INHERITANCE
OF A NUMBER OF DIFFERENTIATING
CHARACTERS IN *TRITICUM DURUM*

by

HOSSEIN ALI SHEYBANI

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ABSTRACT

The mode of inheritance of the seven differentiating characters (awnedness, glume pubescence, stem solidness, grain color, rust resistance, spike density, and growth habit) was studied in the diallel combinations of the following ten varieties of *T. durum*: *leucurum*, *reichenbachii*, *murciense*, *erythromelan*, *provinciale*, Golden Ball, Stewart, Bald Medeah, Kahla, and Camadi.

Monogenic inheritance was found for the four characters awnedness, glume pubescence, stem solidness, and rust resistance. A 3:1 ratio was obtained for awnless vs awned, rust susceptible vs rust resistant and glume pubescent vs glabrous except for crosses involving the pubescent variety Kahla where the ratio was 1:3 glume pubescent vs glabrous. A 1:2:1 ratio of solid: intermediate:hollow was obtained in crosses where varieties differed in stem solidness.

Since a recessive gene conditioning glume pubescence has not been reported previously it is proposed that the gene in Kahla which is recessive to both Hg and hg be designated hg_1.

Digenic inheritance was observed for grain color and growth habit. In crosses involving *murciens* (red seeded) or Camadi (purple seeded) five color classes in a 1:4:6:4:1 ratio were obtained. Either two allelic series R_1^c, R_1, r_1 and R_2^c, R_2, r_2, or three gene pairs Pr, R_1, R_2 could be assigned to ex-

plain the results obtained for this character. In crosses where varieties differed in growth habit, ratios of 3:1, 13:3, and 15:1 spring type vs winter type were obtained. Two allelic series Sp, sp, and W, w, w_1 appear to govern the inheritance of this character.

Spike density was found to be influenced considerably by environment. Since the range of density in progenies of the crosses extended, in some cases, beyond the range of density of the parents involved, transgressive inheritance was considered to be responsible.

Excluding spike density and growth habit, the data obtained in this study were used to determine if linkage relationships existed between different characters. The goodness of fit to the expected ratios for the independant assortment of genes governing any two characters at time was tested by chi-square analysis, and no linkage could be demonstrated between genes governing the characters concerned.

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INTRODUCTION

In wheat there are at least three levels of ploidy: the diploid with seven pairs of chromosomes as in Triticum monococcum, the tetraploid with 14 pairs of chromosomes as in Triticum durum, and the hexaploid with 21 pairs of chromosomes as in Triticum aestivum. The diploid group contains the A genome, the tetraploids either the AB or the AG genomes, and the hexaploids the ABD genomes. Genetic studies in the tetraploid and in the hexploid wheats are usually more difficult than in the diploid species because of a possible duplication of many of the hereditary factors. That is, a gene which governs the inheritance of any specific character, may be found in each of the two genomes of the tetraploids or in each of the three genomes present in the hexaploid wheats.

According to the number of gene pairs involved, the mode of inheritance for a given character may be classified as monogenic, digenic, trigenic, etc. For example, the symbol A is given to designate the awn character in wheats, and at least two genes, A_1 and A_2 have been established. Although several independent reports have indicated digenic inheritance for awnedness, if all varieties concerned were brought together and crossed in diallel, it is conceivable that trigenic ratios may have been obtained. Therefore, a genetic study in the tetraploid or hexaploid group should include as many varieties as is convenient to handle if maximum information is to be obtained.

The most important purpose of genetic studies in wheat, as well as in the other crops, is to understand the relationship between different characters, and the rate of recombination in the offspring of their crosses. Such an investigation is especially valuable particularly if linkage can be established between a hidden important economic character like solidness of stem, and an easy to detect morphological character like awnedness.

If a plant breeder is interested in improving durum wheats, then the inheritance and linkage of as many characters as possible should be investigated. With this in mind, the present study, dealing with the mode of inheritance of awnedness, glume pubescence, stem solidness, rust resistance, spike density, grain color, and growth habit in *Triticum durum*, and their linkage relationship, was initiated. Investigations were made using ten distinctly different durum varieties. The study of the F_1 and the F_2 generations of diallel crosses of these varieties is the subject of this thesis.

REVIEW OF LITERATURE

Although there is considerable information concerning the inheritance of genetic characters for the hexaploid wheats, very few studies have been reported for the tetraploid group of *Triticum*.

Ausemus *et al*. (1) have summarized the characters studied by various investigators in which symbols designating the different characters and their mode of inheritance are described. These are shown in Table I.

Table I. Symbols and the mode of inheritance of some characters in wheat. (After Ausemus *et al.* (1))

Character	Symbol	Mode of inheritance
Awnedness	A	Monogenic
"	-	Digenic
"	-	Trigenic
"	-	Tetragenic
"	Aa	Allel to a
Awn color	Ac	Monogenic
Smooth vs rough awns	Ar	Monogenic
" " " "	-	Digenic
Glume color	Gc	Monogenic
" "	-	Digenic
Hairy glumes	Gg	Monogenic
" "	-	Digenic
" "	Gg^g	Allelic to Gg
Kernel weight	K	Trigenic
" "	-	Multigenic
Kernel length	Kl	Multigenic
Kernel per spiklet	Ks	Digenic
Hairy leaf	Lh	Digenic
Kernel color	R	Monogenic
" "	-	Digenic
" "	-	Trigenic
Stem solidness	S	Monogenic
" "	-	Digenic

Table I (Cont'd.)

Character	Symbol	Mode of inheritance
Stem solidness	-	Multigenic
Spike density	Sd	Monogenic
" "	-	Digenic
" "	-	Multigenic
" "	-	Inhibitor

Awn Character

Several symbols have been reported to designate the genes responsible for awn character. The symbol A has been mentioned by Ausemus *et al.* (1). Howard and Howard (9) used symbols B and T. The same symbols were used by Harrington (4). Watkins and Ellerton (30) used B_1 and B_2; and more recently Tsunewaki and Jenkins (25) have reported the symbols A_1, Hd, B_1, B_2, and A_4.

The mode of inheritance of the awn character, reported in the literature, ranges from monogenic to polygenic. Monogenic inheritance with either a 3:1 ratio of tip-awned to fully awned plants or a 1:2:1 ratio of tip-awned: intermediate: fully awned have been reported by Biffen (2) and by Howard and Howard (9). A ratio of 3:1 awnless vs awned was obtained by Harrington (4). Digenic inheritance with a ratio of 1:4:6:4:1 for the segregation of awn character in the F_2 generation has been reported by Harrington (4), Watkins and Ellerton (30), and Lebsock and Smith (15).

Tsunewaki and Jenkins (25) found five gene pairs governing the awn character, while Heyne and Livers (8), reported a more complex inheritance for this character, assuming that genes affecting awn character are located on at least eight chromosomes.

A monosomic study by Tsunewaki and Jenkins (25) in common wheats has demonstrated that genes A_1, H_d, B_1, B_2, and A_4 are located on chromosomes II, VIII, IX, X, and XVI respectively.

Watkins and Ellerton (30) reported that two gene pairs, B_1 and B_2, control the awn character, and a modifier gene, a_1, influences the action of the major genes B_1 and B_2. Lebsock and Smith (15), reported digenic inheritance and they concluded that there were two factor pairs, one, an awn producing pair of alleles, the other, a pair of inhibiting alleles which were incompletely epistatic over the awn producing allele or alleles.

Glume pubescence

Ausemus et al. (1) reported the symbols Gg and Gg^g for glume pubescence, while Tsunewaki and Jenkins (25) used Hg to designate the hairy character of glume.

An extensive review of the literature by Ausemus et al. (1) indicates that monogenic inheritance with a 3:1 ratio of pubescence vs glabrous is most common. The same ratio has been obtained more recently by Tsunewaki and Jenkins (25). However, Howard and Howard (9) observed digenic inheritance in progenies of crosses between hexaploid and tetraploid wheats with a 15:1

ratio of pubescent vs glabrous. Digenic inheritance was also mentioned by Ausemus et al. (1). Howard and Howard (9), obtaining a 15:1 ratio, assumed that the two factor pairs were carried by separate genomes, and therefore inherited independently.

Stem Solidness

The symbol S has been mentioned by Ausemus et al. (1) to designate stem solidness. Yamashita (31) used the symbol M, and assumed that there is an allelic series for this gene in tetraploid and hexaploid wheats. He stated that the allele Md in T. dicoccum and T. durum conditions the complete pithiness of the stem. With the allele Mp in T. polonicum only the uppermost internode was pithy. The allele Mt in T. turgidum conditions pithiness in the stem only a few centimeters below the spike. A recessive gene mB, for hollowness, is present in the B genome of T. spelta. Moreover, an additional gene, Od, exists in the D genome of T. spelta, and produces the hollow type of the hexaploid wheats (thin-walled culms).

Although digenic and multigenic inheritance of stem solidness have been reported by Ausemus et al. (1), according to the reviews by Putnam (21) and Ausemus et al. (1), most authorities mention only monogenic inheritance. Monogenic inheritance gives a 3:1 or a 1:2:1 ratio with solidness being partially dominant. Sears (19) reported many instances in which a gene pair for hollowness was located in each of the three genomes of hexaploid wheats.

Hollowness was partially dominant, and the three gene pairs had a cumulative effect.

Vavilov and Jakushikina (27), and Von Tschermack (28), reported that in crosses between tetraploid and hexaploid wheats the tetraploid type of pithiness occurs more frequently than the hexaploid type of hollowness.

Thompson et al. (24) observed, in crosses between tetraploid and hexaploid wheats, that the hybrids with 28 chromosomes are not hollow-stemmed with thin walls as are the hexaploid types. They assumed that the factor (or factors) governing stem hollowness in hexaploid wheats, is located in the A and B genomes.

Yamashita (31) reported that an epistatic gene (or genes) is located in the D genome of the hexaploid wheats. He demonstrated that the "e" chromosome of the D genome (Chromosome XX according to Sears' nomenclature) carries a gene for hollowness, epistatic to the genes for solidness located in the A and B genomes. Larson (14) studied inheritance of stem solidness in crosses between Golden Ball, a solid stemmed T. durum variety, and Rescue, a solid stemmed T. aestivum variety, and found that Golden Ball is more solid in the top internode. She observed some increase in the degree of solidness in the top internode of the F_4 lines, over that of Rescue. She assumed that Golden Ball has a stronger allele than Rescue for solidness of the top internode, located on chromosome III.

Grain color

The symbol R for color of grain has been reported by many investigators, as reported by Ausemus *et al.* (1), and Harrington (4). Harrington (4) also used R and R_1 to designate different shades of red, while Hayes *et al.* (6) reported R_1 and R_2 for the same purpose.

Several different ratios have been reported in the literature. Monogenic inheritance has been mentioned by Ausemus *et al.* (1), Biffen (2), Harrington (4), and Lebsock and Smith (15), in which either 3:1 or 1:2:1 ratios were obtained with complete or partial dominance of red color over white color of grain. Digenic inheritance (a 15:1 ratio of red vs white) has been reported by Ausemus *et al.* (1), Nilsson-Ehle, as per Hayes *et al.* (6) and Harrington (4). Trigenic inheritance (a 63:1 ratio of red vs white) has been observed by Howard and Howard (9), Ausemus *et al.* (1), and Nilsson-Ehle, as per Hayes *et al.*

Spike density

Ausemus *et al.* (1) reported the symbol Sd to designate spike density. Nilsson-Ehle, reported by Hayes *et al.* (6), used symbols, C, L_1 and L_2, for factors controlling spike density.

Hayes *et al.* (6) reviewed early studies in which a single gene pair has been reported to govern spike density. Monogenic inheritance has been reported also by Ausemus *et al.* (1), and Unrau (26). Parker, and Nilsson-Ehle, as reported by Hayes *et al.* (6), observed more complex inheritance of spike density. Nilsson-

Ehle in a cross between compact and mid-dense spiked varieties, obtained lax types in the F_2, and indicated that three gene pairs were involved.

Unrau (26), using monosomic and nullisomic lines, observed transgressive inheritance. He demonstrated that the main gene for a dense spike phenotype is carried by chromosome XX of the variety Hymar. Transgressive inheritance has also been mentioned by Stewart as reported by Unrau (26).

The study of Nilsson-Ehle as reported by Hayes *et al.* (6) reveals that the factor C for compactness is epistatic to two factors for length of internode, L_1 and L_2.

Growth habit

Powers as reported by Hayes *et al.* (6) used the symbols A, B, and C to designate the factors controlling growth habit. Recently, Tsunewaki and Jenkins (25) have used the symbol Sg in three allelic series: the first series contains Sg_1, sg_1, and sg_1^w, the second series Sg_2, sg_2, and sg_2^w, while the third series contains only Sg_3 and sg_3.

Monogenic inheritance with a ratio of 3:1 spring habit vs winter habit has been observed by Cooper as reported by Hayes *et al.* (6), Tsunewaki and Jenkins (25), and Unrau (26). Digenic inheritance has been reported by Nilsson-Leissner (16) who obtained a 15:1 ratio of spring vs winter habit. Unrau (26) in a cross between Hymar and 17 of the Chinese Spring monosomes found two gene pairs controlling growth habit, one of which was associated with chromosome IX. Tsunewaki and Jenkins (25) obtained 10:6 and 11:5 ratios of spring vs winter habit, indicating a digenic inheritance of growth habit. According to Hayes _et al_. (6) Powers reported trigenic inheritance with the assumption that the mode of inheritance of growth habit is the result of the interaction of three genes (A, B, and C). Trigenic inheritance has also been reported by Knott (11) and by Tsunewaki and Jenkins (25) who obtained a ratio of 51:13 of spring type to winter type.

The study of Powers as reported by Hayes _et al_. (6), assuming three genes A, B, and C responsible for growth habit, indicates that the gene A is epistatic to b and C, the gene B to a and C, and the gene c to a and b.

Sears (21) from a study of Chinese Spring nullisomics, found that delay in maturity is caused by deficiencies of chromosome II, V, VIII, IX, XIV, and XVIII. Kuspira and Unrau (13), using whole chromosome substitution lines, demonstrated that genes for winter habit of growth were carried by chromosomes XIII and XVIII of Thatcher, while minor genes for spring habit were carried by ten chromosomes of Thatcher, nine chromosomes of Hope, and 13 chromosomes of Timstein. Knott (11), in a monosomic analysis of some varieties including Gabo, stated that chromosome IX of Gabo carries one of the three genes for winter habit of growth. The three allelic series, reported by Tsunewaki and Jenkins (25), are located on chromosomes XVIII, IX, and XIII, respectively.

Stem rust reaction

Ausemus *et al.* used the symbol Sr to designate stem rust resistance. Smith (22), using the same symbol, mentioned Sr^m for seedling reaction of Mindum to physiologic race 147, and Sr^v for seedling resistance of Vernal to race 17. Kenaschuk *et al.* (10) used Sr^d to designate durum genes for resistance to race 15B. The symbol R_b was used by Harrington and Smith as reported by Smith (22) for resistance to races 21, 17, 29, and 36 in the field. Goulden *et al.* as reported by Ausemus *et al.* (6) used R_1 and R_2 to designate resistance to race 36.

The mode of inheritance of stem rust reaction is reported to be monogenic, digenic, and polygenic. Harrington and Aamodt (5) observed a single factor controlling rust reaction of Pentad, a durum variety, to race 34, and in Mindum, another durum variety, to race 1. They stated that it is possible to combine in a single variety, resistance to two races 1 and 34, using varieties which react reciprocally to these two physiologic races. Monogenic inheritance has also been observed by Aamodt as reported by Hayes *et al.* (6), Kenaschuk *et al.* (10), Smith (22), and Knott and Anderson (12).

Digenic inheritance has been mentioned by Goulden *et al.* as reported by Hayes *et al.* (6), Hayes *et al.* (7) with ratios 9:7, 15:1, and 1:15 resistant vs susceptible, and by Kenaschuk *et al.* (10) with a 15:1 ratio of resistant to susceptible to race

15B. A 63:1 ratio of resistant to susceptible has also been reported by Kenaschuk _et al._ (10). These authors stated that Camadi, a durum variety, differed in rust reaction from the other varieties studied by them, and carried a single gene (Srd_6) for high resistance to race 15B.

Linkage relationships

Ausemus _et al._ (1) summarized the results of many investigations on linkage relationships of a number of characters in wheat, and their percentage recombinations. These results are presented in Table II.

Table II. Linkage and percentage recombination of 24 characters in Hexaploid and tetraploid wheats (as per Ausemus *et al.* (1))

Characters linked	Percentage Recombinations
Two non allelomorphic pairs of factors for awnedness (Aa)	35 - 38
Awnedness (A) and beak shape (Bs)	unknown
" (A) " hairy node (No)	0 - 5
" (A) " keeled glume (Gs)	26 - 39
" (A) " head shape	35
Two non allelomorphic pairs of factors for bunt reaction (B)	34
Three non allelomorphic pairs of factors for bunt reaction (B)	2.4 and 28.1
Beak shape (Bs) and width of glume shoulder	unknown
Black chaff and mature plant stem rust reaction (Sr)	"
Coleoptile (Co) and straw color (Sc)	"
Dwarfness (D) and spike density (Sd)	"
Two pairs of factors for dwarfness (D)	"
Gluten strength (G) and glume color (Gc)	30 - 39
Glume color (Gc) and hairy glumes (Gg)	unknown
Stem rust reaction (Sr) and leaf rust reaction (Lr)	"
" " " " " emmer and durum type plant	"
" " " " " seedling reaction to race 41 of stripe rust	"
Leaf rust reaction (Lr) and mildew reaction (Ms)	Unknown and 20.8
Protein (P) and Kernel color (R)	25 - 30
Phenol color reaction of Kernel (Pk and spike (Ps))	unknown
Stem rust reaction (Sr) and seedling reaction	"

Hayes *et al.* (6) reported the results of several studies which indicate a linkage between glume pubesence and chaff color, in crosses of tetraploid wheats with varieties of *T. vulgare*.

Matsumura, reported by Putnam (18), found in a cross between *T. polonicum* and *T. spelta*, that the type of stem solidness of Polish wheat was correlated with the tetraploid chromosome number.

In a study of stem solidness, Larson (14) found for a cross of Golden Ball (*T. durum*) with Rescue (*T. aestivum*) that the solidness of the top internode of Golden Ball was associated with a dense spike, and with the durum type of morphology.

Watkins (29) reported a linkage between the gene K^d for glume thickness and B_1b_1, the gene for awn characters.

Smith (23) in studying the inheritance of head characters in a Mindum durum X Vernal emmer cross found that the clavate head type was conditioned by two factors, a gene C_1 responsible for the clavate head in the absence of another gene I which was epistatic to C1. He assumed that the gene I was in close linkage with the major genes controlling glume tenacity, if it was not itself one of these major genes for glume tenacity. He mentioned that no linkage was found between stem rust resistance and glume tenacity or clavate head type.

Lebsock and Smith (15), in a cross of Ld. 222 x M - V, studied the inheritance of some characters of head and seed color. They assumed that the factor controlling awn character was linked with that responsible for rachis bristle, with a recombination value of 32.3%. Also, they found a linkage between clavate head and glume tenacity. They observed a closer linkage between glume tenacity and red seed color than with amber seed color.

MATERIALS AND METHODS

This study is concerned with inheritance of the following characters in *Triticum durum*: awnedness; glume pubescence; stem solidness; grain color; spike density; rust resistance; and growth habit.

Ten varieties of *T. durum* were used as parents in this study. A brief description of each variety for the seven characters concerned is presented in Table III.

Table III. Classification of ten varieties of *T. durum* for seven differentiating characters.

Code[1]	Variety	Awn[2]	Glume Pub.[3]	Stem Solid[4]	Grain Color	Spike Density[5]	Rust Reaction	Growth habit
A	*leucurum*	+	-	-	Amber	6.6	Susc.	Winter
B	*reichenbachii*	+	+	+	"	6.4	"	Spring
C	*murciense*	+	-	-	Red	6.8	"	"
D	*erythromelan*	+	-	-	Amber	6.4	"	"
E	*provinciale*	+	-	+	"	4.8	"	"
F	Golden Ball	+	+	+	"	7.8	"	"
G	Stewart	+	-	-	"	6.5	"	"
H	Bald Medeah	-	-	-	"	7.8	"	"
I	Kahla	+	+	-	"	6.6	"	"
J	Camadi	+	-	-	Purple	4.6	Resist.	"

1 To avoid repeating the variety names throughout this thesis a code system is established, and will be used in subsequent tables.
2 + indicates awned; - indicates awnless.
3 + indicates pubescent; - indicates glabrous.
4 + indicates solid; - indicates hollow stem.
5 Number of spiklets per inch of rachis.

All varieties except Bald Medeah (H) are awned. Three varieties, reichenbachii (B), Golden Ball (F) and Kahla (I) are pubescent, and the seven others are glabrous. Three varieties, reichenbachii (B), provinciale (E), and Golden Ball (F) are solid stemmed, and seven are hollow stemmed. The variety murciense (C) has red grain, the variety Camadi (J) has purple grain, while the other eight varieties have amber grain. Only one variety, Camadi (J), was resistant to the races of stem rust (either naturally occuring in the field or artificially introduced), whereas the other nine varieties were more or less susceptible to one or more physiologic races. Spike density, shown in Table III, is the average density of seven heads for each variety. Only one variety, leucurum (A), behaved as a winter wheat, while the other nine varieties exhibited spring habit of growth.

Diallel combinations of these ten varieties including reciprocal crosses were available for this study with the exception of reciprocal crosses between erythromelan (D) and Camadi (J).

The F_1 hybrids were grown in the Plant Science Experimental Field during the summer of 1958.

Initial planting of the F_2 generation was made in the greenhouse in the fall of 1958 with approximately 240 seeds sown for each cross. Seeds were sown in greenhouse beds with a spacing of six inches between rows and 1.5 inches within rows.

It was difficult to obtain satisfactory data for some of the characters under study, primarily due to abnormal growth under greenhouse conditions.

A second planting of the F_2 generation was made in the Plant Science Experimental Field in the spring of 1959, where again approximately 240 seeds were sown for each cross. Rows in the field were one foot apart and spacing within rows was three inches.

Since one of the characters to be studied was rust resistance, the field plot was inoculated by spraying three weeks after emergence with a collection of spores of a mixture of several physiologic races of *Puccinia graminis tritici*. It was intended to study the reaction of F_2 plants to all prevalent races of stem rust and not to a particular race. This was to be attempted especially because one of the parent varieties, Camadi (J), was resistant to all physiologic races of stem rust prevalent in the field in 1958, while the other nine varieties were more or less susceptible.

Awn character was studied in the field, and in the laboratory after harvesting. Only two classes, awned and awnless were established and all F_2 plants were classified as awned or awnless.

For glume pubescence, two classes were also established. The F_2 plants were classified as pubescent or glabrous.

Stem solidness was studied after harvesting. Three cuts were made for every plant: the first about two inches below the base of spike, the second in the middle of the first internode below the spike, and the third in the lowest internode of the culm. Three classes were established: Solid, Intermediate, and Hollow. Since there were many degrees of intermediate between solid and hollow, all intermediate plants were placed in one class.

In crosses involving the variety *murciense* (C) five classes for grain color were established: R, R-, BR, B+, and B. These represent a gradation in color from red (R) to amber (B). For crosses involving Camadi (J) five classes were also established: Pr+, Pr, BPr, B+, and B. These represent a gradation in color from purple (Pr+) to amber (B). In the one cross (C x J and J x C) which involved both red and purple, the five classes established were: Pr+, Pr, RPr, R+, and R. These represent a gradation in color from purple (Pr+) to Red (R).

In total, 5697 plants were classified for each of the seven differentiating characters.

For the cross of the variety *murciense* (C) with the variety *provinciale* (E) segregates appeared that could not be accounted for on the basis of parental reactions and therefore, assuming that outcrossing must have accidently taken place, all data from combinations C x E and E x C were discarded.

RESULTS AND DISCUSSION

Experimental results are summarized in a series of tables, each of which accompanies the particular subject under discussion. The linkage relationships of various characters are discussed in a separate section.

F_1 Generation

The hybrids of the diallel crosses of the ten parent varieties were examined, for the seven characters under study, in the field and in the laboratory. Four F_1 plants from each reciprocal cross were studied. The data so obtained are given in Appendix I.

Awnedness Only one variety Bald Medeah (H) is awnless. The hybrids of the nine crosses involving this awnless variety were awnless. Some short tip-awned plants were observed among these hybrids, but they were classified as awnless. The hybrids of the other 34 crosses, involving two awned varieties, were all awned.

Glume pubescence The three varieties, reichenbachii (B), Golden Ball (F), and Kahla (I) are pubescent and the others glabrous. The F_1 plants of the crosses involving two pubescent varieties were pubescent, and the hybrids of the crosses involving two glabrous varieties were glabrous. The F_1 plants of the crosses of either reichenbachii (B) or Golden Ball (F), with each of the seven glabrous varieties were pubescent, whereas the hybrids of the crosses between

Kahla (I) and each of the seven glabrous varieties were glabrous. This would indicate that the gene or genes responsible for pubescence in Kahla (I) are recessive to those in the glabrous varieties.

Stem solidness The three varieties, reichenbachii (B), provinciale (E), and Golden Ball (F), are solid stemmed, and the seven other varieties are hollow stemmed. The F_1 plants of the crosses between any two solid-stemmed varieties were solid stemmed, and those of the crosses between any two hollow-stemmed varieties were hollow stemmed.

The hybrids of the crosses involving a solid-stemmed and a hollow-stemmed variety were intermediate. However, in the F_1 of the reciprocal crosses between Golden Ball (F) and erythromelan (D) (F x D and D x F), three of the four plants under study were solid stemmed instead of intermediate. Similarily, in the F_1 of the cross between Golden Ball and Bald Medeah (Hx F), two of the four plants were solid stemmed instead of intermediate, while in the combination (F x H) of the same varieties all F_1 plants were intermediate. On the contrary, among the hybrids of the cross between Bald Medeah and provinciale (E x H), one of the four plants was hollow stemmed instead of intermediate, whereas all F_1 plants of the combination (H x E) were intermediate.

Grain color The two varieties murciense (C) and Camadi (J), have red and purple color of grain respectively, while the eight other varieties have amber color of grain. The hybrids from the crosses between amber grain varieties all had amber grain. The grain of hybrids from the crosses between Camadi (J) and each of the eight amber varieties were a medium purple in color and those from the crosses between murciense (C) and the amber color varieties were a medium red in color (with the exception of C x E and E x C). The grains of hybrids from the reciprocal crosses involving both Camadi (J) and murciense (C) were also a medium purple in color. The purple and red color of the hybrids concerned were distinctly less intense than the purple and red color of the parents involved.

Spike density This character was studied only visually in the F_1 hybrids. No measurements were made, and therefore no data are presented in this study. The only observation made was that this character is influenced considerably by the environment. A visual observation of the hybrid heads in the field and in the laboratory showed many plants having a spike density more dense than the compact parents or more lax than the lax parents. A considerable range of spike density within a plant or within a cross was observed.

Growth habit Although one variety, leucurum (A), behaved as a winter variety, the hybrids of the crosses of this variety with the other nine exhibited a spring habit of growth. Spring habit of growth was also characteristic of all intra-spring variety crosses and therefore data for growth habit were not included in Appendix I.

Rust resistance The variety Camadi (J) is a rust resistant variety, but the hybrids of crosses between this variety and the other nine varieties were highly susceptible (generally more than 50% infected), with the exception of the three crosses of Camadi (J) with varieties *leucurum* (A), *murciense* (C), and Golden Ball (F), in which some hybrids were more or less resistant to the prevalent physiological races of stem rust present in the field. The hybrids of the diallel crosses of the other nine varieties (susceptible varieties) were highly susceptible.

F_2 Generation

Awnedness Since only one parent, Bald Medeah (H), is awnless, it would be expected that segregation of awn character occurs only in crosses involving this variety. Nevertheless the progenies of the 35 crosses involving two awned varieties were checked, and no segregation for this character was found. Therefore data from the 35 crosses are not presented.

A total of 1253 F_2 plants of nine crosses of Bald Medeah (H) with the nine other varieties were classified for every cross as awned and awnless. The short tip-awned and tip-awned plants were also classified as awnless. No intermediate classes were established.

The experimental results and the chi-square analysis for each of the nine crosses involving Bald Medeah (H) are summarized in Table IV.

Table IV Chi-square analysis for a 3:1 ratio of awnless vs awned in the F_2 generation of crosses involving Bald Medeah (H).

Cross[1]	Observed ratio		Expected Ratio		X^2	P
	Awnless	Awned	Awnless	Awned		
H x A	80	28	81	27	.0493	.80 - .90
H x B	78	25	77.25	25.75	.0218	.80 - .90
H x C	75	26	75.75	25.25	.0296	.80 - .90
H x D	141	51	144	48	.2500	.50 - .70
H x E	103	38	105.75	35.25	.2860	.50 - .70
H x F	98	34	99	33	.0404	.80 - .90
H x G	117	33	112.5	37.5	.7200	.30 - .50
H x I	125	39	123	41	.1300	.70 - .80
H x J	117	45	121.5	40.5	.6666	.30 - .50

[1] The data for each cross in this and subsequent tables represents the combined data from reciprocal crosses.

In each of the nine crosses excellent fits were obtained for a 3:1 ratio as tested by the chi-square test. Therefore, it appears that awnedness is governed by a single gene pair, awnless being dominant over awnedness.

Glume pubescence Three varieties, reichenbachii (B), Golden Ball (F), and Kahla (I) have pubescent glumes, and the others are glabrous. No segregation for this character was found in F_2 plants of crosses between two glabrous or between two pubescent varieties. Segregation occurred only in crosses involving a pubescent and a glabrous parent.

A total of 2500 plants of the F_2 generation of 21 crosses were studied and classified into two classes, pubescent and glabrous. The experimental results are shown in Table V.

Table V Chi-square analysis for the 3:1 ratio of pubescent vs glabrous in the F_2 generation of the 14 crosses involving *reichenbachii* (B) and Golden Ball (F), and for the 1:3 ratio of pubescent vs glabrous in the F_2 generation of the seven crosses involving Kahla (I).

	Observed ratio		Expected ratio			
Cross	Pubescent	Glabrous	Pubescent	Glabrous	X^2	P
B x A	38	12	37.5	12.5	.0266	.80 - .90
B x C	50	15	48.75	16.25	.1288	.70 - .80
B x D	55	17	54	18	.0740	.70 - .80
B x E	52	16	51	17	.0784	.70 - .80
B x G	78	25	77.25	25.75	.0288	.80 - .90
B x H	79	24	77.25	25.75	.1585	.50 - .70
B x J	92	39	98.25	32.75	1.5903	.20 - .30
F x A	49	18	50.25	16.75	.1243	.70 - .80
F x C	108	34	106.5	35.5	.0844	.70 - .80
F x D	103	36	104.25	34.75	.0599	.80 - .90
F x E	105	36	105.75	35.25	.0212	.80 - .90
F x G	115	36	113.25	37.75	.1081	.70 - .80
F x H	101	31	99	33	.1616	.50 - .70
F x J	133	50	137.25	45.75	.5264	.30 - .50
I x A	21	47	17	51	1.2548	.20 - .30
I x C	24	70	23.5	70.5	.0164	.80 - .90
I x D	39	121	40	120	.0333	.80 - .90
I x E	45	113	39.5	118.5	1.0208	.30 - .50
I x G	37	99	34	102	.3529	.50 - .70
I x H	44	120	41	123	.2926	.50 - .70
I x J	46	128	43.5	130.5	.1915	.50 - .70

The 3:1 ratio of pubescent vs glabrous fits very well for all crosses except those involving variety Kahla (I), which gives a 1:3 ratio of pubescent vs glabrous. Therefore, the segregation of this character giving ratios 3:1 and 1:3 shows that glume pubescence is dominant over glabrousness in varieties *reichenbachii* (B) and Golden Ball (F), while it is recessive to glabrous in the variety Kahla (I). The inheritance of glume pubescence is controlled by a single factor.

It seems reasonable to assume that the genes for pubescence and glabrousness of glume in all ten varieties form an allelic series, Hg, hg, and hg_1. Hg, a dominant gene conditions the expression of pubescence in all pubescent varieties tested except in Kahla (I). The gene hg, recessive to Hg but dominant over hg_1, conditions glabrousness when homozygous, or in the heterozygous condition, in crosses involving the variety Kahla (I) which carries the gene hg_1. The gene hg_1 is recessive to either Hg or hg, and it conditions pubescence when homozygous as in the variety Kahla (I).

Therefore, the genotype of the varieties *reichenbachii* (B) and Golden Ball (F), as far as this character is concerned, is HgHg, while the genotype of Kahla (I) is hg_1hg_1, and all glabrous varieties have the genotype hg hg.

3. Stem solidness

Among parent varieties, three varieties are solid stemmed, *reichenbachii* (B), *provinciale* (E), and Golden Ball (F). The others are hollow stemmed.

No segregation was observed in progenies of crosses between two solid or two hollow-stemmed varieties.

The F_2 generation of crosses of the three solid-stemmed varieties with hollow-stemmed varieties were classified into three classes: solid, intermediate, and hollow. A total of 2442 F_2 plants of 20 crosses were examined for this character.

The intermediate class ranged from almost solid to almost hollow. Only the plants fully solid stemmed were classified as solid, and those completely hollow stemmed were classified as hollow, whereas all different degrees of intermediate were considered as one class. However, a careful study of intermediate plants revealed that in some crosses stem solidness was partially dominant (for example, crosses involving Golden Ball (F)), while in the other crosses it was partially recessive (crosses involving provinciale (E)).

Table VI Chi-square analysis for the 1:2:1 ratio of solid: intermediate: hollow, in the F_2 generation of the 20 crosses involving the three solid stemmed varieties: reichenbachii (B), provinciale (E), and Golden Ball (F).

Cross	Observed ratio			Expected ratio			X^2	P.
	Solid	Interm.	Hollow	Solid	Interm.	Hollow		
B x A	15	25	10	12.5	25	12.5	1.0000	.50 - .70
B x C	13	36	16	16.25	32.5	16.25	1.0307	.50 - .70
B x D	17	35	20	18	36	18	.3555	.80 - .90
B x G	26	54	23	25.75	51.5	25.75	.4174	.80 - .90
B x H	32	51	20	25.75	51.5	25.75	2.1851	.30 - .50
B x I	26	47	22	23.75	47.5	23.75	.3473	.80 - .90
B x J	26	73	32	32.75	65.5	32.75	2.2704	.30 - .50

Table VI (Cont'd.)

Cross	Observed ratio			Expected ratio			X^2	P.
	Solid	Interm.	Hollow	Solid	Interm.	Hollow		
E x A	31	53	22	26.5	53	26.5	1.5282	.30 - .50
E x D	36	73	42	37.75	75.5	37.75	.6423	.70 - .80
E x G	44	74	44	40.5	81	40.5	1.2098	.50 - .70
E x H	39	71	31	35.25	70.5	35.25	.9996	.50 - .70
E x I	39	84	35	39.5	79	39.5	.8354	.50 - .70
E x J	40	75	43	39.5	79	39.5	.4177	.80 - .90
F x A	16	36	15	16.75	33.5	16.75	.4029	.80 - .90
F x C	42	72	28	35.5	71	35.5	2.7887	.20 - .30
F x D	32	72	35	34.75	69.5	34.75	.3956	.80 - .90
F x G	39	77	35	37.75	75.5	37.75	.3245	.80 - .90
F x H	35	65	32	33	66	33	.1666	.90 - .95
F x I	32	70	31	33.25	66.5	33.25	.3834	.80 - .90
F x J	56	90	37	45.75	91.5	45.75	3.9945	.10 - .20

In the segregating generation of all 20 crosses a good fit for the 1:2:1 ratio of solid:intermediate:hollow was obtained. This agrees with the result reported by Putnam (18). It appears that stem solidness, in the varieties studied here, is governed by a single factor pair. Neither solidness nor hollowness is completely dominant over its allele.

Grain color

Since only two varieties, murciense (red) and Camadi (purple), differed from the amber color of all remaining varieties, the segregation of color will be discussed only for the F_2 generation of crosses involving either one or both of these two varieties. However, the F_2 generation of all crosses between amber seeded varieties were checked, and no segregation was observed.

In crosses involving murciense (C), a red seeded variety, a range of five different colors from red to amber, R (red like parent C), R- (less intensive red), BR (light red), B+ (dark amber), and B (amber like the other parent) was observed.

The 634 F_2 plants of the seven crosses involving murciense (C) were thus classified into the five classes, and the data are presented in Table VII.

Table VII Chi-square analysis of the 1:4:6:4:1 ratio for the segregation of grain color in the F_2 generation of the crosses involving the variety *murciense* (C).

Cross		R	R-	BR	B+	B	Total	X^2	P. value
C x A	O (1)	4	13	20	9	5	51	2.4297	.50 - .70
	Ex	3.1875	12.75	19.125	12.75				
C x B	O	6	10	19	14	3	52	5.2051	.20 - .30
	Ex	3.25	13	19.5	13	3.25			
C x D	O	10	33	40	27	8	118	1.9869	.70 - .80
	Ex	7.375	29.5	44.25	24.5	7.375			
C x F	O	7	31	50	30	12	130	2.2974	.50 - .70
	Ex	8.125	32.50	48.75	32.50	8.125			
C x G	O	9	31	50	29	8	127	2.5012	.50 - .70
	Ex	7.9375	31.75	47.625	31.75	7.9375			
C x H	O	8	20	35	20	5	88	1.666	.70 - .80
	Ex	5.5	22	33	22	5.5			
C x I	O	5	16	25	15	7	68	2.2156	.50 - .70
	Ex	4.25	17	25.5	17	4.25			

(1) : O, observed - Ex, expected.

The goodness of fit of the 1:4:6:4:1 ratio for each of the seven crosses was confirmed by the chi-square analysis.

In crosses involving Camadi (J) five classes, Pr+(purple like J), Pr (medium purple), BPr (light purple), B+ (dark amber), and B (amber like the other parent), were established, and 1077 were classified accordingly into the five classes.

The data of the seven classes involved are presented in Table VIII.

Table VIII Chi-square analysis of the 1:4:6:4:1 ratio for the segregation of grain color in the F_2 generation of the crosses involving the variety Camadi (J).

Cross		B	B +	BPr	Pr	Pr +	X^2	P. value
J x A †	0	6	20	9 25	21	8	1.4100	.80 - .90
	Ex	5.5625	22.25	33.375	22.25	5.5625		
J x B	0	9	27	28 24	30	7	1.4396	.80 - .90
	Ex	7.8125	31.25	46.875	31.25	7.8125		
J x E	0	8	38	18 41	43	10	.7255	.80 - .95
	Ex	9.875	39.5	59.25	39.5	9.875		
J x F	0	15	44	18 51	41	14	2.4485	.50 - .70
	Ex	11.4375	45.75	68.625	45.75	11.4375		
J x G	0	8	48	19 41	47	16	3.9637	.30 - .50
	Ex	11.1875	44.75	67.125	44.75			
J x H	0	14	35	30 32	43	8	2.8557	.50 - .70
	Ex	10.125	40.5	60.75	40.5	10.125		
J x I	0	14	40	45 18	45	12	1.4250	.80 - .90
	Ex	10.875	43.5	65.25	43.5	10.875		

0, observed - Ex, expected

A ratio of 1:4:6:4:1 was tested by the chi-square analysis, and goodness of fit was obtained.

Similarly, in the F_2 generation of the reciprocal crosses involving both *murciense* (C) and Camadi (J), five classes, Pr+ (purple), Pr (medium purple), RPr (light purple), R+ (dark red), and R (red like parent C).

The 166 F_2 plants of the combinations C x J and J x C were classified into the five classes, and the data so obtained are presented in Table IX.

Table IX Chi-square analysis of the 1:4:6:4:1 ratio for the segregation of seed color in the F_2 generation of reciprocal crosses between *murciense* (C) and Camadi (J).

Cross		R	R+	RPr	Pr	Pr+	X^2	P. value
C x J		6	8	44	11	5		
J x C		5	33	31	18	5		
Total	O[1]	11	41	75	29	10	6.4535	.10 - .20
	Ex	10.375	41.5	62.25	41.5	10.375		

[1] O, observed, - Ex, expected.

A 1:4:6:4:1 ratio of the different shades of purple and red was obtained, and it was tested for goodness of fit by the chi-square analysis.

Since the goodness of fit of the 1:4:6:4:1 ratio is obtained for all 15 crosses, two hypotheses can be presented to explain the results obtained in this study.

1. Grain color may be controlled by two allelic series: R_1^c, R_1, r, and R_2^c, R_2, r_2. The genes r_1 and r_2 are both recessive and condition, when homozygous the amber color grain (r, $r_1r_2r_2$). The genes R_1 and R_2 two dominant genes condition the red color of grain when both are homozygous as in *murciense* (C) ($R_1R_1R_2R_2$). R_1^c and R_2^c two dominant genes condition, when homozygous, the purple color of grain as in Camadi (J) ($R_1^cR_1^cR_1^cR_1^c$).

2. Grain color may be controlled by three gene pairs: Pr, R_1, R_2. In this case, the red color of grain as in *murciense* should have both R_1 and R_2 and pr (R R R R prpr), and the amber seeded varieties should have the complete recessive of all factors ($r_1r_1r_2r_2$prpr). Therefore the purple color of grain as in Camadi (J) should be expressed by either $R_1R_1r_2r_2$PrPr or $r_1r_1R_2R_2$PrPr.

On the basis of the second hypothesis (Pr, R_1, R_2), in progenies of the crosses between Camadi (J), purple grain, and any amber seeded variety, the red color grain should be observed. This was not observed in the results of the present work. However, it is possible that the classification of different shades of purple in those crosses, due to the difficulty of measurement, was more or less erronous, and that some shades of purple like Pr- or B++should have been classified as red.

Since there is no evidence that in the crosses of purple and amber the red color should be observed, the first hypothesis, which assumestwo allelic series, seems to be more probable. On the basis of this assumption, genotypes of the different shades of purple and red, in progenies of the crosses involved, can be explained as follows:

Pr+ : $R_1^cR_1^cR_2^cR_2^c$

Pr : $R_1^cR_1^cR_2^cR_2$, $R_1^cR_1R_2^cR_2^c$, $R_1^cR_1^cR_2^cr_2$, and $R_1^cr_1R_2^cR_2^c$

RPr : $R_1^cR_1^cR_2R_2$, $R_1^cR_1R_2^cR_2$, and $R_1R_1R_2^cR_2^c$

BPr : $R_1^cR_1^cr_2r_2$, $R_1^cr_1R_2^cr_2$, and $r_1r_1R_2^cR_2^c$

R+ : $R_1^cR_1R_2R_2$, and $R_1R_1R_2^cR_2$

R : $R_1R_1R_2R_2$

BR : $R_1R_1r_2r_2$, $R_1r_1R_2r_2$, and $r_1r_1R_2R_2$

R- : $R_1R_1R_2r_2$, and $R_1r_1R_2R_2$

B+ : $R_1r_1r_2r_2$, $r_1r_1R_2r_2$, $R_1r_1r_2r_2$, and $r_1r_1R_2r_2$

B : $r_1r_1r_2r_2$

Rust resistance

The field plot was inoculated by spraying with a mixture of spores of various physiologic races of stem rust. Only one variety, Camadi (J), was found to be resistant to all physiologic races present in the field. However, a slight infection of 1-5% was observed in some plants of this variety, while the nine other varieties were highly infected (60-100%) by at least one physiologic race of stem rust. Therefore, this limit of 5% infection was established arbitrarily as a limit of resistance.

The F_2 generation of crosses involving the variety Camadi (J) showed segregation of resistance vs susceptibility to all prevalent races of stem rust, whereas in the progenies of crosses between any two susceptible varieties no segregation was observed.

A total of 1244 F_2 plants of eight crosses involving Camadi (J) were classified as resistant (completely resistant or less than 5% infected) and susceptible (60% infected or more). However, there may have been less than 60% reaction in some of the F_2 plants, but the difference between resistance and susceptibility was quite clear cut and no difficulty was encountered in differentiation between the two classes.

The experimental results are shown in Table X.

Table X Chi-square analysis for a goodness of fit to a 3:1 ratio of rust susceptible to rust resistant in the F_2 generation of the crosses involving Camadi (J).

Cross	Susceptible	Resistant	χ^2	P
J x A	70	21	.1894	.50 - .70
J x B	97	34	.0636	.80 - .90
J x C	126	40	.0978	.70 - .80
J x E	116	42	.2109	.50 - .70
J x F	138	45	.0163	.80 - .90
J x G	135	44	.0167	.80 - .90
J x H	125	37	.4032	.50 - .70
J x I	134	40	.3754	.50 - .70

A 1:3 ratio of resistant vs susceptible to stem rust was obtained for all crosses. The chi-square test gave P. values of .50 to .70 or higher in all crosses. Therefore it was concluded that resistance is governed by a single recessive gene.

Spike density

The spike density of parent varieties is shown in Table III. The two compact varieties, Golden Ball (A) and Bald Medeah (H), have a spike density of 7.8, measured on the basis of the number of spiklets per inch of rachis. The two lax varieties, provinciale (E) and Camadi (J) have a spike density of 4.8 and 4.6 respectively, while the spike density of the other six varieties ranged between

6.8 and 6.4. In other words, there are three different phenotypes: dense (7.8) in Golden Ball and Bald Medeah, lax (4.6 - 4.8) in <u>provinciale</u> (E) and Camadi, and mid-dense (6.4 - 6.8) in the other varieties involved in this study.

A total of 5229 F_2 plants of 43 diallel crosses were studied for spike density. Six classes, 4, 5, 6, 7, 8, and 9 spiklets per inch, were established, and the head density of every plant was classified to the nearest class (for example, 4.2 into class four and 6.7 into class seven). The experimental results are summarized in Appendix II.

Segregation of this character was observed in F_2 plants of all crosses including the crosses involving the two varieties with the same spike density. Moreover, in many crosses, there were some plants more dense than the compact parent and more lax than the lax parent. This reveals that transgressive inheritance is involved, which is in agreement with results obtained by Unrau (25) using monosomic and nullisomic lines of common wheats.

Since there is considerable influence of environment on the expression of spike density in F_2 (at least under conditions in which this study was conducted), no attempt was made to analyse the genotype of the varieties under study.

<u>Growth habit</u>

Among ten varieties used as parents in this study, variety <u>leucurum</u> (A) showed a winter habit of growth. This variety was sown at the same time as the others, but it remained in the rosette stage and failed to head.

Since the time of sowing of these varieties was very late (early in June), it is possible that environment had some influence on this character, for, Golden Ball, a spring variety, was not completely matured at harvest time in September. However, the F_2 plants of crosses between leucurum (A) and the spring varieties showed a segregation for this character, and 775 F_2 plants of eight crosses involving variety leucurum (A) and the spring varieties, excluding Golden Ball, were classified as spring and winter type and the observed ratios were tested by chi-square analysis. The results are given in Table XI.

Table XI Chi-square analysis of 3:1, 13:3, and 15:1 ratios of spring habit to winter habit in the F_2 generation of the crosses involving leucurum (A).

Cross	Observed		Expected		X^2	P.
	Spring	Winter	Spring	Winter		
3:1						
A x B	50	18	51	17	.0784	.70 - .80
A x C	64	25	66.75	22.25	.4528	.50 - .70
A x D	33	15	36	12	1.0000	.30 - .50
A x I	68	29	72.75	24.25	1.2404	.20 - .30
13:3						
A x E	109	19	104	24	.9200	.30 - .50
A x G	99	21	97.5	22.5	.0920	.70 - .80
A x J	91	19	89.375	20.625	.1575	.50 - .70
15:1						
A x H	108	7	107.8125	7.1875	.0053	.90 - .95

The F_2 generation of four crosses of leucurum (A) with the four varieties, reichenbachii (B), murciense (C), erythromelan (D), and Kahla (I) gave a 3:1 ratio of spring type vs winter type. The F_2 generation of three crosses of leucurum (A) with the three varieties, provinciale (E), Stewart (G), and Camadi (J) give a 13:3 ratio of spring vs winter habit, while in the cross between leucurum (A) and Bald Medeah (H) the ratio 15:1 of spring vs winter habit fits very well with a P. value of .90 to .95.

The cross between leucurum (A) and Golden Ball (F) showed another type of segregation. Among 120 F_2 plants of this cross, 31 spring type, 36 intermediate, and 53 winter type, were observed. Since the intermediate plants were headed at harvest time but green, it is possible to combine the two classes, spring and intermediate. In this case, 67 spring types and 53 winter types would be obtained, with a 9:7 ratio of spring habit vs winter habit.

The ratios obtained for the first eight crosses, 3:1, 13:3, and 15:1, reveal that this character is governed by two allelic series which will be designated as Sp, sp and W, w, w_1. This agrees with the results obtained by Tsunewaki and Jenkins (25) who assumed that three allelic series controlled the growth habit of the hexaploid wheats studied by them in their monosomic analysis. Their studies demonstrated that two of the three allelic series were carried by chromosomes IX and XIII (A and B genomes), and the third one was located on chromosome XVIII (D genome).

On the basis of this assumption, it is possible to assign genotypes to the varieties used in this study, as far as growth habit is concerned.

The variety *leucurum* (A) was assumed to have the genes sp and w, governing winter growth habit. The varieties *reichenbachii* (B), *murciense* (C), *erythromelan* (D), and Kahla (I) were assumed to have the gene w, and a gene Sp, dominant for spring habit and epistatic to w and w_1.

The varieties *provinciale* (E), Stewart (G), and Camadi (J) were assumed to have the genes Sp and w_1, both governing spring habit of growth, but w_1 is hypostatic to the gene w.

The variety Bald Medeah (H) has Sp and W, both dominant genes governing spring habit of growth.

Therefore, the genotypes of these varieties, except for Golden Ball, can be summarized as follows:

(A)	*leucurum*	sp sp w w	Winter habit of growth
(B)	*reichenbachii*	Sp Sp w w	Spring habit of growth
(C)	*murciense*	Sp Sp w w	" " " "
(D)	*erythromelan*	Sp Sp w w	" " " "
(I)	Kahla	Sp Sp w w	" " " "
(E)	*provinciale*	Sp Sp w_1 w_1	" " " "
(G)	Stewart	Sp Sp w_1 w_1	" " " "
(J)	Camadi	Sp Sp w_1 w_1	" " " "
(H)	Bald Medeah	Sp Sp W W	" " " "

Since varieties (B), (C), (D), and (I) have one gene in common with *leucurum* (w) a 3:1 ratio would be expected in F_2.

Varieties (E), (G), (J) differ from leucurum for both genes and Sp is epistatic to w_1, therefore, a 13:3 ratio of spring vs winter should be observed.

Variety Bald Medeah (H) has two dominant genes for spring habit but each of them could condition the expression of spring habit, while leucurum has two recessive genes for winter habit of growth; consequently the cross between these two varieties should give a 15:1 ratio of spring:winter habit of growth.

These theoretical ratios agree with the observed ratios, and are confirmed by chi-square test (see Table XI).

Golden Ball (F) either possesses an allele different from the alleles postulated for the other varieties or has modifying genes that influence some response to environment. When Golden Ball (F) is planted early it is no later in maturity than some of the other varieties classified as spring type in growth habit. At the late date of seeding Golden Ball (F) responded differently to environment than did the other varieties in that it was still quite green where the other varieties were ripe. This sensitivity to environment of Golden Ball (F) could well be the cause of the abnormal ratio obtained in the cross of Golden Ball (F) with leucurum (A).

LINKAGE RELATIONSHIPS

With the exception of spike density and growth habit, data for the five other characters were used to determine if linkage existed between any two characters.

Awnedness - glume pubescence

Only three crosses could be used to study if there was a linkage relationship between these two characters. Bald Medeah (H) is the only awnless variety, and it has a glabrous glume. Three varieties, *reichenbachii* (B), Golden Ball (F), and Kahla (I), have pubescent glumes, and are awned. The analysis of the F_2 generation for each of the three crosses, for goodness of fit to a 9:3:3:1 ratio is presented in Table XII.

Table XII Chi-square analysis of the independant assortment of genes governing awnedness and glume pubescence in the F_2 generation of crosses of Bald Medeah (H) with *reichenbachii* (B), Golden Ball (F), and Kahla (I).

Cross	Awnless Pubescent	Awnless Glabrous	Awned Pubescent	Awned Glabrous	χ^2	P
Theoretical ratio	9	3	3	1		
H x B	59	19	20	5	.4060	.90 - .95
H x F	76	22	25	9	.6868	.80 - .90
Theoretical ratio	3	9	1	3		
H x I	36	89	8	31	2.1896	.50 - .70

A good fit for the 9:3:3:1 ratio was obtained in each cross, indicating independent assortment of the genes governing the inheritance of these two characters.

Awnedness - Stem solidness

Again, only three crosses could be used to study linkage relationship between these two characters. Bald Medeah (H) is the only awnless variety, and it has a hollow stem. Three varieties, reichenbachii (B), provinciale (E), and Golden Ball (F), have solid stems, and are awned. The chi-square test analysis of the F_2 generation for each of the three crosses, for goodness of fit to a 9:3:3:1 ratio is presented in Table XIII.

Table XIII Chi-square analysis of the independant assortment of genes governing awnedness and stem solidness in the F_2 generation of crosses of Bald Medeah (H) with reichenbachii (B), provinciale (E), and Golden Ball(F).

Cross	Awnless Solid	Awnless Hollow	Awned Solid	Awned Hollow	X^2	P
Theoretical ratio	9	3	3	1		
H x B	65	13	19	6	2.9599	.50 - .70
H X E	83	20	27	11	2.3663	.50
H x F	73	25	27	7	.4173	.90 - .95

In each of the three crosses a good fit for the random assortment of genes was obtained, and it is logical to conclude that the two genes are not linked, or if on the same chromosome are at least 50 crossover units apart.

Awnedness - Grain color

The F_2 generation of crosses of Bald Medeah (H) an awnless and amber seeded variety, with murciense (C), awned and red seeded, and Camadi (J), awned and purple seeded, could be used to study if there was a linkage relationship between these two characters. The chi-square test for goodness of fit to a 3:12:18:12:3:1:4:6:4:1 ratio for each of the three crosses is presented in Table XIV.

Table XIV Chi-square analysis of the independant assortment of the genes governing awnedness and grain color in the F_2 generation of crosses of Bald Medeah (H) with, murciense (C), and Camadi (J).

Cross	Awnless					Awned					χ^2	P
	R	R-	BR	B+	B	R	R-	BR	B+	B		
Theoretical ratio	3	12	18	12	3	1	4	6	4	1		
H x C	6	12	28	15	4	2	8	7	5	1	5.0134	.80 - .90

Cross	Awnless					Awned						
	Pr+	Pr	BPr	B+	B	Pr	Pr+	BPr	B+	B		
Theoretical ratio	3	12	18	12	3	1	4	6	4	1		
H x J	5	30	45	25	11	3	13	17	10	3	4.6248	.80 - .90

A very good fit for the random assortment of genes was obtained for both crosses. No linkage could be demonstrated between genes governing awnedness and grain color.

Awnedness - Rust resistance

The progeny of only one cross could be analysed to study the possible linkage relationship between these two characters. The only resistant variety, Camadi (J) is awned, and the only awnless variety Bald Medeah (H) is rust susceptible. The F_2 generation of the cross between these two varieties were tested for a 9:3:3:1 ratio and the data are presented in Table XV.

Table XV Chi-square test of the independant assortment of genes governing awnedness and rust reaction in the F_2 generation of the cross between Bald Medeah (H) and Camadi (J).

Cross	Awnless Susceptible	Awnless Resistant	Awned Susceptible	Awned Resistant	X^2	P
Theoretical ratio	9	3	3	1		
H x J	87	30	38	7	2.1478	.50 - .70

A good fit of the 9:3:3:1 ratio was obtained. Therefore, no linkage could be demonstrated between awnedness and rust resistance.

Glume pubescence - Stem solidness

Thirteen crosses involved varieties that differed in each cross for both glume pubescence and stem solidness. Varieties *reichenbachii* (B), Golden Ball (F), and Kahla (I), are pubescent, the first two are solid stemmed while the latter is hollow stemmed. On the other hand, three varieties *reichenbachii* (B), Golden Ball (F), and *provinciale* (E) which are solid stemmed, are also pubescent except *provinciale* (E) which is glabrous.

The chi-square analysis of the F_2 generation of each of the thirteen crosses for goodness of fit to a 9:3:3:1 ratio was made, and the results are presented in Table XVI.

Table XVI Chi-square test for goodness of fit to a 9:3:3:1 ratio in the F_2 generation of the 13 crosses involving glume pubescence and stem solidness.

Cross	Pubescent Solid	Pubescent Hollow	Glabrous Solid	Glabrous Hollow	X^2	P
Theoretical ratio	9	3	3	1		
B x A	33	5	7	5	2.6007	.30 - .50
B x C	41	9	8	7	4.9348	.10 - .20
B x D	40	16	13	4	.5430	.90 - .95
B x G	61	17	19	6	.4823	.90 - .95
B x H	64	15	19	5	1.9231	.50 - .70
B x J	68	24	31	8	.6399	.80 - .90
F x A	37	12	15	3	1.5995	.50 - .70
F x C	86	24	30	4	3.5775	.30 - .50
F x D	79	24	25	11	.8304	.80 - .90
F x G	88	27	28	8	.3935	.90 - .95
F x H	76	25	24	7	.2557	.95 - .98
F x J	111	22	35	15	5.5778	.10 - .20
Theoretical ratio	3	1	9	3		
E x I	31	14	92	21	4.4077	.20 - .30

Goodness of fit of the 9:3:3:1 ratio, tested by chi-square analysis, showed that no linkage relationship could be demonstrated between these two characters.

Glume pubescence - Grain color

Only two varieties differed for the grain color from the rest of parent varieties. The variety murciense (C) has red grain and Camadi (J) has purple grain, while the remaining varieties have amber grains. These two varieties (C) and (J) are glabrous, whereas among the amber seeded varieties only three, reichenbachii (B), Golden Ball (F), and Kahla (I) are pubescent. Therefore the six crosses involving an amber seeded variety and murciense (C) or Camadi (J) could be used to study if linkage existed between these two characters. The data including the chi-square analysis for goodness of fit of a 3:12:18:12:3:1:4:6:4:1 ratio in the F_2 generation of crosses involving murciense (C) or Camadi (J) are presented in Tables XVII and XVIII respectively.

Table XVII Chi-square analysis for the independant assortment of genes governing glume pubescence and grain color in the F_2 generation of the crosses of *murciense* (C), glabrous and red seeded variety, with *reichenbachii* (B), Golden Ball (F), and Kahla (I), pubescent and amber seeded varieties.

	Pubescent					Glabrous						
Cross	R	R-	BR	B+	B	R	R-	BR	B+	B	χ^2	P
Theoretical ratio	3	12	18	12	3	1	4	6	4	1		
C x B	5	7	15	10	2	1	3	4	4	1	3.9996	.90 - .95
C x F	7	26	39	22	7	0	5	11	8	5	8.4664	.30 - .50
Theoretical ratio	1	4	6	4	1	3	12	18	12	2		
C x I	0	2	5	6	2	5	14	20	9	5	5.5692	.70 - .80

Table XVIII Chi-square analysis for the independant assortment of genes governing glume pubescence and grain color in the F_2 generation of the crosses of Camadi (J), glabrous and purple seeded variety, with *reichenbachii* (C), Golden Ball (F), and Kahla (I), pubescent and amber seeded variety.

	Pubescent					Glabrous						
Cross	Pr+	Pr	BPr	B+	B	Pr+	Pr	BPr	B+	B	χ^2	P
Theoretical ratio	3	12	18	12	3	1	4	6	4	1		
J x B	4	21	37	22	5	3	9	15	5	4	5.9818	.70 - .80
J x F	12	30	53	28	10	2	11	16	16	5	6.4934	.50 - .70
Theoretical ratio	1	4	6	4	1	3	12	18	12	3		
J x I	4	15	13	12	3	8	30	50	28	11	5.8807	.70 - .80

A good fit for the theoretical ratio was obtained. No linkage was demonstrated between genes governing these two characters.

Glume pubescence - rust resistance

Since there is only one resistant variety Camadi (J) which is glabrous, the analysis of the F_2 generation of the three crosses of this variety with three pubescent and susceptible varieties, reichenbachii (B), Golden Ball (F), and Kahla (I) was made to determine if there was linkage between these two characters. The goodness of fit of a 9:3:3:1 ratio is tested by chi-square analysis. The data are presented in Table XIX.

Table XIX Chi-square analysis for the independant assortment of genes governing pubescence and rust resistance in the F_2 generation of crosses of Camadi (J) with reichenbachii (B), Golden Ball (F), and Kahla (I).

Cross	Susceptible		Resistant		χ^2	P
	Pubescent	Glabrous	Pubescent	Glabrous		
Theoretical ratio	9	3	3	1		
J x B	72	25	20	14	8.0201	.10 - .20
J x F	106	32	27	18	4.5745	.20 - .30
Theoretical ratio	3	9	1	3		
J x I	36	98	10	30	.6308	.80 - .90

A good fit was obtained for the 9:3:3:1 ratio and therefore no linkage between genes controlling glume pubescence and rust reaction could be demonstrated.

Stem solidness - Grain color

Two varieties, Camadi (J), purple seeded, and *murciense* (C), red seeded, are hollow stemmed. Among the amber seeded varieties, the three varieties, *reichenbachii* (B), *provinciale* (E), and Golden Ball (F), are solid stemmed. Therefore five crosses (excluding the cross between *murciense* (C) and *provinciale* (E) whose data, as it was mentioned in the section on Material and Methods, was discarded) could be used to study the possibility of linkage between these two characters. The goodness of fit for a 3:12:18:12:3:1:4:6:4:1 ratio was tested for the F_2 generation of each of the five crosses and the results are presented in Tables XX and XXI.

Table XX Chi-square analysis for the independant assortment of genes governing stem solidness and grain color in the F_2 generation of crosses between Camadi (J), and, reichenbachii (B), provinciale (E), and Golden Ball (F).

Cross	Solid					Hollow					X^2	P
	Pr+	Pr	BPr	B+	B	Pr+	Pr	BPr	B+	B		
Theoretical ratio	3	12	18	12	3	1	4	6	4	1		
J x B	6	24	40	16	7	1	6	12	11	2	5.2873	.80 - .90
J x E	8	29	44	27	7	2	14	15	11	1	3.1741	.95 - .98
J x F	13	31	52	40	10	1	10	17	4	5	11.2144	.20 - .30

Table XXI Chi-square analysis for the independant assortment of genes governing stem solidness and grain color in the F_2 generation of crosses between murciense (C), and, reichenbachii (B) and Golden Ball (F).

Cross	Solid					Hollow					X^2	P
	R	R-	BR	B+	B	R	R-	BR	B+	B		
Theoretical ratio	3	12	18	12	3	1	4	6	4	1		
C x B	5	7	14	9	3	1	3	5	5	0	5.5040	.70 - .80
C x F	6	26	36	24	10	1	5	14	6	2	5.1823	.80 - .90

The goodness of fit to the theoretical ratio indicates an independant assortment of the genes governing the inheritance of these two characters.

Rust resistance - Stem solidness

Only one variety was resistant to rust, Camadi (J), which is a hollow-stemmed variety. Three varieties, reichenbachii (B), provinciale (E), and Golden Ball (F), are solid-stemmed and were susceptible to stem rust. Crosses of Camadi (J) with the three above-mentioned varieties, were tested in F_2 for a 9:3:3:1 ratio.

Table XXII Chi-square analysis for the independant assortment of genes governing rust resistance and stem solidness in the F_2 generation of the crosses of Camadi (J), with reichenbachii (B), provinciale (E), and Golden Ball (F), solid stemmed and amber seeded variety.

Cross	Susceptible Solid	Susceptible Hollow	Resistant Solid	Resistant Hollow	X^2	P
Theoretical ratio	9	3	3	1		
J x B	70	27	29	5		
J x E	91	25	25	17	6.6356	.05 - .10
J x F	108	30	38	7	2.9087	.30 - .50

A good fit to the 9:3:3:1 ratio was observed, and therefore, no linkage could be demonstrated between genes governing these two characters.

Rust Resistance - Grain Color

The only resistant variety, Camadi (J), has purple grain. The seven crosses between this variety and the other amber-seeded and susceptible varieties, and a cross of Camadi (J), and *murciense* (C) (red seeded and susceptible) could be used to determine if there was linkage between these two characters.

The goodness of fit of a 3:12:18:12:3:1:4:6:4:1 ratio was tested by chi-square analysis for the F_2 generation of each cross.

The data are presented in Tables XXIII and XXIV.

Table XXIII Chi-square analysis for the independant assortment of genes governing rust resistance and grain seed color in the F_2 generation of the seven crosses involving variety Camadi (J).

	Susceptible					Resistant						
Cross	Pr+	Pr	BPr	B+	B	Pr+	Pr	BPr	B+	B	χ^2	P
Theoretical ratio	3	12	18	12	3	1	4	6	4	1		
J x A	5	17	25	17	3	3	4	9	3	3	5.9037	.70 - .80
J x B	5	16	45	22	7	2	14	7	5	2	13.3844	.10 - .20
J x E	8	32	48	24	4	2	11	11	14	4	7.0255	.50 - .70
J x F	11	35	52	30	9	3	6	17	14	6	7.8814	.50 - .70
J x G	13	33	43	39	5	3	14	17	9	3	7.0229	.50 - .70
J x H	7	29	50	28	11	1	14	12	7	3	6.3367	.70 - .80
J x I	10	34	52	28	10	2	11	11	12	4	4.4189	.80 - .90

Table XXIV Chi-square analysis for the independant assortment of genes governing rust resistance and grain color in the F_2 generation of a cross between Camadi (J) and <u>murciense</u> (C).

	Susceptible					Resistant						
Cross	Pr+	Pr	RPr	R+	R	Pr+	Pr	RPr	R+	R	X^2	P
Theoretical ratio	3	12	18	12	3	1	4	6	4	1		
J x C	7	22	55	32	10	3	7	20	9	1	8.3419	.50 - .70

A good fit to the theoritical ratio was obtained for each cross indicating that no linkage could be demonstrated between genes governing rust reaction and grain color.

GENERAL DISCUSSION AND CONCLUSION

The results reported in this thesis show that of the seven characters studied (awnedness, glume pubescence, stem solidness, rust resistance, grain color, growth habit, and spike density),the first four are controlled by monogenic inheritance, the next two by digenic inheritance and the last one, namely spike density, is so greatly influenced by environment that no inheritance pattern could be determined.

A simple 3:1 ratio of awnless vs awned satisfactorily explains the segregation for this character.

Glume pubescence appears to be controlled by genes in an allelic series, Hg, hg, and hg_1. The gene hg_1, recessive to either Hg, a dominant gene for pubescence, or hg, a recessive gene for glabrousness, conditions the pubescence when homozygous as in the variety Kahla. Since there is no previous report of glume pubescence being controlled by a recessive gene, the evidence in this thesis contributes additional information on the inheritance of this character.

In the case of stem solidness, the ratio of 1 solid:2 intermediate:1 hollow indicates that no complete dominance is involved.

Under the conditions of this study where several physiologic races of stem rust were known to be present, a simple 1:3 ratio of resistant vs susceptible satisfactorily explains the segregation for this character.

The mode of inheritance of grain color and growth habit appears to be digenic. For grain color a 1:4:6:4:1 ratio covering the gradation of colors in the F_2 generation of crosses involving Camadi (purple) or murciense (red) respectively, satisfactorily explains the results. Either two allelic series R_1^c, R_1, r_1 and R_2^c, R_2, r_2, or three gene pairs Pr, R_1, R_2 might be involved. If three gene pairs are involved one gene should be in common in purple and red, one in purple and amber, and one in red and amber. The author favors the allelic series assumption as explaining more accurately the results obtained in this investigation.

The evidence presented indicates that growth habit is governed by two allelic series, Sp, sp and W, w, w_1, giving ratios of 3:1, 13:3, and 15:1 spring vs winter.

No attempt was made to analyse the results obtained for spike density. This character was found to be influenced considerably by environment. The data obtained indicate that transgressive inheritance might be involved.

The chi-square test for the goodness of fit of the theoretical ratios for the assortment of genes governing any two characters, reveals that no linkage relationship could be demonstrated between the characters studied. If the genes governing any two characters are on the same chromosome the distance between them must be at least 50 crossover units.

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Appendix I Characteristics of the hybrids of the diallel crosses including reciprocals between 10 varieties of *T. durum.*

Cross	1 Awnedness	2 Pubescence	3 Rust Resistance	4 Stem Solidness	5 Grain Color
A x B	+	+	S	inter.	B
C x A	+	-	S	-	BR
D x A	+	-	S	-	B
E x A	+	-	S	inter.	B
A x F	+	+	S	inter.	B
F x A	+	+	S	inter.	B
A x G	+	-	S	-	B
G x A	+	-	S	-	B
H x A	-	-	S	-	B
A x I	+	-	S	-	B
I x A	+	-	S	-	B
A x J	+	-	S	-	Pr
J x A	+	-	S	-	Pr
B x C	+	+	S	inter.	Br
C x B	+	+	S	inter.	Br
B x D	+	+	S	inter.	B
D x B	+	+	S	inter.	B
B x E	+	+	S	+	B
E x B	+	+	S	+	B
F x B	+	+	S	+	B
B x G	+	+	S	inter.	B
G x B	+	+	S	inter.	B
H x B	-	+	S	inter.	B

Appendix I (Cont'd.)

Cross	Awnedness	Pubescence	Rust Resistance	Stem Solidness	Grain color
B x I	+	+	S	inter.	B
I x B	+	+	S	inter.	B
J x B	+	+	S	inter.	Pr
C x D	+	-	S	-	RB
D x C	+	-	S	-	RB
C x F	+	+	S	inter.	RB
F x C	+	+	S	inter.	RB
C x G	+	-	S	-	BR
G x C	+	-	S	-	BR
C x H	-	-	S	-	BR
H x C	-	-	S	-	BR
C x I	+	-	S	-	BR
I x C	+	-	S	-	BR
C x J	+	-	S	-	Pr
J x C	+	-	S	-	Pr
D x E	+	-	S	inter.	B
E x D	+	-	S	inter.	B
D x F	+	+	S	+	B
F x D	+	+	S	+	B
D x G	+	-	S	-	B
G x D	+	-	S	-	B
D x H	-	-	S	-	B
H x D	-	-	S	-	B
D x I	+	-	S	-	B
I x D	+	-	S	-	B
E x F	+	+	S	+	B
F x E	+	+	S	+	B

Appendix I (Cont'd.)

Cross	Awnedness	Pubescence	Rust Resistance	Stem Solidness	Grain color
E x G	+	-	S	inter.	B
G x E	+	-	S	inter.	B
E x H	-	-	S	-	B
H x E	-	-	S	inter.	B
E x I	+	-	S	inter.	B
I x E	+	-	S	inter.	B
J x E	+	-	S	inter.	Pr
F x G	+	+	S	inter.	B
G x F	+	+	S	inter.	B
F x H	-	+	S	inter.	B
H x F	-	+	S		B
F x I	+	+	S	inter.	B
I x F	+	+	S	inter.	B
F x J	+	+	S	inter.	Pr
J x F	+	+	S	inter.	Pr
G x H	-	-	S	-	B
H x G	-	-	S	-	B
G x I	+	-	S	-	B
I x G	+	-	S	-	B
G x J	+	-	S	-	Pr
J x G	+	-	S	-	Pr
H x I	-	-	S	-	B
I x H	-	-	S	-	B
H x J	-	-	S	-	Pr
J x H	-	-	S	-	Pr

Appendix I (Cont'd.)

Cross	Awnedness	Pubescence	Rust Resistance	Stem7 Solidness	Grain Color
I x J	+	-	S	-	Pr
J x I	+	-	S	-	Pr

1 + represents awned; - represents awnless.
2 + represents pubescent; - represents glabrous.
3 S represents susceptible; R represents resistant.
4 + represents solid; - represents hollow; and inter. represents intermediate.
5 B represnets amber; BR represents medium red; and Pr represents medium purple.

Appendix II Segregation of the spike density in the F_2 generation of 43 diallel crosses of the ten durum varieties.

Cross	CLASSES						Total
	4	5	6	7	8	9	
A x B	-	2	9	10	28	1	50
A x C	-	3	22	21	18	-	64
A x D	-	3	25	27	8	1	64
A x E	-	8	50	29	9	-	96
A x F	-	-	2	8	19	1	30
A x G	-	-	8	30	12	-	50
A x H	-	-	-	43	56	9	108
A x I	-	-	7	35	26	-	68
A x J	-	24	54	13	-	-	91
B x C	-	-	30	35	-	-	65
B x D	-	-	55	17	-	-	72
B x E	-	30	34	4	-	-	68
B x F	-	13	18	41	-	-	72
B x G	-	-	53	50	-	-	103
B x H	-	-	2	82	19	-	103
B x I	-	-	48	47	-	-	95
B x J	3	79	48	1	-	-	131
C x D	-	28	59	47	-	-	134
C x F	-	1	31	76	33	-	141
C x G	-	-	13	115	9	-	137
C x H	-	-	-	54	47	-	101
C x I	-	-	49	45	-	-	94
C x J	1	84	73	9	-	-	167
D x E	-	48	103	-	-	-	151
D x F	-	1	46	72	20	-	139
D x G	-	-	108	69	-	-	177
D x H	-	2	77	78	35	-	192
D x I	-	41	69	33	-	-	143
E x F	-	16	44	67	14	-	151
E x G	7	73	72	10	-	-	162
E x H	-	29	62	42	8	-	141
E x I	-	53	83	21	-	-	157
E x J	38	78	42	-	-	-	158

Appendix II (Cont'd.)

	CLASSES						
Cross	4	5	6	7	8	9	Total
F x G	-	-	16	61	65	9	151
F x H	-	-	-	32	80	20	132
F x I	-	14	38	40	33	8	133
F x J	4	57	77	39	6	-	183
G x H	-	-	23	61	61	15	150
G x I	-	7	40	59	30	-	136
G x J	11	44	62	43	17	2	179
H x I	-	10	48	60	38	8	164
H x J	9	43	57	34	17	2	162
I x J	13	62	64	35	-	-	174