THE CORRELATION OF CHARACTERS IN HYBRIDS OF *TRITICUM DURUM* AND *TRITICUM VULGARE*

W. P. THOMPSON
University of Saskatchewan, Saskatoon, Canada

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INTRODUCTION

In crosses between *durum* and *vulgare* wheats, correlation of certain *durum* characters has been reported. FREEMAN (1917) found that the *durum* hardness of grain was associated with *durum* shape of head. HAYES, PARKER and KURTZWEIL (1920) reported a correlation between rust-resistance and other *durum* characters, the greatest difficulty being experienced in securing *vulgare*-like segregates with rust-resistance. From his work on the chromosomes of wheat, SAX (1922) concluded that the *durum* characters should be correlated on the one hand, and the *vulgare* characters on the other. Later (SAX 1923) he showed that in the F_3 segregates an actual correlation existed between chromosome number and several characters.

Nevertheless, HAYES and his co-workers (1920) did succeed in securing a few *vulgare*-like segregates which were rust-resistant, a result which has also been obtained by the writer, though according to my observations neither their resistant *vulgare*-like lines nor mine are as resistant as the *durum* parent. Moreover, almost every individual feature characteristic of *durum* wheats is also found in some one or few *vulgare* varieties, and *vice versa*. Some of these varieties are considered by PERCIVAL (1921) to be the result of hybridization.

There is very great need in some regions of developing a *vulgare* wheat with certain *durum* qualities, notably drought-resistance and rust-resistance. *Vulgare* varieties are known which have some degree of resistance to stem rust, but so far none has been found which is resistant to all the biologic forms of stem rust which are found in Western Canada. On the other hand, certain *durum* and emmer varieties are very highly resistant to all the biologic forms which have been discovered here. It is essential, therefore, to determine whether there is such a correlation that this and other characters can not be transferred to *vulgare* types.

THE CHARACTERS CONCERNED AND THEIR INDIVIDUAL INHERITANCE

In the experiments reported in the following pages the *vulgare* parent was the variety Marquis and the *durum* parent was a highly rust-resistant line selected from Iumillo. Thirteen pairs of characters which are readily distinguishable in these parents were chosen for study. Some of these characters, e.g., head form and condition of keel, distinguish nearly all *durum* varieties from nearly all *vulgare* varieties; others, such as length of beards, cannot be considered diagnostic. It was thought that these two kinds of characters might show significantly different behaviors. The characters in question are as follows:

Compactness

When the length of the head in centimeters is divided by the number of spikelets, the range of variation in the *durum* parent is from 0.33 to 0.39, while in the *vulgare* parent it is from 0.43 to 0.54. A similar difference exists between all *durum* and *vulgare* varieties, except that the club wheats, which are generally classified with *T. vulgare*, show the *durum* compactness.

In F_2 the range of variation is from 0.26 to 0.55, with a considerable number intermediate.

Head form

By this term is meant the ratio of the width (1-ranked side) to thickness (2-ranked side). In Iumillo this ratio varies from 0.7 to 1.0 while in Marquis it varies from 1.2 to 1.5: This is a characteristic difference between *durum* and *vulgare*, the only exceptions being a few *vulgare* varieties in which the two dimensions are equal. In F_2 the range of variation extends beyond the extremes of both parents and some plants show variations in different heads, or even in the same head.

Diameter of stem

In 1923 this varied in Iumillo from 1.0 to 1.5 mm measured at a point 2 cm from the base of the head, and in Marquis from 1.75 to 2.25. In F_2 the range of variation again extended beyond the parental extremes, and some plants showed considerable variation in different stems.

Beard length

In Iumillo the beards measure from 10 to 12 cm, in Marquis up to 2 cm. n F_2 the parental and all intermediate conditions are found, but there is a distinct massing of individuals with the shorter beards. The long-bearded condition is characteristic of all but a few varieties of *durum*, but *vulgare* varieties may be long- or short-bearded or beardless.

The remaining characters do not lend themselves to measurement, but are quite distinct in the parent types.

Keel

In *durum* wheats the keel of the outer glume is generally very prominent and extends the full length of the glume; in *vulgare* it is usually less pronounced and extends only part of the length, though in some varieties it is large and extends from tip to base. In Marquis it is better developed than in most *vulgare* varieties. In F_2 intermediate conditions are common.

Middle tooth

The apical tooth of the outer glume is long, sharp and slightly curved in Iumillo, whereas it is short and blunt in Marquis. This distinction applies to most, but by no means all, *durum* and *vulgare* varieties. In F_2 the variation again extends beyond the parental extremes, those longer than the *durum* extreme being few but very conspicuous.

Lateral tooth

In Iumillo this is short and situated close to the middle tooth; in Marquis it is much further away and gives a shoulder-like appearance to this portion of the glume.

Glume shape

In Iumillo the glume is long and narrow, in Marquis short and wide. These differences are generally applicable to *durum* and *vulgare* varieties, though exceptions occur.

Keel hairs

Long and numerous in Iumillo; short and scattered or absent in Marquis. In F_2 the parental conditions and intermediate ones with respect to both length and number are found.

Collar

The collar-like structure at the base of the lowest spikelet extends completely round nearly all the stems in Iumillo and only part way round the stem in Marquis in nearly all cases. In F_1 and some F_2 plants, the collar extends part way round some stems and all the way round others. These are recorded as intermediate.

Cavity of stem

Durum varieties usually have solid stems though some varieties have hollow ones with thick walls; *vulgare* stems are usually hollow with thin walls, though some varieties have solid stems. Iumillo and Marquis are typically *durum* and *vulgare*, respectively. In F_2 very few plants have as thin walls as Marquis, though many have well developed cavities.

Seed hairs

In Marquis there is a thick brush of long hairs at the stigma end of the kernel as in *vulgare* wheats, generally; in Iumillo there are a few short scattered hairs.

Seed form

In *durum* varieties generally the seed is longer, narrower and more tapering than in *vulgare*. In Marquis the bluntness and plumpness is very pronounced.

Other characters

The use of certain other characters was considered but was rejected because it was thought that they might give a false idea of correlation.

For example, the form of the spikelet is very different in the two species, being much broader in *vulgare* than in *durum*, but this form of spikelet very largely determines the character called head form (width : thickness) since width of head depends on width of spikelets. Similarly, the distribution of beards is very different in the parental races, but beard-distribution is in all wheats closely correlated with beard-length. Only those characters were chosen for which there is no external or evident physiological reason for correlation, or which can be separated as shown by the breeding results.

Table 1 shows the results of classifying 57 F_2 plants according to each of the 13 characters. The *vulgare* condition of a character is designated V, the *durum* condition D, intermediate I, intermediate but nearer *vulgare* IV, intermediate but nearer *durum*, ID. In such characters as collar and diameter of stem, I plants were those which had some stems *durum*-like and others *vulgare*-like. In every possible case an F_3 family was grown, though owing to sterility, these families were often small and sometimes missing. The F_2 classification was checked by the F_3 results. In a few cases, particularly of intermediate characters, it was necessary to transfer an F_2 plant to a different class because of the F_3 results.

TABLE 1

CHARACTER	COMPACTNESS	HEAD FORM	KEEL	MIDDLE TOOTH	LATERAL TOOTH	GLUME SHAPE	KEEL HAIRS	COLLAR	BEARDS	CAVITY OF STEM	DIAMETER OF STEM	SEED HAIRS	SEED FORM
V	15	9	14	22	14	10	20	17	26	9	26	33	13
IV	..	..	..	..	..	..	..	..	10	7	..	..	..
I	15	17	14	16	9	19	19	17	9	18	6	12	15
ID	..	..	8	..	..	..	..	..	7	..	..	..	..
D	27	31	21	19	34	28	18	23	5	23	25	12	29

It is difficult to bring the results given in this table into line with Mendelian ratios. Other investigators have reported Mendelian results for some of these characters, but I am unable to reconcile their results with these. In regard to almost every character, the proportion of intermediate F_2 plants is too small for a monohybrid ratio. And any interpretation which is more complex encounters difficulties with the F_3 results. In general the offspring of plants intermediate for any character included a high proportion of *vulgare* plants and *durum* plants, and relatively few intermediates. The *vulgare* plants gave only *vulgares* or some intermediates, and with some characters a few *durum* plants. The *durum* plants behaved similarly. The F_3 results are not given in detail for each character, since we are concerned primarily with the correlation of the whole group of characters.

THE CORRELATION OF CHARACTERS

Experimental data

In table 2 the condition of each of the 13 characters in each of the 57 F_2 plants is shown. The data are given in this extended form because it was desired to ascertain the degree of correlation amongst the whole 13 characters, not merely by pairs, and to compare different plants in regard to the amount of correlation. The letters have the same meaning as in table 1. In each case the classification was confirmed or corrected by reference to the F_3 plants. At the right of the table is shown the number of characters (out of the 13) in each category for each plant.

Analysis of data

In this table it will be observed that the plants fall into three groups: (1) those with *vulgare* characters chiefly and few or no *durum* characters; (2) those with *durum* characters chiefly and few or no *vulgare* characters; (3) those with approximately equal numbers of *durum* and *vulgare* characters and a considerable proportion of intermediate ones. The numbers in these groups are 17, 24 and 16, respectively. The proportion in the latter class is extremely small in comparison with the expectation on a basis of free Mendelian assortment. With 13 pairs of characters nearly all plants in a sample of 57 would be expected to fall into this group. In the columns at the right, the striking thing is that the numbers of *vulgare* and *durum* characters are either large or small,—near zero or near 13,—not mostly 6 or 7 as would be expected. In considering the plants with a large number of D or V characters, it is to be remembered that while this number is less than 13, it is usually less only by approximately the number of intermediate characters.

In short, the great majority of the segregates have either *durum* characters chiefly or *vulgare* characters chiefly.

The correlation is brought out more clearly in table 3. The second column gives the number of characters which remain for each plant when the number of its intermediate characters is subtracted from 13 (the

TABLE 2

The condition of the 13 characters in different F_2 plants.

PEDIGREE NUMBER	COMPACTNESS	HEAD FORM	KEEL	MIDDLE TOOTH	LATERAL TOOTH	GLUME SHAPE	KEEL HAIRS	COLLAR	BEARDS	CAVITY OF STEM	DIAMETER OF STEM	SEED HAIRS	SEED FORM	TOTALS				
														V	IV	I	ID	D
F_1	I	I	ID	I	V	I	D	I	IV, I	V, IV	V	V	I	..	..	..	..	..
1–2–2	V	V	V	V	V	V	V	V	V	V	V	V	I	12	..	1	..	..
1–2–3	I	D	I	D	D	D	I	D	IV	D	D	D	D	..	1	3	..	9
1–2–4	D	D	D	V	D	I	D	D	V	D	D	V	D	3	..	1	..	9
1–2–5	V	V	D	D	D	I	V	I	ID	V	V	V	I	6	..	3	1	3
1–2–6	V	V	V	I	D	V	V	I	V	I	V	D	V	8	..	3	..	2
1–2–7	I	I	V	I	D	D	V	V	V	D	D	D	I	4	..	4	..	5
1–2–9	I	D	D	D	D	D	I	D	D	D	D	D	D	..	..	2	..	11
1–2–10	D	D	D	V	D	D	D	D	V	D	D	D	D	2	..	..	..	11
1–2–11	V	I	ID	D	D	I	I	V	ID	IV	V	I	I	3	1	5	2	2
1–2–12	D	D	V	V	D	D	V	D	V	D	D	I	D	4	..	1	..	8
1–2–13	D	D	D	I	D	D	D	V	V	IV	D	V	I	3	1	2	..	7
1–2–14	D	D	ID	V	I	I	I	D	V	IV	V	V	I	4	1	4	1	3
1–2–15	D	D	D	D	D	D	D	D	ID	D	D	I	D	..	..	1	1	11
1–2–16	D	D	I	I	D	D	I	D	D	D	I	D	D	..	..	4	..	9
1–2–17	D	I	I	V	V	V	V	I	V	I	D	I	D	5	..	4	..	4
1–2–18	V	V	V	D	V	I	I	V	ID	V	V	V	V	9	..	2	1	1
1–2–19	D	D	ID	V	D	I	D	D	I	D	D	V	D	2	..	2	1	8
1–2–20	V	V	V	I	V	I	I	V	IV	IV	V	V	V	8	2	3	..	..
1–2–21	I	I	D	D	V	I	D	I	V	I	V	V	D	4	..	5	...	4
1–2–22	V	I	V	V	I	I	V	I	V	V	V	V	V	9	..	4	..	..

TABLE 2 (continued)

PEDIGREE NUMBER	COMPACTNESS	HEAD FORM	KEEL	MIDDLE TOOTH	LATERAL TOOTH	GLUME SHAPE	KEEL HAIRS	COLLAR	BEARDS	CAVITY OF STEM	DIAMETER OF STEM	SEED HAIRS	SEED FORM	TOTALS				
														V	IV	I	ID	D
1–2–23	V	I	I	V	V	I	I	V	IV	V	V	V	I	7	1	5	..	..
1–2–24	D	D	D	D	D	D	D	D	D	I	V	D	D	1	..	1	..	11
1–2–25	I	I	V	V	D	I	V	V	V	IV	V	V	I	7	1	4	..	1
1–2–26	D	D	ID	V	D	D	D	D	V	I	D	D	D	2	..	1	1	9
1–2–27	I	I	ID	I	I	I	I	I	IV	I	V	V	V	3	1	8	1	..
1–2–28	D	D	V	D	I	D	D	D	D	I	D	I	D	1	..	3	..	9
1–2–29	D	D	I	I	I	D	I	I	V	I	D	V	D	2	..	6	..	5
1–2–30	D	D	I	V	I	I	I	I	V	I	D	V	V	4	..	6	..	3
1–2–31	V	I	I	D	V	V	V	V	I	I	V	V	V	8	..	4	..	1
2–1–27	V	V	V	D	D	I	V	V	I	V	V	V	I	8	..	3	..	2
2–1–28	D	I	D	I	D	D	D	I	IV	I	I	V	D	1	1	5	..	6
2–1–29	I	I	I	V	V	V	V	V	V	I	V	V	I	8	..	5	..	..
2–1–31	I	D	V	V	I	V	V	V	V	I	V	V	V	9	..	3	..	1
2–1–32	D	D	I	V	D	I	V	I	I	D	I	V	D	3	..	5	..	5
2–1–33	D	D	D	I	D	D	I	D	ID	D	D	I	D	..	..	3	1	9
2–1–34	I	I	D	I	D	D	I	I	I	I	V	I	D	1	..	8	..	4
2–1–35	V	V	I	D	D	I	V	I	ID	D	D	V	I	4	..	4	1	4
2–1–36	D	D	D	D	D	D	D	V	D	D	D	D	D	1	..	..	..	12
2–1–38	D	D	D	I	I	D	D	D	IV	D	D	V	D	1	1	2	..	9
2–1–39	D	D	ID	V	D	D	I	I	V	I	V	I	I	3	..	5	1	4
2–1–40	V	I	D	I	I	I	V	V	V	V	V	V	V	8	..	4	..	1
2–1–41	D	D	ID	I	D	D	I	D	I	D	D	D	D	..	..	3	1	9

TABLE 2 (continued)

PEDIGREE NUMBER	COMPACTNESS	HEAD FORM	KEEL	MIDDLE TOOTH	LATERAL TOOTH	GLUME SHAPE	KEEL HAIRS	COLLAR	BEARDS	CAVITY OF STEM	DIAMETER OF STEM	SEED HAIRS	SEED FORM	TOTALS				
														V	IV	I	ID	D
23-4-5	I	D	D	V	D	D	D	I	IV	D	D	I	D	1	1	3	..	8
23-4-6	D	D	D	D	D	D	D	D	V	D	I	D	D	1	..	1	..	11
23-4-7	V	V	I	I	V	V	I	V	V	V	V	V	V	10	..	3	..	..
23-4-8	I	D	I	V	V	V	D	I	V	D	V	I	I	5	..	5	..	3
23-4-9	V	I	V	D	V	V	V	D	V	V	V	V	V	10	..	1	..	2
23-4-10	D	D	D	D	D	D	D	D	ID	D	D	I	D	..	..	1	1	11
23-4-11	I	I	I	D	D	D	V	D	IV	I	I	V	V	3	1	5	..	4
23-4-12	V	V	I	V	V	I	V	V	I	IV	V	V	I	8	1	4	..	..
23-4-13	D	D	ID	V	D	D	I	D	V	I	I	D	D	2	..	3	1	7
23-4-14	I	I	V	D	V	V	V	I	I	IV	V	V	V	7	1	4	..	1
23-4-15	D	D	D	V	D	D	D	D	V	D	D	V	D	3	..	..	..	10
23-4-16	D	D	V	I	D	D	V	D	IV	D	D	V	D	3	1	1	..	8
23-4-18	I	I	D	I	V	I	I	V	V	I	V	V	I	5	..	7	..	1
23-4-19	D	D	D	D	D	D	I	I	I	D	D	I	D	..	..	4	..	9
23-4-20	I	D	D	V	D	D	D	D	IV	D	D	V	D	2	1	1	.	9

total number of characters considered). This is, then, the maximum possible number of D characters after the intermediate ones have been removed from consideration. It will be observed that where the possible numbers are high, the actual numbers are either high or low. The middle numbers (4, 5, 6, 7) occur where the possible numbers are smallest. Their absence where high numbers are possible is striking. Similarly, the plants with the smallest actual numbers of D characters do not occur where the possible numbers are smallest.

The lowest line of this table shows the total number of plants for each number of D characters, intermediate conditions being disregarded. The concentration of the individuals towards the ends of the series is striking. In a typical Mendelian case, the distribution of the numbers would be as in table 4, if no intermediate conditions existed. The chances of getting any plants (out of 57) with few or many *durum* characters are very small. All should have the middle numbers.

TABLE 3

The numbers of plants with the different numbers (0-13) of durum characters.

NUMBER OF INTERMEDIATE CHARACTERS	POSSIBLE NUMBER OF D AND ID CHARACTERS	ACTUAL NUMBER OF D AND ID CHARACTERS													
		13	12	11	10	9	8	7	6	5	4	3	2	1	0
0	13	..	1	1	1	..	..	..	..	..	..	..	..	..	..
1	12	..	2	2	1	2	3	..	..	..	..	..	..	1	1
2	11	..	..	1	..	2	..	1	..	..	..	..	1	..	..
3	10	..	..	..	2	2	1	..	..	..	1	..	2	1	2
4	9	..	..	..	..	2	..	..	..	2	2	..	..	4	2
5	8	..	..	..	..	..	..	..	1	2	3	1	..	..	2
6	7	..	..	..	..	..	..	..	..	1	..	1	..	..	..
7	6	..	..	..	..	..	..	..	..	..	..	..	..	1	..
8	5	..	..	..	..	..	..	..	..	..	1	..	..	..	1
Total		..	3	4	4	8	4	1	1	5	7	2	4	6	8

Table 3 may readily be turned into a similar table for *vulgare* characters, since any character not recorded as I or D is recorded as V.

TABLE 4

NUMBER OF D CHARACTERS	MENDELIAN EXPECTATION FOR 13 CHARACTER PAIRS													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
Number of plants	1	13	78	286	715	1287	1716	1716	1287	715	286	78	13	1

Since this correlation exists with respect to the whole 13 characters, naturally each pair of *durum* or *vulgare* characters shows correlation. For those characters which can be accurately measured, the coefficient of correlation is as follows:

Compactness and head form	0.524 ± 0.054
Compactness and diameter of stem	0.220 ± 0.052
Compactness and beard length	0.096 ± 0.054

Some pairs of characters tend to be associated much more strongly than others. In general, these are the ones which are always or nearly always characteristic of the species. Thus, *durum* compactness and head form are more strongly correlated than either is with long beards. The former two characters distinguish nearly all *durum* varieties from nearly all *vulgare* varieties. On the other hand, though nearly all *durum* varieties have long beards, *vulgare* varieties may have either long or short ones. The more definitely a quality is characteristic of *durum* wheat, the more difficult it is to get it in association with *vulgare* characters.

In no case, however, is the correlation complete. Hybrid lines have been established, for example, even with the *vulgare* looseness and the *durum* ratio of width to thickness. It should therefore not be impossible to break the correlation for any desired character. In actual breeding practice it will not be necessary to get any single *durum* character away from all the others.

Behavior of intermediate segregates

The breeding behavior of those F_2 plants which are intermediate (i.e., which have a high proportion of intermediate characters and approximately equal numbers of *durum* and *vulgare* characters) is characteristic. In the first place they showed a high degree of sterility. Three of the 16 plants produced no offspring at all, and the average number of offspring for the whole 16 was 4.1. The *durum*-like and *vulgare*-like segregates were much more fertile. Though never more than 16 seeds of each plant were sown, the average number of offspring to reach maturity was 9.7. Nevertheless, a considerable number of *durum* and *vulgare*-like segregates did show partial sterility and some of their offspring died before reaching maturity.

In the second place, the offspring of the intermediate plants were generally not intermediate but either *durum*-like or *vulgare*-like. The F_2 plants segregated in the same way as F_1. For example, the offspring of 1-2-29 and 23-4-8 showed a distribution of characters as given in table 5. Thus, combinations of approximately equal numbers of *durum* and *vulgare* characters are not perpetuated in many offspring in later generations. And since these intermediate F_2 plants are relatively few in number and sterile in addition to showing this segregation, a larger and larger proportion of the segregates become *durum*- or *vulgare*-like. On the other hand, plants with a combination of chiefly *durum* characters with a few *vulgare* ones, or *vice versa*, may breed true.

CHROMOSOME NUMBERS IN RELATION TO PLANT CHARACTERS

KIHARA (1919, 1921) and SAX (1922) have shown that in *durum* wheats the haploid chromosome number is 14, while in *vulgare* it is 21 and in einkorn 7. In F_1 hybrids between *durum* and *vulgare* the heterotypic plate shows 14 bivalents and 7 univalents. At the homotypic division, the 7 univalents do not divide, but are distributed at random to either pole. SAX found that the great majority of F_3 plants had either 14 or 21 chromosomes. The 14-chromosome plants were of the *durum* type and the 21-chromosome plants were *vulgare*-like. To account for these results and others, including sterility, he assumes that gametes with 17 and 18 chromosomes do not develop, and that the nearer the chromosome number approaches the parental conditions (14 and 21) the more likely is the gamete to function properly. Most of the offspring will therefore result from the meeting of gametes with 14 or 21 chromosomes.

TABLE 5

Characters of the offspring of intermediate F_2 plants.

PEDIGREE NUMBER	CHARACTERS		
	V	I	D
1-2-29-1	11	1	1
1-2-29-2	1	3	9
1-2-29-3	2		11
1-2-29-4	3	2	8
23-4-8-1	10	1	2
23-4-8-2	3	2	8
23-4-8-3	3	6	4

During the past summer the chromosomes of a considerable number of F_2 plants were studied by the BELLING (1921) method, and these plants have since been examined with respect to the thirteen characters used in this paper. SAX's counts in a similar cross were made in F_3 plants. It was considered desirable to secure information in regard to F_2 conditions, because many of the F_2 possibilities are eliminated through sterility and correlation. It would be very difficult from F_3 plants alone to judge accurately the conditions in a representative F_2 generation, and therefore to estimate the processes which produced them.

Satisfactory counts were obtained in 41 plants, in many cases at both heterotypic and homotypic division. In some other cases in which accurate counts were made, the plants later proved sterile, so that the seed characters could not be studied, and these have not been included in the results. In nearly every case these counts were 16 to 19. Since it is desirable to raise F_3 plants in order to check carefully the F_2 classification of characters, the detailed description of the results is reserved until that generation has been raised, and the results are therefore given only in summary here.

A much larger proportion of plants with chromosome numbers from 16 to 19 were found than SAX (1922) records for F_3 plants. The varieties used may behave differently or the 50 F_3 plants used by him may not give an average representation of the F_2 generation. But the difference is presumably due chiefly to the high degree of sterility of these plants and gametic elimination. If there were no elimination of gametes and no selective fertilization, only 2 F_2 segregates out of about 6000 should have 14 or 21 chromosomes. But even if only 14- and 21-chromosome gametes function, there should be at least twice as many plants with intermediate numbers as with 14 or 21. It is quite possible that the elimination of female gametes is not so extensive as that of males, since there is only one for each ovule and no competition.

Table 6 shows the distribution of the plants with respect to the number of chromosomes and number of *durum* characters (out of a possible 13). Nearly all the plants in the group with chromosome number "14, 15" really had 14. In a few cases it could be stated with certainty that the number was not greater than 15, but it could not be stated definitely whether it was 14 or 15. Similarly, nearly all those in the group "20, 21" really had 21. And most of those in the group "16 to 19" really had 17 or 18.

TABLE 6

Chromosome number and plant characters.

CHROMOSOME NUMBER	NUMBER OF *durum* CHARACTERS													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
14, 15	..	1	..	..	..	..	..	..	3	7	4	1	..	..
16 to 19	1	..	3	1	2	2	3	1	2	1	..	..	..	..
20, 21	2	4	2	..	1	..	..	..	..	..	..	..	..	..

It will be seen that nearly all the plants with 14 or 15 chromosomes had a large number of *durum* characters, while those with 20 or 21 had none or few. It is probable that the single record of one *durum* character in the "14, 15" group is due to an error in records. In those plants with 16 to 19 chromosomes, the number of *durum* characters is for the most part intermediate. A few plants in this group were chiefly *durum*. Some of the 14-chromosome plants lacked one or a few of the most characteristic *durum* features, such as compactness, keel, or head type. And some of the 21-chromosome plants had one or a few of these *durum* characters.

Table 7 shows the distribution of the *vulgare* characters in the same way. Nearly all the 14-chromosome segregates had few *vulgare* characters, while those with 21 chromosomes had many. But there is no unbroken association of any one *vulgare* character with the 21-chromosome condition. The plants with a large number of intermediate characters generally had 16 to 19 chromosomes. On the whole there is a much less settled chromosome condition with numbers 14 and 21 than is reported for F_3 plants and, correspondingly, a much greater variety of character combinations.

TABLE 7

Chromosome number and plant characters.

CHROMOSOME NUMBER	NUMBER OF *vulgare* CHARACTERS													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
14, 15	..	3	8	3	1	..	..	..	..	1	..	..	..	..
16 to 19	..	1	2	4	4	2	2	..	1	..	..	..	..	..
20, 21	..	..	..	..	..	..	1	..	1	2	2	2	1	..

It is also evident that the number of 21-chromosome plants and of *vulgare*-like segregates is less than the number of 14-chromosome and *durum*-like segregates. This has been frequently observed in other experiments.

RUST-RESISTANCE IN RELATION TO OTHER CHARACTERS

The *durum* parent (Iumillo) of this cross is very resistant to stem rust. The pure line which has been used is highly resistant to all the biologic forms which have been found in Western Canada by NEWTON (1922). A brief summary follows of my data on the inheritance of resistance in this cross and the correlation of resistance with other characters.

All records given are from plants artificially inoculated in the greenhouse with a single biologic form of stem rust. This is number XVII of STAKMAN and LEVINE (1922), and is one of the most serious in Western Canada. The rust was supplied from time to time by W. P. FRASER of the DOMINION LABORATORY OF PLANT PATHOLOGY, situated at this University. In the earlier inoculations, F_2 plants were used and any which showed resistance were tested at least twice. Their F_3 offspring were also tested and the F_2 classification confirmed or corrected. Since greenhouse conditions during winter in Western Canada are very unfavorable for wheat because of lack of light, many plants were lost or proved sterile. The F_2 tests were therefore abandoned after a time, and only F_3 plants used, so that no promising line might be lost. When all or most of the plants of a small F_3 family proved susceptible, the F_2 parent was classified as susceptible. Since a few F_2 plants are sterile even under field conditions, no information concerning these was secured when F_3 plants only were used, and the ratios would be inaccurate to that extent. Plants were classified as resistant when they showed no uredinia at all or small, isolated ones surrounded by hypersensitive areas. These would come under types 0, 1 or 2 of STAKMAN and LEVINE (1922). All other plants were classified as susceptible.

Tests with both F_2 and F_3 plants

Total F_2 plants tested	876
Susceptible in F_2 test	771
Resistant or escaped in F_2 test	105
Sterile or dead after F_2 test	35
Susceptible families in F_3 test	18
Final resistant	52

If the sterile and dead F_2 plants are classified with the resistant plants, the ratio of susceptible to resistant is 789:87 or 9.0:1. If they are classified with the susceptible plants, the ratio is 824:52 or 15.8:1. Since sterile plants are generally weaklings and since rust does not develop well on weak plants, they should probably be classified chiefly with the susceptible ones. In any case it is evident that there is no simple Mendelian ratio.

Tests with F_3 plants only

Total number of families tested	2256
Susceptible families	2097
Resistant families	159

Ratio, susceptible : resistant, 13.2 : 1.

HAYES (1920) has reported finding a ratio of 1030 susceptible to 106 resistant or 9.7: 1. His figures, however, include the results with two sets of hybrids, Marquis×Kubanka and Marquis×Iumillo. The factorial conditions in the two *durum* races may not be the same, since they behave differently to certain rust strains.

Characters of resistant segregates

Altogether, in this experiment 211 F_2 plants or F_3 families proved resistant. Of these only 3 possessed chiefly *vulgare* characters, all the others being clearly of the *durum* type. The three *vulgare*-like plants are not as resistant as the *durum* parent, but are much more resistant than the *vulgare* parent. HAYES reports obtaining 2 *vulgare*-like plants in his 106 resistant segregates. According to my observation of their behavior in Western Canada, HAYES'S hybrids also are not so resistant as their *durum* parent.

There is thus evidently a very high degree of correlation between rust-resistance and *durum* characters. This is a particular example of the general correlation of all *durum* characters in this cross. The fact that rust-resistance depends on more than one factor, as shown by the breeding results, makes the correlation more pronounced than in other cases. It is more difficult to get the two or more factors for rust-resistance in the same segregate without taking with them many other *durum* characters, than it would be to get a single factor for resistance free from other *durum* characters.

Some *vulgare* characters are found in resistant segregates much more commonly than others. Thus the *vulgare* laxity and type of head are rarely found in resistant segregates while the keel, length of beards, or seed hairs of resistant plants are frequently of the *vulgare* type.

DISCUSSION

SAX concludes that the correlation of characters as well as the partial sterility is due to the behavior of the extra 7 chromosomes of *vulgare* wheat. The addition to the number 14 of any number less than a complete set of 7 results in an unbalanced condition which kills or greatly handicaps the gametes. Therefore gametes with 14 and 21 chromosomes are the ones which function chiefly. This is supported by his finding that the great majority of F_3 plants studied have a haploid number of either 14 or 21. It should be pointed out, however, that even if all gametes have either 14 or 21 chromosomes, there should be at least as many F_2 plants with an intermediate chromosome number as with 14 and 21. Therefore either the F_2 plants with an intermediate number are sterile or they produce F_3 plants with 14 and 21 only.

Since the 14-chromosome segregates are *durum*-like and the 21-chromosome segregates are *vulgare*-like, it follows from this conception that the *vulgare* characters are due to the extra 7 *vulgare* chromosomes. Fourteen of the *vulgare* chromosomes must be practically the same as fourteen *durum* ones. They mate regularly with them and are interchangeable. According to this view, even if all the 14 chromosomes of an F_2 plant came from the *vulgare* parent, it would still be a *durum*. Then the extra 7 chromosomes must always be the same ones and so unlike any of the *durum* ones, that they rarely mate with them.

But there are several kinds of evidence which seem to be opposed to the conception that the *vulgare* genes are carried only in the extra seven chromosomes, and to the inferences which may be drawn from that conception: (1) Segregates are obtained which are *durum*-like in all but one or a few features, and these features may be the most characteristic of *vulgare*. Similarly, segregates are obtained which are *vulgare*-like in all but one or a few characters. (2) Long-established varieties of wheat are known which present similar combinations. For example, a few races of *durum* wheat are known, which have the *vulgare* hollow stem; others have mealy endosperm, others lax heads, others are beardless. Similarly, some long-established *vulgare* varieties have certain *durum* characters, such as fully-keeled glumes, solid stems, compact heads. (3) It has been shown above that 14-chromosome segregates may actually have some *vulgare* features, even the most characteristic ones, and that 21-chromosome segregates may actually have some characteristic *durum* features. (4) There must really be great differences between the primary 14 chromosomes of *vulgare* and those of *durum*, because several characters quite absent from both appear in some F_2 plants, even the striking adherence of the glumes to the kernel, which is characteristic of emmer wheats. (5) Characters which distinguish *vulgare* from *durum* wheats are commonly present in other 14-chromosome wheats, so that they can not be due to the extra 7 chromosomes. Thus, *T. polonicum* is commonly lax-headed like *vulgare*; *T. turgidum* has the short inflated glumes of *vulgare*; *T. dicoccum* has the brush of hair on the seed. (6) *T. monococcum*, the only species with the primary number 7, has several characters present in *vulgare* but not in *durum*, such as hollow stem, brush of seed hairs, short glumes. It is difficult to see how these characters, which are present in a wheat with 7 chromosomes, absent from one with 14, and present again in one with 21, can be due to duplication of genes, or why they should be present only in the particular 7 extra chromosomes of *vulgare* wheat. (7) There are great variations in the degree of sterility in crosses between different 14-chromosome wheats and *vulgare* wheats. Therefore, it is probably not due to the extra seven chromosomes only.

Owing to these difficulties, one is inclined to view favorably another possibility, namely, the effect of incompatibilities amongst the chromosomes. In this conception, the differences between the *durum* and *vulgare* chromosomes, which must be very great, exist in many or all of them, and not merely in the extra 7. The 14 *durum* chromosomes or the 21 *vulgare* chromosomes work together properly, but the differences between them are so great that combinations of the two sorts may be incompatible. A viable, properly functioning condition may result only when the chromosomes are mostly from the *durum* parent or mostly from the *vulgare* parent.

Then the characters also would be all or chiefly *durum*, or all or chiefly *vulgare*. The substitution of one or a few chromosomes of one species in a set of the other species might not be too disturbing for proper functioning. Thus, the common occurrence of one or a few characters of one species in a segregate of the other type would be accounted for. The other points mentioned in the last paragraph also support this view.

Additional points supporting this conception are: (1) A considerable proportion of the seeds on F_1 plants produce offspring which fail to grow properly to maturity. Therefore, though the gametes form and function, nevertheless the combinations which they produce cannot function properly in the zygote. There would appear to be incompatibilities in the vegetative tissues. (2) A good many plants in F_2 and F_3, which examination shows to have only 14 chromosomes, are weak and partially sterile. In these there can be no effect of an unbalanced chromosome number. Their weakness and sterility are apparently due to chromosome incompatibilities.

It is to be expected that the behavior of these long-established species of wheat should be unlike that of forms in which the chromosome differences are of recent or experimental origin. The species of wheat have been in existence so long (since prehistoric times) that many changes in chromosome constitution must have taken place since the original changes in chromosome number. In recent examples of polyploidy the extra chromosomes presumably carry the same genes as the others, so that any differences in characters are due only to duplications and numerical relationships.

Whatever our interpretation of the causes of the correlation may be, the results show that it is not absolute, that we do get *durum* characters in segregates which are otherwise *vulgare*-like. Even the most characteristic of the *durum* qualities may be found in plants all of whose other characters are *vulgare*. In agreement with this we find 14-chromosome plants with odd *vulgare* characters and 21-chromosome plants with odd *durum* characters. It therefore appears to be premature to conclude that it will be impossible to get any desirable *durum* character in combination with *vulgare* characters in a wheat of *economic* importance.

The difficulties with respect to rust-resistance seem to be greater than with respect to other *durum* characters. This may be due to the fact, as seen from the results, that resistance depends on more than one factor and to carry all over into a *vulgare* type may also involve carrying over other *durum* characters. But rust-resistant *vulgare*-like segregates have actually been secured both by HAYES and by the writer, and have maintained their resistance at many different stations (FRASER 1923). It is true that these are not so resistant as the *durum* parent. Probably not all the factors have yet been carried over into the *vulgare* type, or they may not function so effectively in a set of chromosomes which are mainly *vulgare*. Whether they are sufficiently resistant for practical purposes remains to be seen.

SUMMARY

1. Thirteen pairs of characters which distinguish *Triticum durum* from *T. vulgare* were studied in F_2 and F_3 plants. The condition of each plant (*vulgare*, *durum* or intermediate) with respect to each of them is recorded.

2. The F_2 segregates may be divided into 3 groups: (1) those with *durum* characters only or chiefly; (2) those with *vulgare* characters only or chiefly; (3) those with a considerable number of intermediate characters and approximately equal numbers of *durum* and *vulgare* characters.

3. The *durum*-like segregates commonly showed one or a few *vulgare* features, sometimes even the most characteristic ones. Similarly, the *vulgare*-like segregates commonly showed one or a few *durum* features.

4. The intermediate plants showed a high degree of sterility and produced a high proportion of *durum* and *vulgare* types in F_3. Intermediate types thus tend to disappear in the third and later generations.

5. Chromosome numbers and their relation to the 13 characters is recorded for F_2 plants. A much larger proportion of plants showed chromosome numbers intermediate between those of the parents (14 and 21) than is reported for F_3 plants. The 14-chromosome plants were of the *durum* type and the 21-chromosome plants were of the *vulgare* type, but most plants of each type showed a few characters of the other type, even the most characteristic ones.

6. Results are given concerning the inheritance of rust-resistance in this cross. Records are available for more than 3000 F_2 plants and F_3 families (about 30,000 plants in all) and these show the F_2 ratio of susceptible to resistant to be about 13:1. Of the resistant plants, very few were of the general *vulgare* type, though numerous resistant plants contained a few *vulgare* characters. The few resistant *vulgare*-like plants were not so resistant as the *durum* parent. The correlation of rust-resistance and *durum* characters has been broken, but, owing to the fact that it depends on more than one factor, it may be very difficult to get the full *durum* resistance in *vulgare* types without other *durum* characters.

7. Evidence is brought forward which is considered to indicate that the correlation of characters and partial sterility depends, in part at least, on chromosome incompatibilities, and not entirely on the elimina-

tion, due to unbalance, of gametes with intermediate chromosome numbers.

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