	38	190	2.797	.20-.30
	E	48	95	47			
1035	O	57	94	45	196	1.796	.30-.50
	E	49	98	49			
1041	O	13	27	12	52	0.115	.50-.95
	E	13	26	13			
1042	O	4	21	19	44	10.318	less than .01
	E	11	22	11			
1043	O	26	61	36	123	1.613	.30-.50
	E	31	61	31			
1044	O	27	51	24	102	0.078	.95-.99
	E	26	51	25			
1045	O	37	62	31	130	0.655	.50-.95
	E	33	65	32			
1046	O	36	72	27	135	1.932	.30-.50
	E	34	67	34			
1047	O	29	55	36	120	1.650	.30-.50
	E	30	60	30			
Total	O	324	632	316	1272	0.151	.50-.95
	E	318	636	318			
Sum of the X^2's for the 10 F_1 families						21.754	.30-.50

*R = resistant; Seg = segregating; S = susceptible.

susceptible.

Since the reaction of these three crosses is similar, they may be considered as one cross. A summary of the F_2 reaction of these crosses gave a ratio of 423 resistant and intermediate plants to 152 susceptible. The expected ratio for a 3:1 segregation would be 431 resistant to 144 susceptible. In the F_3 greenhouse studies, 285 families bred true for resistance, 586 segregated, and 326 bred true for susceptibility. Very similar ratios were observed in the F_3 studies in the field. The F_3 ratios observed in these crosses in both the field and greenhouse and their goodness of fit are shown in Table 12. A comparison of F_2 classification with F_3 breeding behavior to crown rust in these crosses is shown in Table 13. The susceptible F_2 plants bred true for susceptibility while one-third of the resistant plants bred true for resistance and two-thirds of them segregated three resistant plants to one susceptible. Counts made in 37 segregating F_3 families of Richland-Fulghum x Fulghum-Victoria and 13 segregating F_3 families of the reciprocal cross gave very good fits to the expected 3:1 ratio and are shown in Table 10. A ratio of 1247 resistant plants to 372 susceptible plants was observed in these counts. Resistance to crown rust in these three crosses like resistance to stem rust was dominant and controlled by one factor. There was very good agreement between field and greenhouse F_3 observations and there appeared to be no difference in the crown rust reaction of seedlings and mature plants in these crosses.

<u>Inheritance of Reaction to Crown Rust in the Anthony-Bond x Richland-Fulghum Cross</u>. Richland-Fulghum has already been described as susceptible to crown rust. Anthony-Bond carries the high resistance of Bond to most

Table 12.--F_3 segregation for crown rust reaction in the field and greenhouse and goodness of fit. Manhattan, Kans., 1941-1942.

Cross	Observed or expected	Field or greenhouse	Number of F_3 families				X^2	Range of P
			R*	Seg*	S*	Total		
Richland-Fulghum x	O	field	36	47	37	120	5.650	.05-.10
Fulghum-Victoria	O	greenhouse	31	45	44	120	10.317	less than
	E		30	60	30			.01
Fulghum-Victoria x	O	field	161	383	180	724	3.434	.10-.20
Richland-Fulghum	O	greenhouse	178	368	178	724	0.199	.50-.95
	E		181	362	181			
Fultex x	O	field	79	177	97	353	1.841	.30-.50
Richland-Fulghum	O	greenhouse	76	173	104	353	4.636	.05-.10
	E		88	177	88			
Summary of three	O	field	276	607	314	1197	2.629	.20-.30
R-F x F-V crosses	O	greenhouse	285	586	326	1197	3.376	.10-.20
	E		299	599	299			
Anthony-Bond x	O	field	50	1002	939	1991	0.337	.50-.95
Richland-Fulghum	O	greenhouse	50	989	952	1991	0.474	.50-.95
	E		54	996	941			

*R = resistant; Seg = segregating; S = susceptible.

Table 13.--Comparison of F_2 classification with F_3 greenhouse breeding behavior to crown rust. Manhattan, Kans., 1941-1942.

Cross	F_2 classification*	F_3 breeding behavior**			
		R	Seg	S	Total
Richland-Fulghum x	R	15	10	1	26
Fulghum-Victoria	I	5	24	7	36
	S	1	3	34	38
Total		21	37	42	100
Fulghum-Victoria x	R	71	64	1	136
Richland-Fulghum	I	5	104	9	118
	S	1	5	74	80
Total		77	173	84	334
Fultex x	R	32	32	1	65
Richland-Fulghum	I	2	29	1	32
	S	--	--	31	31
Total		34	61	33	128
Summary of all	R	118	106	3	227
three crosses	I	12	157	17	186
	S	2	8	139	149
Total		132	271	159	562
Anthony-Bond x	R	27	93	--	120
Richland-Fulghum	2+	6	183	1	190
	X	--	150	8	158
	S	--	63	409	472
Total		33	489	418	940

*F_2 classification, R = resistant plants; I = intermediate types in R-F x F-V crosses; 2+ = nearly resistant intermediate types in A-B x R-F; X = nearly susceptible intermediate types in A-B x R-F; S = susceptible plants.

**F_3 breeding behavior, R = breeding true for resistance; Seg = segregating; S = breeding true for susceptibility.

of the prevalent races of crown rust. The only sign of crown rust infection in plants carrying the Bond type of resistance is a slight flecking where infection occurs. The F_1 hybrids gave an intermediate reaction which was classed as an X type reaction. The crown rust reaction of the hybrids of this cross appeared to be quite complicated. The F_2 hybrids seemed to divide themselves into two main groups, a resistant group and a susceptible group. The resistant group subdivided itself into two more or less distinct classes, truly resistant plants showing slight flecking but no pustules and intermediate types which were nearly resistant but showed slight pustule development and heavy flecking. These near resistant intermediates were called 2± types. The susceptible group subdivided itself into fully susceptible types and intermediate types (X) which were nearly fully susceptible. In many cases it was quite difficult to determine whether a plant should be classed as fully susceptible or as an X type. The same difficulty was experienced in classifying the resistant and 2± types. A summary of the F_2 observations shows that 120 plants were classed as truly resistant, 190 as 2±, 158 as X and 472 as fully susceptible.

The most noticeable thing in the F_3 greenhouse seedling studies was that there were no intermediate types of any kind. The seedlings were inoculated when they were in the primary leaf stage and they were either fully resistant or fully susceptible. This made the greenhouse observations quite simple since the differences were so clear cut and extreme. A very small proportion of them appeared to be breeding true for resistance, while most of the F_3 lines were either breeding true for susceptibility or were segregating. All types of segregation from predominantly resistant lines to predominantly susceptible lines appeared, and it seemed impossible to determine definitely any types of segregation by means of segregation counts. By counting the susceptible and resistant plants in 440 consecutive segregating lines in the greenhouse it was hoped that all types of segregation would be represented proportionately. A summation of the counts made in these 440 segregating lines gave a ratio of 6137 resistant plants to 6836 susceptible plants. A ratio of 50 lines breeding true for resistance to 989 lines segregating to 952 lines breeding true for susceptibility was observed in the greenhouse studies. The F_3 field reaction was similar to the F_3 greenhouse reaction in that the same lines bred true for resistance and susceptibility and the same lines segregated in both the greenhouse and in the field. However, intermediate 2± and X types appeared in segregating lines in the field. By making counts in certain segregating lines in the field it was possible to conclude that the 2± intermediate types appeared resistant in the greenhouse, while the X types appeared fully susceptible in the seedling stage. A hypothesis is presented in Table 14, which explains the crown rust inheritance in this cross on a four factor basis in which two sets of complementary factors were interacting.

A and B are two dominant complementary factors for resistance carried by Anthony-Bond. These factors are inherited independently and due to their complementary nature, both have to be present in a plant to give the expression of the Bond type of resistance. When both of these factors are heterozygous, (Aa Bb) the plant is not truly resistant, but is intermediate giving a 2± reaction. However, if both dominant factors are homozygous, (AABB) or if one is homozygous and the other heterozygous, (AABb, AaBB)

Table 14.--Seedling and mature plant reactions to crown rust expected in the cross Anthony-Bond (AABBccdd) x Richland-Fulghum (aabbCCDD).*

Generation genotype	Phenotypic expression in**			
	Seedling		Mature plant	
	F_1 or F_2 plant	F_3 line	F_1 or F_2 plant	F_3 line
F_1: AaBbCcDd	S	--	X	--
F_2:				
1-AABBCCDD	S	S	S	S
2-AABBCCDd	S	1R:3S	X	1R:2X:1S
2-AABBCcDD	S	1R:3S	X	1R:2X:1S
2-AABbCCDD	S	S	S	S
2-AaBBCCDD	S	S	S	S
4-AaBbCCDD	S	S	S	S
4-AABBCcDd	R	11R:5S	2+	7R:4,2+:4X:1S
4-AABbCcDD	S	3R:13S	X	3R:6X:7S
4-AaBBCcDD	S	3R:13S	X	3R:6X:7S
4-AABbCCDd	S	3R:13S	X	3R:6X:7S
4-AaBBCCDd	S	3R:13S	X	3R:6X:7S
8-AABbCcDd	R	33R:31S	2+	21R:12,2+:12X:19S
8-AaBBCcDd	R	33R:31S	2+	21R:12,2+:12X:19S
8-AaBbCCDd	S	9R:55S	X	5R:4,2+:18X:37S
8-AaBbCcDD	S	9R:55S	X	5R:4,2+:18X:37S
16-AaBbCcDd	S	83R:173S	X	35R:48,2+:52X:121S
1-AABBCCdd	R	R	R	R
2-AABBCcdd	R	R	R	R
2-AaBBCCdd	R	3R:1S	R	3R:1S
2-AABbCCdd	R	3R:1S	R	3R:1S
4-AaBBCcdd	R	3R:1S	R	3R:1S
4-AABbCcdd	R	3R:1S	R	3R:1S
4-AaBbCCdd	R	9R:7S	2+	5R:4,2+:7S
8-AaBbCcdd	R	9R:7S	2+	5R:4,2+:7S
1-AABBccDD	R	R	R	R
2-AABBccDd	R	R	R	R
2-AaBBccDD	R	3R:1S	R	3R:1S
2-AABbccDD	R	3R:1S	R	3R:1S
4-AaBBccDd	R	3R:1S	R	3R:1S
4-AABbccDd	R	3R:1S	R	3R:1S
4-AaBbccDD	R	9R:7S	2+	5R:4,2+:7S
8-AaBbccDd	R	9R:7S	2+	5R:4,2+:7S
1-AAbbCCDD	S	S	S	S
2-AAbbCCDd	S	S	S	S
2-AAbbCcDD	S	S	S	S
2-AabbCCDD	S	S	S	S
4-AAbbCcDd	S	S	S	S
4-AabbCcDD	S	S	S	S
4-AabbCCDd	S	S	S	S
8-AabbCcDd	S	S	S	S
1-aaBBCCDD	S	S	S	S
2-aaBBCCDd	S	S	S	S
2-aaBBCcDD	S	S	S	S
2-aaBbCCDD	S	S	S	S
4-aaBBCcDd	S	S	S	S
4-aaBbCcDD	S	S	S	S
4-aaBbCCDd	S	S	S	S
8-aaBbCcDd	S	S	S	S
1-AABBccdd	R	R	R	R
2-AaBBccdd	R	3R:1S	R	3R:1S
2-AABbccdd	R	3R:1S	R	3R:1S
4-AaBbccdd	R	9R:7S	2+	5R:4,2+:7S
1-AAbbccDD	S	S	S	S
2-AAbbccDd	S	S	S	S
2-AabbccDD	S	S	S	S
4-AabbccDd	S	S	S	S
1-aabbCCDD	S	S	S	S
2-aabbCCDd	S	S	S	S
2-aabbCcDD	S	S	S	S
4-aabbCcDd	S	S	S	S
1-aaBBCCdd	S	S	S	S
2-aaBBCcdd	S	S	S	S
2-aaBbCCdd	S	S	S	S
4-aaBbCcdd	S	S	S	S
1-aaBBccDD	S	S	S	S
2-aaBBccDd	S	S	S	S
2-aaBbccDD	S	S	S	S
4-aaBbccDd	S	S	S	S
1-AAbbCCdd	S	S	S	S
2-AAbbCcdd	S	S	S	S
2-AabbCCdd	S	S	S	S
4-AabbCcdd	S	S	S	S
1-AAbbccdd	S	S	S	S
2-Aabbccdd	S	S	S	S
1-aaBBccdd	S	S	S	S
2-aaBbccdd	S	S	S	S
1-aabbCCdd	S	S	S	S
2-aabbCcdd	S	S	S	S
1-aabbccDD	S	S	S	S
2-aabbccDd	S	S	S	S
1-aabbccdd	S	S	S	S

Expected ratios:

F_2 seedling plants (greenhouse). . . 83R:173S
F_2 mature plants (field). . . 35R:48,2+:52,X:121S
F_3 lines. . . 7R:128Seg.:121S

Expected ratios for the summarization of the segregation in all of the segregating F_3 lines in the seedling stage in the greenhouse.

Number of lines segregating	Number of F_3 plants		
	Type of segregation	Segregation placed on a basis of 256	Segregation on a 256 basis multiplied by the number of lines
4	1R:3S	64R:192S	256R:768S
4	11R:5S	176R:80S	704R:320S
16	3R:13S	48R:208S	768R:3328S
16	33R:31S	132R:124S	2112R:1984S
16	9R:55S	36R:220S	576R:3520S
16	83R:173S	83R:173S	1328R:2768S
28	3R:1S	192R:64S	5376R:1792S
28	9R:7S	144R:112S	4032R:3136S
Total			15152R:17616S
			46.24%R:53.76%S

*A and B are complementary factors for resistance carried by Anthony-Bond. C and D are complementary inhibitors of the expression of A and B and are carried by Richland-Fulghum.

**R = resistant; 1R:3S = a type of segregation; 2+ = nearly resistant intermediate type; X = nearly susceptible intermediate type; S = susceptible.

the plant shows the true Bond resistance to crown rust. Plants breeding true for resistance are homozygous for both dominant factors. If either or both of these factors are recessive (aaBB, aaBb, AAbb, Aabb, aabb) the plant is fully susceptible and will breed true for susceptibility. The inheritance in this cross would be quite simple if only these two complementary factors were involved; however, the inheritance has been complicated by the action of two other independently inherited dominant complementary factors, C and D, which when present together, are capable of inhibiting the expression of the factors for resistance, A and B. The degree to which they inhibit the expression of resistance is determined by two things. First, the number of dominant inhibiting genes present and second, the number of dominant genes for resistance present. It is possible for two, three, or four dominant inhibiting genes to be present and show an inhibiting effect, depending on whether the plant is heterozygous for both (CcDd), heterozygous for one (CcDD, CCDd), or homozygous for both (CCDD). If homozygous for both, four dominant inhibiting genes are acting, masking the resistance of any combination of the genes for resistance and giving a fully susceptible reaction. The progeny of any plant which carries both of these inhibitors in a dominant homozygous condition will breed true for susceptibility to crown rust. If a plant is heterozygous for one inhibitor, and homozygous for the other (CCDd or CcDD), it carries three dominant inhibiting genes whose inhibiting effect on any combination of the genes for resistance, gives an X type intermediate reaction when both genes for resistance are present. If a plant is heterozygous for both inhibitors (CcDd) the inhibitors show their weakest inhibiting effect because only two dominant genes are present.

The inhibitors in this doubly heterozygous condition change the expression of the genes for full resistance (AABB, AaBB, AABb) to that of a 2± intermediate type while if the genes for resistance are already doubly heterozygous (AaBb showing 2± reaction), the interaction of these four genes all in a heterozygous condition (AaBbCcDd) results in an X type rust reaction. All plants which react as X types in the field are fully susceptible in the greenhouse in the seedling stage and all plants which react as 2± in the field are fully resistant in the greenhouse. In the field, an F_2 ratio of 35 resistant plants: 48, 2± type plants : 52 X type plants : 121 susceptible plants would be expected. When placed on a basis of 940 plants, a ratio of 129 resistant : 176, 2± : 191 X : 444 susceptible would be expected. The actual ratio observed was 120 resistant : 190, 2± : 158 X : 472 susceptible. If the resistant and the 2± classes were grouped and also the X and the susceptible classes were grouped, the result is the ratio expected for seedling reaction of the F_2 generation. The observed classes, when grouped in this manner give a ratio of 310 resistant : 630 susceptible which is very close to the expected ratio of 305 resistant : 635 susceptible. The observed F_2 ratios fit very closely to the expected ratios and would fit even more closely had it not been for the difficulty of classifying certain 2± and X types. The F_2 field reaction of this cross is shown in Table 15.

In the F_3 generation according to this hypothesis only 54 of the F_3 lines would be expected to breed true for resistance. Actually, 50 lines were observed in both the greenhouse and the field to be breeding true for resistance. Theoretically, exactly half of the population, 996 lines, would be expected to segregate. In the greenhouse 989 lines

Table 15.--F_2 field reaction of Anthony-Bond x Richland-Fulghum to crown rust and goodness of fit. Manhattan, Kans., 1941-1942.

F_1 family	Observed or expected	Number of F_2 plants: Resistant types* R	2+	Total	Susceptible types* X	S	Total	Total	Goodness of fit of ratio of: Total resistant to total susceptible types X^2	Range of P	Individual classes X^2	Range of P
1033	O	8	14	22	10	38	48	70	0.032	.50-.95	2.240	.50-.95
	E	9.6	13.1	22.7	14.2	33.1	47.3					
1034	O	12	16	28	10	37	47	75	0.833	.30-.50	2.409	.30-.50
	E	10.3	14.0	24.3	15.2	35.5	50.7					
1035	O	6	15	21	8	26	34	55	0.851	.30-.50	3.359	.30-.50
	E	7.5	10.3	17.8	11.2	26.0	37.2					
1041	O	4	9	13	3	30	33	46	0.358	.50-.95	8.210	.01-.05
	E	6.3	8.6	14.9	9.3	21.8	31.1					
1042	O	12	31	43	14	54	68	111	2.014	.10-.20	8.930	.01-.05
	E	15.2	20.8	36.0	22.5	52.5	75.0					
1043	O	9	10	19	11	24	35	54	0.190	.50-.95	0.435	.50-.95
	E	7.4	10.1	17.5	11.0	25.5	36.5					
1044	O	14	31	45	36	92	128	173	3.250	.05-.10	5.325	.10-.20
	E	23.7	32.4	56.1	35.1	81.8	116.9					
1045	O	20	25	45	30	63	93	138	0.003	.95-.99	0.313	.95-.99
	E	18.9	25.8	44.7	28	65.3	93.3					
1046	O	15	16	31	15	42	57	88	0.324	.50-.95	1.239	.50-.95
	E	12.0	16.5	28.5	17.9	41.6	59.5					
1047	O	20	23	43	21	66	87	130	0.028	.50-.95	1.775	.50-.95
	E	17.8	24.3	42.1	26.4	61.5	87.9					
Total	O	120	190	310	158	472	630	940	0.131	.50-.95	9.024	.01-.05
	E	128.5	176.3	304.8	190.9	444.3	635.2					
Sum of X^2's of the 10 families									7.883	.50-.95	34.235	.20-.30

*R = fully resistant; 2+ = nearly resistant intermediate types; X = nearly susceptible intermediate types; S = fully susceptible.

appeared to segregate, while 1002 seemed to be segregating in the field. On the calculated four-factor basis 121 out of each 256 lines of the population, or a total of 941 lines, were expected to breed true for susceptibility. Nine hundred fifty-two lines in the greenhouse and 939 lines in the field appeared to be breeding true for susceptibility. The F_3 field and greenhouse reactions of Anthony-Bond X Richland-Fulghum are shown in Table 16. There was a very close agreement between observed and expected numbers in the F_3 population of this cross. The field and greenhouse reactions were also in very close agreement. The good fits of F_2 and F_3 observed ratios to the expected ratios are further substantiated by the counts made in 440 of the segregating F_3 lines in the greenhouse. If all of the different types of segregation expected by the hypothesis in the F_3 lines are placed on a basis of 256 and then multiplied by the number of lines of each type expected, then all types of segregation will be represented in the exact theoretical proportion. These ratios of resistant to susceptible plants can then be added giving a resultant ratio which is representative of the segregation as a whole. This theoretical ratio is 15,152 resistant to 17,616 susceptible plants. When expressed in percentage, 46.24 percent resistant and 53.76 percent susceptible plants would be expected in the F_3 segregating lines taken collectively. In the 440 lines counted there were 12,973 plants; 5,999 resistant were expected and 6,137 were observed; 6,974 susceptible plants were expected and 6,836 were observed. The agreement between the observed and expected ratios is quite good considering the many different types of segregation that were occurring and also the great variation in the number of F_3 plants in each of the 440 segregating lines.

Table 16.--F_3 segregation of Anthony-Bond x Richland-Fulghum for crown rust reaction in the field and greenhouse and goodness of fit. Manhattan, Kans., 1941-1942.

F_1 family	Observed or expected	Field or greenhouse	Number of F_3 families: R*	Seg	S	Total	X^2	Range of P
1033	O	field	8	84	88	180	2.306	.30-.50
	O	greenhouse	6	81	93	180	1.853	.30-.50
	E		5	90	85			
1034	O	field	4	97	89	190	0.253	.50-.95
	O	greenhouse	2	109	79	190	5.208	.05-.10
	E		5	95	90			
1035	O	field	2	96	98	196	2.110	.30-.50
	O	greenhouse	2	99	95	196	1.853	.30-.50
	E		5	98	93			
1041	O	field	1	26	50	77	10.278	less than .01
	O	greenhouse	2	24	51	77	12.019	less than .01
	E		2	39	36			
1042	O	field	3	77	75	155	0.264	.50-.95
	O	greenhouse	3	75	77	155	0.424	.50-.95
	E		4	77	74			
1043	O	field	8	83	86	177	2.313	.30-.50
	O	greenhouse	11	85	81	177	7.428	.01-.05
	E		5	89	83			
1044	O	field	8	146	121	275	0.960	.50-.95
	O	greenhouse	8	148	119	275	1.500	.30-.50
	E		8	138	129			
1045	O	field	6	143	119	268	1.251	.50-.95
	O	greenhouse	4	135	129	268	1.325	.50-.95
	E		7	134	127			
1046	O	field	8	119	96	223	1.876	.30-.50
	O	greenhouse	8	112	103	223	0.705	.50-.95
	E		6	112	105			
1047	O	field	2	131	117	250	3.868	.10-.20
	O	greenhouse	4	121	125	250	1.829	.30-.50
	E		7	125	118			
Total	O	field	50	1002	939	1991	0.337	.50-.95
	O	greenhouse	50	989	952	1991	0.474	.50-.95
	E		54	996	941			
Sum of X^2's for the 10 F_1 families for field data							25.479	.10-.20
for greenhouse data							34.144	.01-.05

*R = breeding true for resistance; Seg = segregating; S = breeding true for susceptibility

Certain lines were carried into the F_4 generation. The observations in these lines further substantiated the hypothesis. Table 17 shows the reaction of these selected lines.

This hypothesis is in complete agreement with the work of Hayes et al.(1939) and Weetman (1942). These investigators reported that the resistance of Bond was due to two dominant complementary factors. They, however, observed a simple 9:7 ratio because the susceptible parents involved in their crosses did not bring in any dominant inhibitors. Torrie, in 1939, reported the action of a dominant inhibitor in the cross Iowa 444 X Bond. He observed an F_2 ratio of five resistant to 11 susceptible in the field. This is very close to the F_2 ratio of 83 resistant : 173 susceptible which would be expected in the hypothesis which has been outlined if the true resistant and the 2± types are grouped and the true susceptible and X types are grouped. Torrie observed intermediate types in the greenhouse, and was the only investigator to report that the resistance of Bond was not due to two complementary factors.

Relation Between Crown Rust, Stem Rust and Smut Inheritance

No evidence of linkage was found between the factors determining the reactions of these crosses to any of these diseases. The reactions of F_2 hybrids in the field to crown and stem rust are shown in Table 18. A very close fit to the 9:3:3:1 expected phenotypic ratio was obtained. The reactions of F_3 hybrids to both rusts are shown in Table 19. In the Richland-Fulghum x Fulghum-Victoria crosses a fairly good fit was observed to the expected phenotypic ratio, 1:2:1:2:4:2:1:2:1. In the Anthony-Bond

Table 17.--F_2, F_3 and F_4 crown rust reaction of selected lines in the progeny of Anthony-Bond x Richland-Fulghum. Manhattan, Kans., 1941-1942.

F_3 line number	F_2 plant reaction in field*	Reaction of F_3 line* Greenhouse	Reaction of F_3 line* Field	F_3 greenhouse reaction of parent plant of F_4 line*	Reaction of F_4 line in field*
1045-10	R	R	R	R	R
				R	R
				R	R
1045-55	S	S	Seg 1,2±:2X:24S	S	Seg 3R:5,2±:5X:13S
				S	S
				S	S
				S	S
				S	S
				S	S
				S	S
1045-115	2±	Seg 11R:27S	Seg 7R:21,2±:20S	R	R
				R	Seg 14R:5S
				R	Seg 5R:41,2±:18X:15S
				S	S
				S	S
				S	S
				S	S
1045-123	2±	Seg 7R:13S	Seg 9R:8,2±:16S	R	R
				R	R
				R	Seg 3,2±1X:3S
				R	Seg 4R:8,2±:15S
				S	S
				S	S
				S	S
1045-129	R	Seg 26R:4S	Seg 36R:8S	R	R
				R	Seg 13R:5S
				R	Seg 20R:7S
				R	Seg 42R:21S
				R	Seg 30R:10S
				S	S
				S	S
				S	S

*R = resistant; S = susceptible; Seg = segregating.

Table 18.--Reaction of F_2 hybrids in the field to both crown rust and stem rust and goodness of fit. Manhattan, Kans., 1941-1942.

Cross	Observed or expected	Number of F_2 plants: Resistant to both rusts	Resistant to crown rust and susceptible to stem rust	Resistant to stem rust and susceptible to crown rust	Susceptible to both rusts	Total	X^2	Range of P
Richland-Fulghum x	O	46	19	32	7	104	10.735	.01-.05
Fulghum-Victoria	E	58.5	19.5	19.5	6.5			
Fulghum-Victoria x	O	190	68	56	24	338	1.596	.50-.95
Richland-Fulghum	E	190.1	63.4	63.4	21.1			
Fultex x	O	70	30	27	6	133	2.180	.50-.95
Richland-Fulghum	E	74.9	24.9	24.9	8.3			
Summary of all	O	306	117	115	37	575	2.246	.50-.95
three crosses	E	323.5	107.8	107.8	35.9			

Table 19.--Reaction of F_3 hybrids in the greenhouse to both crown rust and stem rust and goodness of fit. Manhattan, Kans., 1941-1942.

Cross	Observed or expected	Stem rust reaction Number of lines	Crown rust reaction Number of lines R	Seg	S	Total	Chi square and range of probability for reaction to Crown rust X^2	Crown rust Range of P	Stem rust X^2	Stem rust Range of P	Both rusts X^2	Both rusts Range of P
Richland-	O	R	7	8	7	22						
Fulghum	E	R	7	15	8	30						
x	O	Seg	14	23	28	65						
Fulghum-	E	Seg	15	30	15	60						
Victoria	O	S	10	14	9	33						
	E	S	8	15	7	30						
	O	Total	31	45	44	120	10.317	less than .01	2.850	.20-.30	17.496	.01-.05
	E	Total	30	60	30							
Fulghum-	O	R	32	83	36	151						
Victoria x	E	R	45	90	46	181						
Richland-	O	Seg	84	177	85	346						
Fulghum	E	Seg	91	181	90	362						
	O	S	62	108	57	227						
	E	S	45	91	45	181						
	O	Total	178	368	178	724	0.199	.50-.95	17.370	less than .01	20.177	.01
	E	Total	181	362	181							
Fultex x	O	R	6	20	40	66						
Richland-	E	R	22	44	22	88						
Fulghum	O	Seg	32	106	48	186						
	E	Seg	44	89	44	177						
	O	S	38	47	16	101						
	E	S	22	44	22	88						
	O	Total	76	173	104	353	4.636	.05-.10	7.878	.01-.05	59.815	less than .01
	E	Total	88	177	88							
Summary of	O	R	45	111	83	239						
crosses	E	R	74	150	75	299						
involving	O	Seg	130	306	161	597						
Fulghum-	E	Seg	150	299	150	599						
Victoria and	O	S	110	169	82	361						
Fultex	E	S	75	150	74	299						
	O	Total	285	586	326	1197	3.376	.10-.20	24.903	less than .01	45.600	less than .01
	E	Total	299	599	299							
Anthony-	O	R	5	155	164	324						
Bond x	E	R	9	159	150	318						
Richland-	O	Seg	13	316	303	632						
Fulghum	E	Seg	17	318	301	636						
	O	S	8	136	172	316						
	E	S	9	159	150	318						
	O	Total	26	607	639	1272	6.039	.01-.05	0.151	.50-.95	10.817	.20-.30
	E	Total	35	636	601							

x Richland-Fulghum cross, the reaction to both rusts gave a good fit to the expected 7:14:7:128:256:128:121:242:121 phenotypic ratio. The Chi square for the fit to this ratio was 10.817 with eight degrees of freedom having a probability of 20 to 30 percent.

The crown and stem rust reaction of smutted F_2 plants are shown in Table 20. All types of rust reaction appeared in these F_2 plants. The F_3 greenhouse stem rust and crown rust reaction of smutted lines are shown in Table 21. In all of the crosses, the smutted lines reacted toward the two rusts in a manner similar to that shown by the entire population.

SUMMARY

The inheritance of reaction to crown rust, stem rust and a mixture of loose and covered smut was studied in four crosses, Richland-Fulghum x Fulghum-Victoria, Fulghum-Victoria x Richland-Fulghum, Fultex x Richland-Fulghum, and Anthony-Bond x Richland-Fulghum. The disease reaction of the first three crosses was the same, but that of the last cross was quite different due to the genetic make-up of the Anthony-Bond parent.

Transgressive segregation for smut susceptibility occurred in the first three crosses. The parents of these crosses were all highly resistant (0.0 percent infection) to the races of smuts used in the investigation. The reaction of the hybrids in the F_2 and F_3 generations indicated that each parent carried a complementary recessive factor pair for susceptibility. When these two independently inherited complementary recessive factor pairs were both present in a hybrid in a fully recessive condition, the plant was susceptible to smut. One-sixteenth of the F_2

Table 20.--Crown rust and stem rust reactions of smutted F_2 plants. Manhattan, Kans., 1941-1942.

Cross	Crown rust* Number of plants			Stem rust* Number of plants		Total number of smutted plants
	R	I	S	R	S	
Richland-Fulghum x Fulghum-Victoria	5	4	1	7	3	10
Fulghum-Victoria x Richland-Fulghum	3	7	2	7	5	12
Fultex x Richland-Fulghum	5	4	5	6	8	14
Summary of the three R-F x F-V crosses	13	15	8	20	16	36
Anthony-Bond x Richland-Fulghum	4	2	4	-	-	10

*R = resistant; I = intermediate; S = susceptible.

Table 21.--F_3 greenhouse crown rust and stem rust reaction of lines showing smutted plants in the field and goodness of fit. Manhattan, Kans., 1941-1942.

Cross or crosses	Observed or expected	Stem rust reaction*	Crown rust reaction*			
			R	Seg	S	Total
Combined	O	R	24	41	32	97
reaction of	E	R	28	57	29	114
R-F x F-V	O	Seg	34	136	61	231
F-V x R-F	E	Seg	57	114	57	228
Fultex x R-F	O	S	30	68	31	129
	E	S	29	57	29	115
	O	Total	88	245	124	457
	E	Total	114	228	115	
Anthony-Bond x	O	R	1	26	39	66
Richland-Fulghum	E	R	2	37	35	74
	O	Seg	2	72	76	150
	E	Seg	4	75	71	150
	O	S	1	39	43	83
	E	S	2	38	35	75
	O	Total	4	137	158	299
	E	Total	8	150	141	

Reaction to	R-F x F-V; F-V x R-F; Fultex x R-F		Anthony-Bond x R-F	
	X^2	Range of P	X^2	Range of P
Crown rust	7.902	.01-.05	5.176	.05-.10
Stem rust	4.279	.10-.20	1.718	.30-.50
Both rusts	21.475	less than .01	8.054	.30-.50

*R = resistant; Seg = segregating; S = susceptible.

hybrids were smutted and nine-sixteenths of the F_3 lines showed one or more smutted plants.

In the Anthony-Bond x Richland Fulghum cross a hypothesis was formulated in which resistance to smut was dominant and the reaction was controlled by three factor pairs. One sixty-fourth of the F_2 plants were smutted and twenty-seven sixty-fourths of the F_3 lines showed smutted plants.

The reaction of all four crosses to stem rust was governed by one factor and resistance was dominant. The crown rust reaction of the three crosses involving Fulghum-Victoria and Fultex was governed by one factor and resistance was dominant.

The crown rust reaction of Anthony-Bond x Richland-Fulghum was controlled by the interaction of four factor pairs, two sets of dominant complementary factors. One set, dominant genes for resistance, was carried by Anthony-Bond and the other set, carried by Richland-Fulghum, were dominant inhibitors epistatic to the genes for resistance. These four factors were only partially dominant resulting in many intermediate type plants. The F_2 reaction gave a ratio of 35 fully resistant : 48 nearly resistant intermediate : 52 nearly susceptible intermediate :and 121 fully susceptible plants. The nearly resistant intermediates were fully resistant and the nearly susceptible intermediates were fully susceptible in the greenhouse in the seedling stage. In the F_3 generation, seven lines were breeding true for resistance, 128 lines were segregating while 121 lines were breeding true for susceptibility.

There was no linkage observed in the disease reaction of any of the crosses studied.

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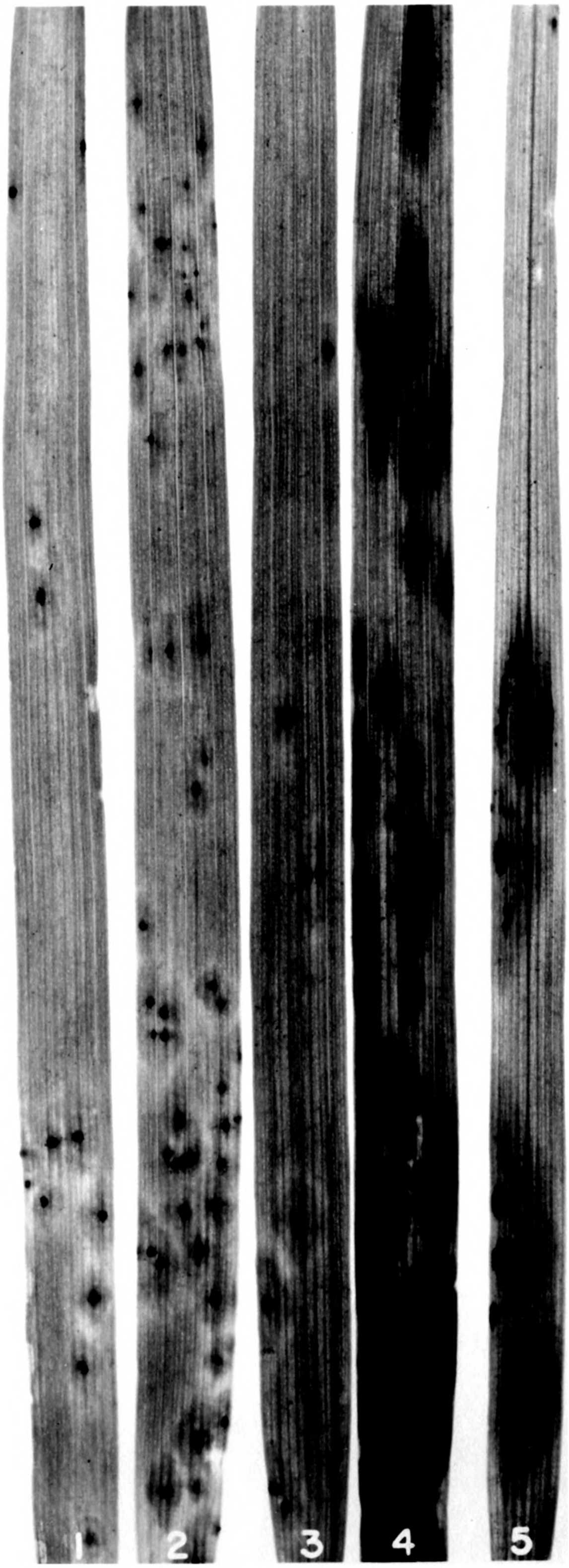
EXPLANATION OF PLATE I

Stem rust reaction of primary leaves of seedling plants to race 2 in the cross Richland-Fulghum x Fulghum-Victoria. No. 1 is the resistant Richland-Fulghum parent; Nos. 2 and 3 are resistant F_3 hybrids; No. 4 is a susceptible F_3 hybrid, and No. 5 is the susceptible Fulghum-Victoria parent.

PLATE I



EXPLANATION OF PLATE II.

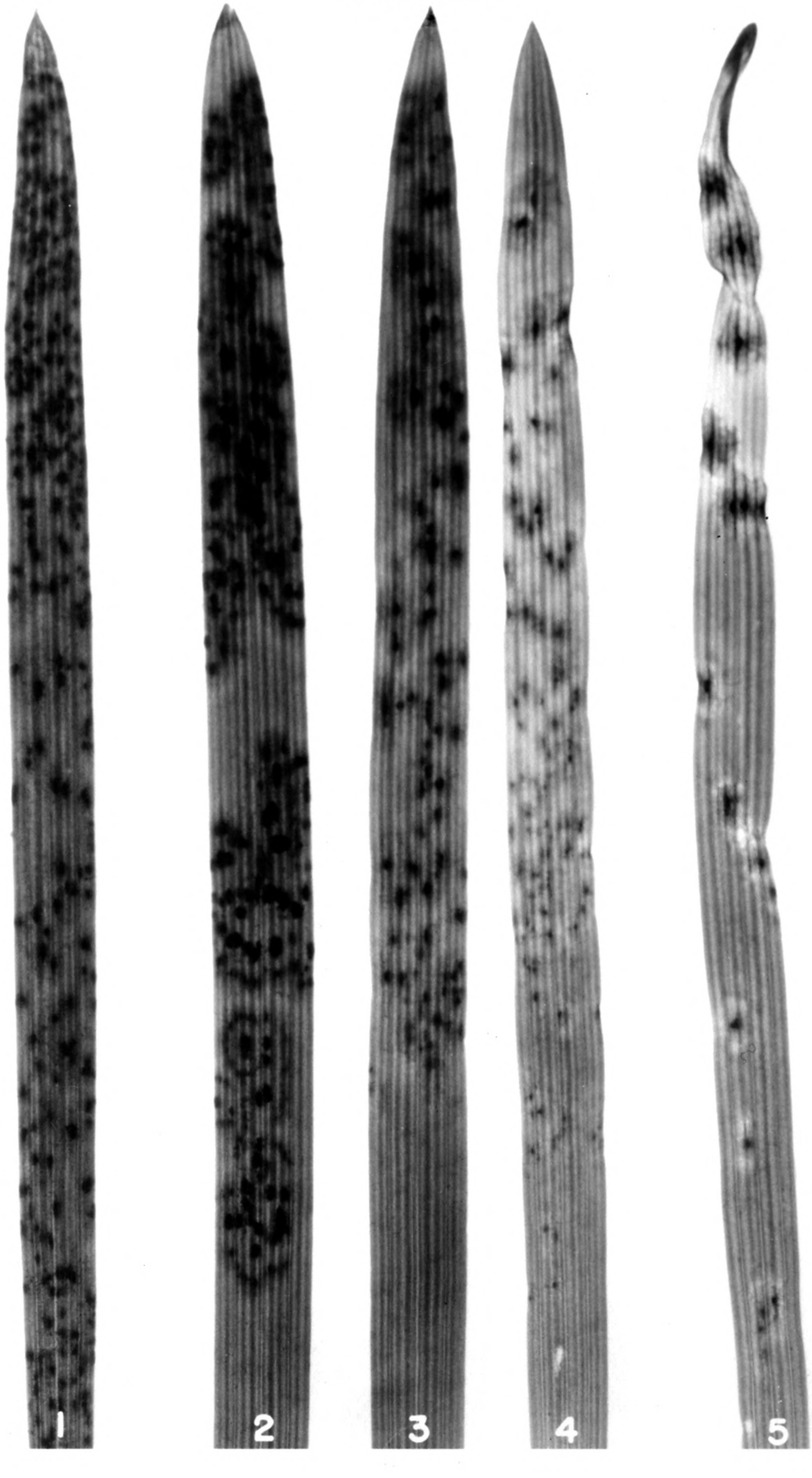
Stem rust reaction of primary leaves of seedling plants to race 8 in the cross Anthony-Bond x Richland-Fulghum. No. 1 is the susceptible Richland-Fulghum parent; No. 2 is a susceptible F_3 hybrid; Nos. 3 and 4 are intermediate F_3 hybrids; No. 5 is a resistant F_3 hybrid, and No. 6 is the resistant Anthony-Bond parent.

PLATE II

EXPLANATION OF PLATE III

Crown rust reaction of primary leaves of seedling plants to race 1 of crown rust in the cross Richland-Fulghum x Fulghum-Victoria. No. 1 is the susceptible Richland-Fulghum parent; No. 2 is a susceptible F_3 hybrid; No. 3 is an intermediate F_3 hybrid; No. 4 is a resistant F_3 hybrid, and No. 5 is the resistant Fulghum-Victoria parent.

PLATE III



EXPLANATION OF PLATE IV

Crown rust reaction of primary leaves of seedling plants to race 1 of crown rust in the cross Anthony-Bond x Richland-Fulghum. No. 1 is the susceptible Richland-Fulghum parent; Nos. 2 and 3 are susceptible F_3 hybrids; No. 4 is a resistant F_3 hybrid, and No. 5 is the resistant Anthony-Bond parent.

PLATE IV