



Chromosome segregation in a *Triticum aestivum* L. em. Thell. by *T. durum* Desf. cross and the production of D genome addition lines
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Abstract:

Seven lines of Chinese Spring, each tetrasomic for one of the chromosomes in the D genome, were crossed to the durum varieties Wells and Lakota. The F₁ from these crosses possessed 15 pairs plus 6 univalent chromosomes at metaphase I of meiosis. Chromosome combinations in the F₂ were determined cytologically and those plants with combinations approaching 15 pairs were selected for advancement to the F₃.

Eight plants with 15 pairs of chromosomes (D diplosomic, i.e. 14 pairs from the A and B genomes plus one pair from the D genome) were obtained in the F₃. Of these eight plants, five proved to be male sterile and three were partially fertile. Two of the fertile plants were presumed to be 4D diplosomics and the third was probably a 5D diplosomic. All F₄ progeny of these three plants had 15 chromosome pairs.

Plants with 15 pairs of chromosomes occurred most frequently in the progeny of F₂ plants having 15 pairs plus one to four univalents. These plants were generally lacking in vigor and either partially or completely sterile. Neither the two durums or the seven tetrasomic hexaploids used as parents affected the chromosome segregation in their F₂ progenies.

In another part of the study, the frequencies of plants with various chromosome combinations in the F₂ of crosses between the hexaploid spring wheat variety Thatcher and the durum varieties Wells, Lakota and Langdon, were determined. As expected the F₁ plants had the chromosome combination 14 pairs plus 7 univalents. Plants with 14 pairs plus zero to seven univalents were observed most frequently in the F₂. A number of plants with 15 pairs plus one to four univalents were also observed. The particular durum variety used in the crosses did not affect the frequencies of various chromosome combinations in F₂ plants.

The hexaploid spring wheat Ceres was crossed to Wells durum and the F₁ was then backcrossed to Wells. The number of univalents present in plants from this cross was used as a measure of the frequencies with which various numbers of univalents were passed through female and male gametes. These frequencies were used to predict the number of chromosomes expected in F_g plants of the Thatcher X durum crosses. Three of the seven possible classes deviated significantly from the expected frequencies.

If the assumption is made that each of the seven univalent chromosomes in F₁ plants has an equal chance of being included in a particular gamete, then the frequencies with which the same univalent is obtained from both female and male gametes can be calculated. This assumption was used to calculate the expected frequencies of various chromosome combinations in F₂ plants of the Thatcher X durum crosses. A comparison of the observed frequencies with the calculated frequencies indicated that three classes (formula not captured in OCR) deviated significantly from the expected. The total chi square value of 49.1 has a probability of 0.25 with 35 degrees of freedom.

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A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree

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ABSTRACT

Seven lines of Chinese Spring, each tetrasomic for one of the chromosomes in the D genome, were crossed to the durum varieties Wells and Lakota. The F_1 from these crosses possessed 15 pairs plus 6 univalent chromosomes at metaphase I of meiosis. Chromosome combinations in the F_2 were determined cytologically and those plants with combinations approaching 15 pairs were selected for advancement to the F_3 .

Eight plants with 15 pairs of chromosomes (D diplosomic, i.e. 14 pairs from the A and B genomes plus one pair from the D genome) were obtained in the F_3 . Of these eight plants, five proved to be male sterile and three were partially fertile. Two of the fertile plants were presumed to be 4D diplosomics and the third was probably a 5D diplosomic. All F_4 progeny of these three plants had 15 chromosome pairs.

Plants with 15 pairs of chromosomes occurred most frequently in the progeny of F_2 plants having 15 pairs plus one to four univalents. These plants were generally lacking in vigor and either partially or completely sterile. Neither the two durums or the seven tetrasomic hexaploids used as parents affected the chromosome segregation in their F_2 progenies.

In another part of the study, the frequencies of plants with various chromosome combinations in the F_2 of crosses between the hexaploid spring wheat variety Thatcher and the durum varieties Wells, Lakota and Langdon, were determined. As expected the F_1 plants had the chromosome combination 14 pairs plus 7 univalents. Plants with 14 pairs plus zero to seven univalents were observed most frequently in the F_2 . A number of plants with 15 pairs plus one to four univalents were also observed. The particular durum variety used in the crosses did not affect the frequencies of various chromosome combinations in F_2 plants.

The hexaploid spring wheat Ceres was crossed to Wells durum and the F_1 was then backcrossed to Wells. The number of univalents present in plants from this cross was used as a measure of the frequencies with which various numbers of univalents were passed through female and male gametes. These frequencies were used to predict the number of chromosomes expected in F_2 plants of the Thatcher X durum crosses. Three of the seven possible classes deviated significantly from the expected frequencies.

If the assumption is made that each of the seven univalent chromosomes in F_1 plants has an equal chance of being included in a particular gamete, then the frequencies with which the same univalent is obtained from both female and male gametes can be calculated. This assumption was used to calculate the expected frequencies of various chromosome combinations in F_2 plants of the Thatcher X durum crosses. A comparison of the observed frequencies with the calculated frequencies indicated that three classes ($16_{III} + 3_I$, $15_{III} + 1_I$ and 14_{III}) deviated significantly from the expected. The total chi square value of 49.1 has a probability of 0.25 with 35 degrees of freedom.

INTRODUCTION

Species of the genus Triticum can be divided into three groups based on chromosome number. The groups and their chromosome numbers are:

(1) diploid, seven pairs; (2) tetraploid, 14 pairs; (3) hexaploid, 21 pairs. The hexaploids are the only group widely grown in the United States. They are divided into the spring wheats and winter wheats. Tetraploid wheats are grown to some extent throughout the world but durum wheats are the only representative of this group commonly grown in the United States. Diploid species are seldom grown commercially.

Hexaploid and tetraploid wheats have been crossed frequently. The purpose of such crosses has usually been to transfer disease resistance or some other characteristic from one species to the other. Usually the end result desired was improvement of the hexaploid. Frequently one or more backcrosses were made to the hexaploid parent to facilitate return to a full hexaploid chromosome complement. Studies of chromosome pairing and chromosome segregation have seldom included that portion of the population which approached 14 pairs.

Aneuploids, (i.e. chromosome numbers other than a simple multiple of the basic chromosome number) have been widely used in genetic studies. Monosomics ($2n-1$) and nullisomics ($2n-1$ pair) have been used to locate genes on chromosomes, to substitute a chromosome pair from one variety into another and to identify genome homologies. Trisomics ($2n + 1$) and tetrasomics ($2n + 1$ pair) have been used to study dosage effects and to locate genes on particular chromosomes as well as for other studies. Trisomics and tetrasomics have been studied at the hexaploid level in wheat but not at the tetraploid level. Matsumura (1952b) produced a

number of haplosomics (14 pairs from the A and the B genomes plus 1 chromosome from the D genome). He also found a diplosomic (14 pairs from the A and the B genomes plus 1 pair from the D genome). The haplosomics were unstable and quickly reverted to 14 pairs. The diplosomic was more stable, but low in fertility.

The use of monosomics, nullisomics and substitution lines has indicated the importance of the D genome chromosomes. Several studies have shown that flour quality and other characteristics are influenced by these chromosomes. These studies (Kuspira and Unrau, 1957; Morris et al., 1966) have indicated that more than one of the D genome chromosomes are capable of affecting quality. For example, chromosomes 4B, 7B and 5D affect strong dough and 4D, 7D and 5D affect loaf volume, crust appearance, and grain and texture of the loaf. Chromosomes 3D, 4D, 5B and 7B are reported to affect protein content. Welsh and Hehn (1964) reported that chromosome 1D affected gluten strength when in the monosomic condition.

In view of these findings it would be of considerable interest to determine the effect of single pairs of D genome chromosomes on flour quality, and on other characteristics carried by D genome chromosomes. If the complete set of D genome diplosomics could be isolated, the characteristics which distinguish the tetraploid wheats from hexaploid wheats could be studied chromosome by chromosome.

The purpose of this study was to determine chromosome segregation in crosses of tetraploid Triticum durum Desf. X Triticum aestivum L. em Thell. and to isolate lines with the seven possible D diplosomics.

REVIEW OF LITERATURE

Cyto-taxonomy and Origin of Common Wheat:

The genus Triticum was one of the first of the plant genera to be investigated cytologically. Sakamura (1918) reported that the group consisted of three ploidy levels with chromosome numbers of 14, 28, and 42. Sax (1923) and H. Kihara (1919, 1924) demonstrated the allopolyploid nature of the 28 and 42 chromosome groups by means of interspecific crosses. Kihara (1929, 1930) developed his genome analyzer method based upon the results of interspecific crosses between the tetraploid and hexaploid wheats and from the results of crosses between the former genus Aegilops and Triticum. The method consists of crossing two species with the same or different chromosome numbers and determining chromosome pairing in the F₁ hybrid. Chromosomes which pair are considered to be related in whole or in part. Those which do not pair are unrelated. The method has been used to determine genome homologies of supposedly different species. As a result, the wheat species have recently been reclassified.

Morris and Sears (1967) and Jenkins (1966) have recently reviewed classification of wheats. Both sources agree that Bowden's (1959) classification is the most realistic. Bowden's classification abandons the old genus Aegilops and includes its species in the genus Triticum. According to this classification the cultivated wheats are grouped into four species (Table I).

A second result of interspecific crossing has been the assignment of genome formula based on chromosome homology. Kihara (1924) and Gaines and Aase (1926) and Aase, (1930) independently proposed that the cultivated

Table I. The groups of varieties (cultivars) of the genus Triticum. After Morris and Sears (1967).

Species	Varietal Group	Based On	Common Name
<u>T. monococcum</u> L.	--	<u>T. monococcum</u> L.	Einkorn
<u>T. turgidum</u> L.	dicoccon	<u>T. dicoccon</u> Schrank (<u>T. dicoccon</u> Schrank)	Emmer
	durum	<u>T. durum</u> Desf.	Durum
	turgidum	<u>T. turgidum</u> L.	Poulard wheat
	polonicum	<u>T. polonicum</u> L.	Polish wheat
<u>T. timopheevii</u> (Zhuk.) Zhuk. var <u>timopheevii</u> var <u>zhukovskyi</u> (Men&Er.) Morris & Sears, comb. nov.	--	<u>T. timopheevi</u> Zhuk.	None
	--	<u>T. zhukovskyi</u> Men. & Er.	None
<u>T. aestivum</u> L. em Thell.	spelta	<u>T. spelta</u> L. + <u>T. macha</u> Dek. & Men.	Spelt
	vavilovii	<u>T. vavilovi</u> Jakubz	None
	aestivum	<u>T. aestivum</u> L. (<u>T. vulgare</u> Host. <u>T. sativum</u> Lam.)	Common wheat
	compactum sphaerococcum	<u>T. compactum</u> Host. <u>T. sphaerococcum</u> Perc.	Club wheat Shot wheat

wheats had the following genome formula: Diploid species, AA; Tetraploid species, AABB; and hexaploid species, AABBDD. This hypothesis, known as the ABD hypothesis, has been amply confirmed by many workers.

Presumably, allopolyploid species are built up by interspecific crossing from two or more diploids, followed by chromosome doubling. Such is held to be the case in wheat. Sax and Sax (1924) crossed Aegilops cylindrica with the common spring wheat variety Marquis. The cross produced a few seed. The F₁ progeny were completely sterile. When pollen mother cells were examined cytologically, 6 or 7 bivalents and 20 or 21 univalents were found at metaphase I of meiosis. This indicates that one of the genomes of A. cylindrica is similar to one of the genomes of common wheat. Therefore, Aegilops was the source of one of the genomes of common wheat. Bleir (1928) crossed A. cylindrica by T. turgidum and found no pairs, indicating genome homologie was between one of the genomes of Aegilops and the D genome of hexaploid wheat.

McFadden and Sears (1944) identified the source of the D genome as Aegilops squarrosa. They crossed T. dicoccoides by A. squarrosa and observed that the amphidiploid closely resembled T. aestivum cultivar spelta. This amphidiploid had good pairing when crossed with T. aestivum.

Thompson (1931) crossed T. monococcum by T. durum and found seven pairs plus seven univalents, thus establishing T. monococcum as the source of the A genome. Sarkar and Stebbins (1956) suggested that on the basis of morphological differences, Triticum speltoides (Aegilops speltoides) was the source of the B genome. Cytological investigations of crosses with T. aestivum have tended to support this view.

Aneuploidy in Wheat:

Sears (1939) found two haploid plants in the F_1 progeny of a cross between Secale cereale and Triticum aestivum var. Chinese Spring. One of the haploids was female sterile but the other set 14 seed upon pollination by Chinese Spring. Sears obtained 13 plants from this seed. These 13 plants produced 5 monosomics, 1 double monosomic, 1 monosomic and trisomic, 2 double monosomic and trisomic, 1 double monosomic plus ring of four, 1 double monosomic plus double trisomic plus ring of four plus nullisomic, and 2 normal plants. The use of aneuploids of wheat in genetic studies received a major impetus from this study. By 1954, Sears had developed the complete series of nullisomics, monosomics, trisomics and tetrasomics. In addition, telosomics and isosomics were described. These aneuploids have been used extensively in determinations of chromosomes carrying particular genes.

Ausemus, McNeal and Schmidt (1967) have recently reviewed the literature concerned with wheat genetics. Their paper shows that aneuploids have been used almost exclusively in assigning genes to a particular wheat chromosome.

Sears (1954, 1966) used crosses of nullisomic and tetrasomic Chinese Spring to show that the 21 different chromosomes of hexaploid wheat fall into seven homoeologous groups of three. The tetrasomic can compensate for the nullisomic of each of the other chromosomes in the same group. These results were supported by the work of Okamoto and Sears (1962) in which they found that pairing in haploids was largely between chromosomes in the same homoeologous group. Sears (1958, 1966) and Okamoto and Sears

(1962) developed a system of chromosome numbering based on identification of genomes as A, B, or D and numbering of the homoeologous groups from one to seven. This system is now widely accepted. There was some doubt about the correct designation of chromosomes 2A and 2B, but this was resolved in a recent paper, (Riley and Chapman, 1966).

Only a few cases of aneuploidy in tetraploid wheats have been reported. Tsunewaki (1963) has described a tetraploid line derived from the durum variety Melanopus which has 13 normal pairs plus two telosomic chromosomes. One of the telosomics was for the right arm and the other for the left arm. The only fertile derivatives of this line were plants with 13 pairs plus two telosomics (1 left and 1 right). Kihara and Tsunewaki (1962) produced trisomics by treating Khapli emmer with the mutagen N_2O . The transmission of the trisomics was lower than for corresponding trisomics of hexaploid wheat. Longwell and Sears (1963) were able to produce nullisomics in tetraploid wheat by adding a pair of compensating tetrasomics from the other genome. So far, aneuploids have contributed little to genetic studies at the tetraploid chromosome level.

Haplosomics and especially diplosomics may offer promise in the study of tetraploid wheat cytogenetics. For example, the chromosomes from the D genome could be studied individually if D haplosomics or D diplosomics for each of the seven D genome chromosomes were available. Matsumura (1952b) produced a number of 29 chromosome plants from a pentaploid wheat cross. These haplosomics were used to study the inheritance of head type, length of glume, stem solidness, size of pollen grains and tillering ability, as determined by chromosomes in the D genome.

Matsumura also reported a 30 chromosome plant (D diplosomic). This diplosomic plant possessed the tetraploid complement of T. turgidum cultivar polonicum and a single pair of D genome chromosomes from T. aestivum cultivar spelta.

The D haplosomics very quickly reverted to 14 pairs, but the D diplosomic was relatively stable. If fertility is not limiting, it should be possible to use the D diplosomics for studies where relatively large populations are desired. Information in the literature regarding the frequency with which D diplosomics can be expected from pentaploid hybrids is limited. Those studies which have been published are not extensive enough to give reliable estimates of the population sizes necessary to produce D diplosomics.

Pentaploid Wheat Crosses:

Kihara (1921, 1924) crossed the Triticum species T. turgidum by T. aestivum cultivar spelta and investigated the chromosome numbers in the F_1 and F_2 . He separated the F_2 progeny into three groups. In those plants with 14_{II} plus $(1 \text{ to } 7)_I$, later generations usually reverted to 14_{II} . Where there were 14_{II} plus X_{II} plus $(7 - X)_I$, the progeny reverted to 21 pairs. The intermediate group was highly sterile and usually disappeared from the population.

Kihara (1924) noted a greater frequency of parental chromosome combinations in the F_2 than would be expected on the basis of random distribution of univalents.

Jenkins and Thompson (1930) looked at chromosome numbers in the F_2 of a small sample (37 plants) from the cross of T. aestivum by T. turgidum

cultivar emmer. Their results supported those of Kihara.

Kihara and Matsumura (1942) suggested that one reason for failure of theoretical expectations to agree with observed was univalent elimination at anaphase II and later stages of meiosis. Univalents tend to be left out of the nucleus at telephase II due to lagging. Such chromosomes appear as micronuclei in tetrads. These micronuclei deteriorate and are lost from the gametes.

Thompson and Cameron (1928) crossed the spring wheats Marquis and Chinese with spring emmer and Iumillo durum with the objective of determining the frequency with which univalents are passed through the male and female gametes. The frequency with which 0, 1, 2, 3, 4, 5, 6 and 7 univalents were passed was determined by backcrossing F_1 pentaploids to each of their respective parents. The backcross progeny were examined cytologically and the number of univalents in each BC_1 plant was determined. Functional gametes from the pentaploid F_1 hybrid passed zero to seven univalents with a higher frequency than expected. Intermediate univalent numbers were correspondingly reduced. The most frequent gamete class was that with 14 chromosomes (i.e. no univalents). There were differences between the crosses in the frequencies with which univalents were passed. The authors concluded that "if gametes with the frequencies found mate at random, the results should be in general like those which have been reported for F_2 ".

Love (1940) investigated crosses of Marquis, Hope, RL-729 and Marquillo hexaploids with the durum variety Iumillo. From these crosses, 336 plants in the F_5 , F_6 and F_7 were examined cytologically. The Iumillo

parent carried rust resistance and the progeny had been selected for rust resistance and hexaploid parent plant characteristics. The following chromosome numbers were found: there were (12), 3, 27, 50, (98), 140, and 6 plants with chromosome numbers of (28), 38, 39, 40, 41, (42) and 43 chromosomes, respectively. In addition there were 14 plants with a heteromorphic bivalent (pairing at metaphase I of meiosis of a normal and telosomic chromosome pair), 14 plants with trivalents, 10 plants with quadrivalents, 8 plants with isosomics, 3 plants with fragments, 1 plant with two trivalents, and 2 plants with two quadrivalents. Evidently, while chromosome numbers tend to approach the parental number, there are several intermediate combinations which are viable.

Summary

Species crosses in the genus Triticum have led to several important conclusions.

1. The similarities between the species of Aegilops and Triticum warrant their inclusion in the same genus.
2. The species of the genus Triticum form a polyploid series from diploid ($n=7$) to hexaploid ($n=21$). In the hexaploid the three genomes are composed of seven homoeologous groups of three. Therefore, hexaploid wheat is an auto-allopolyploid with many of the genes present on chromosomes of one genome duplicated on chromosomes of another genome.
3. Use of aneuploids has made a considerable contribution to the understanding of the cytology and genetics of

wheat. Their continued use should contribute to further advances.

4. The presence of similar genetic material in different genomes allows for considerable buffering against gene loss and allows unusual chromosome combinations to occur.
5. Pentaploid crosses have demonstrated that while chromosome numbers in later generations approaches those of parental types, many intermediate chromosome combinations can be maintained.

Plants with intermediate chromosome combinations could contribute significantly to the study of wheat genetics.

MATERIALS AND METHODS

Experiment I

Seeds derived from single head rows were used for parents in all crosses. All crosses were made in the greenhouse during the winter of 1964-65. They were as follows:

1. Thatcher spring wheat X Wells durum.
2. Thatcher spring wheat X Lakota durum.
3. Thatcher spring wheat X Langdon durum.
4. (T. timopheevi Restorer I X Marquis³) X Ceres²) X Wells durum.

Cross number 4 was backcrossed to Wells durum as the male in the summer of 1965. This latter cross will hereafter be referred to as (Ceres X Wells) X Wells.

The F_1 was grown in the greenhouse during the summer of 1965. Heads from each plant were killed and fixed in Newcomer's Solution, (Newcomer 1953). Pollen mother cells (PMC's) were smeared by the iron acetocarmine technique of Belling (1921). Chromosome pairing was determined at metaphase I of meiosis and checked against total number of chromosomes at anaphase I. The number of cells examined varied but was sufficient to assure correct classification. Where there were insufficient well squashed cells for accurate counts, the plant was excluded from the results.

The F_2 's from the various crosses were grown in the greenhouse during the winter of 1965-66. Heads were collected and chromosome combinations determined, as described earlier. A few F_3 and BC_1 families were grown in the field in 1966 and chromosome combinations determined.

Experiment II:

A set of D genome tetrasomics in the hexaploid variety Chinese Spring were kindly supplied by Dr. E. R. Sears. Seed supplied by Dr. Sears was planted in the greenhouse in the spring of 1965. The tetraploid varieties Wells and Lakota durum were also seeded at this time. Heads from each tetrasomic plant were examined to confirm the expected chromosome combination of $20_{II} + 1_{IV}$. Lines tetrasomic for each of the seven D genome chromosomes were each crossed to Wells and Lakota durum. The durum varieties were used as pollinators.

The F_1 seed was planted in the greenhouse in the autumn of 1965. Each F_1 plant was examined for the expected chromosome combination of $15_{II} + 6_I$. The F_2 seeds from plants with $15_{II} + 6_I$ at metaphase I of meiosis were seeded in the field in 1966. Each F_2 row represented the progeny of a single F_1 plant.

Heads were collected from random F_2 plants in each row. As the head was collected, the plant and the head sample were marked with the row and plant number. The chromosome combination of each F_2 plant was determined as described previously. At maturity F_2 plants were pulled and threshed, and the seed was bagged separately.

The F_3 seeds from F_2 plants with chromosome combinations of from $15_{II} + 1_I$ to $15_{II} + 5_I$ were planted in the greenhouse during the fall and winter of 1966. Heads from each F_3 plant in a family were collected as before and the chromosome combination was determined. At maturity, each F_3 plant was examined. Height, number of tillers, fertility, awning and head type were recorded.

A few F_4 families were grown from selected F_3 plants during the summer of 1967. Chromosome combinations and gross morphology were recorded.

RESULTS

Experiment I:

When hexaploid spring wheat is crossed to tetraploid durum wheat, 14 pairs plus seven univalents are expected at metaphase I of meiosis in F_1 plants. All F_1 plants showed this configuration, indicating that (1) the spring wheats and durum wheats used in the crosses had the expected chromosome numbers, and (2) that crosses were successful.

The frequency with which F_2 plants with various chromosome configurations were observed are reported in Table II. A chi square R X C table (Steel and Torrie, 1960) was used to determine if the three crosses differed in the frequency with which various chromosome combinations occurred. The chi square value of 50.87 (Table II) has a probability of between 0.75 and 0.90. Therefore, the durum variety used in a cross did not affect the frequency with which various gametes were combined in F_2 plants. Some 171 of the 285 plants or 60 percent, had 14_{II} , or $14_{II} + (1 \text{ to } 7)_I$. Plants with each of the possible 21 chromosomes represented at least once made up 23.5% of the sample.

During meiosis the 14_{II} of chromosomes in the pentaploid hybrids should segregate normally, but the seven univalents may go to either pole or become lost (Figure 1). The frequency with which 14, 15, 16, 17, 18, 19, 20, or 21 chromosome gametes are formed can be determined by crossing the pentaploid to either the tetraploid or hexaploid parent. In this study the F_1 pentaploid Ceres X Wells was crossed as female to Wells durum as male. The frequency with which univalents were passed through the female gametes was determined by examining the BC_1 progeny cytologically.

Table II. Observed frequency of chromosome combinations in F₂ progeny of three spring wheat by durum crosses.

Chromosome Pairing	Thatcher X Langdon	Thatcher X Lakota	Thatcher X Wells	Total Observed	Sub Total
14II	2	3	2	7	
14II + 1I	5	12	9	26	
14II + 2I	12	11	8	31	
14II + 3I	8	16	5	29	
14II + 4I	7	13	11	31	
14II + 5I	5	14	4	23	
14II + 6I	3	9	3	15	
14II + 7I	3	4	2	9	171
15II	0	0	0	0	
15II + 1I	1	4	2	7	
15II + 2I	1	0	3	4	
15II + 3I	2	5	3	10	
15II + 4I	1	2	7	10	
15II + 5I	2	2	2	6	
15II + 6I	3	6	3	12	49
16II	0	0	0	0	
16II + 1I	0	0	1	1	
16II + 2I	0	0	1	1	
16II + 3I	0	0	1	1	
16II + 4I	1	4	3	8	
16II + 5I	4	11	1	16	27
17II	0	0	0	0	
17II + 1I	0	0	0	0	
17II + 2I	0	2	0	2	
17II + 3I	0	1	2	3	
17II + 4I	3	4	5	12	17
18II	0	0	0	0	
18II + 1I	0	0	0	0	
18II + 2I	1	1	0	2	
18II + 3I	5	4	1	10	12
19II	0	0	0	0	
19II + 1I	0	1	0	1	
19II + 2I	1	3	0	4	5
20II	0	0	0	0	
20II + 1I	1	2	1	4	4
21II	0	0	0	0	0
Totals	71	135	79	285	285

Chi Square from R X C table = 50.87, P = 0.75 to 0.90

