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Genetic Analysis of Tetraploid and Hexaploid Wheat by Utilization of Monopentaploid Hybrids[1,2]

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Summary. This report deals with a method of analysis which uses existing hexaploid wheat monosomics to establish gene-chromosome associations in a tetraploid variety. Monosomics of *Triticum aestivum* cv. Chinese Spring belonging to the 14 lines of A and B genomes were crossed as female parents with *Triticum durum* cv. Capeiti, a spring type at present widely grown in Italy. For each line, two F_1 populations were obtained, normal pentaploids ($2n = 35$) and monopentaploid ($2n = 34$), in which, in turn, the monosomic A or B chromosome present was supplied by the tetraploid wheat. The morphological and physiological differences observed in the monopentaploid lines are attributed to differential expression of the genetic information concerning the character investigated, carried by the chromosome present in hemizygous condition. Then, only recessive or partially dominant alleles of the variety to be tested can be identified and attributed to a specific chromosome in the F_1 generation.

Eight parameters were analyzed: culm and spike length, length and width of 1st (flag) and 2nd uppermost leaves, days from germination to heading and awn development.

As far as culm length is concerned, although heterotic effect is present, seven chromosomes seem to be responsible for the modification of this character (1A, 2A, 2B, 3B, 4B, 5B, and 6 A); chromosomes 2A and 2B in particular, carry major factor (s) for plant height. A similar picture is presented by spike length which seems to be controlled by factors located in several chromosomes belonging to homoeologous groups 1, 2, 3 and 5, as well as the chromosome 4B.

Leaf length, also, shows a complex pattern of inheritance. Monosomic conditions for chromosomes 1A and 1B increased, while monosomy for 5A and 5B significantly decreased, leaf length. A highly significant correlation was found between the mean lengths of the 1st and 2 nd leaves (= 0.74). Some monosomic lines (4A, 4B, 5A; 5B; 6A; 7A and 7B) had leaves significantly narrower than in the control and only monosomic 2A had broader leaves. The period from germination to heading seems to be influenced by at least 6 chromosomes. Three monosomic lines are significantly earlier (mono 1A, 7A and 5B) and three (mono 5A, 2B and 7B) are significantly later than the hybrid control.

Finally, 8 monosomic lines were found to interfere significantly with awn development. Three lines (mono 2A, 2B and 7A) show a decrease and 5 (mono 1B; 3A, 3B; 4B and 6B) show an increase in awn development. On the basis of evidence in the literature and our own results, it appears that this analysis fits previous results perfectly and actually adds to the picture two further awn-promoting factors, A9 and A10, located on the 7A and 1B chromosomes respectively.

Introduction

Genetic studies in common and *durum* wheats were attempted early this century (Biffen, 1907; Strampelli, 1907; Nilsson-Ehle, 1909, etc.). Although very profitable in some respects — the discovery of the first clear examples of polygenic inheritance (in caryopsis colour, Nilsson-Ehle, *l. c.*) — this work revealed a difficulty in Mendelian analysis and the interpretation of data. We know that this difficulty arises from the polyploid structure of these species and from the scarcity of easily classifiable characters. For each character we should expect the presence and the action of at least one factor for each of the 2 or 3 genomes composing the tetraploid or hexaploid species, respectively. Moreover, if we consider, for each character to be analyzed, the sometimes high number of 'minor' factors which modify or interfere with its expression, and the environmental influences which are always important, we can understand why conventional genetic analysis yielded modest and often inconclusive results over a period of 40 years (Vavilov, 1950). The isolation and identification of aneuploid lines in hexaploid wheat (Sears, 1944, 1954) made available a new, powerful and detailed method of genetic analysis. Since the classic work of Sears (1944), O'Mara (1947) and Unrau (1950), monosomic analysis has been the most fruitful and simple method for the location of genes in hexaploid wheat. Cytogenetical analysis of tetraploid wheat would be quite simple, provided that monosomic lines were available.

For this purpose, several research workers (Kihara and Tsunewaki, 1962; Longwell and Sears, 1963; Tsunewaki, 1964; Camara *et al.*, 1965; Mochizuki, 1968; Bozzini *et al.*, 1969) have isolated monosomic individuals in tetraploid wheats using different methods. From the data available, even if monosomics appear to be viable and partially fertile, their use for

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[2] With the technical assistance for cytological and statistical analyses of P. Mannino.

practical, routine genetic analysis seems difficult. Difficulties arise mostly from the low transmissibility of the monosomic condition to the progeny.

In several laboratories, trisomics and other aneuploids with high transmission rates (e. g. $2n$ + telo etc.), which show some promise, are being isolated in tetraploid wheat, but a complete series is not yet available. Without the possibility of complete analysis using aneuploids in tetraploid wheat, alternative methods are desirable.

Allan and Vogel (1960) tried, without success, to analyze smooth-awn determination by crossing monosomics of Chinese Spring with a *durum* wheat which carried this character. Recently, Kuspira and Millis (1967), using the same technique, attempted to identify the chromosomes controlling heading time in a *durum* variety.

Our research has tried to ascertain the potentialities and the limits of such a method, particularly for characters which are known to be controlled by polygenic systems and which are difficult to analyze by conventional genetic techniques.

We are aware of the fact that the chief weakness of an F_1 analysis is that it is difficult or impossible to determine whether a difference between monosomic and disomic is due to a difference in the genes carried by the two chromosomes concerned, or whether the difference is simply due to a reduced dosage of genes which are the same on the two chromosomes. But it seems that there is no simple way of analyzing tetraploids more precisely, unless *Aegilops squarrosa* could be added to each tetraploid line before making the crosses.

Materials and Methods

Monosomics of Chinese Spring (C. S.) belonging to the 14 lines of A and B genomes were crossed as female parents with *T. durum* cv. Capeiti, a spring type at present widely grown in Italy. For each line, two F_1 populations were obtained, normal pentaploids ($2n = 35$) and monopentaploids ($2n = 34$), in which, in turn, the monosomic A or B chromosome present was supplied by the tetraploid wheat. The chromosome number of each F_1 plant was ascertained by cytological analysis of seedling root tips. For each line, 20 seedlings were analyzed and transferred to growth chambers. The results of this analysis are presented in table 1. The plants were grown in plastic pots containing about 800 cc. of soil and were supplied 5 times with Hoagland's nutrient solution. The plants were given a photoperiod of 18 hrs. of light and 6 of dark. Temperature was maintained at 20° ± 1C in the light and 17° ± 1C in the dark. Under these conditions, the life cycle of spring types of *durum* or bread wheats is completed in about 100—110 days.

Cytological analysis was performed on PMC meiosis in at least two monopentaploid plants for each line.

Eight parameters are here analyzed: culm and spike length, length and width of 1st (flag) and 2nd uppermost leaves, days from germination to heading and awn development. Plant height was measured on the main stem, after ripening, from the crown to the base of the spike. Leaf dimensions were measured at heading time (base of the main spike completely emerged). Spike length was obtained by measuring the rachis of the main stem of each plant after harvest. Awn length was established as that of the longest awn of the main spike. For each character and each line, means and standard errors were calculated. A variance analysis was performed taking into consideration the disomic lines coming from the 14 monosomics of Chinese Spring. As no significant difference was ascertained, all data coming from F_1 disomic hybrids ($2n = 35$) were pooled, and their mean was used in the comparisons. The significance of differences between $2n = 35$ (normal pentaploid plants) and $2n = 34$ plants of each line for each character were then analyzed using Student's „t" test.

Table 1. *Chromosome constitution of F_1 plants coming from Chinese Spring monosomics × Capeiti*

Hybrid and parental lines	No. plants analyzed	No. plants with 34 chromosomes	No. plants with 35 chromosomes	Others
Mono C. S. 1A × Capeiti	21	17	4	—
Mono C. S. 2A × Capeiti	22	11	7	4
Mono C. S. 3A × Capeiti	22	14	7	1
Mono C. S. 4A × Capeiti	22	16	6	—
Mono C. S. 5A × Capeiti	17	16	1	—
Mono C. S. 6A × Capeiti	16	13	1	2
Mono C. S. 7A × Capeiti	21	19	1	1
Mono C. S. 1B × Capeiti	22	17	5	—
Mono C. S. 2B × Capeiti	21	18	3	—
Mono C. S. 3B × Capeiti	14	14	—	—
Mono C. S. 4B × Capeiti	25	20	5	—
Mono C. S. 5B × Capeiti	22	15	7	—
Mono C. S. 6B × Capeiti	22	13	9	—
Mono C. S. 7B × Capeiti	17	14	2	1
C. S. $2n = 42$	20	—	—	—
Capeiti $2n = 28$	20	—	—	—
Total	324	217	58	9

Experimental Results

The results of biometrical and statistical analysis of culm length are presented in table 2. In order to gain a synoptic view of these values, the results have also been represented graphically in fig. 1. For plant height, two main points are apparent from the data: 1) overdominance (heterosis?) effect is present in the pentaploid hybrid; 2) seven monopentaploid lines differ significantly from the hybrid control, and all of them are minus-variants.

A similar picture is presented by spike length determinations (table 2 and fig. 2). Here also, the value of the hybrid control exceeds the values of both parents. However, plus-variation is also present. Factors depressing rachis length are apparently present

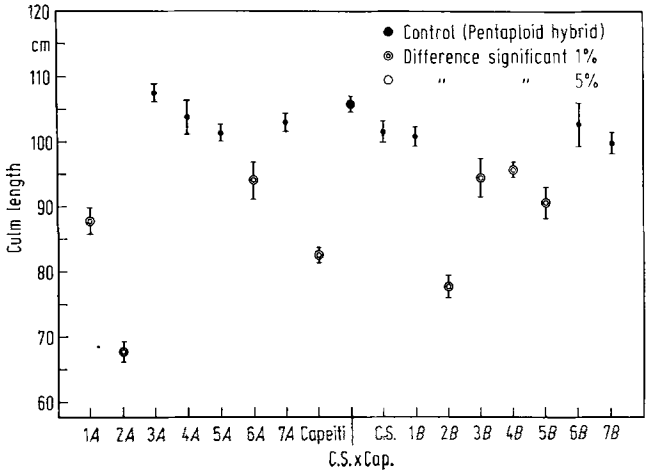

Fig. 1. Diagram showing the means of culm length and standard errors of 14 monopentaploid lines (2 *n* = 34), Chinese Spring (2 *n* = 42), Capeiti (2 *n* = 28) and hybrid control (2 *n* = 35)

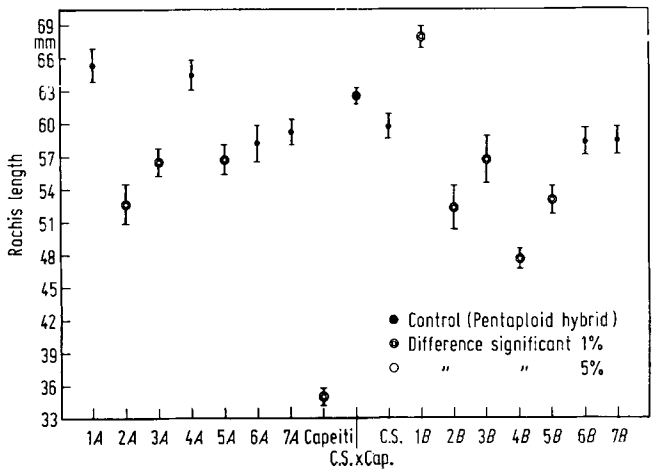

Fig. 2. Diagram showing the means of rachis length (mm) and standard errors of 14 monopentaploid lines (2 *n* = 34), Chinese Spring (2 *n* = 42), Capeiti (2 *n* = 28) and hybrid control (2 *n* = 35)

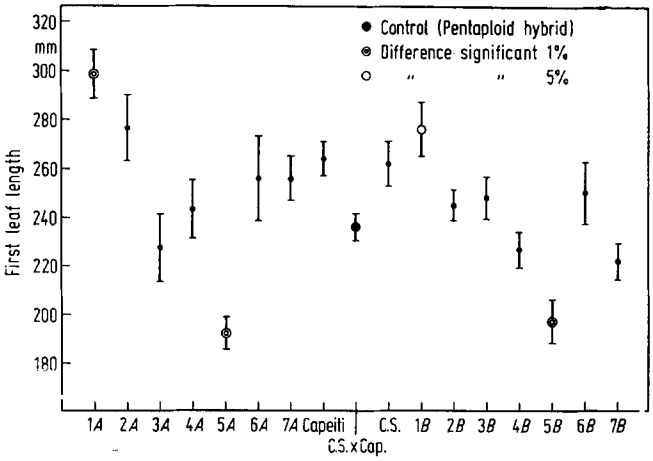

Fig. 3. Diagram showing the means of first leaf length and standard errors of 14 monopentaploid lines (2 *n* = 34), Chinese Spring (2 *n* = 42), Capeiti (2 *n* = 28) and hybrid control (2 *n* = 35)

Table 2. *Biometrical analysis of parents and hybrids between monosomics of Chinese Spring and Capeiti*

Hybrid and parental lines	Culm length	Spike length	Leaves				Days to heading	Awn development
			First leaf		Second leaf			
	cm.	mm.	length mm.	width mm.	length mm.	width mm.		mm.
C.S. 1 A × Capeiti	87.59 ± 1.96**	65.35 ± 1.64	298.63 ± 10.13**	15.84 ± 0.28	394.41 ± 10.90**	14.11 ± 0.23	67.35 ± 1.03**	14.00 ± 1.51
C.S. 2 A × Capeiti	67.75 ± 1.45**	52.78 ± 1.69**	276.88 ± 13.55*	17.94 ± 0.49**	333.63 ± 11.50	15.31 ± 0.28*	73.77 ± 0.75	3.22 ± 0.32**
C.S. 3 A × Capeiti	107.64 ± 1.40	56.64 ± 1.17**	227.29 ± 14.42	16.29 ± 0.24	297.86 ± 13.33	14.25 ± 0.23	73.35 ± 0.97	36.57 ± 2.35**
C.S. 4 A × Capeiti	103.88 ± 2.67	64.56 ± 1.29	243.13 ± 12.59	13.80 ± 0.42**	379.81 ± 11.43	12.50 ± 0.31**	71.37 ± 0.61	11.43 ± 1.78
C.S. 5 A × Capeiti	101.41 ± 1.18	56.88 ± 1.33**	192.38 ± 6.68**	12.84 ± 0.32**	290.56 ± 9.33**	11.78 ± 0.25**	81.00 ± 0.68**	14.88 ± 2.12
C.S. 6 A × Capeiti	94.15 ± 2.86**	58.15 ± 1.68	256.23 ± 16.92	13.54 ± 0.32**	396.00 ± 15.59*	12.85 ± 0.23**	75.23 ± 1.44	17.30 ± 1.92
C.S. 7 A × Capeiti	103.11 ± 1.33	59.16 ± 1.12	256.05 ± 8.77	15.79 ± 0.27	349.21 ± 9.03	12.95 ± 0.17**	67.00 ± 0.76**	4.78 ± 0.47**
C.S. 1 B × Capeiti	101.00 ± 1.51	68.06 ± 0.95**	276.18 ± 10.91*	16.53 ± 0.26	403.06 ± 8.86**	14.06 ± 0.26	72.00 ± 0.66	28.64 ± 2.35**
C.S. 2 B × Capeiti	77.78 ± 1.81**	52.28 ± 2.07**	245.12 ± 6.44	15.97 ± 0.28	325.82 ± 5.93	14.53 ± 0.28	75.74 ± 1.40*	2.77 ± 0.15**
C.S. 3 B × Capeiti	94.64 ± 3.00**	56.64 ± 2.12**	248.36 ± 8.63	16.68 ± 0.24	357.36 ± 9.00	14.00 ± 0.30	70.50 ± 0.92	28.42 ± 3.49**
C.S. 4 B × Capeiti	95.80 ± 1.09**	47.50 ± 0.80**	226.75 ± 7.55	13.48 ± 0.28**	327.75 ± 13.85	12.25 ± 0.24**	72.70 ± 1.33	52.00 ± 1.52**
C.S. 5 B × Capeiti	90.67 ± 2.41**	53.00 ± 1.30**	197.07 ± 9.12**	13.67 ± 0.35**	308.13 ± 14.91	12.27 ± 0.32**	68.28 ± 0.90**	15.50 ± 2.04
C.S. 6 B × Capeiti	102.75 ± 3.39	58.42 ± 1.23	249.92 ± 12.51	15.29 ± 0.34	377.33 ± 14.47	13.83 ± 0.20	71.25 ± 0.65	53.91 ± 1.64**
C.S. 7 B × Capeiti	99.79 ± 1.62	58.50 ± 1.27	222.00 ± 7.69	14.71 ± 0.19*	316.29 ± 11.77	12.89 ± 0.24**	76.07 ± 1.05*	19.21 ± 2.32
Capeiti	82.55 ± 1.15**	34.95 ± 0.68**	264.30 ± 7.08	15.58 ± 0.29	313.55 ± 7.24*	13.40 ± 0.20*	69.50 ± 0.71	99.60 ± 1.38**
Chinese Spring	101.80 ± 1.60	59.70 ± 1.11	262.15 ± 8.94	15.20 ± 0.29	394.70 ± 9.94**	14.45 ± 0.21	77.95 ± 0.49**	0.00 ± 0.00*
C. S. × Capeiti (2 n = 35)	105.98 ± 1.10	62.40 ± 0.64	235.79 ± 5.49	15.96 ± 0.19	341.88 ± 8.65	14.28 ± 0.17	72.03 ± 0.72	15.03 ± 0.82

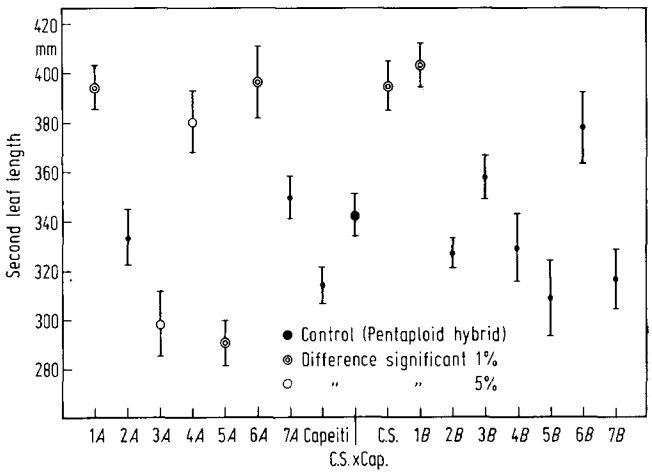

Fig. 4. Diagram showing the means of second leaf length and standard errors of 14 monopentaploid lines ($2n = 34$), Chinese Spring ($2n = 42$), Capeiti ($2n = 28$) and hybrid control ($2n = 35$)

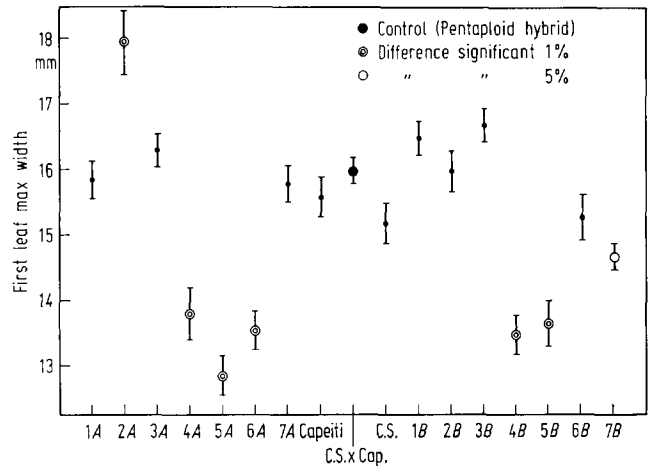

Fig. 5. Diagram showing the means of first leaf max width and standard errors of 14 monopentaploid lines ($2n = 34$), Chinese Spring ($2n = 42$), Capeiti ($2n = 28$) and hybrid control ($2n = 35$)

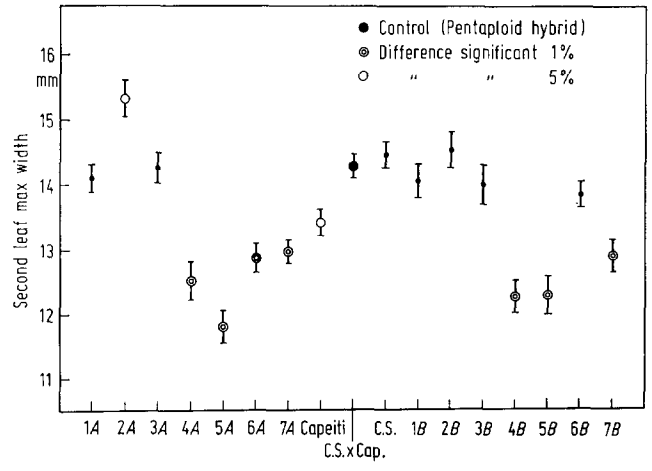

Fig. 6. Diagram showing the means of second leaf max width and standard errors of 14 monopentaploid lines ($2n = 34$), Chinese Spring ($2n = 42$), Capeiti ($2n = 28$) and hybrid control ($2n = 35$)

in monos 1 B (significantly) and 1 A (not significantly) of Chinese Spring. Short rachis is shown by monos 2 A and 2 B (homoeologous to 2 D, controlling the *compactum* factor „C" in hexaploid wheat, Unrau, 1950), as well as 4 B and 5 B.

Like culm length, this character also seems to be controlled by factors located in several chromosomes, and in both cases, overdominance is shown by the hybrid control. A correlation index between culm and rachis length, calculated over all the plants analyzed, was significant at the 1% level of probability.

Measurements of length and width of the first (flag) and second uppermost leaves are presented in table 2 and figs. 3, 4, 5 and 6. Control hybrids did not show heterosis for these characters. Leaf length seems to have a rather complex determination. Monosomic conditions for chromosomes 1 A and 1 B increased, while monosomy for 5 A and 5 B significantly decreased, leaf length. Highly significant correlations were found between the mean lengths of 1st and 2nd leaves ($r = 0.74$).

Some monosomic lines were significantly narrower and only 2 A was significantly broader. A nearly complete parallelism between the widths of 1st and 2nd leaf was observed, the correlation index between the means being very high ($r = 0.88$). The leaves of monos 4 A, 5 A, 6A, 4B, 5B and 7B were distinctly narrower, with a mean decrease varying between 1 and 3 mm.

In order to make a synthetic analysis of the behaviour of the leaf and culm characters and to ascertain the extent of homoeology in controlling the characters considered, differences of the means of monosomic from control lines have been represented in fig. 7 in a pictorial diagram. Values have been grouped in classes, taking into consideration both means and standard errors; for the sake of simplicity, three minus- and three plus-variant classes have been established, in addition to the control class. Parallelism of character trends is very clear: in homoeologous groups 1,5 and 6 for leaf lengths; in homoeologous groups 4, 5, 6, 7 for leaf width; in homoeologous groups 1, 2, 3, 5, 6 for culm and spike length.

Table 2 and fig. 8 present the means and standard errors for the number of days from germination to heading of the 17 lines studied. The two parental lines differ by more than 8 days; the hybrid disomic for the A and B genomes (hybrid control) shows a value closer to the earlier parent, but the difference between them is not significant. The later parent (C. S.) differs significantly from both hybrid control and Capeiti. Three monosomic lines are significantly earlier (mono 1A, 7A and 5B) and three (mono 5A, 2B and 7B) are significantly later than the hybrid control. Therefore, at least six chromosomes have factors which control heading time. Since the two parental varieties should be considered spring types (both, in fact, do not require cold treatment for inflorescence differentiation), the differences found may

be attributed principally to differential reaction to temperature, daylength and light intensity.

In the same way, eight monosomic lines were found to interfere significantly with awn development, as shown in table 2 and fig. 9. Three lines (mono 2 A, 7A and 2B) show a decrease and 5 (3A, 1B, 3B, 4B and 6B) show an increase in awn development. It must be stressed that the two parents are, respectively, practically awnless (C. S.), and with very long awns (Capeiti), while the monopentaploid hybrid (control) is awnletted (15 mm, on average).

Discussion

Genetic analysis of a variety A, to be tested using monosomic lines available in a tester variety B, is based on some general assumptions, which it is convenient to underline before discussing the further limitations presented by using lines of different ploidy level. Monosomic analysis is normally performed both in F_1 and F_2 generations. It is generally assumed that if the expression of a character shown in the disomic F_1 is completely (or partially) modified in a monosomic line of the hybrid, the tester variety carries the dominant (or semidominant) allele. In other words, only recessive or partially dominant alleles of the variety to be tested can be identified and attributed to a specific chromosome in the F_1 generation. All this is based on the assumption that differential expression between disomics and monosomics is caused by the lack of genes on the missing chromosome. The comparison between the segregation ratios of the F_2 progeny of F_1 selfed disomics with the F_2 segregation of each monosomic F_1 line is sufficient to attribute dominant factors to specific chromosomes, while concomitant cytological analysis is required for recessive ones. In crosses between monosomics of hexaploid wheat and normal tetraploid lines, most of the monopentaploid hybrid lines are completely or nearly completely sterile. Therefore there is no practical possibility of carrying the monosomic analysis into the F_2 generation.

Another prerequisite for the validity of monopentaploid analysis exists: attribution of genetic information to specific chromosomes is valid only if homology exists between the A and B genomes of Chinese Spring and Capeiti. This condition, however, should be completely fulfilled, since the A and B chromosomes of *T. aestivum* and *T. durum* are similar both morphologically (Giorgi, Bozzini and Carluccio, 1967) and structurally (Chapman and Riley, 1966). In our F_1's normal pairing was observed (14 II + 7 I in the disomics), and no large structural modifications (e. g. translocations) were present in the hybrid.

This being so, we could assume, with Kuspira and Millis (1967), the validity of F_1 monosomic analysis for our pentaploid hybrids.

Although biometrical and statistical analyses for the 8 characters investigated does not offer particu-

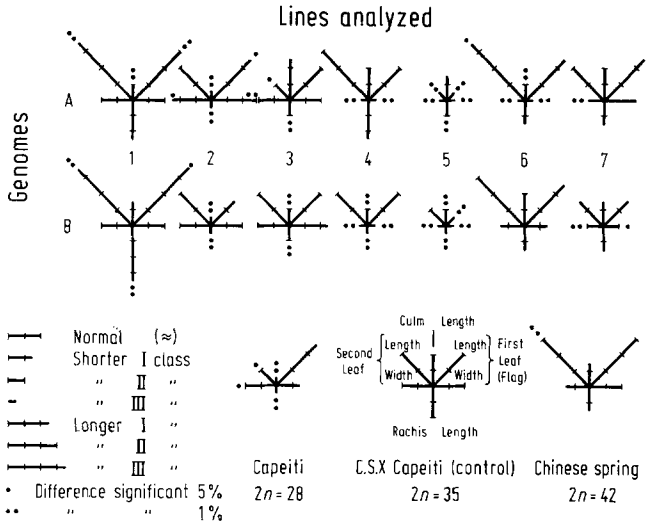

Fig. 7. Pictorial diagram showing the relationship between the homoeologous groups as to the characters investigated

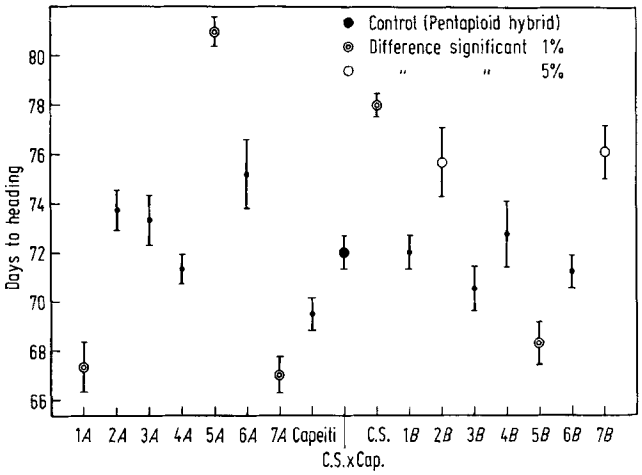

Fig. 8. Diagram showing the means of days to heading and standard errors of 14 monopentaploid lines ($2n = 34$), Chinese Spring ($2n = 42$), Capeiti ($2n = 28$) and hybrid control ($2n = 35$)

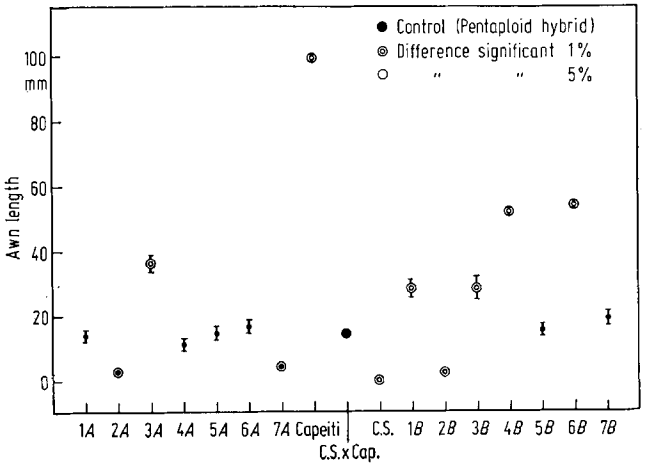

Fig. 9. Diagram showing the means of awn length and standard errors of 14 monopentaploid lines ($2n = 34$), Chinese Spring ($2n = 42$), Capeiti ($2n = 28$) and hybrid control ($2n = 35$)

lar difficulty, the correct genetical interpretation of the data is undoubtedly more difficult. Nearly all the characters investigated rarely show clearcut discontinuous behaviour. The difficulties are increased when a heterotic effect is present, masking real differences between pentaploid and monopentaploid lines. Moreover, for some characters, such as culm and leaf measurement, the paucity of previous genetical investigations increases the degree of uncertainty.

In the case of culm length, all the lines investigated showed a nearly continuous variation, the highest means being those of the control and mono 3A, which are both higher than the mean of Chinese Spring, the taller parent.

In discussing this character it should be kept in mind that if heterosis is due to overdominance (heterozygote superiority), in this case the heterosis effect somewhat increases the apparent difference between short-culm lines and the control. For example, if the control F_1 were the same height as the Chinese Spring parent, differences associated with monos 6A, 3B and 4B would not be significant. If we were to take a midparental value for the hybrid control as an alternative hypothesis, even differences with monos 1A and 5B would be ruled out. In a prudent interpretation, therefore, it could be assumed that monos 2A and 2B should be considered responsible for at least some of the differences in plant height between the two parental lines (20 cm.). As the depression in height is very large, it could be postulated that, as well as determining short straw, these chromosomes — and particularly chromosome 2A of Chinese Spring — have factors present which influence heterotic effect. These findings are in line with results obtained by Sears (1954) in nullisomic analysis: following his data, in fact, nullisomics 2A and 2B are clearly shorter than the control. These results again confirm that several chromosomes participate in the control of plant height.

The large difference in rachis length between Capeiti and Chinese Spring seems to be controlled by an even larger number of chromosomes. Factors affecting rachis length seem to be located in homoeologous groups 1, 2, 3, and 5 and on chromosome 4B. The large number of chromosomes carrying genetic information for this character confirms the extreme complexity of its inheritance pattern, and it may, therefore, be considered among the most difficult to study. However, again our results are in rather good agreement with Sear's *l. c.* findings in nullisomic analysis in C. S.: homoeologous group 1 is considered to determine lax spike, while homoeologous groups 2 and 3 determine shorter rachis.

The significance of the positive correlation between culm and rachis length suggests — in our opinion — the pleiotropic action of a number of factors affecting internode length of both the vegetative and reproductive organs.

The size of the first and second uppermost leaves follows — as may be expected — a similar pattern. Parental lines do not differ in the length of flag leaf, while the second uppermost leaf of Capeiti is clearly shorter than the corresponding leaf of C. S. This differential behaviour has a parallelism in the behaviour of the monosomic lines, differences in the second leaf length being greater than in the case of the first. Chromosomes belonging to homologous groups 1 (clearly) and 6 (possibly) control longer leaves, while group 5 controls shorter leaves.

A reduction in maximum leaf width is present in the monopentaploid lines 4A, 4B, 5A, 5B, 6A and 7 B. It is interesting to note that, for this character also, differences between parental and monosomic lines are higher in the second uppermost than in the flag leaves. A trend toward broader leaves is noticeable in homoeologous group 2, the differences being significant at 1% for 2A and at 5% level for 2B. Similarly, in nullisomics for group 2 of C. S., Sears *l. c.* found broader leaves than in the control.

In table 3 we have tried to summarize data obtained for the parameters analyzed. It appears that all chromosomes, except 7A, carry genetic information for the characters considered, with those belonging to homoloeogous groups 5 and 2 being particularly important.

The difference in heading time between parent lines is rather large (more than 8 days). It seems to be controlled by factors located in at least 6 chromosomes. In Chinese Spring, chromosomes 5A, 2B and 7B carry earliness alleles, while lateness alleles are carried by chromosomes 1A, 7A and 5B. Tsunewaki and Jenkins (1961) identified earliness alleles Sg_2^c and Sg_3 in chromosomes 5A and 2B of Chinese Spring and our data confirm their findings perfectly. An earliness factor was identified by Law and Wolfe (1966) in chromosome 7B of Hope. Capeiti seems to carry at least three other factors, one in 5B (the homoeologous group 5 seems, therefore, to have great influence on the life cycle) and the others on 1A and 7A. Kuspira and Millis (*l. c.*) found control of heading time in chromosomes 5A and 5B, the *durum* variety Caid Eleize showing lateness alleles in both of them. Induction of earliness seems to be rather strong in Capeiti's factors, which are apparently able to counterbalance the lateness alleles in 5A, 5B and 7B. From data in the literature and that presented here, it seems that at least 7 chromosomes control heading time in hexaploid wheat: 1A, 2B, 5A, 5B, 5D, 7A and 7B.

To check the degree of accuracy of monosomic analysis for this character, in which overdominance seems to be absent, positive and negative deviations from the hybrid control were calculated. The difference was positive (+ 7.1 days) and nearly equal to that found between the two parental lines (+ 8.4 days). This should demonstrate that the resolving power of monosomic analysis is quite efficient.

Table 3. *Chromosome mapping of identified factors controlling awn development*

	Genome *A*							Genome *B*							Genome *D*						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7
Chinese Spring (6*x*)		a_1	A_3	A_7	b_1		a_9	A_{10}	a_8	A_6	Hd		B_2			a_2	A_4				A_5
Pawnee (6*x*)		a_1	a_3		b_1						hd		b_2			a_2	a_4				a_5
Kentana 52 (6*x*)		a_1	a_3								hd					a_2	a_4				
Thatcher (6*x*)			a_3	a_7	b_1^a					a_6	Hd[a]		b_2								a_5
Hope (6*x*)					b_1						hd		b_2								
Timstein (6*x*)			A_3	a_7	B_1				a_8		hd		b_2								A_5
Red bobs (6*x*)		A_1			B_1				a_8		hd		B_2			a_2					
Jones fife (6*x*)		a_1			B_1				a_8		hd		b_2			a_2					
Elgin (6*x*)		a_1			B_1				a_8		hd		b_2			a_2					
Prelude (6*x*)		a_1			b_1				a_8		hd		b_2			a_2					
Red-Egyptian (6*x*)		a_1			b_1				a_8		hd		b_2			a_2					
Kharkov (6*x*)		a_1			b_1				a_8		hd		b_2			a_2					
'S-615 (6*x*)		a_1			b_1				a_8		hd		b_2			a_2					
Hymar (6*x*)					B_1																
Marquis (6*x*)					B_1																
Gabo (6*x*)					B_1																
					B_1																
Capeiti (4*x*)		A_1	a_3	A_7	b_1		A_9	a_{10}	A_8	a_6	hd		b_2								

Table 4. *Tentative attribution to A and B chromosomes of factors affecting culm, rachis and leaf size in Chinese Spring and Capeiti after monopentaploid analysis*

Character	1A	2A	3A	4A	5A	6A	7A	1B	2B	3B	4B	5B	6B	7B
Culm length	+	+				+			+	+	+	+		
Rachis length		+	+		+			+	+	+	+	+		
Leaf length	+				+	+		+				+	+	
Leaf width				+	+	+					+	+		+

A similar analysis was performed for awn development. Here also, the difference was positive (+ 93.5 mm) and practically of the same value as the difference between Chinese Spring and Capeiti (+ 99.6 mm). Probably, these results are not completely random events and are related to the resolving efficiency which it is possible to achieve with monosomic analysis if no disturbing factors, such as heterosis, interfere. On the basis of evidence in the literature (see Tsunewaki and Jenkins, *l. c.*) and our own results, it has been possible to summarize in table 3 present knowledge of the factors affecting awn development in polyploid wheats. Our analysis fits previous results perfectly, and adds to the picture two further awn promoting factors, A_9 and A_{10}, located on 7A and 1B, respectively. The extremely complex nature of awn determination is quite clearly attributed to 3 main inhibitors (B_1, B_2 and Hd) and to at least 10 awn promoters.

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