Studies on the Correlations between Morphological Characters, Chromosome-number and Resistance to *Puccinia triticina* in Pentaploid-Bastards of Wheat.

By

Yoshihiko Tochinai, *Nogakuhakushi*
COLLEGE OF AGRICULTURE, HOKKAIDO IMPERIAL UNIVERSITY, SAPPORO,
and
Hitoshi Kihara, *Rigakuhakushi*
COLLEGE OF AGRICULTURE, KYOTO IMPERIAL UNIVERSITY, KYOTO.

Introduction.

Rust-resistance of wheat has been studied mostly in regard to its relation to *Puccinia graminis*, while the studies relating to *Puccinia triticina* are extremely few. In Hokkaido the wheat is very severely attacked by *Puccinia triticina* and the resulting loss is generally considered as far more serious than that due to the ravages of the stem- and yellow-rusts.

The authors have studied the relation between the disease-resistance to *Puccinia triticina* and *P. graminis*, and the genetical characters of wheat-hybrids, especially their intimate relationship to the chromosome-number of hybrid-generations.

The studies have been carried out during the years from 1922 to 1925, mostly in the Phytopathological Laboratory of the College of Agriculture, Hokkaido Imperial University in Sapporo, but a part of the cytological and morphological studies was also done in the Botanical Laboratory of the College of Science, Kyoto Imperial University.

Method.[1]

In fixing pollen-mother-cells, FLEMMING's solution after the formula recommended by BONN, was used after treatment for 1 to 5 minutes with CARNOY's fluid. Sections were cut 12 to 14 microns thick. The preparations were stained generally exclusively with iron-haematoxylin

1) Technic in fixing and staining was previously reported by one of the authors, KIHARA (1919).

in order to make the counting of the chromosome-number easy. In the determination of their number, counts were made through all stages during the maturation-division, especially in the metaphase and anaphase of the first division, and if these counts did not coincide with one another, the chromosome-number of these plants was regarded as unknown.

The observations on the morphological characters of wheat and on rust-resistance were made in the field as well as in the laboratory. The plants in the field were left to natural infection in the University Farm in Sapporo.

The rust-fungi used in the present experiments.

The black-rust of wheat caused by *Puccinia graminis* has been considered to be the most important menace among the rust-diseases of wheat causing the greatest damage, for it attacks the wheat plant in the stem where the passages of the nutrient substances are destroyed. The fungus attacks the wheat plant most severely at its maturing stage and seriously prevents the ripening of the grains. The red-rust caused by *Puccinia triticina*, however, attacks the leaves and sheaths of the wheat plant from an earlier stage of its growth, and the damage caused by an attack of this fungus on wheat has been considered to be relatively unimportant. In Hokkaido, however, the greatest loss in wheat cultivation is caused by the red-rust. The leaves of wheat being severely attacked by the fungus at the most important growing period, the nutrition of the plant is greatly depressed and the resulting loss in the crop is very heavy. The harm caused by *P. graminis* is also of course estimated to be serious, but in Hokkaido the advent or appearance of the black-rust is generally later in the season, when the wheat has almost passed through the most important ripening process. For this reason, study of the red-rust is more important for us in Hokkaido than that of the black-rust.

STAKMAN and LEVINE (1922) reported the occurrence of numerous biologic forms in *P. graminis*. One of us, TOCHINAI, has sent the living uredospores of *P. graminis* collected in Sapporo, and used in the present investigations to Dr. LEVINE, at his request. Dr. LEVINE has kindly informed that the fungus under question was identified with a biologic form of *P. graminis*, *i. e. Puccinia graminis tritici XXI*, according to his infection experiment. Therefore the results obtained in the present investigations concerning *P. graminis* are of *P. graminis tritici XXI* in a strict sense.

Aecidial stage of *P. triticina* was found on the species of *Thalictrum* by JACKSON and MAINS (1921) in America. They have reported on the specific resistance of the species of *Thalictrum* to *P. triticina*, and that *Th. flavum*, *Th. Delavayi* and two other foreign species are susceptible while common American species and *Th. minus* are resistant. The most common species of *Thalictrum* in Hokkaido is *Th. minus* L. var. *elatum* LECOY. TOCHINAI (1922) proved by an infection experiment that this variety is susceptible to *P. triticina*. JACKSON and MAINS suggested the occurrence of biologic forms in *P. triticina* and that their relation to an aecidial host may vary according to the difference in forms. If there are some biologic forms differentiated in *P. triticina* in Hokkaido, the fungus used in the present investigations is a form which develops its aecidial stage most readily and abundantly on *Th. minus* var. *elatum*.

Systematic grouping of wheat.

In 1918, SAKAMURA found the chromosome-number of the species of *Triticum* to be in multiples of 7, and this remarkable find coincides perfectly with the grouping of wheat species studied from various standpoints, previously reported by SCHULZ (1913), TSCHERMAK (1914), VAVILOV (1914) and ZADE (1914). KIHARA (1919, 1921) and SAX (1921) also proved the results reported by SAKAMURA. Further, KIHARA (1924) added data on the number of chromosomes of *Triticum aegilopoides*, *boeticum* and *T. dicoccoides* (from Algeria).

TABLE I.

Showing the systematic grouping of wheat species after SCHULZ and their chromosome-number in haploid.

Monstrosity		*T. polonicum* (14)	
Naked wheat		↑ *T. durum* (14) *T. turgidum* (14)	*T. vulgare* (21) *T. compactum* (21)
Spelt wheat	*T. monococcum* (7)	↑ ↑ *T. dicoccum* (14)	↑ ↑ *T. Spelta* (21)
Wild forms	↑ *T. aegilopoides* (7)	↑ *T. dicoccoides* (14)	
	Einkorn-group	Emmer-group	Dinkel-group

As shown in Table I there are three groups in the species *Triticum*. The chromosome-number of the species belonging to the Einkorn-group is 7, to the Emmer-group is 14 and to the Dinkel-group is 21. Marked differences in the resistance to rust-fungi are found among them.

Susceptibility of pure species of wheat and its allies to rust.

The three groups of wheat are different in their resistance or susceptibility to rust-diseases. In 1914, VAVILOV reported that the Einkorn-group is immune to rust and resistant to mildew, the Dinkel-group is generally susceptible to them and the Emmer-group has an intermediate character in this respect. Before him BIFFEN (1907) reported that the Einkorn-group is extremely resistant to rust. According to several studies on this problem, the relationship between the three groups of wheat and the rust or other diseases is generally believed to be that the Dinkel-group is susceptible, the Emmer-group is partially resistant and the Einkorn-group is very resistant or immune.

About the nature of the immunity of wheat to the rust-diseases, MARSHALL WARD (1905) found that in the case of rust-resistance in wheat, as the protoplasm of the immune species, *e. g. Triticum monococcum*, is very sensitive to the attack of rust-fungi and is readily killed by an invasion of their mycelia, the supply of nutrition of the rust-fungi being interrupted, the starvation of the fungi and the resistance of the wheat follow as a consequence. MARRYAT (1907) and STAKMAN (1915) agreed with his opinion. In the view of MARSHALL WARD, the protein-substances in the protoplasm of the so-called immune or very resistant varieties and species of wheat seem lacking in antitoxic power to neutralize the injurious toxins secreted by the protoplasm of the rust-fungus. In this connection, ZADE (1914) found the serological difference of protein substances in three groups of wheat. KIHARA (1923) examined the effects of hydrogen-ion concentration on the protoplasm of several species of *Triticum* and their bastards, observing the bursting phenomenon of the pollen grains in the nutrient solutions having different hydrogen-ion concentrations of acid side. He found that generally the pollen grains of the Dinkel-group burst most easily, next come those of *T. monococcum*, and lastly those of the Emmer-group. These results accounted for the difference in the colloidal nature of the protoplasm of phylogenical wheat-strains. In each strain the reaction of the protoplasm of pollen to hydrogen-ion concentrations is almost the same. In the hybrid generations the reaction of pollen-protoplasm to hydrogen-ion concentrations shows a tendency to segregation, as it is the case in their morphological characters as well as the number of chromosomes.

These facts may show some possible relationships among rust-resistance, morphological characters, chromosome-number and physiological character of protoplasm in the phylogenical strains of wheat.

The present authors have made observations on the rust-resistance of 9 species of *Triticum* and 3 species of *Aegilops*. The resistance or susceptibility of the plants in question is classified into the following 7 degrees according to the development and number of uredo- and teleutospore sori, and the size and number of spots formed by the discoloured cells killed by the invasion of the mycelium of the rust-fungi, due to their hypersensitive character. The prompt death of the infected cells causes the starvation of these obligate parasites, thus allowing the host plant to escape from being rust-diseased.

rrrr .... Almost perfectly immune; with no sori but with very minute whitish spots.

rrr .... Highly resistant; with no spore-sori but with minute visible whitish spots.

rr ...... Resistant; with a few small spore-sori and many larger spots.

r ...... Somewhat resistant; with not a few, but small, spore-sori and many larger spots.

s ...... Susceptible; with many larger spots almost every one bearing small spore-sori.

ss ...... More susceptible; with many well developed spore-sori which occupy the greater part of the spot.

sss .... Very susceptible; with many vigorously developed spore-sori accompanied by no hypersensitive area.

The results observed in 1922 are shown in the following table:—

TABLE II.

Showing the resistance or susceptibility of pure species of wheat and its allies to the rust-fungi.

Host plants	Resistance or susceptibility to	
	Puccinia triticina	*P. graminis*
T. vulgare	*ss*	*ss*
T. Spelta	*sss*	*sss*

Host plants	Resistance or susceptibility to	
	Puccinia triticina	*P. graminis*
T. compactum	*sss*	*ss*
T. durum	*rrr*	*rrr*
T. turgidum	*rr*	*rr*
T. polonicum	*rr*	*rr*
T. dicoccum	*rrr*	*rrr*
T. dicoccoides	*rrr*	*rr*
T. monococcum	*rrrr*	*rrrr*
Ae. ovata	*rrr*	*rrr*
Ae. triticoides	*rrr*	*rrr*
Ae. squarosa	*rrr*	*rrr*

The species belonging to the Dinkel-group were generally susceptible, but the race of *T. vulgare* examined, *Sapporo-Yu-bo*, showed clearly a less number of spore-sori on its leaves and stems. Among the species belonging to the Emmer-group, *T. durum* and *T. dicoccum* were highly resistant to both rust-fungi, and *T. turgidum* and *T. polonicum* were clearly inferior to them in this connection. *T. monococcum* was almost perfectly immune to both fungi. *T. dicoccoides*, the wild species of wheat, was similar to *T. turgidum* and *T. polonicum* in its resistance to the rust-diseases. Three species of *Aegilops* showed a strong resistance to both rust-fungi, but were not perfectly immune.

F_1-hybrids of a certain two of these *Triticum* species were generally susceptible to both rust-fungi, although some differences in their susceptibility have been observed. F_1-hybrids of Dinkel-wheat and Emmer-wheat were susceptible to both fungi. F_1-hybrids of *T. durum* and *T. vulgare* (*Sapporo-Yu-bo*) were somewhat less susceptible to *P. triticina*, and more resistant to *P. graminis*. F_1-hybrids of *T. turgidum* and *T. compactum* were very susceptible to *P. triticina* and somewhat less so to *P. graminis*. F_1-hybrids of *T. polonicum* and *T. Spelta* were very susceptible to both fungi.

The changes in morphological characters and in chromosome-number.

Concerning the fluctuation of the chromosome-number in species-hybrids of *Triticum*, Kihara (1919, 1921, 1924) described the behavior of chromosomes in F_1-, F_2-, F_3- and F_4-generation in various crosses between Emmer-group ($x=14$) and Dinkel-group ($x=21$)

(*T. durum* × *T. vulgare*, *T. polonicum* × *T. Spelta*, *T. turgidum* × *T. compactum* and *T. polonicum* × *T. compactum*).

He ascertained that in the F_1-hybrids ($2x=35$), there are 14 bivalent or paired and 7 isolated univalent or unpaired chromosomes in the heterotypic division in both pollen- and embryo-sac mother cells. The 14 bivalent chromosomes consist of 14 Emmer- or 14 Dinkel-chromosomes (out of 21), and separate, as usual, in tetrad-formations, *i. e.* reduction of conjugated 14 chromosomes in the first maturation-division and longitudinal splitting in the second. The 7 univalent or unpaired Dinkel-chromosomes which have no homologous chromosomes, however, are divided longitudinally in the first division into 2 daughter-nuclei. The longitudinal splitting of 7 univalent chromosomes occurs in the later anaphase of the bivalent chromosomes. In the second division, these 7 univalent chromosomes do not split longitudinally again. They are distributed in 2 groups, 0 and 7, 1 and 6, 2 and 5, or 3 and 4. Frequently he found diminution of 7 isolated chromosomes which do not reach to the poles in the second division and are degenerated in cytoplasm.

Therefore both the pollen-grains and the egg-cells have the chromosome number represented by the formula 14+i, where "i" is equal to 0, 1, 2, 3, 4, 5, 6 or 7. Fertilization of 14+i gametes with one another gives rise to the plants having 28 to 42 chromosomes. In the formation of gemini of these plants, all possibile combinations will be shown in the following formulae. [See also KIHARA (1921, 1924)].

TABLE III.

Showing the formulae of chromosome-combinations in the formation of gemini of the plants which have from 28 to 42 chromosomes.[1]

Number of chromosomes	Combinatons of chromosomes			
	Formula I	Formula II	Formula III	Formula IV
28	14 b+0 i	—	—	—
29	14 b+1 i	—	—	—
30	14 b+2 i	15 b+0 i	—	—

1) In these formulae "b" means bivalent and "i" means univalent chromosome.

Number of chromosomes	Combinations of chromosomes			
	Formula I	Formula II	Formula III	Formula IV
31	14 b+3 i	15 b+1 i	—	—
32	14 b+4 i	15 b+2 i	16 b+0 i	—
33	14 b+5 i	15 b+3 i	16 b+1 i	—
34	14 b+6 i	15 b+4 i	16 b+2 i	17 b+0 i
35	14 b+7 i	15 b+5 i	16 b+3 i	17 b+1 i
36	15 b+6 i	16 b+4 i	17 b+2 i	18 b+0 i
37	16 b+5 i	17 b+3 i	18 b+1 i	—
38	17 b+4 i	18 b+2 i	19 b+0 i	—
39	18 b+3 i	19 b+1 i	—	—
40	19 b+2 i	—	—	—
41	20 b+1 i	—	—	—
42	21 b+0 i	—	—	—
	Fertile combination	Sterile combinations		

The combination of the first column (Formula I) was found generally. The other combinations (Formulae II, III and IV) were not so often found, and they proved weakly fertile or perfectly sterile (see Table V.).

TABLE IV.

Showing the chromosome-number and the combination of bivalent and univalent chromosomes in the hybrids of *T. durum* and *T. vulgare.*[1]

Number of strain	Metaphase plate of I division	Combinations of b. & i. chromosomes		Diploid number of chromosomes
		Bivalent	Univalent	
30 F_3 28- 5	15	14	1	29
30 F_4 1- 1- 2	14	14	0	28
6	14	14	0	28
9	14	14	0	28
14	14	14	0	28
1- 2- 1	15	14	1	29

1) In this table, the numbers in bold type show sterile combinations of chromosomes.

Number of strain	Metaphase plate of I division	Combination of b. & i. chromosomes		Diploid number of chromosomes
		Bivalent	Univalent	
2	14	14	0	28
4	14	14	0	28
5	14	14	0	28
9	15	14	0	29
16	14	14	0	28
1- 3- 1	14	14	0	28
8	14	14	0	28
15	14			28
1- 6- 2	14	14	0	28
1- 7- 1	15	14	1	29
1- 9- 1	14	14	0	28
13	14	14	0	28
2- 2- 4	**19**	**17**	**2**	**36**
5	**18**	**16**	**2**	**34**
3- 1- 5	14	14	0	28
3- 3- 2	14	14	0	28
3- 4- 1	14	14	0	28
3- 6- 2	14	14	0	28
3- 9- 2	14	14	0	28
3	14			28
5- 9- 3	14			28
5-10- 1	14			28
9- 1- 9	14	14	0	28
12	14	14	0	28
18	15	14	1	29
19	14	14	0	28
21	15	14	1	29
9- 2- 2	14	14	0	28
9 -3- 4	14	14	0	28
12	14	14	0	28
10- 1- 3	14	14	0	28
5	14			28
10- 2- 1	14	14	0	28
8	14	14	0	28

Number of strain	Metaphase plate of I division	Combination of b. & i. chromosomes		Diploid number of chromosomes
		Bivalent	Univalent	
10	14	14	0	28
11- 1- 3	14	14	0	28
11	14	14	0	28
11- 2- 2	14	14	0	28
7	14	14	0	28
11- 3- 3	14	14	0	28
4	14	14	0	28
16- 2- 4	19	16	3	35
19- 1- 1	16	14	2	30
19- 2- 5	14	14	0	28
18	15	14	1	29
21-25- 2	14	14	0	28
4	14	14	0	28
21-28- 2	14	14	0	28
7	14	14	0	28
8	14	14	0	28
9	15	14	1	29
16	14	14	0	28
22- 1- 5	19	17	2	36
22- 2- 3	20	17	3	37
4	19	15	4	34
25- 1- 3	14	14	0	28
5	14	14	0	28
6	14	14	0	28
13	14	14	0	28
25- 2- 5	14	14	0	28
7	14	14	0	28
26- 1- 1	14	14	0	28
5	14	14	0	28
8	14	14	0	28
9	14	14	0	28
10	14	14	0	28
28- 4- 2	14	14	0	28
5	14	14	0	28

Number of strain	Metaphase plate of I division	Combination of b. & i. chromosomes		Diploid number of chromosomes
		Bivalent	Univalent	
8	14	14	0	28
15	14	14	0	28
28	14	14	0	28
37	14	14	0	28
41	14	14	0	28
46	14	14	0	28
50	14	14	0	28
56	14	14	0	28
66	14	14	0	28
30- 3- 1	21	20	1	41
3	21	20	1	41
30-12- 2	20	19	1	39
4	21	18	3	39
5		18	3 (or 2)	?
31- 1- 4	14	14	0	28
6	14	14	0	28
10	14	14	0	28
31- 2- 2	14	14	0	28
4	14	14	0	28

From this reason, it is not easy to obtain homozygous plants with a new constant chromosome-combination, which is not in multiples of 7. They are constant only when the number of chromosomes decreases to 28 or increas s to 42. Occasionally plants having the new chromosome-combination, 20 b+0 i=40, occur in the cross of *T. polonicum* and *T. Spelta*. They are of conspicuously short habit so far as KIHARA (1924, 1925) studied.

In the hybrids of *T. durum* and *T. vulgare*, the plants having 28 or nearly 28 chromosomes are all of the same, or like to *T. durum* in their morphology. In the meioses of the fertile plants having from 29 to 34 chromosomes, we have always found 14 bivalent chromosomes (Formula I). The isolated univalent chromosomes tend to lag behind and often to be left out of the homeotypic nuclei in these hybrids. Succeeding generations tend to return to *durum*-type having 28 chromosomes. At most, they remain the same as the parents in chromosome-number (see Table VI). There is no increase of the number of bivalent chromosomes[1] in the descendants having a small number of chromosomes as from 29 to 34 (diminishing chromosome group).

The plants having from 36 to 41 chromosomes have from 8 to 13 *vulgare*-chromosomes besides 28 pairing chromosomes. In the gemini-formation of these 8 to 13 *vulgare*-chromosomes, the following combinations were generally found in fertile plants, *i. e.* they are fertile combinations: 8=1 b+6 i, 9=2 b+5 i, 10=3 b+4 i, 11=4 b+3 i, 12=5 b+2 i, 13=6 b+1 i.

As shown in Table III, the sum of the bivalent and univalent chromosomes is always 7 (as the whole, 14+7=21) in fertile plants. This fact indicates that in plants having from 8 to 13 chromosomes, at least one set of 7 *vulgare*-chromosomes a, b,....g is included. Each of the 7 chromosomes has individuality and they form no geminus with each other. Therefore, in the plants having 36 chromosomes, only one of them is duplicated, for instance $28+a+a+b+c+d+e+f+g$. In the plants having 37, 38, 39, 40 and 41 chromosomes the duplication of the 7 *vulgare*-chromosomes increases one by one. In case this one set of *vulgare*-chromosomes (a−g) is not acquired in the fertilization of 14+i gametes of F_1-plant (even when only one of them fails), these zygotes will not develop, or if they may develop, they are only weakly fertile and generally become perfectly sterile in the following generations. Therefore in the succeeding generations of the plants of fertile combination having from 36 to 41 chromosomes (Formula I), when the duplication of these unpaired chromosomes occurs, the number of chromosomes consequently increases. Even when the duplication does not occur, the chromosome-number remains unchanged. There occurs no decreasing of chromosome-number in the group of plants having from 36 to 41 chromosomes, while the chromosome-combination is always fertile (Vermehrungsgruppe).[2] The correlation between the chromosome-number and the morphological characters is very clearly recognized in the hybrids of *T. durum* and *T. vulgare*.[3] In the other hybrids, for instance *T. polonicum* × *T. compactum*, *T.*

1) If the number of bivalent chromosomes increased, their combination becomes sterile (cf. Table III).

2) For details see KIHARA (1924).

3) See KIHARA (1924), Plate II.

turgidum × *T. compactum*, however, the correlation was not remarkable at least in relation to the compactness of the spike.

The chromosome-number and the type of the F_4-hybrids of *T. durum* and *T. vulgare* are shown in Table V following.

TABLE V.

Showing the chromosome-number and the type in the hybrids of *T. vulgare* and *T. durum.*[1]

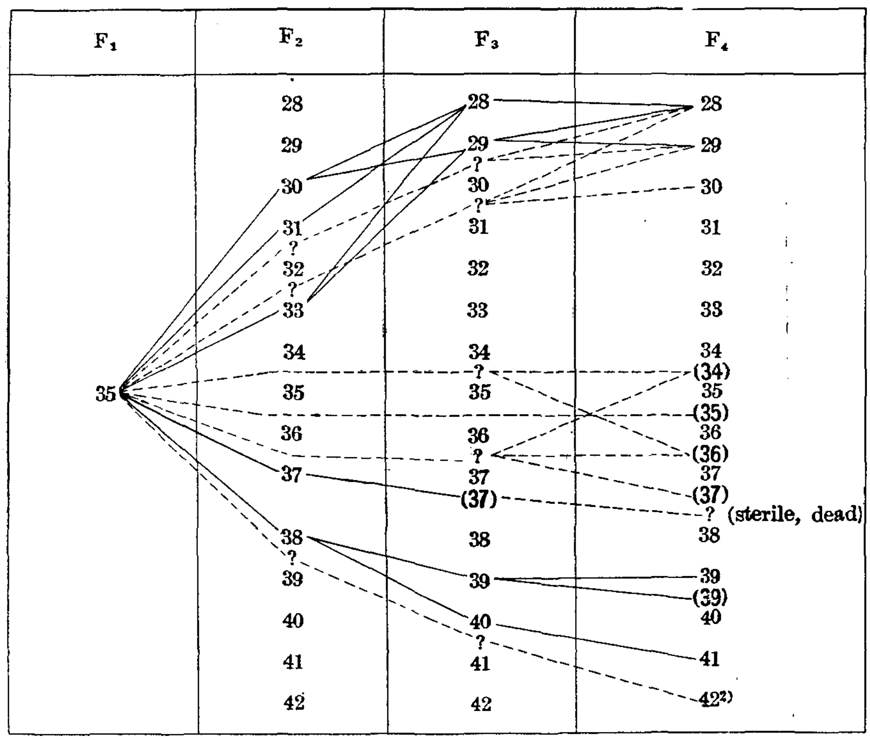
F_1	F_2		F_3		F_4		
	No. of Strain	Chr.-no.	Chr.-no.	No. of plants examined	Chr.-no.	No. of plants examined	
Chromosome-number	1				28	14	*Durum*-Type
					29	3	
	3		28	2	28	6	
	4	31	28	2			
	5				28	2	
	9				28	8	
					29	2	
	10				28	5	
	11				28	6	
	19				28	1	
					29	1	
					28	1	
	21	30	28	7	28	2	
			29	2	28	4	
					29	1	
(35)	25				28	6	
	26				28	5	
	28	33	28	1			
			29	2	28	11	
	31				28	5	
	2				**34**	1	*Vulgare* Type
					36	1	
	13	37	**37**	1	withered		
	16				**35**	1	
	22				**34**	1	
					36	1	
					37	1	
	30	38	39	1	**39**	1	
					39	1	
			40	1	**41**	2	
Total number of plants examined		5	19		93		

1) The numbers in bold type show abnormal combination of chromosomes. The plants having such chromosome-combination possess very poor fertility.

In the following table, the fluctuation of the chromosome-number in these hybrids can be clearly seen.

TABLE VI.

Showing the fluctuation of chromosome-number in the hybrids of *T. vulgare* and *T, durum.*[1]



In Table V, in strain No. 28 the chromosome-number in F_2 is 33 which in F_3 decreases to 29 and 28. As KIHARA (1924) has shown in his Plate II, the plant having 33 chromosomes is similar to *T. vulgare*, but the F_3-plants having 29 and 28 chromosomes show the perfect shape of the spike of *T. durum*. Other strains also prove this fact. In the group of multiplying chromosomes, the duplication of the 7 chromosomes does not cause remarkable changes in the morphology of the spikes. The form of the spike in the F_4-plants

1) See also KIHARA (1924), p. 49.

2) cf. KIHARA (1921), p. 25.

having 41 chromosomes appears very much like that of *T. vulgare*. A F_4-plant having 42 chromosomes (Table IV) shows the characters of *T. vulgare* exactly.

In these cases, it is important to notice that the increase in chromosome-number of the wheat-hybrids progresses slowly and decreases rapidly.

The relationship between the morphological characters, chromosome-number and the rust-resistance in F_4-generation of the wheat-hybrids.

The authors in 1921 and 1922 made observations on the susceptibility and resistance of the F_4-generation of *T. polonicum* × *T. Spelta*, *T. durum* × *T. vulgare* and *T. turgidum* × *T. compactum* to *Puccinia triticina* and *P. graminis*.

These hybrids are variously different in their chromosome-number and morphological characters.

The plants under question were left to natural infection in the field, and some of them were tested by artificial inoculation with uredospore-suspension in green-house. The results obtained by both procedures coincide with each other. The results obtained in the field are shown in the following descriptions and Table VII.

1. F_4-generation of *T. polonicum* × *T. Spelta*.

They have, in general, the morphological characters of *T. Spelta* and 42 or nearly 42 chromosomes. They were extraordinarilly susceptible to both rust-fungi, and were severely attacked by *Puccinia triticina* in the early stage of growth. Many of them were utterly killed before their maturation by the attack of the fungus, having been covered heavily with the uredospore-sori, and the surviving plants were then badly attacked by *Puccinia graminis*. Such a weakness of wheat to the attack of *P. triticina* seems to be unusual in the authors' experience. It is generally known that *T. Spelta* is susceptible and *T. polonicum* is somewhat resistant to rust-fungi, and that their species-bastards are susceptible to the rust in F_1-generation. Such being the case it is very interesting that the segregates which have 42 or nearly 42 chromosomes in advanced generations increase their susceptibility to the rust and become far more weak than their susceptible parent.

2. F_4-generation of *T. turgidum* × *T. compactum*.

They were similar to *T. compactum* in their morphological characters and chromosome-number. They were susceptible to both *P. triticina* and *P. graminis*. But they were not harmed so severely by the fungi as the hybrids above mentioned, and no plant has been killed by the attack of these fungi.

3. F_4-generation of *T. durum* × *T. vulgare*.

These hybrids showed an interesting difference in their rust-resistance correlating to the chromosome-number and morphological characters. In general, the segregates which have 28 or 29 chromosomes and *durum*-like morphological characters are mostly resistant to the rust-diseases, but the degree of the resistance changes variously according to the strains of the hybrids. Sometimes the authors have found plants which are susceptible to the rust-fungi notwithstanding the *durum*-like characters in their morphology and chromosome-number. The segregates which have advanced chromosome-number and *vulgare*-like morphological characters seem to be susceptible to the rust-fungi with no exception. The details of the observation are shown in Table VII following.

In Table VII, the resistance and susceptibility of the plants to the rust-fungi are shown by the symbols used in Table II, and the morphological characters are shown by the following symbols.

ddd .... *T. durum*-type.
ddv .... *T. durum*-type, mixed with some character of *T. vulgare*.
dv...... Characters of both *T. durum* and *T. vulgare* are mixed.
dvv .... *T. vulgare*-type, mixed with some characters of *T. durum*.
vvv .... *T. vulgare*-type.
(*K*) .... Keel develops well.
(*k*) .... Keel develops incompletely.
(*M*) .... Marrow develops well.
(*m*) .... Marrowless or incompletely marrowed.
(*l*)...... Spike is somewhat lax.

TABLE VII.

Showing the chromosome-number, morphological characters and rust-resistance in the F_4-hybrids of *T. durum* and *T. vulgare*.

No. of plant	Metaphase-plate of 1st division	Diploid number	Morphological characters	Resist. or suscept. to	
				P. triticina	*P. graminis*
1- 1- 2	14	28			
6	14	28	*ddv (m. l)*	*rr*	*rrr*
9	14	28			
14	14	28			
1- 2- 1	15	29			
2	14	28			
4	14	28	*ddv (m. l)*	*rr*	*rrr*
5	14	28			
9	15	28			
16	14	28			
1- 3- 1	14	28			
8	14	28	*ddv (k. l)*	*rr*	*rrr*
15	14	28			
1- 4			*ddv (k)*	*rr*	*rr*
1- 5			*ddv (k)*	*rr*	*r*
1- 6- 2	14	28	*ddv (l)*	*rr*	*r*
1- 7- 1	14	28	*ddv (m. l)*	*rr*	*r*
1- 8			*ddv (k)*	*rr*	*r*
1- 9- 1	14	28	*ddv (k)*	*rr*	*r*
13	14	28			
1-10			*ddv (k)*	*r*	*r*
1-11			*dv (k. m)*	*r*	*r*
1-12			*ddv (l)*	*r*	*r*
1-13			*ddv (l)*	*r*	*r*
1-14			*ddv (m. l)*	*r*	*r*
2- 2- 4	19	36	*dvv (K)*	*s*	*s*
5	18	34			
3- 1- 5	14	28	*ddv (m)*	*rr*	*rr*
3- 2			*ddv (m)*	*r*	*rr*
3- 3- 2	14	28	*ddv (m. l)*	*r*	*r*

No. of plant	Metaphase-plate of 1st division	Diploid number	Morphological characters	Resist. or suscept. to	
				P. triticina	*P. graminis*
3- 4- 1	14	28	*ddv* (*m. l*)	*rr*	*rr*
3- 5			*ddv* (*m. l*)	*r*	*r*
3- 6- 2	14	28	*ddv* (*m. l*)	*rr*	*rr*
3- 9- 2	14	28	*ddv* (*m. l*)	*rr*	*rr*
3-10			*ddv* (*m*)	*s*	*r*
3-11			*ddv* (*m*)	*s*	*r*
5- 1			*ddd*	*rr*	*r*
5- 2			*ddd*	*rr*	*r*
5- 3			*ddd*	*rr*	*rr*
5- 4			*ddd*	*rr*	*rr*
5- 5			*ddd*	*rr*	*rr*
5- 6			*ddd*	*rr*	*rr*
5- 7			*ddv* (*m*)	*rr*	*rr*
5- 9- 3	14	28	*ddv* (*m*)	*rr*	*rr*
5-10- 1	14	28	*ddv* (*m*)	*rr*	*rr*
5-12			*ddv* (*m. l*)	*r*	*r*
5-14			*ddv* (*m. l*)	*r*	*r*
5-15			*ddv* (*m. l*)	*r*	*r*
5-16			*ddv* (*m. l*)	*r*	*r*
5-17			*ddv* (*l*)	*r*	*r*
9- 1- 9	14	28			
12	14	28			
18	15	29	*dv* (*k. l*)	*s*	*s*
19	14	28			
21	15	29			
9- 2- 2	14	28	*dv* (*k. l. M*)	*s*	*s*
9- 3- 4	14	28	*dv* (*k. l. M*)	*s*	*r*
12	14	28			
9- 4- 8	14	28	*dv* (*k. l. M*)	*s*	*r*
12	14	28			
10- 1- 3	14	28	*ddv* (*k*)	*s*	*s*
10- 2- 1	14	28			
8	14	28	*dv* (*k. m*)	*s*	*s*
10	14	28			
11- 1- 3	14	28	*ddd*	*r*	*rr*

No. of plant	Metaphase-plate of 1st division	Diploid number	Morphological characters	Resist. or suscept. to	
				P. triticina	*P. graminis*
11	14	28	*ddd*	*r*	*rr*
11- 2- 2	14	28	*ddv* (*m. l*)	*s*	*r*
7	14	28			
11- 3- 3	14	28	*ddv* (*m*)	*rr*	*rr*
4	14	28			
16- 1			*vvv*	*ss*	*ss*
16- 2- 4	19	35	*dvv* (*K*)	*s*	*ss*
19- 1- 1	16	30	*ddv* (*m. l*)	*s*	*ss*
19- 2- 5	14	28	*ddv* (*m*)	*ss*	*ss*
17	15?	29?			
18	15	29			
21- 6			*ddv* (*m. l*)	*rr*	*rr*
21-12			*ddv* (*m*)	*rr*	*rr*
21-16			*ddv* (*m*)	*rr*	*rr*
21-20			*ddv* (*m*)	*rr*	*rr*
21-22			*ddv* (*m*)	*rr*	*rr*
21-25- 2	14	28	*ddv* (*k. m*)	*rr*	*rr*
4	14	28			
21-26			*ddv* (*m*)	*rr*	*rr*
21-28- 2	14	28	*ddv* (*m. l*)	*rr*	*rr*
7	14	28			
8	14	28			
9	15	29			
16	14	28			
21-29			*ddv* (*m*)	*rr*	*rr*
21-41			*ddv* (*m*)	*rr*	*rr*
21-43			*ddv* (*m*)	*rr*	*rr*
22- 1- 5	19	36	*vvv*	*ss*	*s*
22- 2- 3	20	37	*vvv*	*ss*	*s*
4	19	34			
25- 1- 3	14	28	*ddd*	*rr*	*rrr*
5	14	28			
6	14	28			
13	14	28			
25- 2- 5	14	28	*ddv* (*k*)	*rr*	*rrr*

No. of plant	Metaphase-plate of 1st division	Diploid number	Morphological characters	Resist. or suscept. to	
				P. triticina	*P. graminis*
7	14	28	*ddv* (*k*)	*rr*	*rrr*
26- 1- 1	14	28	*ddv* (*m*)	*rr*	*rr*
5	14	28			
8	14	28			
9	14	28			
10	14	28			
26- 2			*ddv* (*m. l*)	*rr*	*rr*
28- 2			*ddv* (*m. l*)	*r*	*rr*
28- 4-(2-66)	14	28	*ddv* (*m. l*)	*r*	*rr*
30- 3- 1	21	41	*dvv* (*K*)	*s*	*s*
2	21	41			
30- 8			*dvv* (*K*)	*s*	*s*
30-12- 2	20	39	*dvv* (*K*)	*s*	*s*
4	21	39			
31- 1- 4	14	28	*ddv* (*m. l*)	*rr*	*rr*
6	14	28			
10	14	28			
31- 2- 2	14	28	*ddv* (*m*)	*r*	*rr*
4	14	28			
$30F_3$ 28- 5	15	29	*ddv* (*m*)	*r*	*r*

Discussions.

On the nature or principle of rust-resistance in wheat, valuable discussions have been given by many authors. The works of MARSHALL WARD (1905), MARRYAT (1907) and VAVILOV (1913, 1914, 1918) have been cited already in the foregoing pages. BIFFEN (1905, 1907, 1912) found that the susceptible character of wheat to *Puccinia glumarum* is dominant in inheritance, and on crossing resistant and susceptible varieties the resulting offsprings are susceptible, which produce on self-fertilization resistant and susceptible descendants in the proportion of one of the former to three of the latter. NILSSON-EHLE (1909), however, did not find any definite ratio of the segregation caused by multiple factors. POLE-EVANS (1911) reported that the hybrids of susceptible and immune wheats are more easily attacked by *Puccinia graminis* than the susceptible parents, and the rust-fungus increases its virulence by passing the hybrids. H. B. HUMPHREY (1917) found several resistant wheats among *T. vulgare*, varieties of *T. durum* and their hybrids. STAKMAN, PARKER and PIEMEISEL (1918) found that the biologic forms of *P. graminis* do not change their parasitic behaviour so rapidly as to interfere with breeding for rust-resistance. HAYES, PARKER and KURTZWELL (1920) reported on the inheritance of resistance to *P. graminis* in the hybrids of *T. vulgare*, *T. durum* and *T. dicoccum*. ARMSTRONG (1922) reported that nitrogenous fertilizers and wide spacing of plants may increase the susceptibility. RAINES (1922) concluded that susceptibility to rust-fungi increases as the vegetative vigour of the host increases. SAX (1923) found a correlation between chromosome-number and morphological characters, and resistance to *P. graminis* usualy in the hybrids of *T. vulgare* and *T. durum*.

In the present investigations *P. triticina*, which causes great damage to wheat cultivation in Hokkaido, was brought under principal consideration as well as *P. graminis*. The authors have found relationship between the rust-resistance and genetical characters of wheats almost analogous to that noticed by former investigators about *P. graminis* and *P. glumarum*. Moreover, they have found somewhat clear correlation between the change of chromosome-number and rust-resistance in pentaploid-bastards of wheats.

As far as our observations are concerned, the change of chromosome-number in the bastards of *T. vulgare* and *T. durum* almost coincides with the change of their morphological characters and rust-resistance. The morphological characters and the rust-resistance of the plants which have 42 or nearly 42 chromosomes closely resemble those of *T. vulgare*. On the other hand, the morphological characters and rust-resistance of the plants which have 28 or nearly 28 chromosomes are almost the same as those of *T. durum*. In these respects, it is highly probable that 7 chromosomes which determine the characteristics of *T. vulgare* play an important role in the susceptibility of wheat to rust-fungi.

As has been stated in the foregoing pages, KIHARA (1924) had assumed that the F_1-generation of the pentaploid-bastard of wheats have the following formula of chromosome-combination, that is

$$14\,b+7\,i, \quad \text{or} \quad 14_{II}+7_{I},$$

and he named each of the 7 univalent chromosomes *a*, *b*, *c*, *d*, *e*, *f*, and *g*. In other words, he considered that certain definite chromosomes, *i. e.*, *a* to *g*, in 21 chromosomes of Dinkel-parent are univalent. Some of these chromosomes ($a-g$) are always found as univalent ones in the plants belonging to the so-called "Vermehrungsgruppe".

Consideration of the reason why the univalent chromosomes in F_1-plant are constantly definite ($a-g$), is very important in order to ascertain the genetical phenomena in the pentaploid-bastards. If 14 bivalent chromosomes of F_1-plants of pentaploid-bastards constantly consist of definite 14 chromosomes of Dinkel-wheat and 14 chromosomes of Emmer-wheat, the remaining 7 univalent chromosomes, from *a* to *g*, may be considered as special chromosomes.

Recently, according to LJUNGDAHL (1924), it has become known that there are two modes of chromosome-conjugation in the gemini-formation of F_1-bastard between poly- and di-ploid-plants:—

1. Allosyndesis, *i. e.* combination of chromosomes of male parent and corresponding chromosomes of female parent;
2. Autosyndesis, *i. e.* combination of chromosomes of one of the parents, for example, in a case of *Papaver*-hybrid which has $7+35$ chromosomes.

As 21 b+0 i chromosomes in the reduction division of the hybrid could be clearly determined, it must be the case that 14 bivalent chromosomes are combined according to autosyndesis and the remaining 7 chromosomes are combined according to allosyndesis.

Now the authors adopt this idea in the case of wheat-hybrids in order to learn whether autosyndesis may occur or not. It is necessary as LJUNGDAHL has already pointed out that the reduced number of chromosomes in one of the parents of the hybrids be at least three times that of the other. Therefore, a hexaploid-plant is needed to cross with a diploid-plant. The crossing of wheat and rye done by KIHARA (1924) is such a case. The hybrid has $21+7=28$ diploid chromosomes. Among these chromosomes, 21 come from wheat (*T. vulgare*) and the remaining 7 come from rye (*Secale cereale*). Observing the reduction division of these hybrids in pollen-mother-cells, (1) there is no geminus, or (2) there are from 1 to 3 gemini. In the former case, there is neither autosyndesis nor allosyndesis. The gemini formed in the latter case are very loose and variable in their number. These gemini differ wholly from those appearing in F_1-generation of pentaploid-bastard. They may be considered as formed due to incomplete allosyndesis. Accordingly we can fully assume that all of the bivalent chromosomes in the F_1-plant of pentaploid-bastard are combined due to allosyndesis.

In view of the foregoing, it becomes evident that autosyndesis never occurs in gemini-formation of wheats. In 14 b + 7 i chromosomes in F_1-hybrid, we name the univalent chromosomes $(a-g)$ D in one set, and each of the two sets of the other 14 chromosomes A and B. Then A, B and D do not combine with each other. Now naming A and B of Emmer-wheat A_E and B_E and those of Dinkel-wheat A_D and B_D, A_E combines with A_D and B_E combines with B_D. However, D never combines with any of them (A_E, A_D, B_E and B_D). In other words, D-chromosomes $(a-g)$ remain constantly as univalent in the pentaploid-bastard F_1.

Each chromosome of these five sets of chromosomes being represented by A_E, B_E, A_D, B_D and D respectively, then the combination of these chromosomes in the parents, F_1-hybrids and homozygous F_2-hybrids of the pentaploid-bastards is as follows (Kihara, 1924, p. 182):

$A_E\ A_E\ B_E\ B_E \times A_D\ A_D\ B_D\ B_D\ D\ D$ .... Parents
(28) (42)

$A_E\ A_D\ B_E\ B_D\ D$ .... F_1
(35)

" Verminderungsgruppe " | " Vermehrungsgruppe "

" Verminderungsgruppe "	" Vermehrungsgruppe "	
$A_E\ A_E\ B_E\ B_E$	$A_E\ A_E\ B_E\ B_E\ D\ D$	
$A_E\ A_E\ B_D\ B_D$	$A_E\ A_E\ B_D\ B_D\ D\ D$	.. Homozygous
$A_D\ A_D\ B_E\ B_E$	$A_D\ A_D\ B_F\ B_E\ D\ D$	F_2
$A_D\ A_D\ B_D\ B_D$	$A_D\ A_D\ B_D\ B_D\ D\ D$	
(28)	(42)	

As shown above, four cases of homozygous combination occur in both groups by combination of every one pair of A and B. As there could be 7 pairs of either A or B, making 14 pairs in all, homozygous combinations among these chromosomes are expected in $(2)^{14}$ cases.

$$(2)^{14}=(1+1)^{14}=1+{}_{14}C_1+{}_{14}C_2+\ldots\ldots+{}_{14}C_7+\ldots\ldots{}_{14}C_{13}+1.$$

1 ... All chromosomes come from Emmer.

${}_{14}C_1$ ... 1 pair of Dinkel-chromosomes and the other 13 pairs of Emmer-chromosomes.

${}_{14}C_2$ ... 2 pairs of Dinkel-chromosomes and the other 12 pairs of Emmer-chrom.

${}_{14}C_7$ ... 7 pairs of either Emmer- or Dinkel-chromosomes.

${}_{14}C_{13}$ ... 13 pairs of Dinkel-chromosomes and 1 pair of Emmer-chromosomes.

1 ... All chromosomes come from Dinkel.

As shown in the above formula, the occurrence of the pentaploid-bastard which has Emmer- or Dinkel-chromosomes only remains as a very rare case. Accordingly even if the plant which has such chromosome-combination as A_E A_E B_E B_E D D be rust-resistant, because it has ample Emmer-chromosomes, such a case will very rarely occur. Especially, the chance of the occurrence of such a plant can hardly be expected in the case of crossing between *T. vulgare* and *T. durum*, for a majority of their bastards belongs to the "Verminderungsgruppe" and the plants belonging to the "Vermehrungsgruppe" are smaller in number. The plants which have such chromosome-combination as A_D A_D B_D B_D may be thought to be rust-susceptible in view of their chromosome-combination. The occurrence of comparatively susceptible plants among the descendants belonging to the *durum*-type seems to indicate the probability of such combination of chromosomes.

NILSSON-EHLE (1909, 1911) found the existence of three pairs of duplicate genes.[1] Considering these genes to exist in chromosomes, A, B and D, the genetical phenomenon, for example the colour of grain in wheat-bastards, can easily be explained. According to him, compactness of ear is determined by 3 pairs of genes, and among them two pairs of duplicate genes (L, M) make the ear long and lax, and genes C make it short and compact (C is epistatic to L and M).

In the present case of pentaploid-bastard of *T. durum* and *T. vulgare*, the gene or genes existing in D which make the ear long and lax seem to be epistatic to genes in A and B which make the ear short and compact. In the present case, the morphology of the ear means its laxity and length, and not the shape of the spikelet and glume which is determined by other genes. The marrowy character of the stalk of *T. durum* has been considered dominant, but the authors think this character to be intermediate and that the presence of genes in D prevents the occurrence of a completely marrowy stalk. The pithiness of straw does not ever occur in the plants belonging to the "Vermehrungsgruppe".

From the physiological point of view, KIHARA (1923) has reported an interesting fact that in the pentaploid-bastards of wheats, the physical character of the protoplasm of their pollen grains changes

1) The existence of duplicate genes may not be confined to the plants with polyploid chromosome-number.

concordantly with the change of chromosome-number and morphological characters.

The rust-resistance, the principal theme in the present investigations, seems to be one of the characters which are weakened also by the presence of genes in D. Accordingly, to breed the rust-resistant wheat-strain by means of crossing Dinkel- and Emmer-wheats seems not to be easily achieved, though one can not dare say it to be impossible.

In the authors' view, the most effective means of producing rust-resistant varieties of wheat is to be sought in the selection and crossing among the races of *T. vulgare*. To breed a resistant strain following this suggestion in a certain locality may be the most practical and easy way. In the Agricultural Experiment Station of the Hokkaido Government, ABIKO (1925) has gained a valuable strain of wheat highly resistant to *P. triticina* in F_5-generation of the hybrid of Turkey-Red and Marchins-Amber.

Further investigations on the descendants of the pentaploid-bastards of wheats, however, are both necessary and interesting in order to find out useful hints for the breeding of rust-resistant wheat.

Summary

1. Former investigations on the relationship between genetical characters and rust-resistance of wheat have been carried out mostly on *Puccinia graminis* and *P. glumarum*, and a little on *P. triticina*. In the present studies, however, the authors have laid stress upon *P. triticina* as well as upon *P. graminis*.

2. Systematic grouping of wheat arranged by SCHULZ (1913) coincides perfectly with the results obtained by the phytopathological studies of VAVILOV (1914), serological studies of ZADE (1914) and cytological studies of SAKAMURA (1918). The results obtained in the observations on the resistance and susceptibility of 9 species of *Triticum* and 3 species of *Aegilops* to *P. triticina* and *P. graminis* coincide well with the results reported by VAVILOV (1914). Three species of *Aegilops*, which has close relationship to *Triticum*, are strongly resistant to both rust fungi, but not immune as *T. monococcum*.

3. The rust-resistance of F_4-generation of wheat-hybrids is most interesting in the case of *T. durum* × *T. vulgare*. In general, the segregates having 28 or 29 chromosomes and *durum*-like morphological characters are mostly resistant, and the segregates having *vulgare*-like characters in their morphology and chromosome-number

are susceptible to both rust-fungi. The degree of the resistance or susceptibility, however, changes variously according to the strains of the hybrids.

4. F_4-generation of the hybrids of *T. polonicum* and *T. Spelta* having, in general, *Spelta*-like shape and nearly 42 chromosomes are unusually susceptible to the attack of *P. triticina*. It is noteworthy that the descendants in the cross of somewhat rust-resistant *T. polonicum* and susceptible *T. Spelta* are far weaker to the rust-fungi than the susceptible parent.

5. F_4-generation of the hybrids of *T. turgidum* and *T. compactum* being similar to or like *T. compactum* in their morphological characters and chromosome-number, are generally as susceptible to both rust-fungi as their susceptible parent.

6. In the crossing of Emmer-wheat and Dinkel-wheat, the combination of the chromosomes of the parents conforms to certain rules. F_1-hybrid has 35 (14 b + 7 i) chromosomes, and in the following generations, the chromosome-number of the descendant plants increasing to 42 or decreasing to 28, the chromosome-combination becomes homozygous when the number of chromosomes coincides with that of parents, *i. e.* 42 or 28. It is important to notice that the chromosome-number increases slowly and decreases rapidly in advancing generations of the hybrids. These fluctuations of the number of chromosomes result from casting off or from duplication of 7 chromosomes which were univalent in F_1-plants. The resistance of wheat to rust-fungi seems also to be one of the characters which are weakened by the presence of genes existing in these 7 chromosomes. Accordingly, a rust-resistant wheat-strain will hardly be obtained by means of crossing Emmer- and Dinkel-wheats, though it may not be utterly impossible. In the authors' view, the most practical means of breeding rust-resistant wheat may be found in selection and crossing among comparatively resistant races of *T. vulgare*. Further investigations on the descendants of the pentaploid-bastards of wheat, however, are both necessary and interesting in the studies of rust-resistant wheat.

The authors wish to acknowledge their heartiest thanks to Dr. Kingo Miyabe, Professor of Botany in the College of Agriculture, Hokkaido Imperial University in Sapporo, for his kind reading and criticism of the present paper.

LITERATURE CITED

ABIKO, K. (1925): On the breeding of wheat resistant to *Puccinia triticina*. (Japanese). Jour. Soc. Agric. and Forest., Sapporo. Year 17, pp. 311–318.

ARMSTRONG, S. F. (1922): The mendelian inheritance of susceptibility and resistance to yellow rust (*Puccinia glumarum* ERIKS. et HENN.) in wheat. Jour. Agric. Sci. Vol. 12, pp. 56–96.

BIFFEN, R. H. (1905): Mendel's laws of inheritance and wheat breeding. Jour. Agric. Sci. Vol. 1, pp. 1–48.

BIFFEN, R. H. (1907): Studies in the inheritance of disease resistance I. Jour. Agric. Sci. Vol. 2, pp. 109–128.

BIFFEN, R. H. (1912): Studies in the inheritance of disease resistance II. Jour. Agric. Sci. Vol. 4, pp. 421–429.

HAYES, H. K., PARKER, J. H. and KURTZWELL, C. (1920): Genetics of rust resistance in crosses of varieties of *Triticum vulgare* with varieties of *T. durum* and *T. dicoccum*. Jour. Agric. Res. Vol. 19, pp. 523–542.

HUMPHREY, H. B. (1917): Cereal diseases and the national food supply. U. S. Dept. Agric. Yearbook 1917. pp. 481-495.

JACKSON, H. S. and MAINS, E. B. (1921): Aecial stage of the orange leaf-rust of wheat, *Puccinia triticina* ERIKS. Jour. Agric. Res. Vol. 22, pp. 151–171.

KIHARA, H. (1919): Über cytologische Studien bei einigen Getreidearten. Mit. I. Spezies-Bastard des Weizens und Weizenroggen-Bastard. Tokyo Bot. Mag. Vol. 33, pp. 17–38.

KIHARA, H. (1921): Über cytologische Studien bei einigen Getreidearten. Mit. III. Über die Schwankungen der Chromosomenzahlen bei den Speziesbastarden der *Triticum*-Arten. Tokyo Bot. Mag. Vol. 35, pp. 19–44.

KIHARA, H. (1923): On the physical nature of protoplasm of the wheats. (Japanese). Jour. Soc. Agric. and Forest., Sapporo. Year 15, pp. 55–68. English abstract in Japanese Jour. Bot. Vol. 2, pp. (8–9).

KIHARA, H. (1924): Cytologische und genetische Studien bei wichtigen Getreidearten mit besonderer Rücksicht auf das Verhalten der Chromosomen und die Sterilität in den Bastarden. Memoirs of the Coll. of Sci., Kyoto Imp. Univ., Series B. No. 1, pp. 1–200.

KIHARA, H. (1925): Weitere Untersuchungen über die pentaploiden *Triticum*-Bastarde. I. Japanese Jour. Bot. Vol. 2, pp. 299–304.

LJUNGDAHL, H. (1924): Über die Herkunft der in der Meiosis konjugierenden Chromosomen bei *Papaver*-Hybriden. Svensk Bot. Tidskr. Vol. 8.

MARRYAT, D. C. E. (1907): Notes on the infection and histology of two wheats immune to the attacks of *Puccinia glumarum*, yellow rust. Jour. Agric. Sci. Vol. 2, pp. 129–138.

MARSHALL WARD, H. (1905): Recent researches on the parasitism of fungi. Ann. Bot. Vol. 19, pp. 1–54.

NILSSON-EHLE, H. (1909): Kreuzungsuntersuchungen an Hafer und Weizen. Lunds. Univ. Arsskrift. Vol. 5.

NILSSON-EHLE, H. (1911): Kreuzungsuntersuchungen an Hafer und Weizen. Lunds. Univ. 'Arsskrift. Vol. 7.

POLE-EVANS, I. B. (1911): South African cereal rusts, with observations on the problem of breeding rust resistant wheat. Jour. Agric. Sci. Vol. 4, pp. 95–104.

RAINES, M. A. (1922): Vegetative vigor of the host as a factor influencing susceptibility and resistance to certain rust diseases of the higher plants. Amer. Jour. Bot. Vol. 9, pp. 183–203 and 215–238.

SAKAMURA, T. (1918): Kurze Mitteilung über die Chromosomenzahlen und die Verwandtschaftsverhältnisse der *Triticum*-Arten. Tokyo Bot. Mag. Vol. 32, pp. 150–153.

SAX, K. (1921): Sterility in wheat hybrids. I. Sterility relationships and endosperm development. Genetics Vol. 6, pp. 399–416.

SAX, K. (1923): The relation between chromosome number, morphological characters and rust resistance in segregates of partially sterile wheat hybrids. Genetics Vol. 8, pp. 301–321.

SCHULZ, A. (1913): Die Geschichte der kultivierten Getreide, I. Halle.

STAKMAN, E. C. (1915): Relations between *Puccinia graminis* and plants highly resistant to its attack. Jour. Agric. Res. Vol. 4, pp. 193–199.

STAKMAN, E. C. and LEVINE, M. N. (1922): The determination of biologic forms of *Puccinia graminis* on *Triticum spp.* Minnesota Agric. Exp. Sta. Technical Bull. 8, pp. 3–10.

STAKMAN, E. C., PARKER, J. H. and PIEMEISEL, E. J. (1918): Can biologic forms of stem rust on wheat change rapidly enough to interfere with breeding for rust resistance? Jour. Agric. Res.

Vol. 14, pp. 111–123.

TOCHINAI, Y. (1922): On the aecidial stage of the red rust of wheat, *Puccinia triticina* ERIKS. (Japanese). Jour. Plant-Protect. Vol. 9, pp. 63–71. English abstract in Japanese Jour. Bot. Vol. 1, p. (32).

TSCHERMAK, E. (1914): Die Verwertung der Bastardierung für physiologische Frage in der Getreidegruppe. Zeitschr. f. Pflanzenzücht. Vol. 2, pp. 201–312.

VAVILOV, N. I. (1913): Beiträge zur Frage über die verschiedene Wiederstandfähigkeit der Getreide gegen parasitische Pilze. Arbeit. d. Versuchsstation f. Pflanzenzücht. am Moskauer landwirtsch. Institute, I Folge.

VAVILOV, N. I. (1914): Immunity to fungous diseases as a physiological test in genetics and systematics, exemplified in cereals. Jour. Genetics Vol. 4, pp. 49–65.

VAVILOV, N. I. (1918): Immunity of plants to infectious diseases. Proc. Petersburg Acad.

ZADE, A. (1914): Serologische Studien an Legminosen und Gramineen. Zeitschr. f. Pflanzenzücht. Vol. 2, pp. 101–151.