THE RELATION BETWEEN CHROMOSOME NUMBER, MORPHOLOGICAL CHARACTERS AND RUST RESISTANCE IN SEGREGATES OF PARTIALLY STERILE WHEAT HYBRIDS[1]

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INTRODUCTION

Crosses between *Triticum vulgare* with 21 gametic chromosomes and *T. durum* with 14 gametic chromosomes result in partially sterile F_1 plants and F_2 segregates with all degrees of sterility. In the reduction divisions of the F_1 pollen mother cells there are 14 bivalent and 7 univalent chromosomes. The bivalent chromosomes divide normally in both divisions, but the univalent chromosomes divide equationally in the first division after the members of the bivalents have passed to the poles, and in the second division the univalent chromosomes pass at random to one pole or the other without dividing. Thus the F_1 gametes contain from 14 to 21 chromosomes, the frequency distribution depending on random assortment of the 7 univalent chromosomes (SAX 1921, 1922).

Sterility in the F_1 and later generations can be attributed to the unbalanced numerical relations of the chromosomes, due to the random distribution of the univalents, and to incompatibility of certain chromosome combinations even among the bivalents. It is assumed that gametic and somatic perfection increase as the chromosome number and constitution approach the parental types. The seven additional chromosomes of *T. vulgare* apparently determine the characters which distinguish the *vulgare* from the *durum* and other 14-chromosome wheats. The above

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conclusions in regard to sterility will explain the partial association of parental characters in F_2 segregates, the occurrence of species of Triticum with chromosome numbers in multiples of seven, and the difficulty in obtaining homozygous segregates combining the desirable characters of the Vulgare and Emmer wheats. Cytological and genetic data are now available which support the above conclusions and show clearly the relation between chromosome number, morphological characters and rust resistance.

STERILITY IN HYBRIDS OF *Triticum vulgare* × *T. durum*

Sterility in wheat hybrids can be measured by grains set per spikelet and by the percentage of obviously poor pollen grains. The amount sterility varies in different species crosses and even in the same species cross with different varieties (SAX 1921). In the F_1 hybrids between *T. vulgare* and *T. durum* the degree of sterility as measured by grains set per spikelet varied from 50 to 83 percent. From 11 to 21 percent of the F_1 pollen grains were obviously aborted as compared with about 1 percent for the parents, but many of the apparently morphologically perfect F_1 pollen grains were probably not functional. It is assumed that all of the fertile egg cells are fertilized because of the large number of pollen grains available in each flower.[2] Some of these F_1 pollen grains are functional and it is probable that there is selective fertilization if gametic perfection increases as the chromosome number approaches 14 or 21.

Since sterility is measured by both male and female gametic development it is of interest to determine to what extent the same factors are involved. Considerable correlation was found in the F_3 segregates of Amby × Kubanka between the percent of imperfect pollen and the number of grains per spikelet ($r = -.49 \pm .07$). One might expect a higher correlation if sterility of pollen grains and egg cells is due to the same causes. However, many apparently morphologically perfect pollen grains may not be functional and the absence of grain development of the plant may be due to weak somatic development and not due to gametic sterility. Considering the various factors which may cause variability in gametic sterility the correlation obtained may indicate that the same factors are involved in the sterility of egg cells and pollen grains.

[2] If fertilization is not effected by the pollen from the same flower the glumes remain open a long time thus permitting cross-pollination instead of the usual self-pollination. It is probable that cross-pollination occurs more frequently in partially sterile hybrids than in completely fertile individuals, but the amount of cross-pollination which occurs would not greatly affect the general cytological and genetic correlations found in such hybrids. The increased susceptibility to ergot which BIFFEN (1912) finds in partially sterile hybrids is undoubtedly due to the long period during which many of the flowers remain open and exposed to the spores of this fungus.

The degree of sterility in the F_2 and F_3 has been obtained for the cross *T. vulgare* (Amby) × *T. durum* (Kubanka). The frequency distribution of sterility as indicated by grains set per spikelet are shown in table 1. In the F_2 and F_3 segregates only the grains set in the outer florets of each spikelet were counted so that 1.8 to 2.0 grains per spikelet would represent the fertility of the parents. The degree of sterility in this particular cross is about 80 percent in F_1, 50 percent in F_2 and 25 percent in F_3. It is evident that the degree of sterility rapidly decreases in successive generations even though much of the sterility in F_2 and F_3 is due to weak somatic development as well as gametic imperfections.

TABLE 1

Sterility in F_2 and F_3 of T. vulgare × T. durum.

Grains per spikelet.

	0-.2	.2	.4	.6	.8	1.0	1.2	1.4	1.6	1.8	2.0 2.2	*n*	Mean	S. D.
F_2 frequency...	7	6	4	3	4	6	1	5	4	9	3	52	1.07 ± .06	.68 ± .04
F_3 frequency...			2		2	1	2	9	8	12	2	38	1.59 ± .04	.38 ± .03

It has been assumed that sterility is due to unbalanced numerical relationships of the chromosomes as a result of random assortment of the 7 univalents, and to incompatibility of certain chromosome combinations even among the bivalents (SAX 1922). If all gametes with 17 or 18 chromosomes rarely function, then the degree of sterility found in F_1 individuals would be largely accounted for. On this basis 70 gametes in a total of 128 would be eliminated. It is probable that gametes with 16 and 19 chromosomes are also less fertile than those with 21 or 14 chromosomes. The frequency distributions of all combinations of univalents and for the 14 bivalents are shown in table 2. It is evident from this table that only 1 gamete in 64 will have either 14 or 21 chromosomes, i.e., either 0 or 7 univalents.

TABLE 2

Recombinations of Emmer and Vulgare chromosomes in F_1 gametes. Frequencies given for the 7 singles and the 14 members of bivalents.

Vulgare...........	0	1	2	3	4	5	6	7							
Frequencies.........	1	7	21	35	35	21	7	1							

Emmer............	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0
Vulgare...........	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Frequencies.........	1	14	91	364	1001	2002	3003	3432	3003	2002	1001	364	91	14	1

It is also clear that unless there is almost complete compatibility among the 14 members of the bivalents, considerable sterility would result. For instance, if combinations of equal numbers of *durum* and *vulgare* chromosomes or 6 chromosomes from one parent and 8 chromosomes from the other parent resulted in non-functional gametes, then 9,438 or 58 percent of the bivalent combinations would be sterile. Evidence to be presented later indicates that most of the sterility can be attributed to the irregular behavior of the 7 univalent chromosomes, so it must be assumed that, with few exceptions, all combinations of *vulgare* and *durum* chromosomes are compatible among the 14 primary chromosomes in the F_1 gametes.

In the F_2, sterility may be due to unfavorable somatic development or to gametic sterility *per se*. In the F_1, two complete sets of chromosomes are present and the F_1 plants are unusually large and vigorous. In the F_2, however, certain chromosome combinations inhibit vegetative development so that many seeds do not germinate or if they germinate they do not pass the rosette stage. Under greenhouse conditions about half of the F_1 seeds produce F_2 plants which bear grain. Under field conditions this proportion may be considerably less. In a cross of *T. vulgare* × *T. polonicum* 309 F_1 seeds gave 97 F_2 plants in 1922.

If the female gametes with 17 or 18 chromosomes do not develop and those with 16 or 19 chromosomes are less perfect than those with 14 or 21 chromosomes the sterility of the female gametes is largely accounted for. Selective fertilization would be expected among the pollen grains, those with 14 or 21 chromosomes being more perfect would function with greatest frequency. In the F_2 and subsequent generations there is further elimination of intermediate types in both somatic and gametic development. As a result of these various factors three classes of segregates would be expected, one group with the chromosome number similar to that of the *durum* parent, another group with the chromosome number similar to that of the *vulgare* parent and a third group with an intermediate chromosome number.

THE CHROMOSOME NUMBER IN F_2 AND F_3 SEGREGATES OF *T. vulgare* × *T. durum* AND *T. polonicum*

The chromosome counts for F_2 and F_3 plants were determined from preparations made by BELLING'S (1921) method. Pollen mother cells were mounted in iron aceto-carmine and counts were made without pressing out the cell contents. In many cases camera lucida drawings were made. It was often difficult to distinguish univalents from bivalent chromosomes, especially in the metaphase, so in correlating chromosome number with morphological characters the total haploid chromosome number was used. In several cases however 14 ± 1 bivalents and 5 to 7 univalents could be counted. It was also difficult in many cases to get the chromosome count more accurate than ± 1. In grouping the chromosome counts the few plants with counts of 15 or 20 were classed as 14 or 21, respectively, and all plants with an intermediate chromosome number were grouped. In table 3 the calculated somatic chromosome number is given for 15 F_2 segregates of Red Fife × Polish and for 46 F_3 segregates of Amby × Kubanka.

TABLE 3

Frequency of chromosome numbers in partially sterile wheat hybrids.

HYBRIDS	DIPLOID CHROMOSOME NUMBER															n
	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	
T. vulgare × *T. polonicum* (F_2)	5				1		1	5	2						1	15
T. vulgare × *T. durum* (F_3)	21		1	1	1	1	1	4	2	1	1				12	46

It is evident that a far greater number of F_2 segregates have either 14 or 21 chromosomes than would be expected if all gametes were functional. With no elimination of gametes and no selective fertilization only 2 plants in 16,384 F_2 segregates would have either 28 or 42 chromosomes. In both F_2 and F_3 segregates the plants with intermediate chromosome numbers could in some cases be attributed to the union of gametes with chromosome numbers similar to the two parental types. The above distributions of chromosome counts show clearly that the functional perfection of the gametes increases as the chromosome number approaches the parental type and that gametes and plants with an intermediate chromosome number are rapidly eliminated.

THE CORRELATION BETWEEN CHROMOSOME NUMBER, MORPHOLOGICAL CHARACTERS AND RUST RESISTANCE

The relations between chromosome number, morphological characters and rust resistance were determined for F_3 segregates of *T. vulgare* × *T. durum* (Amby × Kubanka). Data on rust resistance were obtained in the field. The climatic conditions in 1922 were very favorable for rust development and susceptible varieties were very severely infected. The rust found was *Puccinia graminis* as indicated by the pustules and the shape of the teleutospores, but it was not possible to class it in any of the 38 biologic forms described by STAKMAN and LEVINE (1922). In my cultures Einkorn was very resistant, Kubanka was moderately resistant, at least, while Marquis and a club wheat very similar to Little Club were both extremely susceptible. A scale of rust resistance similar to those used by previous investigators was adopted. Data on pollen-grain size and variability were obtained from measurements of about 60 pollen grains from each F_3 plant. The following code was used in describing the F_3 plants.

CODE FOR DESCRIPTIONS OF WHEAT HYBRIDS

K = Kubanka. A = Amby.

a. Rust resistance
  1. Very resistant but not immune, K
  2 to 5. Intermediate stages
  6. Very susceptible A
b. Mean pollen-grain diameter in microns; A = 60, K = 55
f. General type of head
  1. Vulgare type, A
  2. Intermediate
  3. Emmer type, K
g. Diameter of culm in mm; A = 2.2, K = 1.5
h. Spikelet shape
  1. Open as in Amby
  2. Intermediate
  3. Compressed as in Kubanka
i. Keel hape
  1. Small as in Amby
  2. Intermediate
  3. Large as in Kubanka
j. Length of longest beard in cm; A = 0, K = 17
n. Compactness of head
  1. Compact as in Kubanka
  2. Intermediate
  3. Open as in Amby
o. Chromosome number, (haploid); A = 21, K = 14
q. Standard deviation of pollen-grain diameter
r. Percent of poor pollen
s. Grains per spikelet

In each case the characters of the two parents are indicated. For correlations between different morphological characters, data on 52 plants are available; for the relation between rust resistance and morphological characters 49 plants are described; for the relation between chromosome number and morphological characters 38 plants are described and for correlations between chromosome number and rust resistance 37 plants are available. The different numbers used are largely due to the fact that many plants for which chromosome counts were made had only one head and the latter was used for chromosome counts. Chromosome counts were obtained for 25 F_3 families. In practically all cases members of the same family,—i.e., descendants of the same F_2 plant,—had the same chromosome number.

The classification of characters into broad categories and the bimodal frequency distribution in many cases made the use of the correlation coefficient, as a measure of association, of doubtful value. Accordingly, for such cases the coefficient of contingency η was used (PEARSON 1913).[3] The probable error of the coefficient of contingency was taken as four-thirds of the probable error of the correlation coefficient for the same value of n and r. In cases where only one side of the correlation table was classed in large groups the correlation ratio, r_c, was used. When both sides of the correlation table were classed in numerical measurements the correlation coefficient was used.

The correlations between chromosome number, morphological characters, and rust resistance are shown in table 4. There is a very high degree of correlation between chromosome number and rust resistance, head type, keel shape, spikelet shape, and head shape. All of these characters are those which distinguish the *durum* and *vulgare* wheats. For instance the *durum* wheats have head type 3, keel shape 3, spikelet shape 3, while the *vulgare* wheats have the first type for each of these characters (see description of characters p. 306). There is not much correlation between awn length and chromosome number, because awned and awnless segregates were found in both 14- and 21-chromosome types. This relation is in accord with taxonomic differences, because both *durum* and *vulgare* wheats may be awned or awnless although the *durum* wheats usually have long awns. It will be noted that all segregates with very long awns, i.e., 12 cm or longer, have 14 chromosomes, while the segregates which are true awnless types have more than 14 chromosomes. This again is in accord with taxonomic differences, as only the *vulgare* wheats have true awnless varieties like Amby, and the awns of the awned types do not exceed 10 cm in length. The awns of *durum* varieties vary from 12 to 23 cm in length and in Kubanka are about 17 cm long. The correlation between chromosome number and culm diameter is not high, because culm diameter varies greatly, depending on the vigor of the plant.

It is evident that all of the distinguishing characters of the *durum* parent are found only in 14-chromosome segregates and that the typical *vulgare* characters are found in the 21-chromosome segregates. In the first correlation table one segregate with 14-chromosomes was classed as a

[3] The writer is indebted to Dr. JOHN W. GOWEN for suggesting and demonstrating the use of this method.

vulgare type, but a detailed classification of the distinguishing characters did not sustain this classification. One 21-chromosome segregate was consistently classed as a *durum* type, but on looking up the original chromosome counts it was found that this plant had 14 ± 1 bivalents and 6 ± 1 univalents, so that it resembled the F_1 in chromosome number and re-

TABLE 4

Showing correlation between chromosome number and morphological and physiological characters in F_3 segregates of a cross of T. vulgare × T. durum.

CHARACTERS CORRELATED			CHROMOSOME NUMBER 14	16–19	21	
f. Head type	(V)	1	1	4	8	r_c
		2	6	2	3	$-.73 \pm .07$
	(E)	3	12	1	1	
i. Keel shape	(V)	1		3	9	r_c
		2	4	3	2	$-.88 \pm .03$
	(E)	3	15	1	1	
h. Spikelet shape	(V)	1		4	9	r_c
		2	5	1		$-.82 \pm .05$
	(E)	3	14	2	3	
n. Head shape	(E)	1	16	1	1	r_c
		2	3	5	4	$.87 \pm .03$
	(V)	3		1	7	
g. Diameter of culm		1.0 to 1.2	1			
		1.2	4			
		1.4	6	2		η
		1.6	4	1	6	$.46 \pm .09$
		1.8	2	1	1	
		2.0	1	2	1	
		2.2	1	1	1	
		2.4 to 2.5			2	
j. Length of beards		0		2	3	
		0–2	9	2	4	
		2–4	4		1	
		4–6	2		2	η
		6–8		2		$.15 \pm .11$
		8–10			1	
		10–12		1	1	
		12–14	2			
		14–16	1			
		16–18	1			

TABLE 4 (continued)

CHARACTERS CORRELATED			RUST RESISTANCE 1	2	3	4	5	6	
	(E)	14	2	14	2				r_c
o. Chromosome number		16–19			2		1	4	.87 ± .04
	(V)	21		1	1	2	3	5	
	(V)	1			3		4	7	r_c
f. Head type		2		8	1	1	1	3	−.79 ± .05
	(E)	3	7	11	1	1		1	
	(V)	1			2	1	4	6	r_c
i. Keel shape		2	1	2	1		1	5	−.82 ± .03
	(E)	3	6	17	2	1			
	(V)	1			2	1	3	7	r_c
h. Spikelet shape		2		4	2		1	3	−.77 ± .05
	(E)	3	7	15	1	1	1	1	
	(E)	1	7	16	2	1	1		r_c
n. Head shape		2		3	2		2	6	.78 ± .05
	(V)	3			1	1	2	5	
	(V)	0					1	4	
		0.2	1	11	1			7	
		2–4	1	3	1		2		
		4–6		2			2		
j. Length of beards		6–8	1		2				η
		8–10				1			.59 ± .06
		10–12		1					
		12–14	1		1	1			
		14–16	2	1					
	(E)	16–18	1	1					

sembled the *durum* parent in most respects. This plant was relatively sterile and had only 0.9 grains per spikelet. Two other segregates classed as 21-chromosome types had at least several lagging chromosomes.

Since these differentiating characters of the parents are all closely associated with chromosome number they should be more or less closely associated with each other. We do find a very high correlation between the various morphological characters. The coefficient of contingency for keel shape and spikelet shape is .99 ± .02, for keel shape and head shape .91 ± .02, and the correlation ratio for keel shape and diameter of culm is −.66 ± .05. In general the shape of the keel alone could be used satisfactorily as a means of classifying segregates into *durum* or *vulgare* types.

There is a striking relation between chromosome number and pollen-grain size in the cultivated species of wheat (SAX 1922). There is also a high correlation between chromosome number and pollen-grain size in the F_3 segregates ($\eta = .77 \pm .05$). The average size of the pollen grains could be used as an indication of the approximate chromosome number in parents or segregates.

It is evident from table 4 that rust resistance is also closely associated with morphological characters. Segregates which have the chromosome number and morphological characters of the resistant *durum* parent are in general resistant to rust while the segregates which have 21 chromosomes and resemble the *vulgare* parent are usually susceptible. Especially interesting is the relation between rust resistance and length of awns. The true awnless segregates are very susceptible, while the segregates with very long awns are resistant to rust. The segregates with short awns which would ordinarily be classed as awnless, may be either susceptible or resistant, but with an increase in awn length resistance increases. The number of segregates with the Vulgare type of awn is too small for conclusive results, but it is perhaps significant that the most important resistant varieties of *T. vulgare*, Kanred and Kota, and other Crimean selections, are all awned.

The association of rust resistance and morphological characters in segregates of *T. vulgare* × *T. durum* has been attributed to chromosome linkage by HAYES, PARKER and KURTZWEIL (1920) and by WALDRON (1921). WALDRON has suggested that the linkage of *durum* head characters and rust resistance in the segregates might be due to the association of these characters in two chromosomes of the same pair and that crossing-over would produce the occasional resistant *vulgare* type which is occasionally found. FREEMAN (1917) describes linkage between shape of head (the same character which is called shape of spikelet in the present paper) and hardness of grain, in F_2 segregates of *T. vulgare* × *T. durum*. In view of the cytological and genetic data here presented it is clear that the association of rust resistance and morphological characters is not due to chromosome linkage in the usual sense of the term, but is due to the fact that most of the surviving segregates have 14 or 21 chromosomes and that rust resistance and distinguishing morphological characters are in general associated with chromosome number.

The fact that chromosome number is so clearly associated with rust resistance and morphological characters in segregates of *T. vulgare* × *T. durum* and in the cultivated species, suggests that the 7 additional chromosomes of the *vulgare* parent determine the distinguishing characters of the *vulgare* wheats. The effect of the 7 additional chromosomes may be due either to the numerical relations causing a reduplication of hereditary factors, or to specific factors in these chromosomes which are not possessed by the 14 chromosomes of the Emmer wheats. If the latter hypothesis were correct it would be expected that these 7 chromosomes which determine the distinguishing characters of the Vulgare wheats would not pair with the Emmer chromosomes and thus no 14 chromosome segregates would possess the physiological and morphological characters of the Vulgare wheats. In either case it would be impossible to combine the desirable characters of the Emmer and Vulgare wheats in a homozygous fertile segregate.

The genetic data show that the characters which are common to the two groups of species may combine and segregate with the usual Mendelian results. For instance, in a cross of *T. vulgare* × *T. durum*, LOVE and CRAIG (1919) find a 15 : 1 ratio for color of chaff and for color of grain, and a ratio approximating 3 : 1 for the segregation of awnless and awned segregates. The awned condition is associated to some extent with differences in chromosome number, as I have shown, so that a clear case of simple segregation would not be expected. PERCIVAL (1921) finds normal segregation of glume color in a similar cross. The characters found in both groups of species are apparently determined by the 14 primary chromosomes. Since there is in most cases an orderly behavior of these chromosomes normal segregation and recombination would be expected. On the other hand, the characters peculiar to the Vulgare wheats are dependent on the assortment of the 7 univalent chromosomes and as a result these characters, in a homozygous condition, are, with few exceptions, found only in segregates with 21 chromosomes.

In species hybrids which are relatively sterile, such as Amby × Kubanka, the 7 additional chromosomes of the Vulgare parent may be quite unlike any of the 14 Emmer chromosomes and would rarely combine with them. In more fertile combinations of Emmer and Vulgare wheats, such as *T. dicoccum* or *T. turgidum* × *T. vulgare*, some of the 7 additional chromosomes of the Vulgare parent might in some cases pair with the 14 chromosomes of the Emmer parent. The greater compatibility of the chromosomes in such hybrids would not only increase the fertility, but would perhaps result in some relatively fertile segregates combining some of the characters of both parents. With increased sterility, on the other hand, the intermediate types would be rapidly eliminated and the fertile homozygous segregates could be classed as either Emmer or Vulgare types.

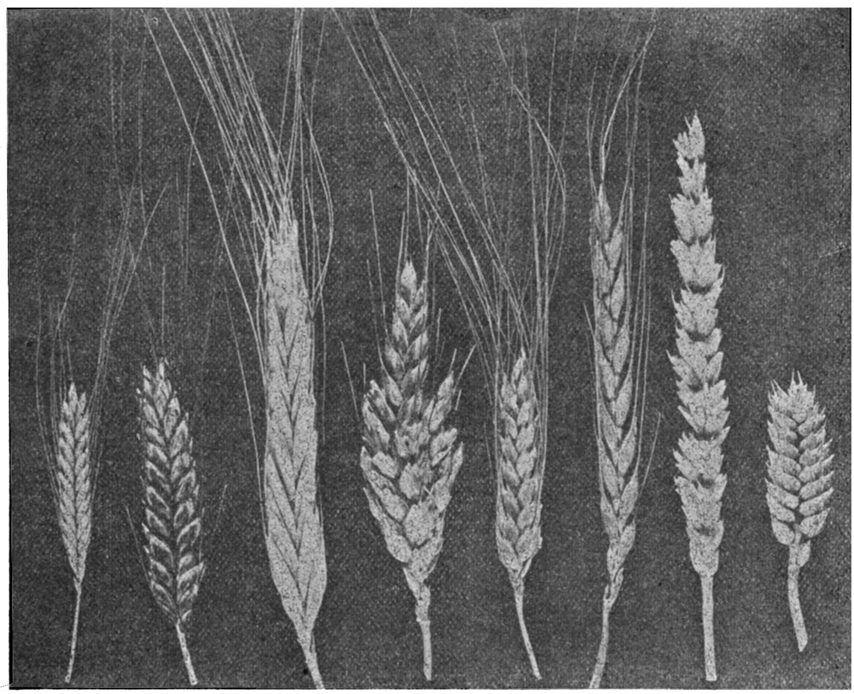
The primary 14 chromosomes of the Vulgare wheats are not, in most cases at least, of the same factorial constitution as the 14 chromosomes of the Emmer wheats. This is shown by the various types of Emmer wheats obtained on crossing members of the two groups. For instance crosses of *T. vulgare* × *T. durum* result in some typical *T. dicoccum* segregates and the cross *T. vulgare* × *T. turgidum* results in segregates resembling *T. dicoccum*, *T. durum*, *T. Spelta* and *T. compactum*. *T. polonicum* or *T. turgidum* crossed with *T. vulgare* produces many segregates like *T. durum*, which are homozygous. LOVE and CRAIG (1919) found 2 segregates resembling *T. dicoccoides* in a cross of *T. vulgare* × *T. durum*. Such a result is not unexpected since *T. dicoccoides* has 14 chromosomes. It does not necessarily mean, however, that all 14-chromosome wheats can be obtained in this way.[4] There is also some incompatibility in certain combinations of the 14 bivalents in Emmer × Vulgare crosses as indicated by the partial sterility of certain 14-chromosome segregates.

In view of the fact that morphological and physiological characters of the Vulgare wheats are associated with the 7 additional chromosomes, it is improbable that the desirable characters of the Emmer and Vulgare wheats can be combined in homozygous fertile segregates. This conclusion is substantiated by the results of a large number of breeding experiments in all parts of the world. FARRAR (1898) recognized the value of combining the rust resistance of the Emmer varieties with the bread wheats, and made numerous species crosses with this end in view, but he was apparently unsuccessful in obtaining the desired results. Crosses between the Emmer and Vulgare wheats have also been made by VILMORIN in France, TSCHERMAK in Austria, BIFFIN in England, and by a large number of plant breeders in various parts of the United States. In Minnesota alone (HAYES and GARBER 1921), over 20,000 F_3 segregates of such hybrids have been studied and only a few plants were found which had the morphological characters of the Vulgare parent and were resistant to rust. So far as I have been able to determine no segregate of economic value has been originated by combining the desirable characters of the Emmer group with the desirable characters of the Vulgare group.

[4] I have found 14 chromosomes in *Aegilops ovata*, but Aegilops is almost if not quite sterile with all of the cultivated species of wheat (PERCIVAL 1921). The sterility relationships, taxonomic characters, pollen-grain shape, and pollen-grain size, all support the contention that Aegilops deserves its generic rank.

THE RELATION BETWEEN CHROMOSOME NUMBER AND MORPHOLOGICAL AND PHYSIOLOGICAL CHARACTERS IN WHEAT SPECIES

The association between chromosome number and morphological and physiological characters found in segregates of *T. vulgare* × *T. durum* is even more striking in the cultivated species of wheat (figure 1). The Einkorn group, consisting of one species, *T. monococcum*, has 7 chromosomes. It is a very homogeneous species with only a few varieties. It is adapted to barren rocky soil where other wheats will not grow. All



1 2 3 4 5 6 7 8

FIGURE 1.—Representatives of the cultivated species of wheat:
Einkorn group: 1. *Triticum monococcum.*
Emmer group: 2. *T. dicoccum;* 3. *T. polonicum;* 4. *T. turgidum;* 5. *T. durum.*
Vulgare group: 6. *T. Spelta;* 7. *T. vulgare;* 8. *T. compactum.*

varieties are bearded, the empty glumes are strongly keeled and the ears are flattened across the face. The Emmer group, consisting of *T. dicoccum*, *T. turgidum*, *T. polonicum* and *T. durum*, has 14 chromosomes. According to PERCIVAL there are about 150 "forms" (agronomic varieties) in this group. These species are in general restricted in adaptability to dry warm regions and under semi-arid conditions will yield more than other wheats. Most of the varieties in this group are bearded and the beards are usually very long. The empty glumes are strongly keeled, the ears are usually flattened across the face, and the culms are pithy or, if hollow, have thick walls. The Vulgare group, consisting of *T. vulgare*, *T. Spelta* and *T. compactum*, has 21 chromosomes. The species of this group are very adaptable and are grown in all parts of the world where wheat can be grown. PERCIVAL describes more than 500 varieties in this group. Bearded and beardless forms are found in about equal numbers but the beards of the bearded types are relatively short. The empty glumes are slightly keeled, and with the exception of *T. Spelta*, the ears are square in cross section or broader across the face. The culms are usually hollow and thin-walled.

Of even greater importance than the morphological characters is the relation of rust resistance and bread-making qualities in these three groups of wheat species. VAVILOV (1914) classes Einkorn as immune to rust and mildew; species of the Emmer group are classed as resistant, although *T. dicoccum* has both resistant and susceptible forms; and the species of the Vulgare group are classed as susceptible. In 1918 VAVILOV found all Vulgare wheats tested to be susceptible except Black Persian. PERCIVAL'S (1921) results show, however, that Black Persian is a variety of *T. dicoccum*. According to BIFFEN (1907) Einkorn is notoriously rust-resistant and in ERIKSSON'S trials it was the only variety immune to the three common wheat rusts. MELCHERS and PARKER (1922) also find all strains of Emmer and Einkorn to be more or less resistant. The work of these and other investigators (see PERCIVAL 1921) shows that the Einkorn group is very resistant to rust, the species of the Emmer group are relatively resistant, while the members of the Vulgare group, with the exception of *T. Spelta* and a few varieties of *T. vulgare* and *T. compactum*, are susceptible to rust.[5] Similar relations are found in respect to resistance to mildew (*Erysiphe graminis*) and bunt (*Tilletia tritici* and *T. levis*).

Although the *durum* and other wheats in the Emmer group usually have a higher protein content and a greater yield of flour than the Vulgare wheats, they do not possess the quality of gluten necessary for the manufacture of light bread. Some of the *durum* wheats do, however, make a better quality of flour than some of the soft wheats in the Vulgare group.

[5] STAKMAN and LEVINE (1922) find *T. monococcum* relatively susceptible to most of the 38 biologic forms of *P. graminis*. These results, contradictory to a large amount of data collected in Europe and America, may perhaps be attributed to differences in the distribution and prevalence of the various biologic forms of rust. The species of the Emmer group were found to be relatively resistant.

The wheats of the Emmer group are commonly used in the manufacture of macaroni, or mixed with "strong" flour of Vulgare wheats. Most of the Emmer varieties have hard flinty grains, but varieties of *T. turgidum* and *T. dicoccum* have starchy grains and the flour is used in the manufacture of biscuits and pastry. Only in varieties of the Vulgare wheats are the characters found which make a flour of high quality. LeClerc, Bailey and Wessling (1918) made milling and baking tests with several species of wheat. Their conclusions are of so much interest that they are quoted.

> "When these flours were baked into bread, the bread made from Einkorn was the least desirable, not only in volume, but in color, elasticity, and in taste or flavor. . . . . That made from Emmer was somewhat better, although not equal to bread made from spring-wheat flour in color, volume and elasticity. The Polish-wheat [Emmer group] bread had a better color than the Emmer bread, but the volume was not quite so large. . . . . The spelt [Vulgare group] bread on the other hand compared favorably in most respects to the ordinary-wheat bread, except that the color was a little darker. There was no difference in taste and appearance from ordinary-wheat bread."

It is evident that the species of wheat with different chromosome numbers are differentiated by distinct morphological characters, by differences in susceptibility to disease, and by differences in quality of grain. As the chromosome number increases, the variability and adaptability of the species increases, its propagation becomes more dependent on artificial methods, its susceptibility to plant diseases increases, and its economic value is greater. A similar correlation is found in the species of oats. Vavilov (1918) finds *Avena brevis* and *A. strigosa* most resistant to rust in Russia. Durrell and Parker (1920) find *A. barbata*, *A. brevis* and a few varieties of *A. sativa* very resistant to crown rust (*P. coronata*). *A. barbata* was also very resistant to stem rust (*P. graminis*). The species *A. brevis*, *A. barbata* and *A. strigosa* have 7 or 14 chromosomes as compared with 21 for *A. sativa* (Kihara 1919). Here we find, again, greater disease resistance in the species with the smaller chromosome number and greater economic value of species with the increased chromosome number. The relation between chromosome number and the various characters described may be attributed to the greater opportunity for mutations to occur in species with larger chromosome number, to a greater number of possible combinations in fertile hybrids, and to the cumulative effect of reduplicated factors or the combined effect of many different factors (see East 1915, and Bridges 1922).

THE NATURE OF RUST RESISTANCE

Rust resistance has been found to be dependent on a single hereditary factor in several Vulgare crosses (BIFFEN 1912, ARMSTRONG 1922). The work of ARMSTRONG is especially valuable as his F_2 classification was verified by F_3 data. It is of interest to note that BIFFEN found a simple 3 : 1 ratio for susceptibility to rust in a cross of resistant and susceptible varieties of *T. vulgare*, but that he obtained no Mendelian ratios in a cross of *T. turgidum* × *T. vulgare* in which about 2000 F_2 segregates were obtained. HAYES, PARKER and KURTZWEIL (1920) conclude that linkage prevents free assortment of factors for rust resistance in crosses of Emmer × Vulgare wheats. The non-Mendelian inheritance of rust resistance in partially sterile hybrids can be easily explained in view of the cytological analysis of such hybrids.

It has been suggested that resistance to rust infection may depend on the size of the stomata, the resistant varieties having stomatal openings too small for the hyphae to enter. This view would agree very nicely with the degree of resistance found in the cultivated species of wheat because stomata size is closely associated with chromosome number. Under the same environmental conditions the relative size of stomata for the Einkorn, Emmer, and Vulgare groups is in the ratio of 10, 14 and 18.

Although the assumption that susceptibility is due to the large size of the stomata may be a very attractive hypothesis, the works of WARD (1905), MARRYAT (1907), GARBER (1922) and others show clearly that it is untenable.[6] These investigators find that the rust hyphae enter the stomata of immune species and varieties about as frequently as in the susceptible varieties, or that stomatal size is not associated with resistance. In case the hyphae enter the stomata of such a resistant species as Einkorn the host cells shrink and break down and the hyphae are starved. In less resistant varieties the host cells have a more protracted struggle with the fungus and a few pustules may be formed, while in completely susceptible varieties there is no retardation in the growth and development of the fungus. Susceptibility to rust is apparently dependent directly or indirectly, on physiological factors. The exact nature of these factors is unknown, but VAVILOV (1918) states that immunity to rust is not due to osmotic pressure or hydrogen-ion concentration in the host cells.

[6] Dr. RUTH ALLEN (1923) has recently published a very complete account of the factors involved in rust resistance in wheat. She finds resistance in Kanred wheat to be due to small size of stomatal openings, to heavy walls adjoining pathological cells, and to a true physiological immunity.

The fact that nitrogenous fertilizers, and wide spacing of plants may increase susceptibility (ARMSTRONG 1922) also supports the assumption that susceptibility is due to physiological factors. RAINES (1922) concludes that susceptibility to rust increases as the vegetative vigor of the host increases. Thus, increased vigor in segregates due to heterosis might have considerable effect on susceptibility or resistance. Since so many factors might affect the physiological balance of an individual, especially in species crosses, it is not surprising that unusual results are found and that transgressive segregation frequently occurs in hybrids between susceptible and resistant species or varieties.

The occasional appearance of segregates in Emmer × Vulgare crosses, which resemble common wheat and are also resistant, may be due to physiological conditions, and it is perhaps significant that few if any of these segregates are of economic value. Vegetative vigor, in general, increases as the chromosome number increases, within a given genus, and thus the relative susceptibility of the various species of wheat might be explained. However, genetic studies show that the physiological balance which makes a plant resistant or susceptible may, in the Vulgare wheats at least, depend on a single hereditary factor. ARMSTRONG has found certain varieties immune to rust under all environmental conditions available.

Nearly all varieties of *T. vulgare* and *T. compactum* are susceptible to rust. Marquis was at one time considered resistant, but it was found that it simply escaped rust because of its early maturity. Recently several resistant varieties have been found. WALDRON and CLARK (1919) find Kota to be a resistant variety, but it has from 5 to 15 percent rust infection in North Dakota and is slightly more susceptible in other localities. MELCHERS and PARKER (1922) have made 3 selections of Crimean wheat which are relatively resistant. Kanred, the best of these selections, had from 40 to 70 percent rust in 1915, but usually it is very resistant. Kota and Kanred as well as the other two selections, are very similar in morphological appearance and both belong to the Crimean group of Vulgare wheats which were originally obtained from southern Russia. They are awned, lax-eared, and have comparatively long beaks on the outer glumes. Resistant wheats are not confined to beardless types although these are of most economic value. Fern, a variety of *T. vulgare*, is awnless and is as resistant as Kanred (MELCHERS and PARKER 1922).

A comparison of the resistance of different species and varieties to rust and bunt shows that the factors which cause resistance to rust also cause resistance to bunt. GAINES (1918) finds Turkey, a variety in the Crimean group, to be relatively resistant to bunt. Stephens and Woolman (1922) find most Vulgare wheats susceptible to bunt in Oregon. A large number of Crimean selections from the Kansas Agricultural Experiment Station were found to be highly resistant. Although most of the resistant varieties were awned Crimean wheats, several awnless varieties were found to be resistant. Gaines (1920) crossed Turkey with Florence, both resistant varieties, and obtained a number of segregates even more resistant than the parents and either awned or awnless resistant types could be obtained.

Through the courtesy of Doctor Gaines data have been obtained for bunt resistance in the various species of wheat. Gaines finds Einkorn to be completely immune. The percentage of infection in *T. polonicum* was 8, in *T. dicoccum* 10, in *T. durum* 29, in *T. turgidum* 33. In the Vulgare group, *T. Spelta* was comparatively resistant with only 10 percent infection, but the percentage of bunt found in *T. vulgare* was 70 and in *T. compactum* it was 64. In general, the species and varieties of wheat which are resistant to rust are resistant to bunt and *vice versa*. It is probable then, that varieties found to be resistant to rust in the middle west would be valuable disease-resistant varieties for the Pacific coast where bunt is the most important cereal disease. Likewise the valuable results in breeding bunt-resistant wheats on the Pacific coast could be utilized in regions where rust is prevalent. In many cases resistant segregates might not be adapted to the region where they were originated but would perhaps be suited to other climatic conditions.

In selecting disease-resistant varieties of wheat for breeding work the chances for successful results are much greater if the parents are selected within the Vulgare group. Several disease-resistant varieties of *T. vulgare* are known and these can be used in breeding varieties suited to local conditions. *T. Spelta* may also be of value since it is relatively resistant to disease and is very hardy, but it is possible that resistance may be associated with *Spelta* morphological characters even in hybrid segregates.

SUMMARY

Previous investigation has shown that the cultivated species of wheat may be divided into 3 groups according to their taxonomic, sterility and cytological relationships. These groups are the Einkorn group with 7 haploid chromosomes, the Emmer group with 14 chromosomes, and the Vulgare group with 21 chromosomes.

It has also been found that in F_1 hybrids of Emmer × Vulgare wheats there are 14 bivalent and 7 univalent chromosomes in the meiotic divisions. The bivalent chromosomes divide normally in both reduction divisions, but the univalents lag and divide equationally in the first division and pass at random to one pole or the other without dividing in the second division. Thus the F_1 gametes contain from 14 to 21 chromosomes. There is considerable sterility in F_1 and subsequent generations.

A cytological examination of 46 F_3 segregates of *T. vulgare* × *T. durum* shows that most of the segregates have either 14 or 21 chromosomes or an intermediate number which could result from the union of a 14-chromosome gamete with a 21-chromosome gamete. It is evident that the segregates with an intermediate chromosome number tend to be eliminated because of their sterility and that the ultimate homozygous fertile segregates will have either 14 or 21 chromosomes.

A very high degree of association was found between chromosome number and morphological and physiological characters in the F_3 segregates. The plants with 14 chromosomes were similar in morphological characters and rust resistance to the *durum* parent, while segregates with 21 chromosomes had the morphological characters and susceptibility to rust of the *vulgare* parent. Apparently the 7 additional chromosomes of the Vulgare varieties determine the distinguishing characters of the common wheats due to a reduplication of hereditary factors or to specific factors in these chromosomes.

The cytological and genetic data would indicate that many of the desirable characteristic properties of the Emmer and Vulgare wheats cannot be combined in a homozygous condition. This conclusion is supported by breeding experiments in all parts of the world and involving hundreds of thousands of segregates. So far as the writer has been able to determine no variety of economic importance has been originated by combining the desirable characters of the Emmer and Vulgare wheats.

There is a striking correlation between chromosome number and morphological and physiological characters in the cultivated species of wheat. With an increase in chromosome number, 7–14–21, there is an increase in variability and adaptability, an increased susceptibility to rust, mildew and bunt, a better quality of gluten in the grain, and the economic value is greater. The relation between chromosome number and morphological and physiological characters may be attributed to the greater opportunity for mutations to occur in species with the larger chromosome number, to a greater number of possible combinations in fertile hybrids, and to the cumulative effect of reduplicated factors or the combined effect of many different factors.

The resistance to rust appears to depend on the physiological condition of the host. This condition may depend on a single hereditary factor in some varietal crosses, but in species hybrids many factors, acting either directly or indirectly, may influence the physiological balance which determines resistance or susceptibility. Rust and bunt resistance apparently depend on the same factors, so that results in breeding wheats resistant to rust can be applied to bunt, and *vice versa.*

Pollen-grain size may be used as an approximate measure of chromosome number in wheat species and hybrid segregates.

The breeding of wheat varieties to combine disease resistance with high yield and quality of grain is much more likely to be successful if the parents are selected within the Vulgare group.

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