INHERITANCE OF REACTION TO SEVERAL RACES OF CROWN RUST, PUCCINIA CORONATA AVENAE ERIKSS., IN TWO CROSSES INVOLVING UKRAINE OATS

by

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ABSTRACT

The oat variety Ukraine is resistant to a large number of crown rust races, including race 263, a race which is pathogenic on almost all commercial oat varieties in North America. Approximately 200 random F_3 lines made up of 60 to 80 lines from the Fortune x Ukraine cross and 110 to 140 lines from the Garry x Ukraine cross were classified as resistant, segregating, or susceptible to races 213 and 263 of crown rust. Thirty selected F_3 lines from the Fortune x Ukraine cross and sixty selected F_3 lines from the Garry x Ukraine cross were tested to a total of ten races of crown rust. The tests indicated that a single dominant gene in Ukraine governed resistance to races 213, 202, 202A, 209, 212A, 235, 236, 239, 239B, and 240, and that another dominant gene in Ukraine, linked with a crossover value of the order of 7 per cent, governed resistance to race 263. Tests with lines from one family of the Garry x Ukraine cross showed that the Garry resistance to races 229, 235, and 240 is associated in inheritance, and tests with lines from a second family showed that Garry resistance to races 209, 236, and 239 is also associated in inheritance. The Ukraine and Garry genes were

shown to be independent of one another, with the gene for the higher type of resistance epistatic to the gene for the lower type in all cases.

A number of F_3 lines were isolated which combined the field resistance of Ukraine and Garry to crown rust, including race 263, with the field resistance to stem rust of Garry. These lines may prove very useful in a plant breeding program.

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INTRODUCTION

Crown rust or leaf rust of oats, caused by *Puccinia coronata avenae* Erikss., occurs in most countries where oats are grown. According to Simons and Murphy (28) it is the most serious disease of oats in the Eastern half of the United States. Peturson (24) reported that crown rust often causes severe crop losses in Eastern Canada, and in Manitoba and Eastern Saskatchewan. In some years it is of minor importance, but in other years crown rust may occur in epidemic proportions, as in 1935, 1937, and 1944.

Crown rust is a long cycle, heteroecious rust. Following the urediospore or "red spore stage" which occurs on the oat plant in summer, the rust overwinters in the teliospore or "black spore stage" on stubble and certain grasses. In the spring these teliospores germinate producing sporidia which can infect only the buckthorn, of which the most common species in Western Canada is *Rhamnus cathartica* L. The aeciospores produced following the sexual stage on the buckthorn infect the oat plant on which urediospores develop, thereby completing the rust life cycle. Crown rust is not a single entity, but consists of many physiologic races which differ in ability to parasitize different varieties of oats.

The control of crown rust has been of great economic importance in Canada and the United States. The main control used has been the development of varieties resistant to the pathogen.

Sources of resistant germ plasm must be found, and when found, the factors for resistance must be transferred to the commercial varieties of the area concerned. The ease with which such transfers of germ plasm can be made depends on (1) the number of genes involved, (2) dominance or recessiveness of the genes concerned, (3) allelic relationships with factors for resistance from other varieties, and (4) ease of crossing between parental varieties. Information on these points is available from studies of the F_2 (second generation) and F_3 (third generation) segregations of crosses involving resistant and susceptible varieties.

Simons (25) reported a new race of crown rust in 1954, identified as race 263. Ukraine is the best known source of resistance to this race. If this race becomes prevalent in the next few years, the Ukraine resistance will be of extreme value.

This study was undertaken, therefore, to determine (1) the mode of inheritance of the Ukraine reaction to race 263 and other races of crown rust, (2) the mode of inheritance of the Garry reaction to certain races, and (3) the degree of association between the inheritance of factors for resistance in Ukraine and Garry.

REVIEW OF LITERATURE

Oats belong to the genus *Avena*, one of the numerous subdivisions of the great grass family, Gramineae. There are several species of oats and within each species there are a number of varieties. In general the oat varieties grown in North America are of the *A. sativa* type, the exception being the varieties of *A. byzantina* grown in the Southern United States. Varieties of *A. byzantina* have furnished the plant breeder with valuable breeding material for disease resistance. Cytologically oats may possess 42, 28, or 14 chromosomes in the diploid phase. The species *A. sativa* and *A. byzantina* fall into the 42 chromosome number group, and may be readily intercrossed. Zillinsky (32) reports that crosses within all chromosome number groups are highly compatible, but those between groups are often incompatible. The diploid group, particularly *A. strigosa*, possesses considerable disease resistance, especially to crown rust. Work done by Zillinsky and others in the production of autotetraploids of *A. strigosa* and amphiploids of *A. abyssinica* (28 chromosomes) x *A. strigosa* may soon make the germ plasm of the diploid group available for the improvement of the hexaploid oats.

Physiologic Specialization of the Pathogen

Hoerner (13) was the first to demonstrate physiologic specialization within the organism causing crown rust. Murphy (18) and Murphy and Levine (19) worked out a system of thirteen differential hosts. By 1953 races numbered from 1 to 113 had been identified by workers in Canada, the United States and South America.

Simons and Murphy (28) introduced a new set of ten differential hosts made up of four varieties from the old set plus six added varieties. Most workers in crown rust have used this new set in the identification of cultures collected since 1951. Races identified according to this set have been numbered from 201 to over 288.

Some of the investigations reported in this paper used races identified by the old set of thirteen differentials, while others used races identified by the new set. The races used in the present investigation were identified by the new set. Cultures identified as race 57 by the old set would be race 202A by the new set, race 109 would be race 228 or 229 by the new set, and race 45 would be race 202.

Types of Resistance

Ausemus (1) states that there are two major types of resistance to stem rust of wheat, namely seedling and adult. Seedling resistance is due to incompatibility of the pathogen and host cells. Adult plant resistance may be due to morphological or functional characteristics of the plant. Varieties possessing seedling resistance are invariably resistant in the adult stage, while varieties with adult plant resistance may be susceptible as seedlings. Simons (26) found a number of lines of oats which were susceptible to crown rust in the seedling stage but which gave good adult plant resistance. The reactions of the upper and lower leaves of these lines were tested in the greenhouse. All lines in which the upper leaves were resistant under greenhouse conditions were highly resistant in the field. Lines in which the lower leaves were resistant and the upper leaves susceptible were not always resistant in the field. Peturson (23) found that the varieties Ajax and Erban possessed adult plant resistance only.

Sources of Resistance

Victoria was first used in crosses for disease resistance in 1930 and Bond in 1932. A number of varieties with Victoria resistance were released in the early 1940's but were later unpopular because of their susceptibility to Victoria blight caused by Helminthosporium victoriae M. and M. Many varieties released in the late 1940's depended on Bond for their resistance. These varieties are susceptible to the races of crown rust which have become prevalent since that time. Varieties such as Garry (New) and Rodney have some of the Victoria genes for crown rust resistance, but not the gene for susceptibility to Victoria blight. Varieties with the Santa Fe and Landhafer resistance, which have been released from several stations in the United States, have superior resistance to crown rust as well as resistance to Victoria blight.

Inheritance of Resistance

Biffen (2), working with stripe rust of wheat, caused by Puccinia glumarum (Schm.) Erikss. and Henn., crossed resistant and susceptible varieties and found that the F_2

segregated in a ratio of three susceptible to one resistant. This was shortly after the re-discovery of Mendel's laws of heredity, and was one of the first proofs that disease resistance may be inherited in a simple Mendelian manner. Investigations by Parker (22) and Gaines (9) on the inheritance of rust and smut resistance in oats also found resistance to be inherited in a simple Mendelian manner.

Dietz and Murphy (4) studied the response of F_1, F_2, and F_3 generations of crosses involving Sunrise 23 and Fulghum oats to a single physiologic race. Resistance was found to be dominant with two factors involved, one of which was an inhibitor.

Practically all of the more recent work has involved studies of seedling resistance. The different varieties concerned in published studies of this kind will be dealt with individually.

1. <u>Ukraine</u>

Weetman (30) concluded that Ukraine resistance to a portion of race 1 is due to two complementary genes allelic to the Bond genes for resistance. Finkner <u>et al</u>. (6) investigated the mode of inheritance of Ukraine reaction to races 57 (now designated 202A) and 109 (228 and 229). The data indicated that a single gene in Ukraine governs resistance to race 57 and susceptibility to race 109. This gene is epistatic to the Clinton gene for resistance to race 109. The Ukraine gene for resistance was found to be allelic and dominant to one of the two Santa Fe genes and epistatic to the other. The F_2 plants, when classified for resistance to race 109, indicated that the

Ukraine gene is dominant to one Santa Fe gene and conditions susceptibility to this race in the absence of the other dominant linked Santa Fe gene. The other Santa Fe gene is epistatic to the Ukraine gene if the Santa Fe gene is in the homozygous condition or if the Ukraine gene is in the heterozygous condition.

Finkner (7) found that the reaction in F_3 of crosses of Ukraine with Trispernia, Santa Fe, Anthony-Bond x Boone, and Clinton indicated that duplicate dominant genes linked with a crossover value of $22.88 \pm .04$, condition resistance to race 57. One of the linked gene pairs was shown to be allelic to the gene in Santa Fe, with the Ukraine gene dominant and epistatic. The same gene in Ukraine is allelic to one of the Trispernia genes and to one of the two complementary Bond genes.

2. Victoria

This variety is resistant to most of the races of crown rust found in North America but susceptible to a soil-borne disease known as Victoria blight. Weetman (30) and Litzenberger (17) demonstrated that Victoria resistance to races 1 and 45 is conditioned by a single dominant gene and completely linked with Victoria blight susceptibility. Cochran et al. (3) indicated that Victoria resistance to race 1 is conditioned by a single dominant gene. Murphy et al. (20) found that Victoria resistance to races 1 and 45 is governed by a single dominant gene. Finkner (7) and Finkner (5) showed that a single dominant gene linked with Victoria blight susceptibility conditioned resistance to races 57 and 109. Welsh et al. (31) also found a single dominant gene completely linked with Victoria blight susceptibility which governed resistance to race 57 as well as to races 4, 5, and 34A. However, these investigators discovered three independent genes governing resistance to races 1, 2, 3, 6, 24, 34, 38, and 45. One of these genes for resistance was completely independent of the gene for Victoria blight susceptibility while one was completely linked. Vallega (29) found that the varieties Klein Mar and Tama, which derived their resistance from Victoria, each had a single dominant gene for resistance to race 1 and another for resistance to race 45. It should be noted, however, that the South American biotypes used in the above study may be different from those in North America.

Tama and the original Garry appeared to carry all the Victoria genes for resistance to crown rust but were susceptible to Victoria blight. Rodney and Garry (New) possess the gene for susceptibility to crown rust race 57 and resistance to Victoria blight. The gene for resistance to race 45 and associated races has been retained.

Finkner (7) showed that the single gene in Victoria for resistance to race 57 was allelic to one of the complementary genes in Bond and non-allelic to the genes in Ukraine, Landhafer, Santa Fe, and Trispernia.

3. Bond

Hayes *et al.* (12), Hayes (11), Weetman (30), Cochran *et al.* (3), and Ko *et al.* (16) found that the Bond resistance to races 1, 3, and 6 is conditioned by two dominant complementary genes. Finkner (7) concluded that resistance to race 57 is governed by two independent duplicate partially dominant genes.

4. Santa Fe

This variety is considered resistant to all races found in North America except for races 263, 264, and 276. Litzenberger (17) working with races 1 and 45, Vallega (29) working in South America with races 1, 55, and 56, and Finkner (7) working with race 57, found resistance governed by a single dominant gene. Finkner (7) found this Santa Fe gene to be allelic to one of the genes in Ukraine, in Trispernia, and in Bond, but to be independent from genes in Landhafer and Victoria. Osler and Hayes (21) indicated that resistance to races 45 and 57 is due to two dominant complementary genes and/or an independent dominant gene. They also showed that at least one of the complementary Bond genes for resistance is not allelic to the genes controlling Santa Fe type resistance. Finkner *et al.* (6) concluded that resistance to races 57 and 109 is governed by two duplicate genes linked with 28.8 per cent crossing over and that the Ukraine gene for resistance to race 57 is allelic to one of the two genes in Santa Fe.

5. Landhafer

Litzenberger (17) demonstrated that a single dominant gene in Landhafer conditioned resistance to races 1 and 45. Finkner (5) found the Landhafer gene for resistance to races 57 and 109 to be only partially dominant. Kehr and Hayes (14) discovered a single dominant gene governing resistance to races 1, 3, 4, 5, 6, 33, 45, 57, and 68, independent from the two complementary Bond genes. Finkner (7) postulated a single dominant gene for resistance to race 57, independent from the genes in Santa Fe, Victoria, Ukraine, Trispernia, and Bond.

6. Trispernia

Finkner (5) found two duplicate genes in Trispernia for resistance to races 57 and 109. One of these genes was allelic to the gene in Victoria. Finkner (7) showed that plants of this variety may have one, two or three gene pairs for resistance to race 57.

7. Ascencao

Simons (27) demonstrated that the oat variety Ascencao has the Victoria gene for moderate resistance to race 263 and other races as well as susceptibility to Victoria blight. Simons discovered a new gene for resistance to race 202 which he designated as "E". This gene is independent from the genes for resistance in Victoria, Landhafer, Santa Fe, and Trispernia.

MATERIALS AND METHODS

The varieties used as parents in this study are as follows:

(1) Ukraine was introduced into the United States from Russia in 1930 and into Canada from the United States in 1945. This variety is valuable in breeding for crown rust resistance, particularly for race 263.

(2) Garry is from the cross Victory x Victoria x (Hajira-Banner) . The original Garry, developed at the Cereal Breeding Laboratory, Winnipeg, was released in 1947. It was withdrawn and replaced in 1952 by a new selection which was resistant to Victoria blight and susceptible to some races of crown rust. This variety is being grown widely in Canada and the United States.

(3) Fortune is from the cross Victory x (Victory-Richland) x (Markton-Victory). This variety, developed at the University of Saskatchewan, was licensed and accepted for registration in 1948. It is grown mainly in Saskatchewan.

The seed of all three parents was from the stocks of the Cereal Breeding Laboratory at Winnipeg. The reaction of Rodney, used as an accessory host in the identification of races, and the reactions of the parental varieties to the races of crown rust studied are shown in Table I.

TABLE I

Seedling Reaction of Parent Varieties and Rodney to 12 Races of Crown Rust

Races of Crown Rust	Varieties Ukraine	Garry	Fortune	Rodney
202A	R	S	S	S
212A	R	S	S	S
213	R	S	S	S
239B	R	S	S	S
263	R	S	S	S
202	R	R	S	R
209	R	R	S	R
235	R	R	S	R
236	R	R	S	R
239	R	R	S	R
240	R	R	S	R
229	S	R	S	R

The two crosses studied, namely Garry x Ukraine and Fortune x Ukraine, were made in the greenhouse at the Cereal Breeding Laboratory at Winnipeg during the winter of 1954-55. Seven F_1 plants from each cross were grown in the field at Winnipeg in 1955, together with the parents of each F_1 plant. Three families of each cross and their parents were grown in the field at the Central Experimental Farm, Ottawa, in 1956. All tests on crown rust reaction were made in the greenhouse of the Plant Science Department, University of Manitoba during the winter of 1956-1957 and the greenhouse of the Cereal Breeding Laboratory in the spring and summer of 1957.

<u>Techniques of Testing Lines</u>

In this paper the term "family" is used to refer to a group of F_2 plants or F_3 lines derived from a single F_1 plant.

The term "line" or "F_3 line" refers to the progeny of a single F_2 plant. Sixty to eighty F_3 lines from each family were selected at random to determine their reaction to races 263 and 213. Groups of 30 lines were selected on the basis of their reaction to these races for testing to other races of crown rust.

From each line 15 to 30 seeds were planted in 4-inch pots. The seedlings were inoculated in the one-leaf stage using the following method:

(1) The leaves were wetted with a hand atomizer.

(2) Fresh crown rust spores taken directly from an infected plant or a talc-spore mixture was used. The inoculum was applied to the plant by rubbing gently onto the leaves with the thumb and index finger.

(3) Two types of incubation chambers were used. In early tests a polyethylene-covered frame was fitted over the pots on the greenhouse bench. In later tests the pots were placed in upright polyethylene-covered chambers. The pots were sprayed with water and kept overnight in the chamber under reduced temperature.

The pots were then kept on the greenhouse bench at a temperature of approximately 70-75° F. for 12 to 14 days. The seedlings were classified according to pustule type, the lines were then classified as resistant, segregating, or susceptible. In all cases the parents were used as checks.

In some of the later tests, the plants were inoculated with two different races by means of the method described by Knott and Anderson (15). In the one-leaf stage the plants were inoculated with the first race and seven to eight days later the second leaf was inoculated with the second race at about the time the first leaf was beginning to show flecking. In all tests the parents and hybrid lines gave consistent reactions on both first and second leaf.

Pure races were obtained from Dr. B. Peturson of the Plant Pathology Laboratory, Winnipeg. These races were classified on the set of ten differentials suggested by Simons and Murphy (28) with Rodney and Garry used as accessory hosts. Several of the races used were subraces differentiated in Canada on the basis of these two accessory hosts. The purity of races was usually checked on the differential hosts both before and during tests.

The data were statistically analysed using the Chi-square test as described by Goulden (10). The correction for continuity was applied in all cases where there was only one degree of freedom. The P values were taken from the table of Fisher and Yates (8).

EXPERIMENTAL RESULTS

Tests with Race 213

Ukraine is almost immune to this race while Garry and Fortune are completely susceptible. A total of 86 random F_3 lines from the cross Fortune x Ukraine and 137 random F_3 lines from the cross Garry x Ukraine were classified as resistant, segregating, or susceptible to race 213 and fitted to a 1:2:1 ratio. The data from these tests, presented in Table II, indicate that in both these crosses a single factor is operative, as shown by P values of 0.70 - 0.80 and 0.20 - 0.30, respectively. The P value for the totals of both crosses is 0.30 - 0.50.

TABLE II

Goodness of Fit to a 1:2:1 Ratio of F_3 Lines for Reaction To Race 213 of Crown Rust in Crosses of Resistant Ukraine with Susceptible Fortune and Garry

Cross	Classes: Resistant Obs.	Resistant Exp.	Segregating Obs.	Segregating Exp.	Susceptible Obs.	Susceptible Exp.	Chi-square	P
Fortune x Ukraine	24	21.50	40	43.00	22	21.50	0.61	0.70-0.80
Garry x Ukraine	40	34.25	70	68.50	27	34.25	2.53	0.20-0.30
Total	64	55.75	110	111.50	49	55.75	2.04	0.30-0.50

If a single gene conditions resistance to race 213, as the data in Table II indicate, plants within segregating lines should occur in a ratio of 3 resistant to 1 susceptible. When the observed numbers are fitted to the expected 3:1 ratio, a poor fit is obtained for both crosses as indicated in Table III by the P values of 0.02 - 0.05 for the Fortune x Ukraine cross and less than 0.001 for the Garry x Ukraine cross. However, owing to the greater reliability of data on the classification of F_3 lines, the single gene hypothesis is acceptable.

TABLE III

Goodness of Fit to a 3:1 Ratio of Plants Within Segregating F_3 Lines for Reaction to Race 213 of Crown Rust in Crosses of Resistant Ukraine with Susceptible Fortune and Garry

Cross	Classes: Resistant Obs.	Resistant Exp.	Susceptible Obs.	Susceptible Exp.	Chi-square	P
Fortune x Ukraine	746	778.5	292	259.5	5.26	0.02-0.05
Garry x Ukraine	1050	1110.0	430	370.0	12.54	0.001
Total	1796	1888.5	722	629.5	17.92	0.001

Tests with Race 263

The reaction of the parental variety Ukraine varied in different tests from a resistant type (1) pustule to a moderately susceptible type (3) pustule, while the parents Garry and Fortune gave susceptible type (4) pustules. A total of 180 random F_3 lines consisting of 68 lines from the cross Fortune x Ukraine and 112 lines from the cross Garry x Ukraine were classified as resistant, segregating, or susceptible to race 263 and fitted to a 1:2:1 ratio. The data presented in Table IV indicate that in both the Fortune x Ukraine and Garry x Ukraine crosses a single gene conditions resistance to race 263, as shown by P values of 0.30 - 0.50 and 0.05 - 0.10, respectively. The P value for the totals of both crosses is 0.10 - 0.20.

TABLE IV

Goodness of Fit to a 1:2:1 Ratio of F_3 Lines for Reaction to Race 263 of Crown Rust in Crosses of Resistant Ukraine with Susceptible Fortune and Garry

Cross	Classes						Chi-square	P
	Resistant		Segregating		Susceptible			
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.		
Fortune x Ukraine	13	17	38	34	17	17	1.44	0.30-0.50
Garry x Ukraine	32	28	62	56	18	28	4.78	0.05-0.10
Total	45	45	100	90	35	45	3.33	0.10-0.20

When the observed numbers of resistant and susceptible plants within the 38 lines of the cross Fortune x Ukraine and the 62 lines of the cross Garry x Ukraine which segregated for reaction to race 263 are fitted to a 3:1 ratio, as shown in Table V, P values of 0.70 - 0.80 and 0.02 - 0.05, respectively, are obtained. The P value for the totals of both crosses is 0.10 - 0.20. Therefore, the hypothesis of a single dominant gene in Ukraine for resistance to race 263 is acceptable.

TABLE V

Goodness of Fit to a 3:1 Ratio of Plants within Segregating F_3 Lines for reaction to Race 263 of Crown Rust in Crosses of Resistant Ukraine with Susceptible Fortune and Garry

Cross	Classes: Resistant Obs.	Resistant Exp.	Susceptible Obs.	Susceptible Exp.	Chi-square	P
Fortune x Ukraine	706	711	242	237	0.12	0.70-0.80
Garry x Ukraine	1151	1113	333	371	5.05	0.02-0.05
Total	1857	1824	575	608	2.31	0.10-0.20

Association Between Inheritance of Reaction to Races 213 and 263.

The relationship between the inheritance of reaction to races 213 and 263 was determined for 64 random F_3 lines of the Fortune x Ukraine cross and for 94 random F_3 lines of the Garry x Ukraine cross. The majority of the lines which were classified as resistant, segregating, or susceptible to one race gave a similar classification to the other race, as indicated in Table VI.

TABLE VI

Frequency Distribution Showing the Relationship Between the Seedling Reaction of F_3 Lines to Races 213 and 263 of Crown Rust in Two Crosses

Cross	Reaction to Race 263	Reaction to Race 213 Res.	Seg.	Susc.	Total
Fortune x Ukraine	Res.	12	1	1	14
	Seg.	6	28	0	34
	Susc.	0	0	16	16
	Total	18	29	17	64
Garry x Ukraine	Res.	20	4	1	25
	Seg.	4	48	1	53
	Susc.	0	0	16	16
	Total	24	52	18	94

Eighteen lines did not follow this pattern. Two of these lines were classified as susceptible to race 213 and resistant to race 263. Ten lines were resistant to race 213 and segregated for reaction to race 263, while five lines segregated for reaction to race 213 and were resistant to race 263. One line was susceptible to race 213 and segregated for reaction to race 263.

The above data indicate that the gene for resistance to race 213 is closely linked to the gene for resistance to race 263. It was not possible to estimate the linkage intensity using the product method, since the sum of the classes making up the factor "b" was equal to zero in both crosses. The linkage intensity was estimated using the following method:

1. The nine observed classes were combined into the five classes as shown below:

   Class I - lines resistant to both races.

   Class II - lines resistant to race 213 and segregating or susceptible to race 263, and lines segregating to race 213 and susceptible to race 263.

   Class III - lines segregating to both races.

   Class IV - lines resistant to race 263 and segregating or susceptible to race 213, and lines segregating to race 263 and susceptible to race 213.

   Class V - lines susceptible to both races.

2. The expected frequencies of these five classes were calculated for several linkage values. Table VII indicates the method in which the classes were bulked. Classes I and V are non-recombinant classes, class III is almost all non-recombinant, and classes II and IV are recombinant classes.

3. The observed ratios of the five classes were fitted to the expected ratios for different linkage values using the Chi-square test. The Chi-square values of 2.5 and 2.1 for 7 per cent linkage for the Fortune x Ukraine and Garry x Ukraine crosses,

respectively, are lower than the Chi-square values for 6 per cent or 8 per cent linkages, as shown in Table VIII. In all cases the P values are very high.

The above data indicate that the gene for resistance to race 213 and the gene for resistance to race 263 are linked with a crossover value of the order of 7 per cent. Since the reaction to race 263 of the Ukraine parent and of hybrid lines possessing the Ukraine gene varies from resistant to moderately susceptible under different environmental conditions, some of the lines may have been misclassified for their reaction to race 263. For this reason, and because of the method of calculation used in estimating the linkage value, 7 per cent linkage should be considered as only an approximation of the true value.

TABLE VII

Expected Genotypic Classes for Reaction of F_3 Lines to Races 213 and 263 Grouped into Five Classes for Estimating Linkage

Reaction to race 213	Reaction to race 213					
		Res.		Seg.		Susc.
Res.	I	AABB		AaBB aABB	IV	aaBB
Seg.		AABb AAbB	III	AaBb AabB aABb aAbB		aaBb aabB
	II					
Susc.		AAbb		Aabb aAbb	V	aabb

TABLE VIII

Goodness of Fit for Different Linkage Values of Observed Frequencies of Classes of F_3 Lines Tested for Reaction to Races 213 and 263

Crossover value in per cent	Fortune x Ukraine		Garry x Ukraine	
	Chi-square	P	Chi-square	P
6	2.8	0.50 - 0.70	2.5	0.50 - 0.70
7	2.5	0.50 - 0.70	2.1	0.70 - 0.80
8	2.6	0.50 - 0.70	3.8	0.30 - 0.50

Tests of Several Races on Selected Lines

1. Fortune x Ukraine

Ukraine is resistant and Fortune is susceptible to races 202, 202A, 209, 213, 236, and 239. Thirty F_3 lines from one family of this cross were selected on the basis of their reaction to race 213. Nine lines were resistant to this race, nine segregated for reaction, and twelve were susceptible. These lines were tested for their reaction to races 202, 202A, 209, 236, and 239. All lines classified as resistant, segregating, or susceptible to race 213 gave a similar classification to the other five races. These results indicate that the single dominant gene in Ukraine which conditions resistance to race 213 also conditions resistance to races 202, 202A, 209, 236, and 239.

The observed numbers of resistant and susceptible plants within the lines which segregated for reaction to race 213 and other races are recorded in Table IX. In all

TABLE IX

Goodness of Fit to a 3:1 Ratio of Plants Within Segregating F_3 Lines for Reaction to Races 202, 202A, 209, 236, and 239 of Crown Rust in a Cross of Resistant Ukraine with Susceptible Fortune

Cross	Resistant Obs.	Resistant Exp.	Susceptible Obs.	Susceptible Exp.	Chi-square	P
202	141	141.75	48	47.25	0.01	0.99-1.00
202A	108	108.00	36	36.00	0.00	1.00
209	134	127.50	36	42.50	1.03	0.30-0.50
236 + 239	122	131.25	53	43.75	2.33	0.10-0.20
Total	505	508.50	173	169.50	0.06	0.80-0.90

cases the data show a good fit to the expected ratio of 3 resistant to 1 susceptible. This provided further evidence in favor of the hypothesis that a single dominant gene in Ukraine conditions resistance to the races of crown rust studied.

2. Garry x Ukraine

(a) Thirty F_3 lines from one family of this cross were selected on the basis of their reaction to race 213. Eleven lines were resistant to this race, ten segregated for reaction, and nine were susceptible. These lines were inoculated with races 202A, 212A, 239B, and 263, to which Ukraine is resistant; race 229 to which Garry is resistant; and races 235 and 240 to which both parents are resistant. The results from these tests are shown in Table X and are discussed below.

TABLE X

Reaction of F_3 Lines of One Family of the Cross Garry x Ukraine to Eight Races of Crown Rust

Parents and F_3 lines	Races of Crown Rust							
	213	202A	212A	239B	263	229	235	240
Ukraine	R	R	R	R	R	S	R	R
Garry	S	S	S	S	S	R	R	R
1	R	R	R	R	R	Seg	R	R
2	R	R	R	R	Seg	S	R	R
3	R	R	R	R	R	Seg	R	R
4	R	R	R	R	R	Seg	R	R
5	R	R	R	R	R	Seg	R	R
6	R	R	R	R	R	R	R	R
7	R	R	R	R	R	R	R	R
8	R	R	R	R	-[1]	R	R	R
9	R	R	R	R	Seg	Seg	R	R
10	R	R	R	R	-	Seg	R	R
11	R	R	R	R	-	Seg	R	R
12	Seg	Seg	Seg	Seg	Seg	Seg	Seg	Seg
13	Seg	Seg	Seg	Seg	Seg	Seg	Seg	Seg
14	Seg	Seg	Seg	Seg	Seg	Seg	Seg	Seg
15	Seg	Seg	Seg	Seg	Seg	Seg	Seg	Seg
16	Seg	Seg	Seg	Seg	Seg	Seg	Seg	Seg
17	Seg	Seg	Seg	Seg	Seg	Seg	Seg	Seg
18	Seg	Seg	Seg	Seg	Seg	R	R	R
19	Seg	Seg	Seg	Seg	Seg	R	R	R
20	Seg	Seg	Seg	Seg	Seg	R	R	R
21	Seg	Seg	Seg	Seg	Seg	R	Seg	Seg
22	S	S	S	S	S	R	R	R
23	S	S	S	S	S	R	R	R
24	S	S	S	S	-	R	R	R
25	S	S	S	S	-	R	R	R
26	S	S	S	S	S	S	S	S
27	S	S	S	S	S	S	S	S
28	S	S	S	S	S	S	S	S
29	S	S	S	S	-	Seg	Seg	Seg
30	S	S	S	S	-	Seg	Seg	Seg

1 - lines left blank did not show the same reaction in separate tests to race 263.

i) Races 202A, 212A, and 239B. In all cases the reaction of the thirty lines to these races was the same as their reaction to race 213. This indicates that the Ukraine reaction to all four races is governed by the same gene.

ii) Race 263. In most cases the reaction of the lines to race 263 was the same as their reaction to race 213. However, two lines which were resistant to race 213 segregated for reaction to race 263 in two separate tests. The lines for which no reaction is indicated gave different reactions in separate tests with the same line. The data support the conclusion that the gene for resistance to race 263 is closely linked to the gene for resistance to race 213.

iii) Race 229. The reaction of the lines to this race differed from their reaction to race 213. This indicates that the gene or genes from Garry for resistance to this race are independent from the Ukraine gene.

iv) Races 235 and 240. All lines which showed either the Ukraine resistance to race 213 or the Garry resistance to race 229 were resistant to races 235 and 240. All lines which were susceptible to both of races 213 and 229 were susceptible to races 235 and 240. The remainder of the lines segregated for reaction to these two races. These data indicate that the Ukraine gene for resistance to race 213 controls resistance to race 235 and 240 and that the Garry gene or genes for resistance to race 229 also controls resistance to races 235 and 240.

(b) Thirty F_3 lines from a second family of the cross Garry x Ukraine were selected on the basis of their reaction to race 213. Nine lines were resistant to this race, thirteen segregated for reaction, and eight were susceptible. These lines were inoculated with races 202A and 263 to which Ukraine is resistant and with races 209, 236, and 239 to which both parents are resistant. The results from these tests are shown in Table XI and are discussed below.

i) Race 202A. The reactions of the thirty lines tested to this race were the same as their reaction to race 213. This indicates that the Ukraine resistance to races 213 and 202A is governed by the same gene.

ii) Race 263. In most cases the reaction of the thirty lines to race 263 was the same as their reaction to race 213. However, four lines were exceptions to this pattern. One line resistant to race 213 segregated for reaction to race 263. One line which segregated to race 213 was resistant to race 263, and of two lines which were susceptible to race 213, one segregated and one was resistant to race 263. The classification of these four lines to race 263 was based on three or more separate rust tests all giving the same reaction. The six lines for which no classification is given were not tested to race 263. These data support the hypothesis that the gene for resistance to race 263 is closely linked to the gene for resistance to race 213. As the data comes from lines selected on

TABLE XI

Reaction of F_3 Lines of a Second Family of the Cross Garry x Ukraine to Five Races of Crown Rust

Parents and F_3 lines	Races of Crown Rust					
	213	202A	263	209	236	239
Ukraine	R	R	R	R	R	R
Garry	S	S	S	R	R	R
1	R	R	R	R	R	R
2	R	R	-[1]	R	R	R
3	R	R	Seg	R	R	R
4	R	R	R	R	R	R
5	R	R	R	R	R	R
6	R	R	R	R	R	R
7	R	R	-	R	R	R
8	R	R	-	R	R	R
9	R	R	R	R	R	R
10	Seg	Seg	Seg	R	R	R
11	Seg	Seg	Seg	Seg	Seg	Seg
12	Seg	Seg	Seg	Seg	Seg	Seg
13	Seg	Seg	Seg	R	Seg	Seg
14	Seg	Seg	Seg	Seg	R	R
15	Seg	Seg	R	Seg	Seg	Seg
16	Seg	Seg	-	R	R	R
17	Seg	Seg	Seg	R	R	R
18	Seg	Seg	Seg	Seg	Seg	Seg
19	Seg	Seg	Seg	R	R	R
20	Seg	Seg	Seg	Seg	Seg	Seg
21	Seg	Seg	Seg	Seg	-	-
22	Seg	Seg	Seg	Seg	-	-
23	S	S	Seg	-	-	-
24	S	S	-	Seg	Seg	Seg
25	S	S	S	-	S	S
26	S	S	S	R	R	R
27	S	S	S	-	S	S
28	S	S	R	Seg	-	-
29	S	S	S	S	-	-
30	S	S	-	S	S	S

1 - lines left blank were not tested to race 263.

the basis of crown rust reaction rather than from random lines, an analysis of linkage intensity was not made.

iii) Races 209, 236, and 239. All thirty lines gave similar reactions to these races. The nine lines that were resistant to race 213 gave the Ukraine type of resistance to these three races. All thirteen lines that segregated for reaction to race 213 segregated or were resistant to these races, while the eight lines susceptible to race 213 were resistant, segregated or were susceptible to the three races. This indicates that the Ukraine gene for resistance to race 213 also controls resistance to races 209, 236, and 239, and in addition that the Garry gene or genes control resistance to the same three races.

DISCUSSION

These investigations were undertaken with the assumption that the parental varieties were homogeneous for crown rust reaction. Rust tests were made on hybrid progenies from four parental plants of Ukraine and two parental plants of Garry. As there did not appear to be a significant variation in results between different families of the same cross, no evidence was found of heterogeneity for crown rust reaction.

The F_3 reactions of the Fortune x Ukraine and Garry x Ukraine crosses indicate that the Ukraine resistance to race 213 is controlled by a single dominant gene and that Ukraine resistance to race 263 is also controlled by a single dominant gene. It was concluded that the gene for resistance to race 213 is linked to the gene for resistance to race 263 with a crossover value of the order of 7 per cent. The gene for resistance to race 213 also governs resistance to races 202, 202A, 205, 209, 212A, 235, 236, 239, 239B, and 240. Tests of F_3 lines from one family of the Garry x Ukraine cross indicated that the Garry resistance to races 229, 235, and 240 is associated in inheritance. Tests of F_3 lines from a second family of this cross indicated that the Garry resistance to races 209, 236, and 239 is associated in inheritance. The data did not reveal if the inheritance of resistance to the two groups of races is controlled by the same gene or genes. The gene for resistance in Ukraine and Garry are independent of one another, with the gene for the higher type of resistance epistatic to the gene for the lower type in all cases.

Finkner _et al_. (6) stated that a single dominant gene in Ukraine gives resistance to race 57 and that this Ukraine gene conditions susceptibility to race 109, even in the presence of the Bond gene for resistance to this race. The present study agrees with the results of Finkner _et al_. in finding a single gene for resistance to race 202A (new designation for race 57). No crosses with Bond were made, but it was found that the Ukraine gene did not inhibit the Garry gene for resistance to race 229 (new designation for race 109). Finkner (7) concluded that Ukraine resistance to race 57 is controlled by duplicate dominant linked genes rather than by a single dominant gene as found in this study. This difference in results could be explained by the fact that Ukraine is not homogeneous for crown rust reaction and therefore genetically different Ukraine plants may have been used as parents in these investigations.

Finkner (5) and Finkner (7) reported a gene in Victoria for resistance to race 57 and susceptibility to Victoria blight. Welsh _et al_. (31) indicated that this gene is lacking in Garry, but that Garry has a single dominant gene for resistance to a large number of races. This gene governs resistance to races 2, 29, and 38 (which are now grouped as race 239); 3 and 24 (grouped as race 240); and 2b (now designated 229). The present investigation revealed the Garry resistance to races 229, 235, and 240 to be associated in inheritance, and resistance to races 209, 236, and 239 to be also associated in inheritance. Resistance to the races used in this study is probably conditioned by the same gene as that studied by Welsh <u>et al</u>. (31) which was shown to condition resistance to races 229, 239, and 240, therefore, the same gene must give resistance to all six races.

Finkner (5) and Finkner (7) found allelism between the gene or genes in Ukraine and the gene or genes in Santa Fe, Trispernia, and Bond. The Ukraine gene was independent of genes in Landhafer and Victoria. In this investigation only the Ukraine gene and the Garry gene were studied. This Garry gene is not the same gene as that controlling resistance to race 57 (202A) in Victoria, and its allelic relationships had not been previously studied. It was found to be independent of the Ukraine gene.

Future Use of Ukraine and Garry Resistance

In North America there are at least three races of crown rust, races 263, 264, and 276, which will attack most of the commercial varieties of oats. Simons[1] calls these races, pathogenic on Santa Fe and Landhafer, the "Landhafer races". Usable sources of resistance to these races are not positively known except in the case of Ukraine resistance to race 263. These races appeared in epiphytotic proportions in Florida in the winter of 1956-1957. Of the twenty to thirty cultures of these races obtained from Florida by Simons

1 Personal correspondence, letter from Dr. M. D. Simons, July 29, 1957.

in the spring of 1957, the majority proved to be race 264. In addition, there was one culture of race 263 and a number of cultures of a previously unidentified race. The reactions of Ukraine and Victoria to these races appeared to be somewhat influenced by environmental conditions.

A number of lines from the Garry x Ukraine cross possess the seedling resistance to crown rust of both parents. Some of these lines, selected in the field, were found to combine the field resistance to crown rust of Ukraine and Garry with the field resistance to stem rust of Garry. These lines may be very useful in the future as breeding material.

Field reactions determined at Winnipeg in 1957 under artificially induced epidemic conditions show that the Ukraine resistance to the races of crown rust prevalent in Western Canada is equal to that of Landhafer and Santa Fe. Ukraine also controls resistance to one or more of the Landhafer races in the seedling stage. According to former investigators the genes for resistance in Ukraine and Santa Fe are allelic and therefore the resistance from both sources cannot be combined in one genotype. The Ukraine and Landhafer genes, on the other hand, were shown to be independent of one another and therefore the resistance of these two varieties can readily be combined. The changes in race population in the crown rust organism over the past few years have been very rapid and great effort will be required to maintain commercial varieties resistant to the prevalent races of this pathogen.

SUMMARY

Crown rust tests conducted with F_3 lines of the crosses Fortune x Ukraine and Garry x Ukraine indicated that a single dominant gene in Ukraine governed resistance to races 213, 202, 202A, 209, 212A, 235, 236, 239, 239B, and 240, and that another dominant gene in Ukraine, linked with a crossover value of the order of 7 per cent, governed resistance to race 263. Tests with lines from one family of the Garry x Ukraine cross showed that the Garry resistance to races 229, 235, and 240 is associated in inheritance, and tests with lines from a second family showed that Garry resistance to races 209, 236, and 239 is also associated in inheritance. The Ukraine and Garry genes were shown to be independent of one another, with the gene for the higher type of resistance epistatic to the gene for the lower type in all cases.

A number of F_3 lines were isolated which combined the field resistance of Ukraine and Garry to crown rust, including race 263, with the field resistance to stem rust of Garry. These lines may prove very useful in a plant breeding program.

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