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THE INHERITANCE OF HULL-LESSNESS IN OAT HYBRIDS¹

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THE purpose of this paper is to set forth some results obtained in certain crosses between the hull-less types of oats and some of the hulled forms.

The hull-less types belong to the species *Avena nuda*. The origin of these forms is not definitely known, although, according to Carleton,² they appear to have come from central and eastern Asia. Reports are to the effect that a certain form of this oat has been cultivated in China for a thousand years or longer. These types are not generally cultivated in any other countries and perhaps due to this fact little study has been made of the various hull-less types and their possible origin. From some observations made on our material it seems quite possible that these hull-less forms may have originated through mutative changes. For example, in a pure line of the variety Sixty Day certain spikelets suddenly appeared which were very similar to the true hull-less forms in having the caryopsis loosely held in the glumes and an increased number of flowers per spikelet. These seeds were tested, but did not reproduce this hull-less tendency. A large number of similar cases have been observed particularly with hybrids, although none of these

¹ Paper No. 68, Department of Plant Breeding, Cornell University, Ithaca, N. Y.

² "The Small Grains," 1916.

has been tested as to its inheritance as yet, but it is planned to do so.

Trabut³ says in regard to the possible origin of hull-less oats that "the study of the domestication of *Avena* presents, from the genetic point of view, some rather substantial arguments in favor of an ambient medium, a modifying agent causing fluctuations which end in the formation of varieties well characterized and fixed by selection."

PREVIOUS WORK

A number of investigators have studied hybrids between varieties of *Avena nuda* and *Avena sativa*. Norton⁴ was the first investigator in America to hybridize these forms. He reports that

the spikelet of the naked varieties usually has more than three grains, while in the hulled types three grains is the limit. The first generation plants produced a head naked at the top and hulled at the bottom. In the second generation, one fourth of the progeny were typical naked plants, one fourth were hulled, and one half like the first generation hybrids. The naked plants all had long spikelets with more than three grains, while the hulled plants had spikelets with the usual two or three grains. In future generations no exception to this rule has been found except that one second generation plant of a cross between European Hull-less and Garton's Tartar King which seems to have become fixed in the intermediate hybrid type. In this example we have an extremely rare case of the fixation of a heterozygote or hybrid type.

Gaines⁵ reports having made some hybrids between hulled and hull-less oats and first separated the F_2 types into two groups, hulled and hull-less. In making such a grouping the heterozygous types were put into the group which it resembled most. He obtained from one cross 48.7 per cent. hulled and 51.3 per cent. hull-less plants and says, "this indicates an intermediate about half-way between hulled and hull-less for the heterozygous types. As was mentioned above, the separation was made arbitrarily into hulled and hull-less, according to the type any given plant most nearly resembled."

³ *Journal of Heredity*, Vol. 5, p. 84, 1914. Translation of original paper.

⁴ American Breeders' Association, Vol. III, p. 285, 1907.

⁵ Washington Agr. Expt. Sta. Bul. 135, p. 58, 1917.

In another cross Gaines found 77.1 per cent. hulled to 22.9 per cent. hull-less, which caused him to conclude that the two crosses were not similar in their behavior. This would seem to be the case from the data at hand, yet in 1914 Gaines made a number of other crosses, among which according to the pedigree numbers is another one between these two sorts, Black (Wash. No. 665) and Hullless (Wash. No. 680) which gave, this time, results very similar to all the other crosses reported as made that year, which indicated a 1:2:1 ratio. Gaines did not offer any explanation as to the different behavior of these two crosses between the same two sorts.

From these experiments Gaines concludes,

the percentage of hulled type suggests a simple Mendelian recessive although in every case there are a few too many hulled plants. The percentage of hull-less plants is not only very irregular in the different crosses but is also irregular in the different families within the same cross with the exception of the two families of Sixty Day \times Hull-less, which gave a ratio approaching 1:2:1. The intermediate types showed great variation. Plants could be found with only one or two spikelets that showed the hull-less character. Others could be found that showed the hulled character in only one or two spikelets, and plants were obtained with every degree of hull-lessness between these extremes. However, most of the intermediates produced more than half hulled oats. A curve fitted to these intermediate variations in Black Tartarian \times Hull-less shows larger numbers at either extreme and few numbers showing per cents. of hulled oats ranging from 30 to 50. This is just the opposite of what we would expect if the hull-less character was caused by a single Mendelian unit which produced an intermediate in the F_1 .

In a paper by Zinn and Surface⁶ results are given of a cross between a hull-less and hulled oat. The sorts used were *Avena sativa patula* var. Victor, and *Avena sativa nuda* var. *inermis*. The results indicate that their forms agree very closely with those reported by Norton and Gaines. The following paragraph gives part of their conclusions.

The F_1 generation is distinctly intermediate in most characters. In regard to the glumes, both naked and firmly hulled grain as well as intermediate forms are found on the same panicle and even in the same

⁶ *Journal of Agricultural Research*, Vol. X, No. 6, pp. 310-311, 1917.

spikelet. As shown in Table I, the spikelets near the top of the panicle are either entirely naked or nearly so, while those spikelets near the base of the panicle tend to be firmly hulled. A similar but less marked relation is to be observed between the spikelets at the tip and base of each whorl.

In the F_2 generation a large number of intermediate forms appear. In addition to the two parental hull types, four intermediate classes were distinguished. These intermediate forms contain all gradations from the plants with perfectly hulled grain to the perfectly naked forms.

As shown in Table II, the inheritance of the hull characters presents a simple Mendelian relation giving 1 hulled, 2 intermediate, 1 naked. Likewise, in respect to grain color, there are 3 black plants to 1 white, in the second generation.

MATERIAL AND METHODS

In connection with some experiments in oat breeding a number of hybrids between the hulled and hull-less forms have been made. While in these crosses the inheritance of other characters such as color of glumes, pubescence, awns and the like, are very interesting, the present paper will be confined to the discussion of the inheritance of the hull-less and hulled characteristics. A more complete discussion of the various characters is being prepared for a later publication.

The authors want to take this opportunity to express their appreciation for the valuable assistance in note-taking and tabulation of results rendered by W. T. Craig and Miss A. M. Atwater. Their work has been of great aid in conducting these experiments.

The hull-less oat used for the various hybrids was typical of the *Avena nuda* group and differs from the *Avena sativa* forms by three important characters: (1) The lemma, or flowering glume, and palet do not clasp the kernel as in other forms, and the kernel is therefore loose, or free, within the hull; (2) The rachillæ of the three to many-grained spikelet are so elongated that the uppermost grains are borne above the empty glumes; (3) The glumes and the lemmas are similar in texture. The illustration (Fig. 1) will give a fair idea of the par-



FIG. 1. THE FEMALE PARENT (*Avena nuda*) USED IN SERIES 382.

ticular characteristics which separate *Avena nuda* from the hulled species. This type is typical of the hull-less forms used in the following hybrids.

The hulled forms were all varieties of *Avena sativa* with one exception. In this case *Avena fatua* was used

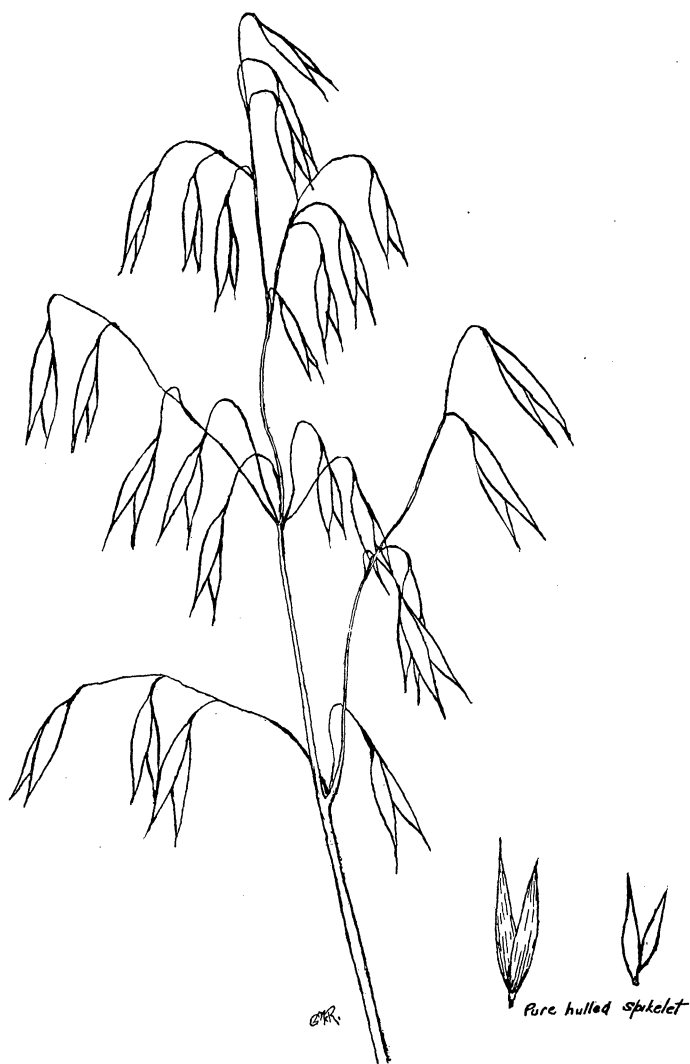


FIG. 2. THE MALE PARENT (*Avena sativa*) USED IN SERIES 382.

as the hulled parent. Fig. 2 shows the hulled variety, Sixty Day, used in one of the crosses. It is typical of a hulled oat.

The first crosses of this sort were made in 1910 and the F_1 plants grown in the greenhouse the following winter. The first cross was between Hulless and Black Tar-

tarian. Here the hull-less form was used as the female parent. The male parent possessed, as indicated by its name, black glumes, and was a typical hulled oat. The other cross was between Danish Island and Hulless in which the hulled type was used as the female parent. In each case the F_1 type was typical of the F_1 types as described by the authors mentioned above. This form is intermediate in that both kinds of kernels, hulled and hull-less, are found on the same head. The type of panicle resembles the hull-less parent more than it does the hulled and may be considered as intermediate in type. There are some spikelets with hulled and some with hull-less kernels and also some with both hulled and hull-less kernels. As a usual thing the hulled spikelets occur towards the base of the panicle while the hull-less kernels occur near the terminal spikelet which is almost invariably hull-less if such kernels are present at all in the panicle.

There are fewer hulled than hull-less kernels on the F_1 types. The percentage of hulled kernels does not usually run very high. In Fig. 3 is shown a typical form of F_1 panicle of a cross between a hulled and hull-less oat.

The F_2 generation of these two crosses were grown in the field in the summer of 1913. The plants were then sorted into two groups, hulled and hull-less, or hull-less like. All those plants having any indication of hulllessness were placed in the hull-less class. The result of these counts was as follows:

Series Number	Varieties Crossed	Hull-less	Hulled
111	Hulless \times Black Tartarian.....	129	37
51	Danish Island \times Hulless.....	364	93
		493	130

Although the ratio deviates considerably from 3:1 it indicates that this character behaves as a simple monohybrid and that there is one factor pair concerned. In

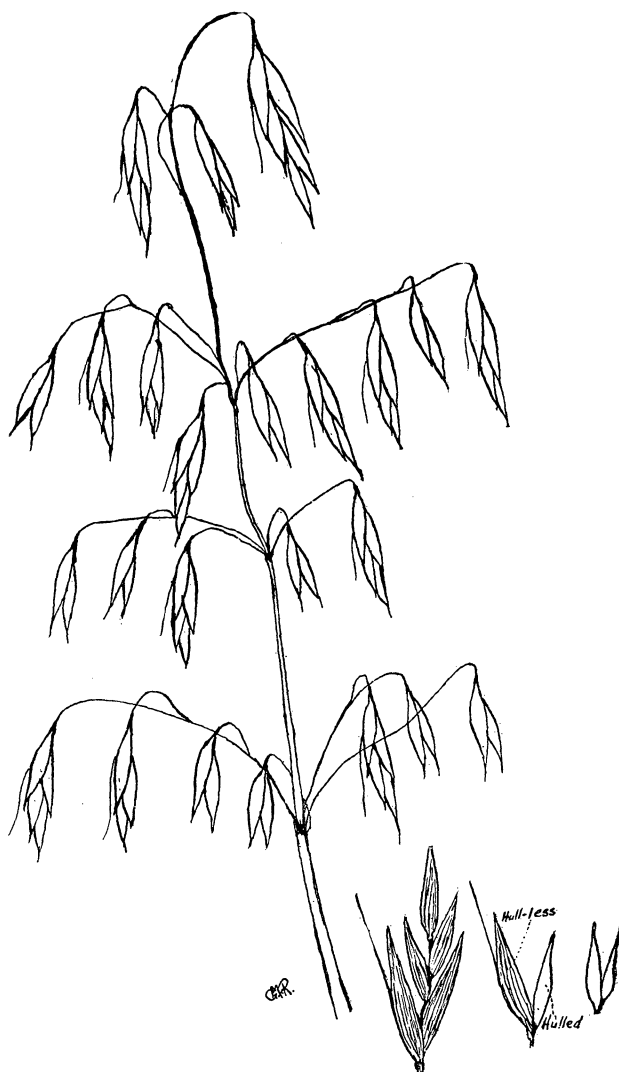


FIG. 3. F_1 INTERMEDIATE TYPE OF A CROSS BETWEEN HULL-LESS AND HULLED.
Series 382.

order to test this out more fully all plants from which good seed could be obtained were grown in the following year. The results obtained from these plants showed without doubt that the segregation followed a simple monohybrid ratio. That is, the pure hulled and hull-less plants bred true to these characteristics, while the inter-

mediate types reproduced the three types again. The second generation plants tested as to their composition gave the following results in the third generation:

Series Number	Varieties Crossed	Pure Hulled	Intermediate	Pure Hull-less
111	Hulless \times Black Tartarian	37	85	38
51	Danish Island \times Hulless	115	216	114
		152	301	152

It is apparent from these results that certain plants were classed as intermediate in the second generation, which were in reality pure hulled plants. It is evident that the hulled-hull-less character is inherited in a simple Mendelian fashion so far as its general behavior is considered.

The heterozygous plants produced in the third generation were examined as to the relative amounts of hulled and hull-less kernels present. This was done by threshing a representative head from each plant by hand and counting the hulled and naked kernels and expressing the result as the percentage of hulled kernels.

In order to determine whether the results from a single head fairly represented the type of the plant a number of plants were examined and recorded a head at a time. The percentage of hulled kernels for a representative head was then compared with that for the entire plant. The average percentage was the same for the results from single heads as it was for the entire plant. Although there was some deviation in the individual determinations, the correlation between the two methods is very high.

The result of determining the percentage of hulled kernels was to indicate the great variation existing, which was from a very low to a very high percentage. As a result of these observations it was apparent that while in the hybrids under consideration the usual 1:2:1 ratio was observed, some factor or factors were pres-

ent which affected the heterozygous forms in such a way as to modify the amount of hulled or hull-less kernels present.

In order to determine this effect in a more definite way it was planned to sow seed from heterozygous individuals which differed as to the percentage of hulled kernels present. A rather large number of such seeds were planted in 1915. The plants were severely injured by a storm, so that accurate percentage determinations could not be made.

In the meantime, however, a number of other crosses had been made in which the *Avena nuda* was used as one parent. The following sorts were crossed with the naked oats: Swedish Select, Sixty Day and *Avena fatua*. Other crosses are being studied but these will be reported on later.

As regards the hull-less character the F_1 individuals of these crosses were all similar to the description of the first generation given earlier in this paper. Regarding the other characters, the cross between the hull-less form and *Avena fatua* showed some very interesting variations. These will not now be discussed.

Seeds of these various F_1 plants were sown and the resulting plants harvested. From each plant a head was saved and threshed separately by hand and the plants then sorted into hulled, intermediate and hull-less. The result of the several crosses is given here:

Series Number.	Varieties Crossed	Hulled	Intermediate	Hull-less
379	Hullless \times <i>Avena fatua</i>	68	111	78
202	Hullless \times Swedish Select	41	90	36
382	Hullless \times Sixty Day	75	193	53
	Observed	184	394	168
	Expected	186.5	373	186.5

The probable error is ± 7.98 and the observed numbers agree fairly well with the expected numbers. The number of hull-less plants is too low and the number of intermediates too high. It is possible that in some cases

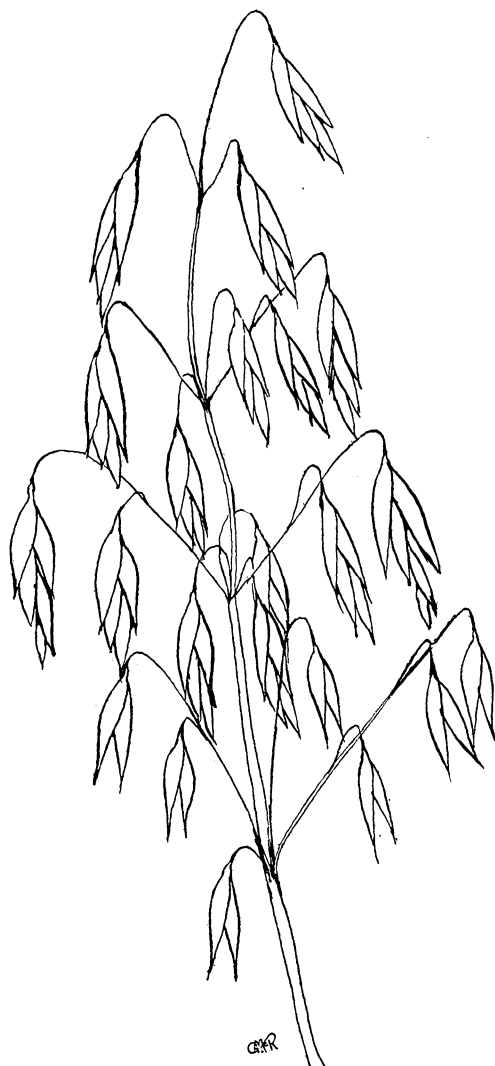


FIG. 4. HETEROZYGOUS TYPE F_4 POSSESSING 10 PER CENT. OF HULLED KERNELS.
Series 382.

hull-less plants may have been recorded as intermediates although the error from this source is not large. When the results are considered on a 1:3 basis and the hull-less and intermediates are grouped together we find that there is a percentage of 24.66 ± 1.07 hulled plants.

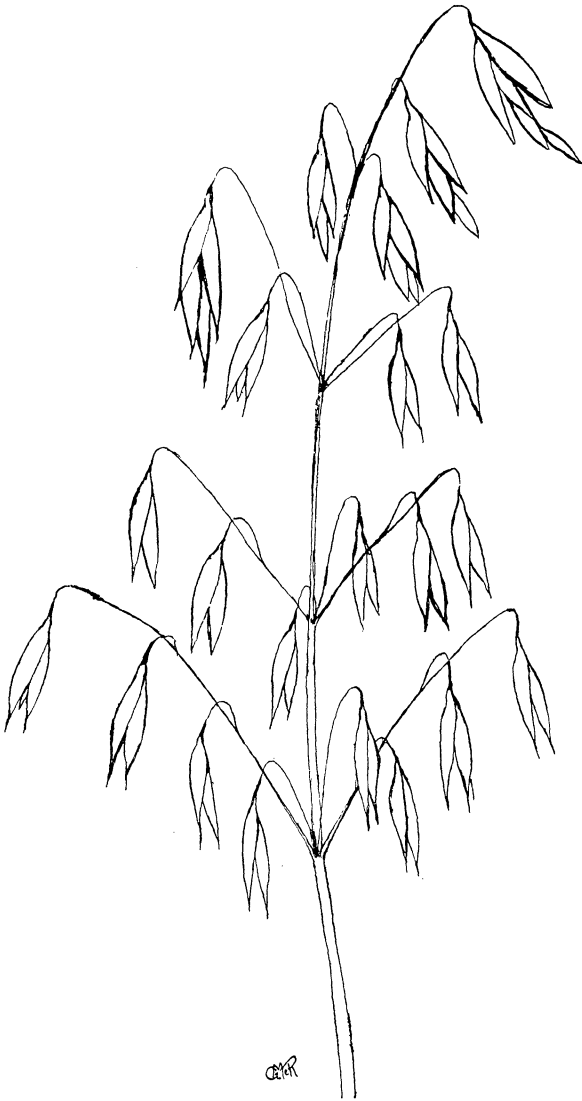


FIG. 5. HETEROZYGOUS TYPE F_4 POSSESSING 87.9 PER CENT. OF HULLED KERNELS.
Series 382.

The results of these different hybrids show that hull-lessness is inherited in a simple monohybrid manner and that without doubt the difference between hulled and hull-less oats in this regard is represented by one pair

of factors. An analysis of the different heterozygous or intermediate individuals of these second generation plants showed that for these hybrids also there was a great amount of variation in the percentage of hulled or hull-less kernels in the individual plants, the variation ranging all the way from less than 5 per cent. to 95 per cent. or more. In Figs. 4 and 5 are shown two forms of heterozygous plants, one very low and one very high, in percentage of hulled kernels. These percentages were obtained from the heterozygous individuals by sorting the kernels from one head of each plant into hulled and hull-less as outlined earlier. The percentage of hulled kernels on the heterozygous plants of the second generation for the three series is given in Table I.

TABLE I

SHOWING PERCENTAGE OF HULLED KERNELS ON THE HETEROZYGOUS PLANTS OF THE SECOND GENERATION IN CROSSES BETWEEN HULLED AND HULL-LESS OATS.

Series Number	Varieties Crossed	Percentage of Hulled																				
		2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	67.5	72.5	77.5	82.5	87.5	92.5	97.5	
379	Hulless \times <i>Avena fatua</i>			2	3	5	4	4	3	4	4	7	5	5	8	4	6	5	7	10	13	15
202	Hulless \times Swedish Select	10	4	4	4	3	5	8	2	1	7	6	3	4	2	5	3	3	6	3	4	6
382	Hulless \times Sixty Day		5	5	5	4	4	6	6	8	20	15	22	21	15	13	17	11	7	4	4	1
		15	11	12	12	13	18	11	13	31	28	30	30	25	22	26	19	20	17	21	22	

From this table it is seen that there is considerable difference in the percentage of hulled kernels on the different heterozygous plant. The range is from a very low percentage or one which indicates nearly all hull-less to a very high percentage or one which is nearly all hulled. There is no general grouping near the middle of the series, as might be expected with the exception of series 382. This may be due to lack of numbers or to a segregation of the different types which give percentages ranging from low to high without any tendency to grouping. That it is not due to lack of numbers is probably

borne out by the fact that in series 51, where over 900 plants of the third generation were sorted into the different classes, there was no indication of a grouping near the middle classes, in fact, the slight indication of grouping was near the lower values. The distribution is as follows:

TABLE II

SHOWING PERCENTAGE OF HULLED KERNELS IN THE HETEROZYGOUS PLANTS OF THE THIRD GENERATION IN A CROSS BETWEEN DANISH ISLAND AND A HULL-LESS OAT.

Percentage of Hulled Kernels	Frequency	Percentage of Hulled Kernels	Frequency
0 — 4.9	89	50.0 — 54.9	42
5.0 — 9.9	80	55.0 — 59.9	48
10.0 — 14.9	60	60.0 — 64.9	43
15.0 — 19.9	49	65.0 — 69.9	26
20.0 — 24.9	59	70.0 — 74.9	35
25.0 — 29.9	48	75.0 — 79.9	33
30.0 — 34.9	47	80.0 — 84.9	32
35.0 — 39.9	53	85.0 — 89.9	26
40.0 — 44.9	52	90.0 — 94.9	21
45.0 — 49.9	46	95.0 — 99.9	15

It was planned to carry some of this work further to answer in general two questions which are: (1) Does the percentage of hulled plants obtained from any heterozygous parent vary with the percentage of hulled kernels possessed by that parent? (2) Do the hulled and hull-less kernels of a heterozygous plant give approximately the same results in their offspring?

In order to obtain data on these questions two of the series have been continued. The hull-less-*Avena fatua* series has not been carried further as yet but it is planned to do so.

RESULTS FROM SERIES 202—SWEDISH SELECT \times HULLLESS

The first series to be discussed is the Swedish Select-Hull-less cross. Seed from two hulled and two hull-less plants of the second generation were grown in the third generation and each bred true to type. In addition to these plants twenty heterozygous plants were selected for planting. These varied as to the amount of hulled

kernels. The range was from 3.2 per cent. to 92.0 per cent. The number of seed was not large, therefore the number of plants obtained was not as large as desired, yet from the consistency of the results certain conclusions are justified. The offspring from these twenty plants were sorted into the three classes, hulled, intermediate and hull-less. The intermediate plants were again threshed and the percentage of hulled kernels determined.

In Table III is given the percentage of hulled condition in the parent plant, the segregation into the three groups, the percentage of hulled kernels in the heterozygous offspring, the grouping into hulled and hull-less and (where both hull-less and intermediate plants are grouped together) the percentage of hulled plants with the probable error.

TABLE III

SHOWING SEGREGATION IN F_3 OF CERTAIN F_2 PLANTS TOGETHER WITH THE PERCENTAGE OF HULLED SEED IN PARENT TYPE AND THE AVERAGE PERCENTAGE IN THE HETEROZYGOUS OFFSPRING.

	Segregation Obtained from Plants Sown and Resulting Percentage of Hulled Kernels on Intermediate Forms.							
	Per Cent. of Hulled Kernels in Plants Sown	Hulled	Intermediate	Hull-less	Per Cent. Hulled in Intermediate Offspring	Hulled	Hull-less and Intermediate	Per Cent. Hulled and P. E.
202al-4...	44.9	27	63	22	44.8	27	85	24.11 \pm 2.76
6...	25.0	34	51	40	21.0	34	91	27.20 \pm 2.61
9...	20.9	27	35	60	12.8	27	95	22.13 \pm 2.64
10...	83.0	42	63	34	39.5	42	97	30.22 \pm 2.48
11...	92.0	42	62	17	52.6	42	79	34.71 \pm 2.65
22...	65.1	13	36	7	60.6	13	43	23.21 \pm 3.90
25...	90.3	14	36	9	55.3	14	45	23.73 \pm 3.80
26...	76.6	14	37	21	56.3	14	58	19.44 \pm 3.44
29...	30.7	12	19	15	44.1	12	34	26.09 \pm 4.31
31...	56.8	16	43	21	47.6	16	64	20.00 \pm 3.27
38...	10.5	21	26	40	22.3	21	66	24.14 \pm 3.13
40...	82.4	19	33	19	53.6	19	52	26.76 \pm 3.47
46...	16.7	14	20	22	24.7	14	42	25.00 \pm 3.90
51...	56.6	25	41	10	47.1	25	51	32.89 \pm 3.35
60...	74.3	7	10	4	46.0	7	14	33.33 \pm 6.37
66...	3.2	10	26	32	22.7	10	58	14.71 \pm 3.54
77...	65.4	15	21	14	34.9	15	35	30.00 \pm 4.13
92...	35.3	12	10	8	36.0	12	18	40.00 \pm 5.33
120...	44.7	14	18	8	33.9	14	26	35.00 \pm 4.62
121...	9.5	13	11	23	20.2	13	34	27.66 \pm 4.26
Totals		391	661	426		391	1087	26.45 \pm .76
Expected....		369.5	739	369.5				

The results of the segregation into the three classes gave 391 hulled, 661 intermediate and 426 hull-less. Here the hull-less plants are too great in number, while the number in the intermediate class is too small. The expected numbers are 369.5:739:369.5, with a probable error of ± 11.23 . It is possible that some intermediate plants were classed as hull-less. Such a condition is possible since some intermediates are found bearing only one or two hulled kernels, and if these should be lost through shattering, such plants would be classed as hull-less when in reality they are intermediates. When the grouping is made into the two groups, hulled and hull-less, it is seen that the 3 to 1 ratio is approximated very closely, as there are 391 hulled plants to 1087 hull-less, giving a percentage of $26.45 \pm .76$ hulled.

An examination of this table shows further that some of the families do not give ratios close to 1:2:1. This is true with regard to certain families particularly with certain of those coming from plants low in percentage of hulled, and some of those relatively high in this respect. The results of some of these families have been brought together in Table IV.

TABLE IV

SHOWING SEGREGATION OF OFFSPRING COMING FROM SOME INDIVIDUALS LOW OR HIGH IN THE PERCENTAGE OF HULLED KERNELS.

Family Number	Percentage of Hulled Seed in Plants Sown	Segregation of Offspring Into Different Types.		
		Hulled	Intermediate	Hull-less
6	25.	34	51	40
9	20.9	27	35	60
38	10.5	21	26	40
46	16.7	14	20	22
66	3.2	10	26	32
121	9.5	13	11	23
Total.....		119	169	217
10	83.	42	63	34
11	92.	42	62	17
25	90.3	14	36	9
26	76.6	14	37	21
40	82.4	19	33	19
Total.....		131	231	100

In this table the plants from parents having 25 or less per cent. of hulled kernels give 119 hulled:169 intermediate:217 hull-less. From this result it appears that those plants having a low percentage of hulled or high percentage of hull-less kernels tend to produce a relatively high number of hull-less plants. On the other hand, those plants having more than 75 per cent. of hulled kernels do not give results so striking. There are more hulled than hull-less plants, yet not strikingly so, and the hulled do not run higher than the intermediates. It may be, however, that the degree of hull-lessness as expressed by the percentage may influence the segregation in the following generations. This can not be definitely stated from this cross, and further evidence will be needed.

TABLE V

SHOWING THE RELATION BETWEEN THE PERCENTAGE OF HULLED KERNELS ON THE HETEROZYGOUS PARENT PLANTS AND THE PERCENTAGE OF HULLED KERNELS ON ITS OFFSPRING

Percentage of Hulled Oats on Plants Sown	Percentage of Hulled Oats on Offspring																	
	0-4.9	5.0-9.9	10.0-14.9	15.0-19.9	20.0-24.9	25.0-29.9	30.0-34.9	35.0-39.9	40.0-44.9	45.0-49.9	50.0-54.9	55.0-59.9	60.0-64.9	65.0-69.9	70.0-74.9	75.0-79.9	80.0-84.9	85.0-89.9
3.2	12	3	3	1	1				1		1				1	1		26
9.5	1	1	2	2	1		1	1										11
10.5		5	2	3	6	6	1	1		1								26
16.7	2	3	3	4	2	1	2		2				1					20
20.9	9	10	7	4	1	2			1	1								35
25.0	5	12	4	6	5	2	9	2	4	1								51
30.7	1	1	1	1	1	1	2	2	2	2	1	1		1	2	1		19
35.3		2		1	1	1	1	1	1									10
44.7	1	1	1		2	4	3				2	2	1					18
44.9	4	3	6		3	1	6	3	2	3	4	7	7	6	0	6	2	63
56.6	1	3	1	1	3	3	2	6	3	3	2	3	3	3	1	2	2	41
56.8			5	1	1	4	3	2	2	4	2	5	6	2	3	2	1	43
65.1	2	3									6	4	2	4	2	6	4	36
65.4	1	5	1	1	1	4			2	1			1		1	1	1	21
74.3	1	1		1			1		1	1	1		1	1	1		4	10
76.6			1	2	3	2	1	1	1	3	4	5		1	1	1	6	37
82.4			1	1	2		2	3	3	4	3	3	1	1	2	2	2	33
83.0	5	1	2	8	4	5	2	7	5	2	5	3	3	5	2	1	2	63
90.3	4	2	2		1	1			3	3	3	3	1	7	1	5	3	36
92.0	1	4	2	1	3	3	2	3	2	5	5	6	4	2	4	4	7	62
	50	60	37	39	41	39	39	30	32	36	39	42	32	34	18	32	32	15
																		12
																		2
																		661

The relation between the percentage of hulled kernels on the parent and the percentage of hulled kernels on the heterozygous offspring for this series is shown by the correlation table given above. The correlation coefficient is $.421 \pm .022$, which shows a very definite relation between the percentage of hulled in the parent and offspring.

This relation is also better shown by means of a curve (Fig. 6) in which the parents are represented by the dotted line beginning with the lowest and increasing to the highest value. On the same ordinate is plotted the average value for the heterozygous offspring, and to this line has been fitted a straight line whose equation is $y = 20.1999 + 1.9579x$.

Certain of these families show a decided grouping; for example that represented by 20.9 per cent. shows a decided tendency to be grouped in the lower classes, while that represented by 65.1 per cent., with five exceptions, shows a grouping around the higher classes.

RESULTS OF SERIES 382—SIXTY DAY \times HULL-LESS

From the second generation of this cross six heterozygous plants were selected for further study. The results of three of these will be discussed here. These plants possessed different amounts of hulled kernels, which expressed in percentages were as follows, 73.3, 37.7, 49.3. Thus, there was one high, one low and one medium plant. The offspring of these gave the following results when grouped in the three classes:

	Hulled	Intermediate	Hull-less
382a1-7.....	23	55	20
8.....	15	37	24
9.....	53	105	49
	91	197	93

These figures agree very well with the expected 1:2:1 ratio. Single heads of the heterozygous plants of these three families were threshed and the percentage of hulled

kernels per plant determined as before. The three families gave the following distribution:

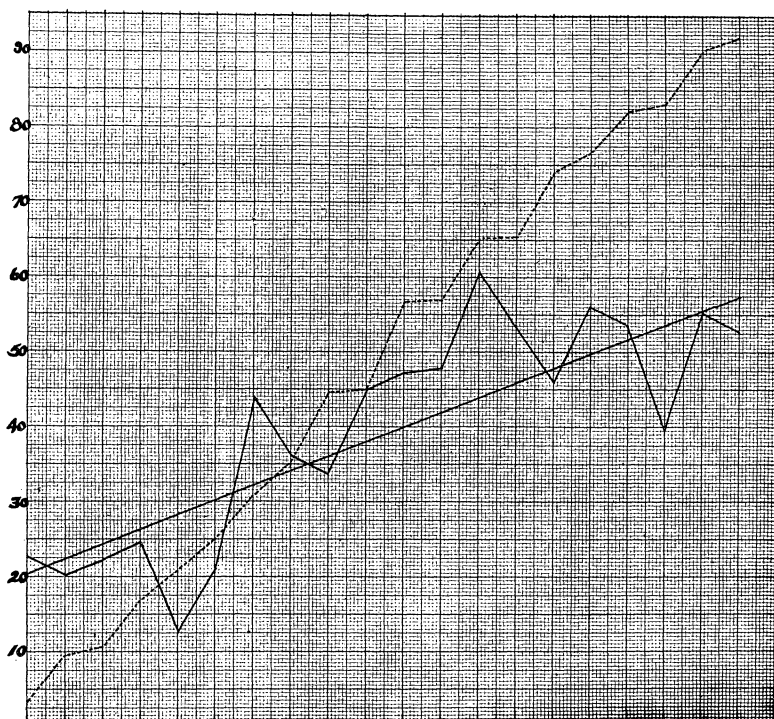


FIG. 6. These curves show the relation between the percentage of hulled grain on the heterozygous plant used as parent and the average percentage of hulled kernels on its heterozygous offspring. Dotted line represents the value for the parents and the solid line that of the heterozygous offspring. Series 202.

From these distributions it is clear that the percentage of hulled kernels on the parent form influences the amount of the hulled condition. The average percentage of the offspring in each case agrees closely with that of the parent forms.

From these three families several plants differing in their percentage values were selected to continue the study in the fourth generation. As observed from the frequency distribution just given it is noted that series 7 is of high value, while 8 is relatively low and 9 varies from very low to high. The plants selected then in gen-

eral represented the types of their lines; that is, those from 7 were generally high, those from 8 generally low, and those from 9 both low and high. The offspring of these various selections are arranged in a table similar to that for series 202.

Series No.	Per-centage Hulled Seed in Plants Sown	Percentage of Hulled in Offspring																			Totals	A ver- age Per Cent. of Hulled Ker- nels on Off- spring
		0-4.9	5.0-9.9	10.0-14.9	15.0-19.9	20.0-24.9	25.0-29.9	30.0-34.9	35.0-39.9	40.0-44.9	45.0-49.9	50.0-54.9	55.0-59.9	60.0-64.9	65.0-69.9	70.0-74.9	75.0-79.9	80.0-84.9	85.0-89.9	90.0-94.9		
382al-7	73.3					1				1	3	5	5	5	6	12	10	6	1		55	67.3
8	37.7	1	1	2	3	3	6	4	5	2	5	2	1	2							37	33.7
9	49.3	1	1	3	6	7	6	5	4	4	14	5	8	11	11	7	8	1	1	2	105	50.1
		2	2	5	9	11	12	9	9	7	22	12	14	18	17	19	18	7	2	2		

TABLE VI

SHOWING SEGREGATION IN F_4 OF CERTAIN F_3 PLANTS TOGETHER WITH THE PERCENTAGE OF HULLED SEED IN PARENT TYPE AND THE AVERAGE PERCENTAGE IN THE HETEROZYGOUS OFFSPRING

Segregation Obtained from Plants Sown and Resulting Percentage of Hulled Kernels on Intermediate Forms.								
	Per Cent. of Hulled Kernels in Plants Sown	Hulled	Inter-mediate	Hull-less	Per Cent. Hulled in Inter-mediate Offspring	Hulled	Hull-less and Inter-mediate	Per Cent. Hulled and P. E.
382al-7-10..	63.6	22	31	25	63.1	22	56	28.21 \pm 3.31
11..	53.0	24	34	10	46.0	24	44	35.29 \pm 3.54
32..	77.0	28	38	22	70.5	28	60	31.82 \pm 3.11
33..	70.3	21	53	26	62.7	21	79	21.00 \pm 2.92
37..	80.0	8	31	19	57.5	8	50	13.79 \pm 3.84
45..	81.7	13	27	13	75.1	13	40	24.53 \pm 4.01
55..	63.0	19	39	28	67.8	19	67	22.09 \pm 3.15
8-14..	43.6	26	34	19	37.6	26	53	32.91 \pm 3.29
17..	38.2	28	63	23	44.1	28	86	24.56 \pm 2.74
22..	23.2	15	36	14	25.3	15	50	23.08 \pm 3.62
23..	17.0	4	9	9	19.2	4	18	18.18 \pm 6.23
28..	60.8	12	30	13	49.8	12	43	21.82 \pm 3.94
35..	17.2	22	43	24	20.5	22	67	24.72 \pm 3.10
61..	59.6	13	27	11	50.6	13	38	25.49 \pm 4.09
64..	9.8	16	36	14	25.3	16	50	24.24 \pm 3.60
9-9..	14.0	4	29	7	19.2	4	36	10.00 \pm 4.62
44..	62.4	24	50	15	49.1	24	65	26.97 \pm 3.10
94..	23.6	15	21	20	22.2	15	41	26.79 \pm 3.90
166..	79.7	16	27	22	81.2	16	49	24.62 \pm 3.62
175..	87.9	19	32	17	67.2	19	49	27.94 \pm 3.54
Totals		349	690	351		349	1041	25.11 \pm .78
Expected ...		347.5	695	347.5		347.5	1042.5	

The total number of plants in the hulled, intermediate and hull-less classes agree very closely with the expected numbers. The same is true for the 3:1 grouping, since the percentage of hulled is $25.11 \pm .78$, which shows without doubt that the various families give offspring which follow the 1:2:1 expectancy.

In this series there is little evidence that the percentage condition of the parent plant affects the type of segregation in the following generation. In general the segregation of the various families follows a 1:2:1 ratio regardless of the percentage condition of the parent.

To show the relation between the hulled condition of the parent forms and that of the heterozygous offspring a correlation table was made in which the different families were arranged according to their percentage values. The coefficient of correlation here is $.726 \pm .012$, which

TABLE VII

SHOWING THE RELATION BETWEEN THE PERCENTAGE OF HULLED KERNELS ON THE HETEROZYGOUS PARENT PLANTS AND THE PERCENTAGE OF HULLED KERNELS ON ITS OFFSPRING

Percentage of Hulled Oats on Plants Sown	Percentage of Hulled Oats on Offspring																				
	0-4.9	5.0-9.9	10.0-14.9	15.0-19.9	20.0-24.9	25.0-29.9	30.0-34.9	35.0-39.9	40.0-44.9	45.0-49.9	50.0-54.9	55.0-59.9	60.0-64.9	65.0-69.9	70.0-74.9	75.0-79.9	80.0-84.9	85.0-89.9	90.0-94.9	95.0-99.9	
9.8	2	2	4	5	4	5	7	2	3	2										36	
14.0	2	7	7	3	1	2	2	1	2	2										29	
17.0	1		2	1	3	1	1													9	
17.2	2	7	6	11	4	5	3	1	3					1						43	
23.2	2	2	4	5	4	7	2	3	2											36	
23.6	2			6	7	2	1	1			1									20	
38.2					2	3	12	11	11	8	7	3	1	3					2	63	
43.6			2		5	2	4	5	6	6	1	2	1							34	
53.0		1	1	2	1	3		2	2	6	5	6	1	2	1		1			34	
59.6						1		4	2	4	8	4	2	1	1					27	
60.8				1		2	1	3	4	3	6	2	3	3	2					30	
62.4	4	2	2	1			1	4	2	3	5	9	6	4	4	1			2	50	
63.0	1						2			1	2	5	1	6	5	8	5	1	2	39	
63.6				1			2	1	1	2	2	2	1	9	1	2	6	1		31	
70.3						1	1	2	2		7	9	7	9	5	6	1	3		53	
77.0			1				1			1		4	1	5	9	6	5	3	1	37	
79.7								1		1	1			2	1	4	4	1	10	27	
80.0	1	1				3			1	3	4	1	3	6	2	3	1	1		31	
81.7										1			3	3	5	8	3	3	1	27	
87.9				1				1		2	4	2	4	3	2	2	5	4	1	31	
	17	22	29	37	31	35	45	41	42	46	54	49	34	57	38	40	31	17	17	5	687

is considerably higher than it was with the 202 series. One reason for this may be that perhaps there is a difference between this series and the former or that the result is caused by grouping the three families. When a correlation table is made for each of the three families

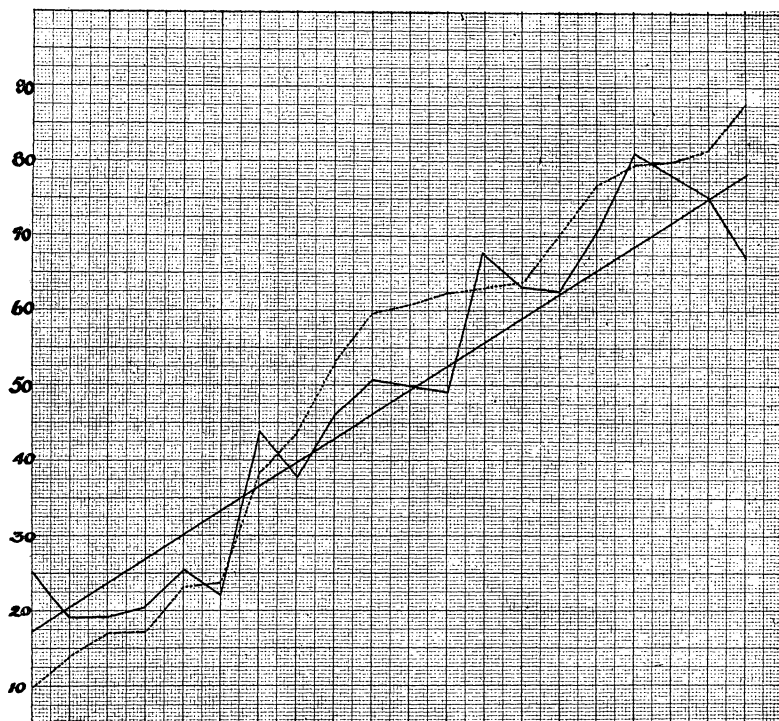


FIG. 7. These curves show the relation between the percentage of hulled grain on the heterozygous plant used as parent and the average percentage of hulled kernels on its heterozygous offspring. Dotted line represents the value for the parents and the solid line that of the heterozygous offspring. Series 382.

separately, correlation coefficients of $.296 \pm .039$, $.623 \pm .025$ and $.741 \pm .024$ are obtained. Thus it is seen that within any family correlation exists to a greater or less degree. Putting the three families in one table does increase the correlation somewhat over the average value for each alone. Another and possibly more plausible reason is the fact that these plants are of the fourth generation, while those of 202 are of the third.

The three parent series from which these were taken were of three types as mentioned before, therefore the parent plants selected from them carried the tendency to produce high or low as the case may be, and when they are all arranged in a correlation table naturally a high coefficient is obtained. In other words, the three parent forms were more nearly homozygous, so to speak, for high or low values. More will be said on this point later.

This relationship was further shown by means of a graph showing the relation between the parent percentage condition and the average value for the offspring, the same as was done in Fig. 7.

In this case the relationship is higher than in the former series. The equation to the straight line is $y = 17.2411 + 3.2062x$.

That the plants arising from heterozygous plants having a low or high percentage of hulled kernels did not segregate in a manner indicating any influence of the hulled condition of the parent plant, as was the case to some extent with series 202, is shown in Table VIII.

TABLE VIII

SEGREGATION OBTAINED WHEN SOWING SEED FROM HETEROZYGUS PLANTS
HAVING LOW OR HIGH PERCENTAGES OF HULLED SEED

Percentage of Hulled Kernels in Plants Sown	Segregation of Offspring Into Different Types		
	Hulled	Intermediate	Hull-less
9.8	16	34	14
14.0	4	29	7
17.0	4	9	9
17.2	22	43	24
23.2	15	36	14
23.6	15	21	20
	76	172	88
77.0	28	38	22
79.7	16	27	22
80.0	8	31	19
81.7	13	27	13
87.9	19	32	17
	84	155	93

It is clear that the percentage of hulled seeds does not seem to influence the segregation as far as these data are concerned.

HULLED COMPARED WITH HULL-LESS KERNELS

In order to learn whether there was any difference in the ratios produced by the hull-less kernels from the heterozygous plants the seed from the third generation plants used was separated and planted separately; that is, the hulled and hull-less from family 382a1-7-45 was planted separately so that the ratio may be determined on each lot of plants. This was done for all the families. These results are given in Table IX.

TABLE IX

RESULTS OBTAINED FROM SOWING HULLED AND HULL-LESS SEED FROM THE SAME HETEROZYGUS INDIVIDUAL SEPARATELY

Family No.	Segregation Obtained from Hulled Seeds			Segregation Obtained from Hull-less Seeds		
	Hulled Plants	Intermedi-ate Plants	Hull-less Plants	Hulled Plants	Intermedi-ate Plants	Hull-less Plants
382a1-7- 45.....	11	26	12	2	1	1
7- 10.....	18	22	20	4	9	5
7- 11.....	19	27	10	5	7	0
7- 32.....	18	28	17	10	10	5
7- 33.....	20	39	21	1	14	5
7- 37.....	8	25	19	0	6	0
7- 55.....	14	31	25	5	8	3
8- 14.....	18	19	8	8	15	11
8- 17.....	10	28	12	18	35	11
8- 22.....	3	7	4	12	29	10
8- 23.....	4	6	6	0	3	3
8- 28.....	9	18	8	3	12	5
8- 35.....	5	16	7	17	27	17
8- 61.....	9	19	9	4	8	2
8- 64.....	3	7	4	13	29	10
9- 9.....	3	6	3	1	23	4
9- 44.....	16	35	13	8	15	2
9- 94.....	7	8	7	8	13	13
9-166.....	13	22	14	3	5	8
9-175.....	19	30	16	0	2	1
Totals	227	419	235	122	271	116
Expected Nos.	220.25	440.5	220.25	127.25	254.5	127.25

In many of the cases the numbers are too small to give good ratios, yet the important point is obtained from the summation of the two series. In each case these agree very closely with the expected numbers. If there was any difference we might expect the hulled kernels to produce relatively more hulled plants and the hull-less rela-

tively more hull-less. The facts are the reverse. In the series from the hulled kernels the hull-less plants are in the majority and the opposite is true for the hulled plants from the hull-less seed. It is very evident that there is no relation between the kind of kernel (hulled or hull-less) sown from a heterozygous plant and the offspring produced.

GENERAL DISCUSSION

From the foregoing data it seems without doubt that the inheritance of the hulled condition follows a simple Mendelian ratio giving in general 1 hulled, 2 intermediate, 1 hull-less. This is in accord with the results obtained by Norton, Gaines, Zinn and Surface, and others.

In regard to the relation between the hulled condition of the heterozygous parent plants and of the offspring, it is clear that there is a very close agreement in regard to the hulled percentage. When high or low plants are selected they produce heterozygous offspring giving high or low percentage. In most cases, however, the usual 1:2:1 ratio is obtained. This is true in general in all cases of the 382 series but not so for 202. Whether the 202 series behaves differently or whether in reality it will agree with 382 will have to be determined with further work.

The percentage relation shows that there is a variation from very low to a very high percentage. Owing to this fact and that any heterozygous plant tends to reproduce a simple monohybrid ratio, in which the heterozygous plants tend to follow the percentage relation, it seems at first that we are dealing with a case of multiple factors, in which one primary factor pair determines the hulled or hull-less condition and the other factors influence the hulled condition of those plants only that are heterozygous for the primary factors. This may be so, as the results of selecting high or low individuals seem to indicate. If, however, we assume a multiple factor series to

account for the facts, it is evident that, assuming all the factors involved to have equal value, we must have an F_1 type that is very nearly intermediate as regards its percentage condition. This we have not observed in any of our series. The F_1 type, while being generally intermediate, is not so as regards its hulled condition, for it always contains fewer hulled kernels than hull-less. Thus, so far as the percentage relation is concerned, we do not have a strict intermediate. To be sure, there is a reduction of the multiple-flowered spikelet and other changes which cause the F_1 type to appear as an intermediate.

With the usual multiple factor hypothesis assuming ordinary segregation, there must be a larger number of individuals ranging from 30 to 70 per cent. than we have at the extremes. With series 379 and 202 we do not have any indication of such a condition. On the other hand, there is a slight suggestion that series 382 does tend more nearly to a frequency distribution such as would usually be expected with the ordinary multiple factor hypothesis. When the third generation distribution of series 202 is observed (Correlation Table V) it is apparent that there is more of a tendency to pile up nearer the lower values. When the size of the classes is doubled a decided skew curve is obtained with the mode at class 0-9.9. As stated above, the seed sown to obtain the plants used in this distribution was selected from plants of high, low, or medium value, and this may influence to some extent the type of distribution. Yet, when one examines the percentages of the plants used as parents, it is apparent that they are fairly evenly distributed. If, as suggested above, the nearly dominant primary factor pair influences the hulled or hull-less condition and the other factors influence the hulled condition of plants heterozygous for the primary factor, then we would expect a piling up near the lower values.

With series 382 there is a tendency for both the third and fourth generation percentage distributions to be

grouped around the middle classes. This is especially true with regard to the fourth generation, especially when the size of the classes is doubled.

The results of the different series are rather conflicting and it does not seem possible at present to explain all of them on a simple multiple factor hypothesis. It seems quite possible to explain series 382 on this basis (except the first generation) but the other types do not at present seem capable of such an explanation.

The distribution in Table II, which is the third generation of a cross between Danish Island and Hull-less, is skewed much the same as for the third generation of series 202. No doubt for these series there is some disturbing factor which causes such distributions and more data will be needed before a suitable explanation can be found to fit all of these cases. It may be that, since in crosses between two hulled sorts we have found some hull-less spikelets, we have combinations such that there is a tendency to produce an excess of hull-less kernels. This would influence the type of distribution considerably.

At first one might assume that those individuals nearer the lower part of the distribution were like the F_1 types, however, from all the plants tested where the percentage of hulled kernels has been low the frequency distribution of the percentage of hulled kernels from the heterozygous plants has been low in general and has not ranged from very low to very high, as would be the case with seed from F_1 plants. These facts would help support the statement just made, which is to the effect that it is possible certain crosses tend to produce an excess of hull-less kernels.

SUMMARY

From the results presented it is evident that hull-lessness exhibits a simple Mendelian ratio of 1 hulled, 2 intermediate, 1 hull-less.

The intermediates show all gradations of hull-lessness from those nearly hulled to those nearly hull-less.

The percentage of hulled kernels on the heterozygous plants seem, to indicate to some extent the percentage of hulled kernels on the heterozygous offspring.

No matter what percentage of hulled kernels is present on the heterozygous individual, it tends in general to produce a 1:2:1 ratio.

The hulled and hull-less kernels from intermediate plants reproduce similar 1:2:1 ratios.