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IT IS generally recognized that disease-resistant varieties are of particular importance in that they eliminate some of the hazards in crop production, thus tending to stabilize production by the control of one of the major causes of seasonal variability. Stem-rust resistant varieties of oats, including Anthony and Minrus, bred in Minnesota, Rainbow from North Dakota, and Iogold from Iowa, which have been grown extensively in Minnesota, have proved valuable in this respect.

The Bond variety of oats appears to be one of the most promising introductions made in recent years by the United States Department of Agriculture. According to Stanton and Murphy (1933) it was received from Australia in 1929. They quote Wenholz as stating that Bond resulted from crossing a strain of *Avena sterilis* with Golden Rain. Bond appears of particular value as a parent in crosses because of its high resistance to many strains of crown rust and smut, strength of straw, plump seeds, and ability to yield well under unfavorable conditions.

This bulletin reports correlated studies of inheritance of reaction to stem rust, crown rust, and smuts in relation to agronomic and botanical characters, particularly those that differentiate cultivated varieties of *A. byzantina* from *A. sativa.*

REVIEW OF LITERATURE

Short summaries that have been made by Stanton and others (1934) show that from crosses of Victoria with varieties of oats grown in Iowa it is comparatively easy to combine resistance to stem rust, crown rust, and smuts in a single variety. It seems unnecessary here to review the extensive studies made previously on inheritance of disease reaction. Concise summaries are given by Roemer and others (1938) who include references to much of the more important literature.

Coffman, Parker, and Quisenberry (1925) have made extensive studies of variability in Burt oats and have described certain characters of the base of the lower floret and methods of floret disjunction that are of particular value in relation to the studies reported in this bulletin. The following summaries are taken from their studies.

[1] The writers gratefully acknowledge the help of the following people who contributed to the progress of the work in various ways and at various times: A. R. Downie, Martin Schlegtendal, Karl Manke, F. R. Immer, and H. K. Wilson.

Spikelet disarticulation has been defined as the separation of the lower floret of the oat spikelet from the axis of the spikelet. Three groups were described: (1) abscission, leaving a well-defined, deep, oval cavity or "sucker mouth" in the face of the callus on the base of the lemma of the lower grain; (2) disarticulation, by fracture resulting in a rough fractured surface with little or no cavity in the base of the lemma, a method characteristic of cultivated varieties of *A. sativa*; (3) disarticulation by semi-abscission, more or less intermediate between (1) and (2).

Floret disjunction is defined as the method of separation of the second floret from the first or lower floret. Three groups are of interest in relation to the present study: (1) disjunction by basifracture, the rachilla segment breaking near its base and remaining firmly attached to the base of the upper floret, the method of common occurrence in *A. byzantina*; (2) disjunction by disarticulation at the apex of the rachilla segment, the rachilla segment remaining attached to the lower floret, the normal method in *A. sativa*; (3) disjunction by heterofracture, the rachilla segment breaking transversely in the middle portion.

Basal hairs refer to conspicuous bristles at the base of the lower floret. Three classifications are given: abundant long, abundant mid-length, and few.

Previous studies by Fraser (1919), in crosses between Burt and Sixty Day, gave an intermediate type of base in F_1, with few basal hairs and disjunction by basifracture, using the terminology of Coffman and others. Segregation in F_2 was on a 3:1 basis for each pair of characters. Strong linkage was reported between the Burt type of base and the presence of medium long basal hairs, between the fully awned condition and the presence of medium long hairs on the base, and between the Burt base and the fully awned condition.

MATERIALS AND METHODS

The materials consisted of three varieties of oats grown commonly in Minnesota—Anthony, Iogold, and Rainbow; two strains of double crosses from hybrids between (Minota × White Russian) and Black Mesdag; and the Bond variety obtained from the United States Department of Agriculture (Stanton and Murphy, 1933).

Anthony and the two double-cross parent strains have the type of resistance to stem rust, *Puccinia graminis avenae* Erikss. and Henn., that is characteristic of the White Russian variety, i.e. moderate resistance under greenhouse and field conditions to physiological races 1, 2, and 5. Iogold and Rainbow are resistant to races 3 and 7 in addition to 1, 2, and 5, and it seems probable that these two types of resistance and susceptibility are dependent upon a series of three allelic factors (Smith, 1934).

All varieties used in these studies are susceptible to crown rust, *Puccinia coronata* Corda, under field conditions in Minnesota except Bond, which is resistant to many physiologic races of crown rust found in the United States. Rainbow often shows some degree of resistance to crown rust under field conditions, although it is susceptible to some common races.

The two double crosses have proved resistant to both species of smut, *Ustilago avenae* (Pers.) Jens. and *Ustilago levis* (Kellerman and Swingle) Magn., in trials at University Farm, St. Paul. Bond also has proved smut resistant, while the remaining varieties are susceptible.

During recent years at University Farm, conditions have in general been unfavorable for small grains, because of unusually high temperatures and low precipitation, particularly in the latter part of the growing season. This has given opportunity to observe the reaction to drouth of varieties used as parents in this study. Comparative performance, including date of heading, per cent of lodging (the percentage of the plot that is lodged), degree of lodging (the angle made by the stem with the perpendicular), per cent of plumpness of grain on the basis of 100 as completely plump, and yield in bushels for 1935 to 1937 is given in table 1. These data give some idea of the ability of Bond to withstand unfavorable conditions to a greater extent than the recommended varieties of oats now grown in Minnesota.

Table 1. Comparative Performance of Bond and Other Varieties in Yield Trials at University Farm, 1935-37, in Replicated Rod-row Trials

Variety	Year	Date heading	Per cent lodged	Degree lodged	Per cent plumpness grain	Yield, bu.
Anthony	1935	7/2	100	80	65	67.1
	1936	6/28	0	0	24	21.3
	1937	6/26	85	48	36	17.8
	Average	6/29	62	65	42	35.4
Iogold	1935	6/26	100	86	45	50.4
	1936	6/21	0	0	33	33.0
	1937	6/21	100	76	44	38.2
	Average	6/23	67	81	41	40.5
Rainbow	1935	6/30	100	85	56	51.8
Double Cross II-22-220	1935	6/28	100	88	60	71.2
	1936	6/24	50	8	24	24.1
	1937	6/23	85	70	39	28.5
	Average	6/25	78	64	41	41.3
Bond	1935	6/26	100	43	91	71.3
	1936	6/19	0	0	65	41.2
	1937	6/21	0	0	81	51.8
	Average	6/22	33	43	79	54.8

One of the double-cross strains has been grown for many years in nursery trials under the designation II-22-220. The second strain has not been tested in rod rows. These two selections from (White Russian × Minota) × Black Mesdag are referred to in the studies as Double Cross A and Double Cross B, respectively. The low yields of Anthony in 1936 and 1937 with low plumpness of grain show that conditions were particularly unfavorable for midseason oats. Iogold and Bond have similar dates of heading and maturity. The average per cent plumpness of grain of Iogold and Bond is 41 and 79, respectively. These data show to what extent Bond is outstanding in appearance of kernel under unfavorable conditions. During these three years Bond yielded more than any other variety, averaging 54.8 bushels an acre compared with 40.5 bushels for Iogold, with a similar time of maturity. In percentage and degree of lodging Bond was also much superior to the four varieties with which it was compared.

Data are available also from the Southeast Experiment Station at Waseca during 1935 and 1936, being a part of the rod-row yield trials grown in cooperation with the United States Department of Agriculture. Under these conditions, which were somewhat more favorable, Bond gave good yields, yielding more than any other variety except Double Cross II-22-220, which yielded six bushels more on an average than Bond. This double-cross selection has proved rather outstanding in yielding ability, but is decidedly lacking in kernel type and has rather strong awns.

Table 2. Comparative Yields of Bond and Other Varieties in Replicated Rod-row Trials at the Waseca Branch Station, 1935 and 1936

Variety	Year	Date heading	Per cent lodged	Degree lodged	Per cent plumpness grain	Yield, bu.
Anthony	1935	7/5	......	......	78	59.0
	1936	......	30	13	85	58.2
	Average	......	......	......	82	58.6
Iogold	1935	6/26	97	74	50	55.1
	1936	6/20	0	0	92	63.9
	Average	6/23	49	74	71	59.5
Rainbow	1935	7/1	......	......	92	58.0
	1936	6/25	0	0	90	70.6
	Average	6/28	......	......	91	64.3
Double Cross II-22-220	1935	6/29	20	90	87	77.0
	1936	6/22	0	0	92	63.7
	Average	6/26	10	90	90	70.4
Bond	1935	6/25	......	......	90	69.1
	1936	6/20	0	0	95	60.1
	Average	6/23	......	......	93	64.6

The oat crosses were made during the summer of 1933, and the F_1 generations were grown in the greenhouse the following winter and under field conditions in 1934 under stem and crown rust epidemic conditions in the nursery. Both parents were labeled for each cross made so that the parents could be compared with the hybrids in all cases and in order to check up on any marked variations in the parents. Pure lines of each plant used as a parent were compared with the hybrids during the segregating generations. As the different selections of the parents showed no marked variations in disease reaction within each variety, it seems unnecessary to report on them in detail.

Data on crown-rust reaction were taken in the field nursery on F_1 and F_2 plants and the parents of each cross. Three different types of rust reaction were noted: (1) resistant, small pustules generally surrounded by a dead area; (2) intermediate, small pustules averaging somewhat larger in size than group 1, without definite killing of areas surrounding each pustule; (3) susceptible, large, numerous pustules with no sign of resistance. When there was some doubt about the classification, group 2 was used. The data on crown rust were taken before the plants were mature, while the leaves were green.

Classification for stem rust was made by placing the plants in two classes, resistant and susceptible. This was done in the field when the plants were harvested and was checked later in the laboratory.

Data in the laboratory were taken by two persons working together. Notes were taken on awn development by classifying each plant on the basis of percentage of lower florets with awns and on development of awns, three groups being used: strong, intermediate, and weak.

Each plant was classified also for type of base, using three groups: B, with the type of spikelet disarticulation classified as abscission, typical of *A. byzantina;* S, with disarticulation by fracture, typical of *A. sativa;* and I, intermediate, more or less intermediate between B and S, although with a very definite enlargement of the base and with definite basal cavity. In the intermediate group there was, as a rule, rather marked variation, but there were no florets with basal cavity so well developed as in Bond.

Classification was made, also, on the manner of floret disjunction, referring to the method of separation of the second from the first or lower floret. Each of the two workers studied four florets, taken at random from each plant, taking care to select well-developed florets near the top of the panicle. The upper floret was pulled from the lower by holding to the upper grain, bending it away from the lower floret and observing the manner of disjunction. Three groups were made: B, disjunction by basifracture, the rachilla segment breaking near its base and remaining firmly attached to the upper floret, characteristic of Bond; S, disjunction by disarticulation, the rachilla segment remaining attached to the lower floret as in *A. sativa*; and I, including an intermediate group containing all plants not belonging to B or S. Considerable variation was observed in this group, some florets showing disjunction by heterofracture, the rachilla segment breaking transversely in the middle portion, others approaching the B or S type.

The number of basal hairs was recorded in several groups as 0, 0-10, 10-25, 0-B, and B, the number in the B class being 30 or more. Typical spikelets of Anthony and Bond are given in figure 1 which illustrates type of base and floret disjunction of Anthony and Bond. The basal hairs characteristic of Bond are shown also.

Figure 2 shows spikelets of all varieties used in the crosses. There is a marked contrast in awn development between Bond and Double Cross A. Note particularly the short plump grain of Bond in contrast to that of Double Cross A, Iogold, and Rainbow. Anthony produces a somewhat plumper grain than the other *sativa* varieties.

In the crown- and stem-rust nursery, from the time of heading to maturity, surface irrigation was practiced when necessary in order to prevent premature dying of the plants, so that the rust epidemics could develop normally. The epidemics of stem rust, crown rust, and the smuts were produced in the following manner.

Urediospores of crown and stem rusts grown on seedling plants in the greenhouse were injected by means of hypodermic needles into the shoots of susceptible plants in border rows in the nursery. The inoculations were started when the plants were about six inches high and continued until an abundance of inoculum was available or until the plants headed. In addition, inoculum was increased by spraying small areas, about 3 by 8 feet, with a heavy spore suspension and incubating them under a canvas-covered frame. Later, on cloudy days and at night when the plants were wet with dew or rain, the entire nursery was sprayed frequently with spore suspensions. Surface irrigation aided greatly in holding free moisture on the leaf surfaces for longer periods of time.

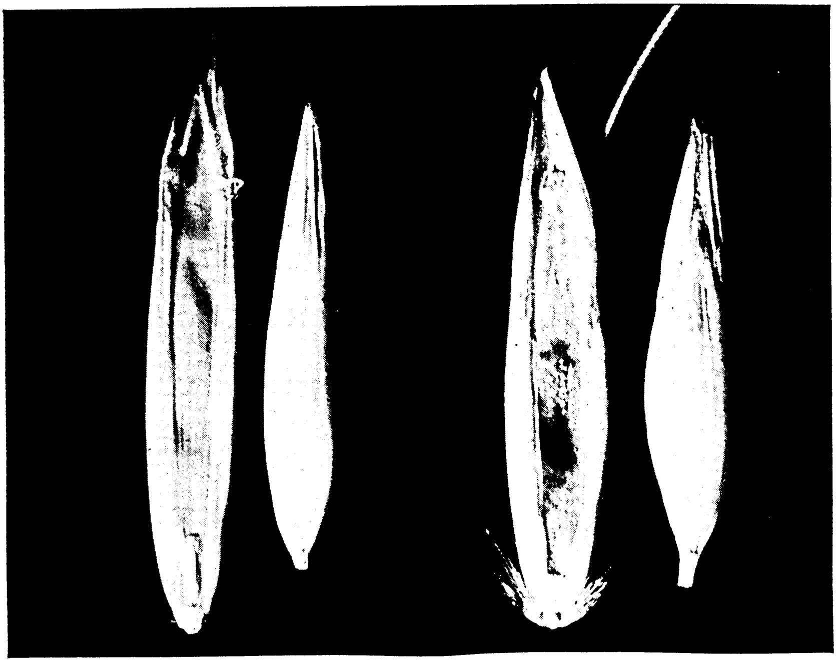

FIG. 1. CHARACTERISTIC SPIKELETS OF ANTHONY (LEFT) AND BOND (RIGHT)

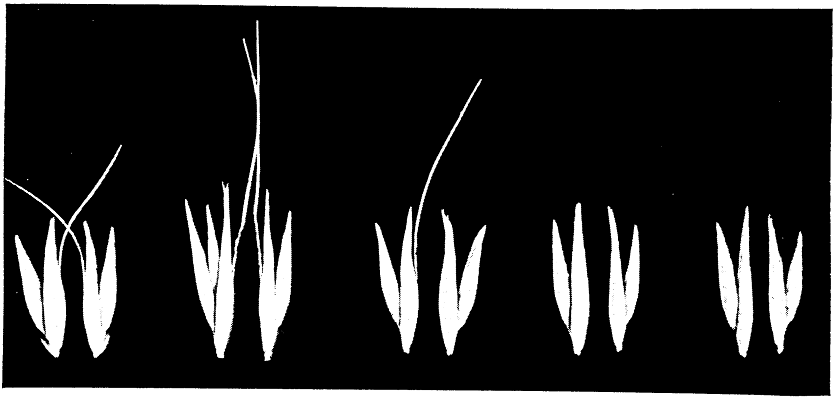

FIG. 2. AVERAGE SPIKELETS OF BOND, DOUBLE CROSS A, ANTHONY, IOGOLD, AND RAINBOW (LEFT TO RIGHT)

Before planting, the seed of each selection was inoculated with a composite of several collections of loose and covered smuts, essentially according to the partial-vacuum method described by Zade (1928-29) and modified by Haarring (1930). The seed was immersed in an aqueous suspension of smut spores and subjected to a partial vacuum for 12 to 15 minutes. The excess water was then poured off and the seed dried and stored for a few days until needed for planting. Under favorable soil conditions this method resulted in the production of 80 to 100 per cent of smut in susceptible varieties and lines.

EXPERIMENTAL RESULTS

Data on individual character reactions will be summarized to determine, as far as possible, the mode of inheritance of the character and this will be followed by studies of association between characters.

Crown-rust Reaction

The parents and F_1 crosses were grown in 1934 under an artificially induced epidemic of crown rust. The Bond variety in 1934 uniformly proved highly resistant to crown rust and susceptible to stem rust. The other varieties of *A. sativa* used as parents were in all cases susceptible to crown rust and resistant to stem rust. The F_1 crosses were resistant to stem rust and resistant or semi-resistant to crown rust. The individual plants of the F_1 and F_2 generations were classified into three groups for crown-rust reaction: resistant, semi-resistant, and susceptible.

Data on the parents and F_2 plants are given in table 3. The different parent plants within the different crosses gave similar hybrid progenies and for this reason were not summarized in relation to the particular parent plants used in making the cross.

The results for the different crosses appear rather similar with the exception of the cross between Bond and Rainbow which was grown a year later than the remainder of the F_2 progenies. The other crosses were tested in F_3 by studying their hybrid progenies. The disease reactions in 1936 were not so definite as in previous years and for this reason it was impossible to study the F_3 breeding behavior of the greater part of the Bond × Rainbow cross, although the epidemic was sufficiently good in 1936 to make further selections for crown-rust resistance possible. From the data given in table 3, it appears that if resistant and intermediate types of infection are combined, in the cross between Bond × Rainbow the ratio in F_2 approaches 3:1, with resistance dominant over susceptibility. A random selection of a few progenies of F_2 plants was tested under field conditions in 1935 and gave 5 homozygous resistant, 3 near resistant, 16 segregating, and 11 susceptible lines, which agrees fairly well with a hypothesis that one major factor pair differentiates resistance and susceptibility in this cross.

The F_3 breeding behavior of F_2 plants of known crown-rust reaction was obtained for other crosses in the field under epidemic conditions in 1935. Two kinds of material are given in table 4: Group A, random selections of particular crosses, and Group B, plants that were classified in F_2 as resistant to crown rust and selected for further trial in F_3. The random selections consisted of certain F_2 families where the number of F_2 plants approximated the number that could be tested in F_3. The reaction of the parent F_2 plants under field conditions was known, which gave an opportunity to test the accuracy of the F_2 classification based on the F_3 breeding behavior.

Table 3. Crown-rust Reaction of Individual Plants of the Parent Varieties and of the F_2 of Crosses Between Them

Plants of parents and F_2	Reaction classes*			Total
	R	I	S	
Bond	121	....	1	122
Double Cross A	....	....	60	60
F_2, Bond × Double Cross	192	104	372	668
Double Cross × Bond	159	36	215	410
Anthony	....	....	5	5
F_2, Anthony × Bond	121	23	115	259
F_2, Bond × Anthony	24	12	18	54
Double Cross B	....	....	10	10
F_2, Bond × Double Cross B	162	70	309	541
F_2, Bond × Rainbow	274	159	116	549
F_2, Bond × Iogold	191	45	244	480
Total	1,023	449	1,389	....
Total of R and I	1,472			

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

Table 4. Breeding Behavior of F_3 Lines from Random Selections of F_2 Plants (A) and from F_2 Plants that were Resistant to Crown Rust (B)

Parent rows and F_3 lines	F_2 reaction	F_3 breeding class*					
		R	R and R- or R-	RS	SR	S	Total
Bond		38	......	......	......	......	38
Double Cross A		......	......	......	......	15	15
Bond × Double Cross A, F_3	A, R	4	......	20	19	......	43
Bond × Double Cross A, F_3	A, I	......	......	7	9	2	18
Bond × Double Cross A, F_3	A, S	......	2	7	9	43	61
Bond × Double Cross A, F_3	B, R	7	......	29	34	4	74
Double Cross B		......	......	......	......	9	9
Bond × Double Cross B, F_3	A, R	5	......	7	15	1	28
Bond × Double Cross B, F_3	A, I	......	......	3	7	1	11
Bond × Double Cross B, F_3	A, S	......	......	......	5	39	44
Bond × Double Cross B, F_3	B, R	3	......	13	31	4	51
Anthony		......	......	......	......	7	7
Bond × Anthony, F_3	A, R	4	1	28	14	1	48
Bond × Anthony, F_3	A, I	2	......	2	2	2	8
Bond × Anthony, F_3	A, S	......	1	1	2	49	53
Bond × Anthony, F_3	B, R	7	......	7	5	1	20
Iogold		......	......	......	......	9	9
Bond × Iogold, F_3	A, R	3	......	13	20	......	36
Bond × Iogold, F_3	A, I	1	......	2	4	1	8
Bond × Iogold, F_3	A, S	......	......	......	2	33	35
Bond × Iogold, F_3	B, R	7	......	18	12	3	40

* R, containing only resistant plants; R-, somewhat less resistant than R; RS, segregating with more resistant than susceptible plants; SR, segregating with as many (or more) susceptible as resistant plants; S, containing only susceptible plants.

The epidemic of crown rust in 1935 was satisfactory, 50 plant progenies being grown for each F_3 line and frequent plots of the parents also being included to test the accuracy of reaction of homozygous material. All plots of the susceptible parents proved susceptible, as may be noted from the table, while Bond in each of 38 plots distributed throughout the nursery was highly resistant.

The F_3 lines and plots of the parents were classified for crown rust reaction into the following groups:

R, containing only resistant plants
RS, segregating with more resistant than susceptible plants
SR, segregating with as many or more susceptible than resistant plants
S, containing only susceptible plants

F_3 lines classified as RS or SR were made by careful inspection of each plot, two investigators working together to obtain a combined judgment of the type of segregation.

From the results given in table 4, it may be concluded that all crosses behaved in a similar manner in F_3. The results of breeding behavior may be summarized for the various crosses by comparing the breeding behavior in F_3 with the F_2 classification.

Table 5. Comparison of F_2 Classification with F_3 Breeding Behavior

Cross	F_2 classification	F_3 breeding behavior* R	Seg	S	Total
Bond × Double Cross A	R	4	39	......	
Bond × Double Cross B	R	5	22	1	
Bond × Anthony	R	4	43	1	
Bond × Iogold	R	3	33	......	
	Total	16	137	2	155
Bond × Double Cross A	I	......	16	2	
Bond × Double Cross B	I	......	10	1	
Bond × Anthony	I	2	4	2	
Bond × Iogold	I	1	6	1	
	Total	3	36	6	45
Bond × Double Cross A	S	......	18	43	
Bond × Double Cross B	S	......	5	39	
Bond × Anthony	S	......	4	49	
Bond × Iogold	S	......	2	33	
	Total	......	29	164	193

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

On the basis of the F_3 trials, as given in table 5, there is little difference in breeding behavior of the plants classified as I, or intermediate in rust reaction, and those classified as R, although a somewhat larger percentage of plants classified as I bred true for susceptibility than for those classified as R. As the number of F_2 plants classified in the I group is relatively small, it seemed desirable to place the R and I plants together. The actual ratios in F_2 were corrected for each cross, based on F_3 breeding behavior. For example, in Bond × Double Cross A and the reciprocal, 43 R and 18 I plants in F_2 were subjected to progeny tests in F_3. Of these, 59 showed resistance in F_3 and 2 proved susceptible, giving the percentage of those showing resistance as 96.7 and the percentage as breeding true for susceptiblity as 3.3. There was a total of 491 R and I plants in F_2, which, when classified as above, leads to the proportion of 475 R : 16 S. Plants classified as susceptible in F_2 from this same cross were tested in F_3 and gave a ratio of 18 showing resistance to 43 that bred true for susceptibility. There were 587 F_2 plants classified as susceptible from this cross. Correcting this on the basis of 29.5 per cent resistant and 70.5 per cent breeding true for susceptibility gives the ratio of 173:414. This when added to 475:16 gives the corrected F_2 ratio based on F_3 breeding behavior of 648:430.

Correcting the three other crosses in a similar manner gives the following ratios:

Cross	Resistant to Susceptible	Probability of Agreement with a 9:7 Ratio
Bond × Double Cross A	648 : 430	P between .01 and .02
Bond × Double Cross B	254 : 287	P <.01
Bond × Anthony	180 : 133	P between .50 and .70
Bond × Iogold	245 : 235	P between .02 and .05
Total	1327 : 1085	

While three of the crosses deviated rather widely from a 9:7 ratio, when tested by X^2 and P, the total of resistant to susceptible is 1327:1085. The X^2 test gives a P value between .20 and .30.

Where sufficient seed was available, F_3 progenies of F_2 plants were tested also for their reaction to crown rust under greenhouse conditions, by growing approximately 25 seedlings of each F_2 plant and inoculating with the same collection of crown rust used in the field trials.

The following illustrates the type of notes taken in these studies and shows the method of classification.

1934 Plant	Infection types				Total plants	Classified as
	0	1 and 2	x	3 and 4		
Bond	24				24	R
Double Cross A				23	23	S
Hybrids						
716-1				22	22	S
716-2		8	1	11	20	H
717-1	16				16	R
718-1	4	2		14	20	SR
718-2	16			3	19	RS
739-2	12	1	1	10	24	H

Seedlings classified in 0, 1, and 2 reaction classes were considered resistant. Those in classes x and in 3 and 4 were considered susceptible.

Where the ratio of resistant to susceptible approached 3:1 and did not fall below 2:1, the line was classified as RS. When the ratio of susceptible to resistant did not fall below 2:1 the segregating line was classified as SR. Other segregating lines, where the number of resistant and susceptible plants was approximately the same, and including all where the ratio of resistant to susceptible varied from 1.9:1 to 1:1.9, were classified as H.

It is of interest to compare the F_3 seedling and F_3 field breeding behavior for crown-rust reaction. This may be accomplished by arranging the material in correlation tables. The first group given in table 6 consists of F_2 plants that were selected because they were of desirable agronomic habit and were classified as resistant to both crown and stem rusts. Table 7 is a summary of the same crosses and represents F_3 progenies from F_2 plants selected at random.

The data given show in general a good agreement between greenhouse and field reaction. The number of seedling plants that could be grown was not sufficient to be sure of the accuracy of the classification, while under field conditions no attempt was made to differentiate between progenies that were classified as H and SR in the greenhouse. Data on crown-rust reaction in the field must be taken in a comparatively short time, which greatly limits the amount of detailed information that can be obtained.

Table 6. Comparison of Seedling and Field Reaction to Crown Rust of F_3 Lines from 4 Crosses Where the F_2 Parent Plants were Selected Because They Were Classified as Resistant to Both Stem and Crown Rusts

Bond × Iogold

Greenhouse Reaction†	Field Reaction* R	RS	SR	S	Total
R	3	2			5
RS	1	2	2	1	6
H	3	10	5	1	19
SR		4	10	1	15
S					0
Total	7	18	17	3	45

Bond × Anthony

Greenhouse Reaction	Field Reaction R	RS	SR	S	Total
R	5		1		6
RS		3	1	1	5
H	2	1	2	1	6
SR		1	1		2
S			1	3	4
Total	7	5	6	5	23

Bond × Double Cross A

Greenhouse Reaction	Field Reaction R	RS	SR	S	Total
R	6	1			7
RS		7	7		14
H		13	17	2	32
SR		1	8	1	10
S			1	5	6
Total	6	22	33	8	69

Bond × Double Cross B

Greenhouse Reaction	Field Reaction R	RS	SR	S	Total
R	5	1	1		7
RS		4	1		5
H		5	16	2	23
SR		6	19	2	27
S				1	1
Total	5	16	37	5	63

* R, containing only resistant plants; RS, segregating with more resistant than susceptible plants; SR, segregating with as many (or more) susceptible as resistant plants; S, containing only susceptible plants.

† S and R, as for field reaction; RS, with ratio of R:S approaching 3:1 and not less than 2:1; SR, with ratio of S:R not below 2:1; H, ratio of R:S falling within 1.9:1 to 1:1.9.

From the 4 crosses summarized in table 6, 200 F_2 plants were selected that were resistant to stem and crown rust. Of this number, only 9 bred true for susceptibility showing the accuracy of the F_2 selection. Of the remaining 191 lines the following results were obtained for breeding behavior in the seedling stage.

Breeding true to resistance	25 lines
Segregating approximately 3 R : 1 S	30 lines
Segregating approximately 1 R : 1 S	80 lines
Segregating approximately 1 R : 3 S	56 lines

The results given in tables 6 and 7 show that it is difficult to differentiate the two types of segregation under field conditions by the manner of reaction in the greenhouse, and accordingly it seems unwise to attempt an explanation of the causes of the different types of segregations under greenhouse conditions. While the x type of reaction was considered as susceptible in making this summary, it is possible that a considerable number of these types of seedling reaction might prove resistant in the field.

Table 7. Comparison of Seedling and Field Reaction to Crown Rust of F_3 Lines from 4 Crosses Where the F_2 Parent Plants were Collected at Random

Bond × Iogold

Greenhouse Reaction†	Field Reaction*: R	RS	SR	S	Total
R	3				3
RS		7	7	1	15
H		2	8		10
SR		2	7	1	10
S				26	26
Total	3	11	22	28	64

Bond × Anthony

Greenhouse Reaction	Field Reaction: R	RS	SR	S	Total
R	3	1			4
RS		7	5		12
H		9	7	1	17
SR			1	1	2
S				28	28
Total	3	17	13	30	63

Bond × Double Cross A

Greenhouse Reaction	Field Reaction: R	RS	SR	S	Total
R	3				3
RS		9			9
H		7	7	1	15
SR		4	14	1	19
S				29	29
Total	3	20	21	31	75

Bond × Double Cross B

Greenhouse Reaction	Field Reaction: R	RS	SR	S	Total
R	3				3
RS	1	6	5		12
H		3	11		14
SR			4	2	6
S				26	26
Total	4	9	20	28	61

* R, containing only resistant plants; RS, segregating with more resistant than susceptible plants; SR, segregating with as many (or more) susceptible as resistant plants; S, containing only susceptible plants.

† S and R, as for field reaction; RS, with ratio of R:S approaching 3:1 and not less than 2:1; SR, with ratio of S:R not below 2:1; H, ratio of R:S falling within 1.9:1 to 1:1.9.

From the random selections under field conditions the following summary is obtained, which includes some F_3 progenies where seed was insufficient for the greenhouse trial.

Cross	F_3 Breeding Behavior, Field: R	RS	SR	S
Bond × Iogold, F_3	4	15	26	34
Bond × Anthony, F_3	8*	31	18	52
Bond × Double Cross A, F_3	6*	34	37	45
Bond × Double Cross B, F_3	5	10	27	41
Total	23	90	108	172

* Two progenies in each of these groups were less resistant than Bond.

Comparing this to the ratio of 1 R : 8 Seg.: 7 Sus., by combining the RS and SR types of segregation, and X^2 for goodness of fit gives a P value of between .90 and .95.

Adding the results of the four crosses and combining the R, RS, and SR progenies in one group gives a ratio of 221 showing resistance to 172 breeding true for susceptibility. Comparing this with 9:7 by X^2 for goodness of fit gives a P value greater than .99.

It may be concluded that the results of these four crosses may be explained on the basis of complementary factors for rust reaction, both present in a homozygous dominant condition in Bond and carried in a recessive condition in the double crosses, Iogold, and Anthony. It seems probable that Rainbow may carry one of these factors in a homozygous dominant condition and the other in a recessive condition. Further studies would be necessary with a single strain of rust to explain minor causes of variability in crown-rust reaction.

Stem-rust Reaction

Stem-rust reaction was studied also, using the plants that were classified for their reaction to crown rust. The plants were placed in two classes, resistant and susceptible. The results are given in table 8.

Table 8. Inheritance of Reaction to Stem Rust in Parents and F_2 Generations of Crosses Between Bond and Several Other Varieties of Oats

Variety or cross	Classification groups*		Corrected		Total
	R	S	R	S	
Bond	....	117	....	....	....
Double Cross A	60	....	....	....	....
Bond × Double Cross A, F_2 and recip.	773	305	809	269	1,078
Double Cross B	10	....	....	....	....
Bond × Double Cross B	401	140	....	....	541
Anthony	5	....	....	....	....
Bond × Anthony and recip.	206	107	249	64	313
Iogold	46	....	....	....	....
Bond × Iogold	329	151	340	140	480
Bond × Rainbow	442	107	....	....	549

* R, resistant; S, susceptible.

Seedling F_3 progenies were grown in the greenhouse in much the same manner as for crown rust and inoculated with stem-rust race 1. The progenies were classified into three groups: (1) breeding true for resistance, (2) segregating, and (3) breeding true for susceptibility. This made it possible to study the accuracy of the field classification. The results of these studies are given in table 9.

From a total of 198 plants classified as resistant under field conditions, 67 bred true for resistance, 1 bred true for susceptibility, and 130 segregated, giving both resistant and susceptible plants.

The classification for susceptibility in F_2 was relatively accurate for three of the crosses, but much less accurate for the cross of Bond × Anthony, where, out of 17 plants classed as susceptible, 7 gave progenies that showed segregation and 1 bred true for resistance. After correction based on the accuracy of classification as shown by the greenhouse trials,

Table 9. Breeding Behavior in F_3, on the Basis of Seedling Reaction, Compared with F_2 Classification

Cross	Reaction of F_2 plants	F_3 seedling reaction*			
		R	Seg	S	Total
Bond × Double Cross A	R	23	35	......	58
	S	......	2	15	17
Bond × Double Cross B	R	18	30	......	48
	S	......	......	13	13
Bond × Anthony	R	11	32	1	44
	S	1	7	9	17
Bond × Iogold	R	15	33	......	48
	S	......	1	13	14

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

the corrected ratio for resistant and susceptible is given in table 8. The combined ratio, exclusive of the Bond × Rainbow cross, was 1799 R : 613 S which closely approximates 3:1. The segregation in the Bond × Rainbow cross obtained in F_2 was 442:107 which indicates a single factor pair is probably responsible in this cross for differentiating resistance and susceptibility to stem rust, although the agreement with a 3:1 segregation is not very close. These results are similar to those obtained by previous investigators.

Smut Reaction

Seed of F_2 plants selected at random and from plants of the parents was inoculated with smut as outlined under experimental methods. There was no consistent difference in the row inoculated with a single smut race from that inoculated with a mixture of races. The data from the two treatments are summarized together for each F_3 line and parental row. As there were only a few parental plots included with the random F_3 lines, the smut reaction of parental plots distributed throughout the breeding nursery is summarized in the lower part of table 10 in addition to the smut reaction of parental plots grown with the random F_3 lines.

The 35 plots of Bond and the 16 plots of Double Cross A showed no smut infection. Double Cross B gave 6 plots with no infection and 2 with slight infection. The 6 plots of Anthony ranged in infection from the 7 to 9 plants class to the 19 to 21 class. Iogold showed lower infection than Anthony, on the average.

In the crosses between Bond and Double Cross A there were 112 F_3 progenies grown, 11 of these showing some infection.

In addition to the F_3 lines selected at random, other F_3 lines were grown that were progenies of F_2 plants resistant to stem and crown rust and of desirable type. The F_4 progenies of both groups may be used to determine the accuracy of classification in F_3. Sixty-four F_3 lines were studied that showed no smut infection. Their F_4 progenies were each grown from the seed of a plant selected in F_3. Of these, 45 were free from smut in F_4 and 19 gave some plants infected. One of these 19 gave a F_4 progeny with 15 plants infected that was as susceptible as the Anthony or Iogold varieties. From 19 lines with 1 or 2 infected plants in F_3, 9 gave F_4 progenies without infection and 10 showed some infection in F_4. One F_3 line with 8 plants infected was tested in F_4 by growing 4 separate progenies. The numbers of plants infected in these 4 F_4 lines were 4, 5, 6, and 11, respectively.

The Double Cross B parent gave 2 plots out of 8 that showed some infection in 1935. In 1936, 11 plots were grown of both Bond and Double Cross B. Ten plots of each gave no infection and 1 plot of Bond showed 1 infected plant while 1 plot of Double Cross B gave 9 infected plants. It does not seem wise to discuss the cross Bond × Double Cross B, as the Double Cross B parent is somewhat variable in its smut reaction.

Table 10. Smut Reaction of F_3 Lines in Crosses between Bond with Varieties of *Avena sativa* and in Plots of the Parental Varieties

Variety or cross	Smut reaction classes (Number of smutted plants)								
	0	1-3	4-6	7-9	10-12	13-15	16-18	19-21	Total
	Number of lines or plots								
Bond	8	......	......	......	......	......	......	......	8
Double Cross A	3	......	......	......	......	......	......	......	3
Bond × Double Cross A, F_3	101	9	1	1	......	......	......	......	112
Double Cross B	2	......	......	......	......	......	......	......	2
Bond × Double Cross B, F_3	69	8	4	1	1	......	......	......	83
Anthony	......	......	......	1	......	......	......	2	3
Bond × Anthony, F_3	53	35	13	3	3	1	1	......	109
Iogold	......	......	1	......	......	......	1	......	2
Bond × Iogold, F_3	33	24	6	7	3	2	1	3	79
Bond	27	......	......	......	......	......	......	......	27
Double Cross A	13	......	......	......	......	......	......	......	13
Double Cross B	4	1	1	......	......	......	......	......	6
Anthony	......	......	......	......	......	1	1	1	3
Iogold	1	2	1	......	4	......	......	......	8

These results from the cross of Bond with Double Cross A are similar to those of Stanton, Reed, and Coffman (1934) who obtained susceptibility in F_3 from crosses of Markton × Black Mesdag where both parental varieties were free from smut. They used the explanation of complementary factors for smut susceptibility. Smut resistance appears dominant to susceptibility, as a rule, and it is apparent that the factor or factors responsible for resistance are different in Bond and the Double Cross A. A very few lines in F_4 from the crosses were highly susceptible, which would be difficult to explain on the basis of minor modifying factors that condition smut reaction in these crosses. In a previous study, where Black Mesdag was used as a resistant parent (Hayes and others, 1928), it was concluded that at least two factors were responsible for resistance. The double-cross parent in these studies very probably has the same factors for smut resistance as the Black Mesdag parent.

In the random F_3 lines of Bond × Anthony, 54 gave no infection and 55 showed some infection, a part of these being as severely injured as the Anthony and Iogold parents.

Thirteen out of 27 lines that showed no infection in F_3 were free from smut in F_4 and 14 lines that gave 0 infection in F_3 contained some susceptible plants in F_4. From 20 F_3 lines that showed intermediate infection, 1 to 6 plants, all but 2 gave F_3 progenies that showed some infection. Two F_3 lines with 13 plants infected in each line bred true in F_4 to susceptibility with 15 and 11 infected plants, respectively.

If approximately half of the F_3 lines with no infection were heterozygous, as the results indicate, approximately 27 F_3 lines out of 109 from the Bond × Anthony cross bred true for resistance to smut. These results can be explained on the basis of a single factor in Bond for resistance to smut.

In the Bond × Iogold cross, 33 F_3 lines out of 79 selected at random showed no infection in F_3. From 27 F_4 lines grown from these random selections, and from the breeding plots that showed no infection in F_3, only 8 were free from infection in F_4, although 11 others gave only 1 or 2 plants infected. From 23 F_3 lines of intermediate infection in F_3, 1 to 4 plants infected, 20 lines showed some infection in F_4, although there were several lines with very low infection both in F_3 and F_4. There were 16 out of 57 lines in F_3 with more than 7 plants infected. Eight of these lines tested in F_4 gave smut infection, although 4 of these gave some progenies with low infection. The results of the Bond × Iogold cross can be explained on the basis of a single dominant factor for resistance in Bond. A greater variability in infection was obtained in this cross than for the cross of Bond × Anthony. With Bond × Iogold there is some evidence of minor modifying factors or of greater environmental effects on smut infection.

Spikelet Disarticulation

The mode of separation of the lower floret of the spikelet from the axis of the spikelet, or spikelet disarticulation, is one of the major characters used in differentiating varieties of *A. sativa* from *A. byzantina*. The mode of inheritance is, therefore, of considerable interest. It is probable also that there is some economic importance in the method designated as disarticulation over that described as abscission, the latter being characteristic of cultivated varieties of *A. byzantina*. In the hybrids there was a noticeable correlation between the manner of spikelet disarticulation and shattering of the grain, the *A. sativa* type being noticeably more resistant to shattering than the *byzantina* type of base.

The individual plants of the parents and of the F_2 generations of five separate crosses are classified in table 11 on the basis of spikelet disarticulation, placing the material in three classes, S, I, and B, characterized by the three types of spikelet disarticulation, disarticulation by fracture, semi-abscission, and abscission, respectively.

The plants in the table designated as S and B appeared similar to the parent varieties of *A. sativa* and *A. byzantina,* respectively Those designated as I have the intermediate type of base which has been previously called disarticulation by semi-abscission. The basal cavity is somewhat smaller than in plants of the Bond parent and the edges of the base are somewhat roughened, showing a partial fracture instead of a break by abscission.

Table 11. Inheritance of Type of Spikelet Disarticulation in F_2 of Crosses of Bond with Other Varieties of Oats of the Avena sativa Group

Variety or cross	Spikelet disarticulation classes*		
	S	I	B
Bond	....	.....	122
Double Cross A	60	.....	....
Bond × Double Cross A, F_2	802	17	259
Double Cross B	10	.....	....
Bond × Double Cross B, F_2	395	16	130
Anthony	5	.....	....
Bond × Anthony, F_2	230	48	35
Iogold	46	.....	....
Bond × Iogold, F_2	352	9	119
Bond × Rainbow, F_2	373	20	156

* S, *sativa* type; B, *byzantina* type; I, intermediate.

The plants of intermediate type of floret disarticulation were added to those of the typical B group. The ratio of plants with an abscission type of spikelet disarticulation to those with a more or less well-developed basal cavity approached 3:1 in F_2. Testing the five crosses in table 11 by means of X^2 for goodness of fit to a 3:1 ratio gives satisfactory agreement in all crosses except Bond × Rainbow which gave a calculated P value less than .01. P values in the other crosses lay between .50 and .70 in two crosses, between .30 and .50 in one cross, and between .20 and .30 in the other cross.

As the four crosses, Bond × Double Cross A, Bond × Double Cross B, Bond × Anthony, and Bond × Iogold gave similar types of segregation, their breeding behavior may be discussed together.

Thirteen lines from F_2 plants classified as B were grown in F_3, approximately 30 plants being available from each line. These 13 lines were distributed as follows:

6 Bond × Double Cross A	3 Bond × Anthony
3 Bond × Double Cross B	1 Bond × Iogold

Of these 13 lines, 6 bred true in F_3 and 4 gave mostly B plants, the segregations being 28 B:1 I:1 S, 22 B:1 I:3 S, 29 B:1 S, and 28 B:1 I:1 S. Three gave ratios as follows: 5 B:23 I:2 S, 18 B:7 I:4 S and 13 B:17 S. It is apparent that while B is a simple recessive to S, there is considerable deviation from expectation in F_3. While an occasional mistake might be made in handling large quantities of material, care was taken in these studies to prevent such mistakes. Seed of individual F_2 plants was threshed by hand in order to guard against possible mixtures. The only explanation that appears at all tenable is that there is some genetic cause for these deviations from expectation. It is recognized, however, that plants classified as I showed rather wide variations, sometimes approaching the S group and in other cases the B group.

Of the plants classified as S in F_2, 35 lines were grown and examined in F_3. Of this number, 11 bred true to the S habit, 13 gave normal segregation, and 11 showed rather wide deviations from normal segregation, the classifications being as follows: 2 lines with 18 S:12 B; 1 line each as follows: 2 S:23 I:5 B, 11 S:2 I:9 B, 15 S:15 B, 28 S:3 I, 21 S:8 I, 19 S:11 B, 11 S:10 I:9 B, 10 S:11 I:9 B, 9 S:15 I:5 B.

Only five plants with intermediate types of base in F_2 were studied by examination of progenies in F_3. All five behaved as if they should have been classified as S in F_2, three of the five giving only S and B plants in a ratio of 3:1, one segregating into 22 S:1 I:7 B and the other giving a segregation of 9 S:14 I:7 B.

Further discussion of the breeding behavior of type of base will be given after presenting data on basal hairs.

Manner of Floret Disjunction

The classification of parent plants and F_2 crosses is given in table 12. Disjunction by basifracture was typical in all plants of Bond, which are placed in the B group. The two double-cross parents were characterized by an intermediate type of floret disjunction, although in this group there was wide variability in the different florets on the same plant, some being

Table 12. Inheritance of Manner of Floret Disjunction in Crosses between Bond and Varieties of *A. sativa*

Variety or cross	Rachis adherence groups*		
	S	I	B
Bond	....	....	122
Double Cross A	....	51	9
Bond × Double Cross A, F_2	4	341	733
Double Cross B	....	10	....
Bond × Double Cross B, F_2	4	143	394
Anthony	5	....	....
Bond × Anthony, F_2	33	121	159
Iogold	46	....	....
Bond × Iogold, F_2	55	270	155
Bond × Rainbow, F_2	112	295	142

* S, *sativa* type; B, *byzantina* type; I, intermediate.

characterized by basifracture, others by disarticulation at the apex of the rachilla segments, the segment remaining attached to the lower floret, and still others showing an intermediate type, the rachilla breaking transversely in the middle portion, called heterofracture.

It is apparent that the double crosses have an intermediate type of floret disjunction, and there is some doubt as to the correctness of the classification for the eight plants classified in group S. It is probable that only a single factor pair differentiates the intermediate break of the double-cross parents from the type of the Bond parent.

The studies of floret disjunction in F_3 were made in those families grown to test the breeding behavior of the type of spikelet disarticulation as it was apparent that it was very difficult to classify the type of floret disjunction. Twenty-two F_3 progenies of Bond × Double Cross A were studied for type of floret disjunction in F_3. Of this number, 16 were classified as of B type of floret disjunction in F_2. Four of the 16 bred true to the B type, 3 were classified in F_3 as breeding true to the I type, and the remainder gave plants in both groups. Of the F_2 plants classified as having the I type of floret disjunction in F_2, all gave segregation in F_3, 2 of the 4 progenies being classified as segregating for the S and I groups.

Entirely comparable results were obtained for the other Bond × Double Cross, where 10 progenies were tested in F_3. Of these, 6 were classified as B in F_2, 1 of the 6 breeding true for the B habit of floret disjunction in F_3, and the other 5 giving both B and I types of plants in F_3. Of the 4 I plants tested in F_3 all showed segregation.

In the Bond × Anthony cross, the F_3 progenies of 8 F_2 plants classified as B for floret disjunction were studied in F_3. One bred true to the B type of floret disjunction, showing basifracture in all 30 plants, 2 bred true for the I type, and the other 5 gave F_3 progenies with some plants in all 3 groups, S, I, and B. One of the 3 plants tested in F_3 that was classified as I in F_2 bred true to this habit of floret disjunction, the other 2 gave F_3 progenies segregating for S and I.

In the Bond × Iogold cross, one plant classed as B gave an F_3 progeny containing both B and I plants, one classified as S gave an F_3 progeny containing both S and I plants. Of the 7 classified as I, one bred true to the I habit of floret disjunction in F_3, 3 gave S and I plants in F_3, and 3 gave I and B plants.

From these results it is apparent that floret disjunction is dependent upon more than a single factor pair for its differentiation. The classification is difficult, the expression of the character being easily influenced by environmental conditions. The double-cross parents may very probably contain one of the genetic factors that is responsible for the Bond type of floret disjunction. In the other 2 crosses it is probable that at least 2 factor pairs are involved.

Basal Hairs

Individual plants of the F_2 crosses and of the parents were studied for the development of hairs on the base of the lower floret. The Bond parent has a heavy production of basal bristles, with 30 or more hairs on the base. Some plants of Bond, however, showed florets with scarcely any hairs, but no plants of Bond, so far as examined, were found that did not have over 30 hairs on the base of some florets.

Only one of the plants of the Double Cross A parent was recorded as having hairs on the base, this plant varying from 0-8 hairs, the remaining plants having no hairs on the base of the lower floret. One of the plants of the Double Cross B parent was recorded as having from 15 to B hairs, the other 9 plants studied being divided into two groups, 0-10 and 0-20 hairs. The 5 plants of Anthony studied gave from 5 to 15 hairs per base. The Iogold parent gave 1 plant with a reading of 0-15 hairs, several with no hairs, and the larger number with 0-5 hairs.

For the purposes of classification, the data on the F_2 plants were placed in four groups, 0-10, 0-25, 0-B, and B. The data for the parents and F_2 progenies are given in table 13.

Table 13. Inheritance of Basal Hairs in Parent Lines and in F_2 Crosses Between Them

Parent or cross	Basal hairs classes*			
	0-10	0-25	0-B	B
Bond	....	....	26	96
Double Cross A	60	....	....	....
Bond × Double Cross A, F_2	796	48	90	144
Double Cross B	4	5	1	....
Bond × Double Cross B, F_2	280	118	46	97
Anthony	....	5	....	....
Bond × Anthony, F_2	176	61	8	68
Iogold	45	1	....	....
Bond × Iogold, F_2	259	93	24	104
Bond × Rainbow, F_2	213	171	9	156

* Number of hairs with B similar to the Bond variety.

In these studies no attempt has been made to study minor differences. All F_2 crosses gave some plants in each of the four groups. The plants in groups 0-B and B were combined to represent the *byzantina* type of basal hairs, the other two groups being combined also. These then represent character differences that may be used to help differentiate *sativa* from *byzantina* plants. The data are summarized for the separate crosses and P values calculated by X^2 for goodness of fit to a 3:1 ratio.

Two of the six crosses have rather wide deviations from a 3:1 ratio. The total of all crosses agrees very well with a 3:1 ratio, giving a P value between .50 and .70.

Cross	Segregation Ratio	P Value
Double Cross A × Bond	844 : 234	Between .01 and .02
Double Cross B × Bond	398 : 143	Between .30 and .50
Anthony × Bond	233 : 76	Between .80 and .90
Iogold × Bond	352 : 128	Between .30 and .50
Rainbow × Bond	384 : 165	Less than .01
Total	2211 : 746	Between .50 and .70

These results show two crosses where the deviation from a 3:1 ratio was greater than could have been expected on the basis of random variation. Taking all of the results together, there is close approximation to a 3:1 ratio with the presence of a large number of basal hairs of the Bond parental type recessive to the development of basal hairs in the various types found in the *sativa* parents.

Fifty-three progenies were studied in F_3 to determine the breeding behavior of F_2 plants. Of this number, 40 families were the progeny of F_2 plants in one or the other of the two classes 0-10 or 0-25. Of this number, 11 bred true for the few hairs of the *sativa* type. Several of the F_3 lines from Bond × Double Cross A bred true for 0 hairs, others from this cross bred true for from 0-10 basal hairs. Twenty-nine lines segregated in F_3 with the larger proportion of plants in the two groups for low hair production, about one third of the plants being of the Bond parental type.

One plant in F_2 from the Bond × Iogold cross was classified as producing 15-30 basal hairs. Its F_3 progeny consisted of 4 plants with 0-10 hairs, 6 plants with 0-15 hairs, 3 plants with 0-B hairs, and 17 plants with the B type of basal hairs, this being an unusual type of segregation.

Seven plants that in F_2 were classed as 0-B or B for basal hairs bred true for the B type of basal hair production. The progenies of six other F_2 plants of the B group segregated in a peculiar manner in F_3. One line was classified as having 29 plants with B hairs and 2 with 0-10 hairs. Another that in F_2 was noted as having B short hairs gave an F_3 progeny consisting of 29 plants with B hairs and 1 with 0-10 hairs. Two lines that were classified in F_2 as of the 0-B or B types of basal hairs gave the normal segregation in F_3 expected from F_2 plants in either of the 2 lower groups for basal hair production. Another plant classified in F_2 as having 5-B basal hairs gave an F_3 progeny of 3 plants with 0-10 hairs, 1 plant with 10-25, 8 with 0-B hairs, and 14 with B hairs.

It is apparent from these results that the segregation approximated 3:1 but that there were some exceptions. These exceptions happened rather frequently in plants that deviated also in the type of base. For example, plants with an I base usually had fewer hairs than were found on plants with a type of spikelet disarticulation characterized by the B type of base. Certain families of this type were studied further in F_4 and will be discussed after the data on association have been presented.

Awn Development

Data were taken on awn development by placing the plants in four groups for the presence or absence of awns on the lower floret and designating the strength of the awn on the basis of three classes: strong, intermediate, and weak. The results are given in table 14.

From the results given in the table it appears that weak awns are dominant over strong awns in these crosses. This, however, may not be a simple case of dominance, as there appears to be a strong correlation between the *byzantina* type of base, basal hair production, and the development of weak awns. It is apparent also that there are genes for few awns as well as genes for weak awns.

In the cross between Double Cross B and Bond, where both parents produced awns in the 100 group, i.e. approximately 100 per cent of the florets that are awned, all except a very few F_2 plants were placed in this group, with a ratio of approximately 3 plants with weak awns to 1 with

Table 14. Inheritance of Awn Development in F_2 Crosses Between Bond and Varieties of *A. sativa*

Variety or cross	Awn development classes*										
	S100	S75	S50	I100	I75	I50	I25	W100	W75	W50	W25
Bond	......	......	......	......	......	......	......	122	......	......	......
Double Cross A	4	......	......	41	5	......	......	6	4	......	......
Bond × Double Cross A, F_2	13	......	......	184	6	......	......	856	14	5	......
Double Cross B	......	......	......	10	......	......	......	......	......	......	......
Bond × Double Cross B, F_2	10	1	......	114	1	......	......	410	4	1	......
Anthony	......	......	......	......	......	5	......	......	......	......	......
Bond × Anthony, F_2	7	1	1	53	9	2	1	219	13	7	......
Iogold	......	......	......	......	......	......	1	......	1	1	32
Bond × Iogold, F_2	2	......	......	26	5	1	1	387	27	24	7
Bond × Rainbow, F_2	......	......	......	1	2	1	......	159	7	40	75

* S, strong; I, intermediate; W, weak awn. Classes are based on percentage of lower florets with awns.

intermediate and strong. Similar results were obtained in the Bond × Anthony cross. In Bond × Iogold, where the Iogold parent had a large proportion of its plants in the 25 per cent awned group, there were more plants with few awns than in other crosses.

It is recognized that environmental conditions affect awn development to a marked extent and for this reason it is impossible to make an accurate analysis without the accumulation of many more data.

Vigor of Plant and Plumpness of Seed

The parent plants and F_2 crosses were pulled in the field at maturity, wrapped with cheesecloth to prevent loss of seeds and hung in the drying shed until after the notes were taken. The seeds that shattered at the

Table 15. Number of Seeds per Plant of Parents and F_2 Crosses

Variety or cross	Number of seeds per plant					
	0-50	51-100	101-150	151-200	201-250	251 up
Bond	51	68	3	......	......	......
Double Cross A	6	31	9	5	3	5
Bond × Double Cross A, F_2	304	530	121	65	20	24
Double Cross B	1	2	3	1	......	2
Bond × Double Cross B, F_2	80	167	110	107	32	45
Anthony	1	4	......	......	......	......
Bond × Anthony, F_2	97	120	44	27	12	13
Iogold	......	10	8	9	6	13
Bond × Iogold, F_2	69	183	107	52	19	49

time of examination were discarded to help in preventing mixtures. Results given in table 15 show that in the F_2 crosses there was a considerable proportion of F_2 plants that excelled in number of seeds per plant.

Bond was outstanding in plumpness of grain and excelled all other varieties in this respect. Several F_2 crosses produced a considerable percentage of their plants that were as desirable in grain plumpness as the Bond parent. These results are summarized in table 16 and give some reason for the hope that the addition of this character to the type of oats now grown may not be too difficult.

Table 16. Classification of Parents and F_2 Crosses for Plumpness of Grain

Variety or cross	Percentage plumpness of grain			
	0-25	26-50	51-75	76-100
Bond	1	6	54	61
Double Cross A	5	28	26	......
Bond × Double Cross A, F_2	48	102	534	381
Double Cross B	1	2	6	......
Bond × Double Cross B, F_2	27	46	283	185
Anthony	......	......	4	1
Bond × Anthony, F_2	13	20	125	155
Iogold	1	7	31	7
Bond × Iogold, F_2	45	69	268	97

STUDIES OF ASSOCIATION BETWEEN CHARACTERS

The data were taken in a correlated manner in order to study association between characters. Data on F_2 plants were used in most cases, although smut reaction was determined by studying the F_3 progeny of F_2 plants selected at random. X^2 for independence was used to determine the extent of association, if any. Table 17 summarizes studies of association by means of X^2 for independence.

There was a definite association between reaction to stem rust and crown rust in crosses between Double Cross A with Bond, a larger proportion of the plants resistant to crown rust being susceptible to stem rust and vice versa than would be expected on the basis of random sampling. No evidence of such association was present in other crosses, and as all crosses except Bond × Rainbow gave similar types of segregation no reason can be given for linkage of the factors involved in stem- and crown-rust reaction in one cross with an absence of such linkage in another. This does not seem at all likely as Double Cross A presumably carries the same genetic factors for reaction to stem rust as Double Cross B and Anthony.

Crown rust showed some tendency for association with per cent plumpness of grain in two crosses, but these cases are rendered somewhat doubtful as the P values in three other crosses lay between .70 and .90. Two of the six hybrid populations showed a distinct association between stem-rust reaction and per cent plumpness of grain. This relationship would be expected if rust infection came sufficiently early so that it interfered with normal processes of metabolism in the plant.

Data were not taken in all cases for extent of shattering of the grain. The plants were pulled as they approached maturity, the plants from a culture being tied together and the panicles wrapped with cheesecloth. The bundles were hung in the field house until they were examined in the winter. Extent of shattering was determined on the basis of spikelets that had lost their grain. There was a high association between the manner of spikelet disarticulation and shattering.

There was no indication of close association between any of the factors responsible for reaction to stem rust or crown rust and smuts and other characters studied. Consequently there would seem to be no reason for any combination of these characters being difficult to attain.

There was strong association between the characters that differentiate *A. byzantina* from *A. sativa,* including spikelet disarticulation, floret disjunction, basal hair development, and awn development. Oats with the *A. byzantina* type of base, basal hairs, and floret disjunction rather uniformly produced a small, weak awn on the lower floret, whereas *A. sativa* types differed in strength of awn as well as the percentage of spikelets with an awn on the lower floret. A few plants of the *A. byzantina* type were classified as having intermediate awns. None of these was grown in F_3 so it is impossible to be sure of their genotype.

The rather close linkages between various characters are summarized here. As all crosses gave similar relationships it does not seem necessary to present each separately. Table 18 summarizes the associations between classes for basal hairs and spikelet disarticulation.

Table 17. A Study of Independence or Association of Characters in the F_2 Generation of Crosses by Means of X^2 and P

Cross	N	P value
Crown rust vs. stem rust		
Bond × Double Cross A	668	<.01
Double Cross A × Bond	410	<.01
Bond × Double Cross B	541	.70-.80
Anthony × Bond	259	.10-.20
Bond × Iogold	480	.95-.98
Bond × Rainbow	549	.50-.70
Crown rust vs. articulation		
Bond × Double Cross A	668	.80-.90
Double Cross A × Bond	410	.90-.95
Bond × Double Cross B	541	.10-.20
Anthony × Bond	259	.70-.80
Bond × Iogold	480	.30-.50
Bond × Rainbow	549	.90-.95
Crown rust vs. awn development		
Bond × Double Cross A	668	<.99
Double Cross A × Bond	410	.50-.70
Bond × Double Cross B	541	.50-.70
Anthony × Bond	259	.70-.80
Bond × Iogold	480	.30-.50
Bond × Rainbow	285	.02-.05
Crown rust vs. per cent plumpness		
Bond × Double Cross A	655	.05-.10
Double Cross A × Bond	410	.70-.80
Bond × Double Cross B	541	.80-.90
Anthony × Bond	159	.70-.80
Bond × Iogold	479	.80-.90
Crown rust vs. smut		
Anthony × Bond	109	.50-.70
Bond × Iogold	79	.70-.80
Crown rust vs. shattering		
Bond × Double Cross A and reciprocal	417	.80-.90
Stem rust vs. articulation		
Bond × Double Cross A	668	.70-.80
Double Cross A × Bond	410	.70-.80
Bond × Double Cross B	541	.05-.10
Anthony × Bond	259	.02-.05
Bond × Iogold	480	.50-.70
Bond × Rainbow	549	.90-.95
Stem rust vs. awn development		
Bond × Double Cross A	668	.30-.50
Double Cross A × Bond	410	.80-.90
Bond × Double Cross B	541	.70-.80
Anthony × Bond	259	.50-.70
Bond × Iogold	480	.30-.50
Bond × Rainbow	285	.95-.98
Stem rust vs. per cent plumpness		
Bond × Double Cross A	655	<.01
Double Cross A × Bond	410	.30-.50
Bond × Double Cross B	541	<.01
Anthony × Bond	259	.50-.70
Bond × Iogold	479	.80-.90
Stem rust vs. smut		
Anthony × Bond	109	.80-.90
Bond × Iogold	79	.05-.10
Stem rust vs. shattering		
Bond × Double Cross A and reciprocal	417	.80-.90
Smut infection vs. plumpness of grain		
Anthony × Bond	109	.50-.70
Bond × Iogold	79	.95-.98
Smut infection vs. spikelet distribution		
Anthony × Bond	109	.02-.05
Bond × Iogold	79	.70-.80
Spikelet disarticulation vs. shattering		
Bond × Double Cross A and reciprocal	417	<.01
Bond × Double Cross B	165	<.01
Anthony × Bond	55	<.01
Bond × Iogold	62	<.01

Table 17—Continued

Basal hairs vs. spikelet disarticulation

Cross	N	P value
Bond × Double Cross A	668	<.01
Double Cross A × Bond	410	<.01
Bond × Double Cross B	541	<.01
Anthony × Bond	259	<.01
Bond × Iogold	480	<.01
Bond × Rainbow	549	<.01

Basal hairs vs. awn development

Cross	N	P value
Bond × Double Cross A	668	<.01
Double Cross A × Bond	410	<.01
Bond × Double Cross B	541	.01-.02
Anthony × Bond	259	<.01
Bond × Iogold	480	<.01
Bond × Rainbow	285	<.01

Basal hairs vs. floret disjunction

Cross	N	P value
Bond × Double Cross A	668	<.01
Double Cross A × Bond	410	<.01
Bond × Double Cross B	541	<.01
Anthony × Bond	259	<.01
Bond × Iogold	480	<.01
Bond × Rainbow	549	<.01

Spikelet disarticulation vs. floret disjunction

Cross	N	P value
Bond × Double Cross A	668	×.01
Double Cross A × Bond	410	<.01
Bond × Double Cross B	541	<.01
Anthony × Bond	259	<.01
Bond × Iogold	480	<.01
Bond × Rainbow	549	<.01

The I class for spikelet disarticulation has a smaller basal cavity than the B type and a somewhat more irregular base with less well defined callus and greater irregularity of disarticulation, i.e. in type of disarticulation it seems definitely intermediate between that which characterized Bond and the cultivated varieties of *sativa.* On the basis of study in F_3 and F_4, it seems probable that the plants classified as having I base and B type of basal hairs should have been classified as of the B type of spikelet disarticulation. Placing I and B types of spikelet disarticulation in one class and 0-10 + 10-25 basal hairs together and the classes 0-B and B together gives a dihybrid ratio of 2118 : 19 : 81 : 727. Calculating the linkage by the product method gives a cross-over value of 2.7 ± 0.3. The wide deviation in the two intermediate classes is correlated with the I group of floret disarticulation that may be due to abnormal chromosome pairing or other abnormality not a result of simple Mendelian inheritance.

Table 18. Linkage between Basal Hairs Classes and Spikelet Disarticulation in the F_2 Plants of Crosses between Bond and Varieties of *A. sativa*

		Basal hairs classes				
		0-10	10-25	0-B	B	
Spikelet disarticulation classes	S	1687	431	14	5	2137
	I	14	33	22	40	109
	B	10	24	141	524	699
		1711	488	177	569	2945

Studies of floret disjunction were more difficult than other characters and both the double-cross parents were intermediate in type of floret disjunction. In F_2 from crosses of Bond with these two double crosses the results were obtained as summarized in table 19.

Table 19. Association between Classes for Basal Hairs and Floret Disjunction in the F_2 of a Cross between Bond and the Two Double-cross Hybrid Varieties of *A. sativa*

		Basal hairs classes				
		0-10	10-25	0-B	B	
Floret disjunction classes	S	6	1	1	0	8
	I	416	46	12	15	489
	B	653	125	123	226	1127
		1075	172	136	241	1624

There is considerable doubt of the correctness of the classification of those F_2 plants designated with the S type of floret disjunction, as both of the double-cross parents appeared to be breeding true for an intermediate type of disjunction and because of the difficulty of classification. For this reason, it seems probable that these eight plants should have been placed in the I group for floret disjunction. There is no doubt that in this case the linkage between the gene for floret disjunction that differentiates I from B and the gene for basal hair development has been broken. Five F_4 families bred true for the B type of floret disjunction and for the *sativa* type of basal hairs. One of these had no basal hairs on any plant except one. Two F_4 lines were obtained that bred true for B type of basal hairs and for an I type of floret disjunction.

Table 20. Association between Classes for Basal Hairs and Floret Disjunction in the F_2 Crosses between Bond with Anthony, Iogold, and Rainbow

		Basal hairs classes				
		0-10	10-25	0-B	B	
Floret disjunction	S	122	62	4	3	191
	I	411	203	21	46	681
	B	103	56	16	279	454
		636	321	41	328	1326

If the few plants classed as S are placed in the I group, and if two classes are made for basal hairs by combining 0-10 and 10-25, and also 0-B and B, an F_2 dihybrid ratio in the repulsion phase of 778 : 469 : 349 : 28 is obtained. This gives a calculated linkage value of 24.0 $\pm$2.3.

The F_2 data from the crosses between Bond with Anthony, Iogold, and Rainbow for basal hair development and type of floret disjunction are combined and given in table 20.

These results present further evidence for a linkage relation between factors that differentiate floret disjunction and basal hair development.

Table 21. Association in F_2 of Spikelet Disarticulation and Floret Disjunction in Crosses between Bond with Double Crosses A and B

		Spikelet disarticulation			
		B	I	S	
Floret disjunction	B	363	22	742	1127
	I	26	10	448	484
	S		1	7	8
		389	33	1197	1619

Because of the difficulty of classification for floret disjunction in crosses between *sativa* oats with an S type of floret disjunction and oats of the *A. byzantina* type, it seems unwise to attempt a study of the association between the genetic factors involved when more than a single factor pair is involved for type of floret disjunction, as in the crosses between Bond with Anthony, Iogold, and Rainbow.

The two most interesting characters and those used more commonly to differentiate *A. byzantina* from *A. sativa* are spikelet disarticulation and floret disjunction. These are summarized in table 21 for crosses between Bond with Double Cross A and Double Cross B.

The *sativa* type of spikelet disarticulation is dominant over the *byzantina* type while the method of floret disjunction characterized by *byzantina*

Table 22. Association between Spikelet Disarticulation and Floret Disjunction in F_2 of Crosses between Bond with Anthony, Iogold, and Rainbow

		Spikelet disarticulation			
		B	I	S	
Floret disjunction	B	193	42	221	456
	I	85	33	568	686
	S	32	2	166	200
		310	77	955	1342

is dominant over the *sativa* type. Combining the few plants in the S class of floret disjunction with the I group and the B and I types of spikelet disarticulation gives a dihybrid ratio of 742 : 455 : 385 : 37. The calculated linkage value from the repulsion phase is 25.7 ± 2.3.

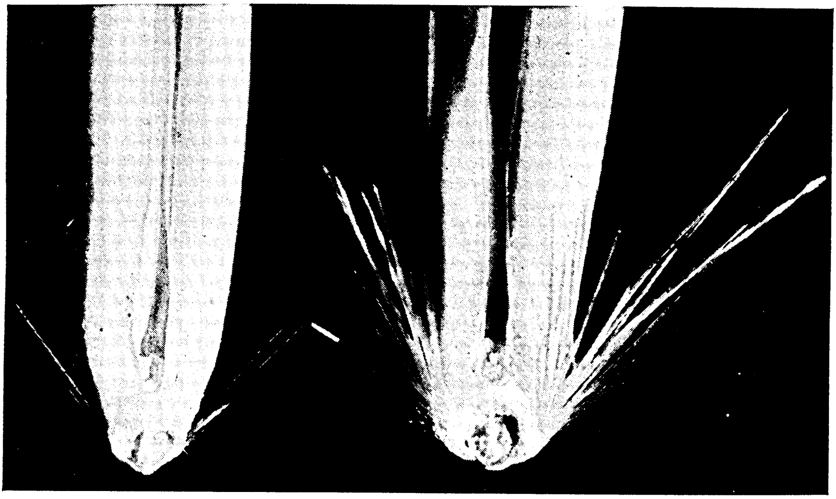

FIG. 3. TYPICAL LOWER FLORETS OF PLANTS OF AN F_4 FAMILY SHOWING THE CHARACTERISTIC TYPE OF BASE OF PLANTS CLASSED AS I AND B, RESPECTIVELY

Data from the crosses of Bond with Anthony, Iogold, and Rainbow are given in table 22.

These results indicate a linkage between one of the factors involved in floret disjunction and the factor pair for spikelet disarticulation.

A number of F_3 and F_4 lines were grown to determine the breeding behavior of the I or intermediate base.

An F_3 line of the cross between Bond with Double Cross A gave several plants that were classified in F_3 as having a B type of base, with hairs on different spikelets ranging from 5 to 20. Several plants were selected and F_4 progenies grown. One such F_4 line contained 14 plants classed as I base with less than 25 hairs, and 9 plants with B base with many hairs. Typical kernels illustrating the differences observed are shown in figure 3.

F_4 line 805 gave 24 plants with I base and from 10 to 30 hairs, 2 with S base, and 7 with B base. F_4 line 806 gave 13 plants with an I base, 11 with a B base, and 2 that were classified as having an S type of base. Characteristic plants of these three groups are shown in figure 4.

F_4 lines 809, 810, and 811 were derived from F_3 plants that were classified as having the B type of base for spikelet disarticulation and the B type of floret disjunction with from 0 to 5 hairs. All bred true for the B type of floret disjunction. Family 809 approached most closely to the B type of spikelet disarticulation. Figure 5 shows that these plants have a somewhat less developed base than the Bond parent and most plants were classified as having the B type of base. This family approaches closer to the B type of base with few basal hairs than any F_3 or F_4 line. A few spikelets in most plants of this F_4 line approached the B type of basal hairs.

F_4 line 811 bred true for an intermediate type of base and few basal hairs. Range of variability for basal development is given in figure 6.

The results presented for the inheritance of floret disjunction indicate that more than a single factor pair is involved. One of these factors that differentiate the B type of floret disjunction from an intermediate or S type appears to be rather closely linked with the factor or factors responsible for the *byzantina* type of spikelet disarticulation and basal hair development.

It seems probable that the factors for basal hairs and for spikelet disarticulation are very closely linked. It is probable that they are of a cumulative nature and that the factor responsible for basal hair development of the Bond type may interact with a factor for spikelet disarticulation to give a more strongly developed base than in the presence of the factor for few hairs.

Some species of *Avena* have a haploid chromosome number of 7 while cultivated varieties of *A. sativa* and of *A. byzantina* are polyploids of the amphidiploid type with three different genoms. In speltoid wheats and fatuoid oats the results have been explained on the basis of abnormal pairing of one pair of chromosomes of set B with a pair in set C. As has been emphasized by several writers, the difficulties of studying inheritance

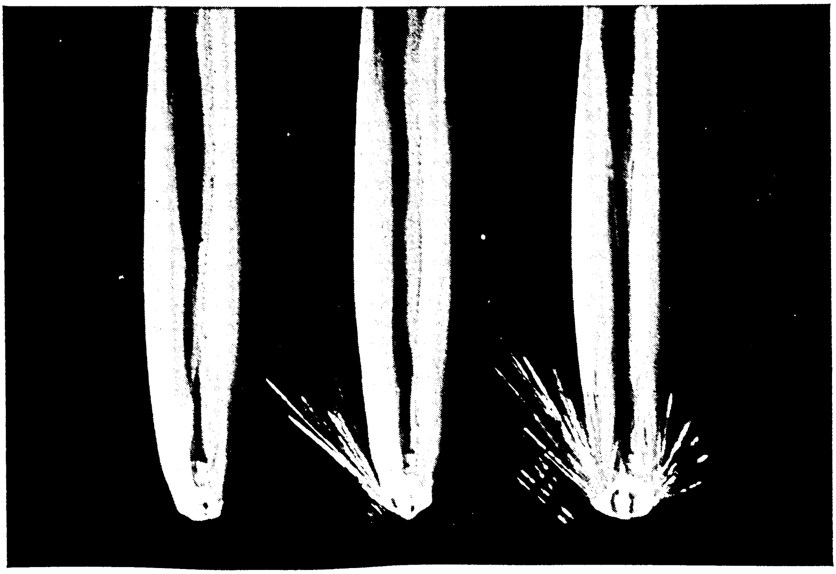

FIG. 4. PLANTS CLASSIFIED AS HAVING S, I, AND B TYPES OF BASE FROM LINE 806

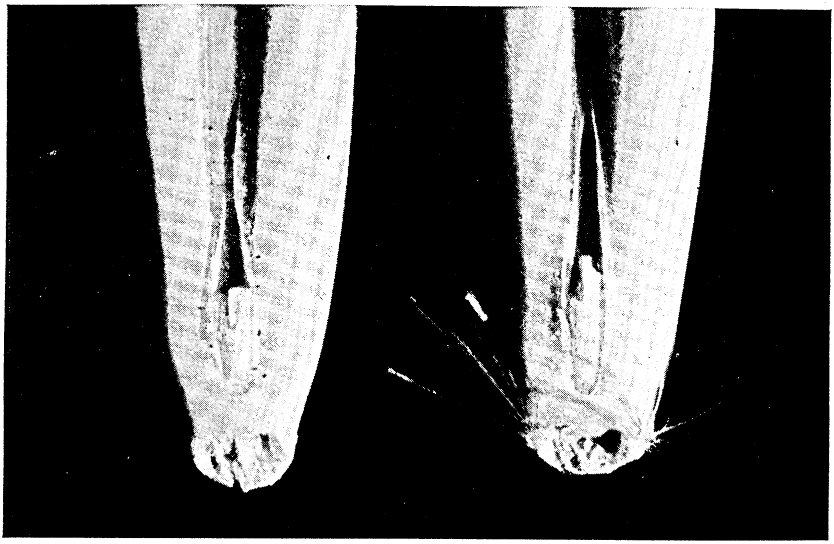

FIG. 5. RANGE OF VARIABILITY IN THE TYPES OF BASE OF F_4 PLANTS FROM LINE 809

These plants approach rather closely to the *byzantina* type with lower development of basal hairs than found in any Bond progeny studied. The basal cavity is somewhat less developed than in Bond.

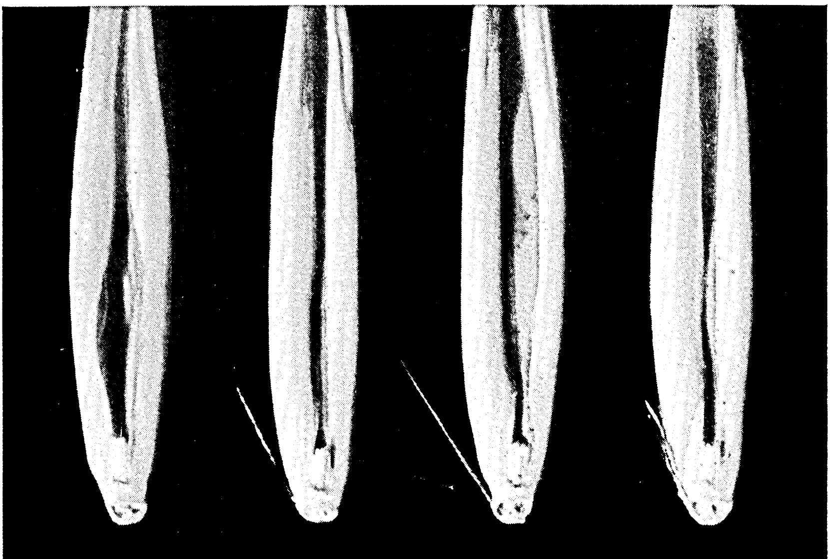

FIG. 6. RANGE OF VARIABILITY IN TYPES OF BASE IN F_4 FAMILY 811

Classified as breeding true for an intermediate type of base with few basal hairs.

in polyploids of the amphidiploid type are due, presumably, to two main causes: (1) the presence of duplicate or polymeric factors, (2) abnormalities in pairing owing to occasional pairing of some members of one set with those of another. It seems probable that for type of abscission of the lower floret, and for basal hairs, only a single major factor pair was responsible in the case of each pair of contrasting characters. Abnormalities in segregation in later generations may be due to a change in pairing in the hybrids where the chromosomes carrying these factors occasionally pair with members of a different chromosome set.

SUMMARY

1. The material consisted of crosses between Bond, *Avena byzantina,* and several varieties of *Avena sativa,* including Anthony, Iogold, Rainbow, and two selections called Double Cross A and Double Cross B, respectively, from previous crosses of (Minota × White Russian) × Black Mesdag. Correlated studies were made with particular reference to the manner of inheritance of those characters which differentiate varieties of *Avena byzantina* and *A. sativa,* and reaction of these varieties to stem rust, crown rust, and smuts.

2. Stem-rust resistance was dominant to susceptibility, and segregation in F_2 and F_3 was explained on the basis of a single factor difference. The physiologic races of stem rust used in creating the epidemic consisted of those to which White Russian was resistant.

3. Bond proved resistant to all physiological races of crown rust used in the studies. (During 1937 and 1938, late in the season, a race of crown rust appeared to which Bond was susceptible.) The F_1 generation of all crosses proved resistant although the degree of resistance was lower than in the Bond variety. The F_2 generation of the cross between Bond and Rainbow approached a ratio of 3 resistant to 1 susceptible, indicating only a single factor difference, while the other crosses gave a segregation of resistant to susceptible in a 9:7 ratio, indicating two major factors for differentiating resistance and susceptibility.

4. For both stem rust and crown rust there was good agreement between seedling reaction in the greenhouse to a single race and field reaction to the collection of races used in the studies.

5. Bond and the Double Crosses A and B proved resistant to the smuts in the field. In the cross between Bond and Double Cross A, some susceptible lines were obtained in F_3, showing that the factor or factors which conditioned resistance were unlike in the Bond and Double Cross A parents. In the crosses of Bond with Iogold and Anthony there were indications of a single major factor difference, although there

was some evidence of minor modifying factors. Previous studies indicated that at least two major factors were necessary to explain resistance of the Black Mesdag type, the type of resistance exhibited in the double crosses used in these studies.

6. For mode of separation of the lower floret of the spikelet from the axis of the spikelet, the *sativa* type of abscission appeared dominant over the *byzantina* type, designated as disarticulation, and the ratio in F_2 approached 3:1.

7. The floret disjunction of the *sativa* varieties, with the exception of the double crosses, showed disarticulation at the apex of the rachilla segment; the double crosses were characterized by heterofracture, although there was considerable variability in different florets and the Bond parent showed disjunction by basifracture. Segregation in the crosses between Bond and the double crosses was explained on the basis of a single major factor difference. In the remainder of the crosses it was apparent that the type of floret disjunction was dependent upon more than a single factor for its differentiation.

8. The Bond parent had a heavy growth of basal hairs on the lower floret, although some plants of Bond showed some florets with scarcely any hairs on the base. The *sativa* varieties showed a lower number of basal hairs than Bond, and some plants had no basal hairs. Segregation in F_2 approached a ratio of three plants with the *sativa* type of basal hairs to one with the Bond type.

9. Studies of awn development were made with the parents and F_2 crosses. Segregation occurred and the type of segregation was strongly influenced by the characteristics of the particular parents used in the crosses. It was impossible to determine the genetic factors involved.

10. The Bond parent was outstanding in plumpness of seed and excelled all other varieties in this respect. Segregation in F_2 indicated that it was possible to transfer this character to plants that were classified as typical of *Avena sativa*.

11. A study was made of independence or association of characters in the F_2 generation of crosses by means of X^2 and P. Associations of importance are summarized here. One of the five crosses studied showed a negative association between degree of crown-rust infection and plumpness of seed, and two of the five crosses showed a similar association between the plumpness of seed and degree of stem-rust infection.

12. Spikelet disarticulation was strongly associated with shattering of the seed, with type of floret disjunction, and with the type of basal hair development. Basal hair development was strongly associated with floret disjunction and awn development.

13. The association between spikelet disarticulation and basal hair development was explained on the basis of genetic linkage with a crossover value of 2.7±0.3. In the crosses of Bond with the two double crosses, the association between one of the genes conditioning floret disjunction and the major factor for basal hair development showed a calculated linkage value of 24.0±2.3. The two most interesting characters commonly used in differentiating *A. byzantina* and *A. sativa* are spikelet disarticulation and floret disjunction. In the crosses of Bond with the double-cross parents there was a calculated linkage value of 25.7±2.3 for the two pairs of factors involved.

14. Several F_3 and F_4 lines were studied to determine whether it was possible to obtain true breeding types with an intermediate type of base on the lower floret and with basal hairs similar to those in *sativa* varieties. Several F_4 lines appeared to breed true for these characters. In several cases, peculiar types of ratios were obtained which differed widely from the types of segregation in F_2. It was suggested that these results might be due to abnormal types of chromosome pairing that have been used in previous cases to explain abnormal segregation in polyploid species, and which may be similar to the types of chromosome behavior that have been observed as characteristic of speltoid wheats and fatuoid oats.

15. The evidence obtained indicates that it should be relatively easy to combine resistance to the three major diseases, stem rust, crown rust, and the smuts, with the characters of cultivated varieties of *A. sativa* and with plumpness of grain, an outstanding character of the Bond variety.

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