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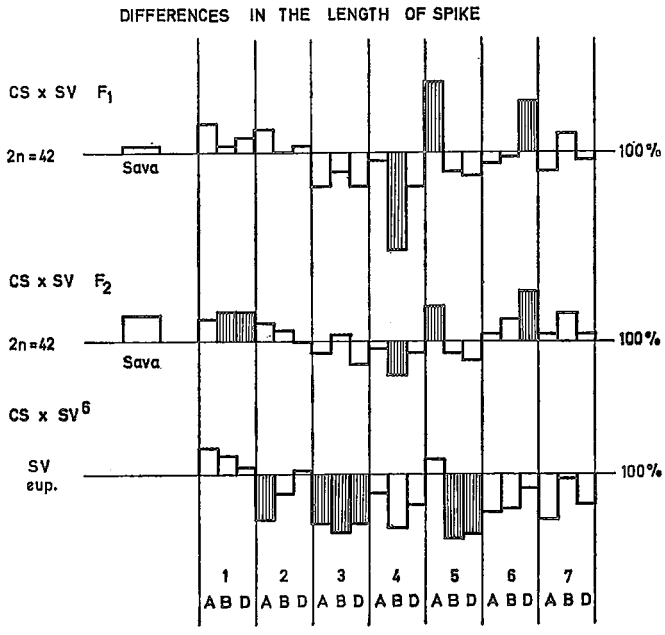

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No. 49 May, 1979

I. Research Notes

Expression of heterosis and combining ability for grain protein in a diallel wheat cross

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Improvement of the nutritional value of common winter wheat by breeding new varieties or creating hybrid wheat, which is one of the main tasks in many wheat breeding programmes, requires good knowledge and data on expression of heterosis and combining ability for grain protein content, since the protein content in wheat grain is an important constituent in determining the nutritional quality of wheat.

The purpose of the present study was to investigate heterosis and combining ability for protein content in wheat grain and to evaluate parents and F_1 hybrids in two different environments (two years), as well as to relate the findings to breeding practice.

Materials and Methods

Three winter wheat varieties Sava, Bezostaja-1 and Kavkaz, and one spring wheat variety Cajeme 71 were crossed by hand in a diallel system excluding reciprocals in 1972 and 1974. The wheat varieties were chosen on the basis of both assumed genetic differences for grain protein content and genetic diversity of origin. In each of the six possible cross combinations enough seed was produced to set up a replicated trial with normal sowing density.

The four parental varieties and the resulting six F_1 hybrids were grown in field in a randomized complete block trial with three replications during 1973 and five replications during 1975. The plot unit was one row, 1 m long with 0,2 m between rows. An standard agricultural practice was applied.

In each year the trial was hand harvested and the seeds from all the plants of the F_1 hybrids and parental varieties in each replication were mixed to form a composite sample. Protein percentage determinations were made on all samples by a colorymetric method using the apparatus Prometar MK–2.

Combining ability variances and effects were obtained by analysing the diallel table following GRIFFING (1956), method 2, model 1.

Results and Discussion

Heterosis. – Two of the 6 F_1 hybrids had significantly higher grain protein percentage than the better parent in the cross for 1% (Bezostaja 1× Kavkaz) and 10% (Sava × Bezostaja-1) in 1973, and only one for 3% (Sava×Kavkaz), in 1975, showing positive heterosis. However, the rest of F_1 hybrids showed no heterosis for grain protein percentage. This suggests that the considerable amount of heterosis for grain protein percentage may be encountered only in certain F_1 hybrids, and that this depends strongly on the environmental conditions. GRIFFING and ZSIROS (1971) reported that plant density and environmental conditions has an effect on the amount of heterosis in wheat, which agrees with the results obtained in this study regarding the grain protein content. From the stand point of the practical hybrid wheat growing and development of a breeding programme it is neccessary for F_1 hybrids to express heterosis under local environmental conditions. Because of this the obtained results approved the need that the breeders should evaluate the F_1 hybrids and parents under local environmental conditions.

Combining ability. – The analysis of variance for combining ability for grain protein percentage showed that both, general (GCA) and specific (SCA) combining ability variances were highly significant in 1973 as well as in 1975. In 1975 the GCA variances were larger than the SCA variances with the ratio of GCA/SCA being 4,71, while in 1973 the SCA variances were larger than the GCA variances, with the ratio of GCA/SCA being 0,047.

The relatively higher magnitude of the GCA variance than that of the SCA variance indicates the predominance of additive (fixable) gene effects in the genetic control of the grain protein percentage among parents used in the diallel cross. On the other hand, the significant SCA variance suggests considerable amount of non-additive (dominance and overdominance) variance among the parents used for the diallel crossings. CHAPMAN and MCNEAL (1970); RAM and SRIVASTAVA (1975), and KETATA *et al.*, (1976); BHULLAR *et al.*, (1978), also reported that additive gene effects in grain protein content were significant in all crosses and consistently greater than dominance effects, while Brown *et al.*, (1966) found the predominance of non-additive gene effects to be significant.

Of particular importance to the wheat breeder seeking improvement of grain protein content is the predominance of additive gene action for this attribute, because it suggests that the improvement of this character can be achieved through the standard breeding procedure, from which may result superior pure-line varieties. The occurence of a rather pronounced non-additive gene action, as was found in this study, could also be of practical value to the wheat breeder. If this is a general phenomenon, it may be possible to obtain higher protein content by hybrid wheat breeding through appropriate choice of crossing parents for producing the F_1 hybrid seeds.

The comparison of GCA performances of individual varieties (Tab. 1) shows that Cajeme–71 and Sava had positive GCA effects in 1973 and Kavkaz and Cajeme–71 in 1975.

It should be pointed out that expression of GCA effects of parents used in this study depended on the year in which the hybrids were tested. In both years Bezostaia–1 had negative GCA effects and Cajeme–71 positive GCA effects, while Sava and Kavkaz had in one year positive and in one year negative GCA effects. The variety Cajeme–71 proved to be the best general combiner and Bezostaja–1 very poor general combiner for the grain protein content. The other tested varieties were an average in this respect.

The estimates of SCA effects for the character studied (Tab. 2) show that out of the total 6 cross combinations three of them had negative and three positive SCA effects in 1973, while four of them had negative and only two positive SCA effects in 1975. No one cross combination showed positive SCA effects in the both years which indicates a strong influence

Table 1. Estimates of GCA effects for grain protein percentage in parental varieties on the bases of F_1 hyrbids from a 4×4 diallel wheat cross

Parental varieties	1973		1975	
	GCA	Rank	GCA	Rank
Sava	0, 0342	2	−0, 1333	3
Bezostaja-1	−0, 0425	3	−0, 6833	4
Kavkaz	−0, 0742	4	0, 7833	1
Cajeme-71	0, 0825	1	0, 0333	2
S.E. (gi)	±0, 0127		±0, 0405	
S.E. (gi-gj)	±0, 0208		±0, 0661	

Table 2. Estimates of SCA effects for grain protein percentage in a 4×4 diallel wheat cross

Parents	SCA effects with			Parent mean (%)	
	2	3	4		
		1973			
1. Sava	1, 16	−0, 51	0, 28	15, 1	
2. Bezostaja-1		0, 42	−1, 09	15, 2	
3. Kavkaz			−0, 41	15, 6	
4. Cajeme 71				16, 3	
S.E. (sij)			0, 03	LSD:	
S.E. (Sij-Sik)			0, 04	0, 05	0, 11
S.E. (Sij-Skl)			0, 05	0, 01	0, 15
		1975			
1. Sava	−0, 04	1, 19	−0, 76	14, 2	
2. Bezostaja-1		−0, 56	0, 19	14, 2	
3. Kavkaz			−0, 38	16, 8	
4. Cajeme 71				15, 9	
S.E. (Sij)			0, 10	LSD:	
S.E. (Sij-Sik)			0, 13	0, 05	0, 33
S.E. (Sij-Skl)			0, 15	0, 01	0, 45

of the environmental factors on the expression of SCA effects. HALLORAN (1975) reported similar findings with the F_4 wheat diallels tested in the two different environments.

The highest positive SCA was shown by the combination Sava × Bezostaja–1 (1,16) in 1973 and Sava × Kavkaz (1, 19) in 1975. Because of the preponderance of additive effects in these cross combinations they could be assumed as promising combinations for selection of superior pure-line varieties.

Although the wheat grain protein content in numerous studies has shown to be of a resonable strong heritability (RAM and SRIVASTAVA, 1975; DUFFIELD *et al.*, 1972 and others), the data in this experiment pointed out that genetic control of this character appeared to change with environment. This behavior again points to the need to conduct protein inheritance and selection studies under environmental conditions closely appropriate to those for which higher protein genotypes are required. It seems that season to season selection within the one environment should be resonable effective in retaining a genetically high protein component of the population. The greatest advance in protein content would be expected from selection within the highest protein crosses.

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Epicuticular wax of wheat. Alkane composition of 29 ditelosomic lines.

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JENSEN and DRISCOLL (1962) report the results of a number of investigators who as early as in the thirties studied some phenotipic aspects of wax production in wheat. These studies dealt mainly with inheritance patterns of the waxiness character in segregating generations derived from interpsecific crosses (e.g. *Triticum vulgare* × *T. compactum*; *T. turgidum* × *T. vulgare*; *T. pyramidale* × *T. durum*; *T. dicoccoides* × *T. persicum*). These early genetic studies gave results difficult to interpret owing to the complexity of the various levels of ploidy present in that material. JENSEN and DRISCOLL (1962) made use of the glaucous line 5075, a 42 chromosomes strain derived from a series of interspecific crosses involving tetraploid *Long Kernel* which in turn arose from a cross of *T. dicoccoides* and *T. polonicum*.

The character glaucous appeared dominant in the F_1 generation with a typical monomendelian 3:1 segregation in F_2.

In another paper DRISCOLL and JENSEN (1964) were able to localize a gene affecting wax production (decrease) on the short arm of chromosome 2A. By means of ditelosomic lines DRISCOLL (1966) localized the gene inhibiting wax production at 42–50 map units from the centromer. Furthermore, DRISCOLL and JENSEN (1964) cited a studies by Muramatsu on nullisomics of Chinese Spring from which the investigator localized genes controlling wax production on chromosomes 2A, 4B and 6B.

Further results by other Authors are worth being cited: ALLAN and VOGEL (1960) located on chromosome 2A a gene responsable of the large wax production of a durum wheat; an inhibitor, on the contrary, was found by TSUNEWAKI (1962) on chromosome 2D of a synthesized hexaploid wheat. Furthermore TSUNEWAKI (1964) confirmed MURAMATSU and DRISCOLL and JENSEN findings that a gene associated with waxiness is located on chromosome 2A of Chinese Spring.

It is clear from the foregoing literature survey on studies concerning the identification of chromosomes or genes associated with wax (glaucousness) character that the limiting factor of such studies was the difficulty of a proper evaluation of the amount and the chemical composition of wax.

More recently, NEWTON-BARBER and NETTING (1968) resumed the problem applaying an up to date more complete approach comparing genetic constitution of lines of wheat with

chemical composition of waxes, paying particular attention to the amount of β-dicarbonyl compounds present in the wax.

The authors were able to demonstrate that both the glaucous and non-glaucous lines are waxy and the phenotypical differences depend on the presence of β-diketones and hydroxy β-diketones on the glaucous lines.

We have resumed the subject on the relationships between genetical constitution and chemical composition of the wax, taking advantage of the availability of ditelosomic lines developed in *Triticum aestivum* var. Chinese Spring by SEARS (1954). As well known, each ditelosomic line carries a homozygous deletion for a particular chromosome arm. Any morphological and chemical variation detected in the ditelosomic line can be related with the specific missing arm of the chromosome. Because of the complexity of the analysis required for a complete analysis of all the components of the wax, we have made a preliminary screening on the alkane fractions of Chinese Spring variety and of 29 derived ditelosomic lines.

Materials and Methods

Plants of *Triticum aestivum* variety Chinese Spring and of 29 derived dietelosomic lines kindly supplied by Dr. LAW (Cambridge, England) were grown in the open in the Po Valley near Milan during 1976. The plants were collected at the stage of maximum wax production when the flag leaf was completed and the spike was emerging from the sheath (late boot stage). Wax extraction was carried out by dipping the shoots into chloroform for approximately 60 sec. Evaporation of the solvent under reduced pressure in the rotary evaporator gave the derived wax sample. Each extracted material was chromatographed over a silica gel column (with carbon tetrachloride for 7A-L, 7D-S and the parent plants, while cyclohexane was used for the remaining lines) to obtain the n-alkane fraction as a colourless crystalline substance. IR absorption bands: ν_{max} 2920, 2860, 1460, 1385,

Table 1 Per cent composition of n-alkane fractions of waxes isolated

Chain length	C.S.* test	1A-S	1A-L	2A-S	3A-S	3A-L	4A-α	5A-L	6A-α	7A-S	7A-L	1B-S	1B-L	2B-L
21	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	2.3	tr.	tr.	2.1
22	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	5.0	tr.	tr.	tr.
23	2.7	3.6	2.6	2.0	3.7	2.4	3.9	2.1	3.7	1.8	9.7	5.0	4.0	5.3
24	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	8.1	tr.	tr.	1.6
25	3.9	5.1	4.8	4.0	5.0	4.2	6.3	4.2	5.7	2.8	10.8	9.2	5.2	6.2
26	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	7.0	1.9	tr.	1.7
27	13.6	12.5	17.7	14.7	16.6	16.5	20.5	17.2	19.2	13.5	14.3	24.4	15.3	18.7
28	1.3	1.8	1.9	1.9	1.7	1.3	1.8	0.1	2.3	1.1	4.0	3.1	1.5	1.7
29	51.0	51.1	44.8	54.2	50.8	48.8	45.6	41.4	37.1	50.8	25.0	36.7	53.2	37.7
30	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.
31	22.9	22.9	21.9	20.1	19.8	22.1	18.2	26.2	23.2	24.1	10.6	16.4	18.6	19.1
32	—	—	—	—	—	—	tr.	tr.	tr.	tr.	tr.	tr.	—	tr.
33	4.6	3.0	6.3	3.1	2.4	4.7	3.7	8.8	8.8	5.9	3.2	3.3	2.2	5.9

* See text.

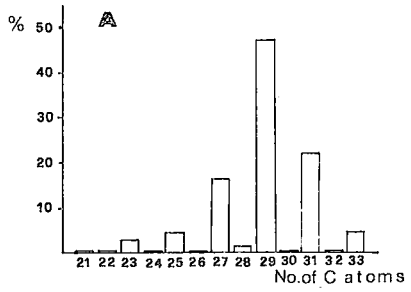

Fig. 1a

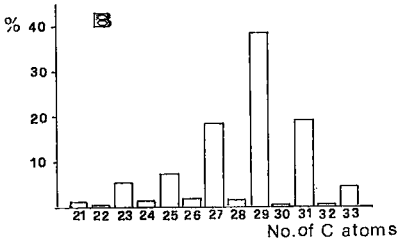

Fig. 1b

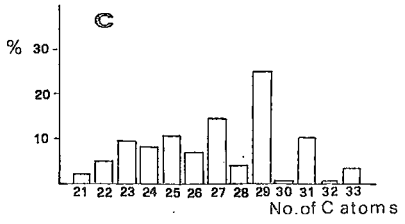

Fig. 1c

Fig. 1 – Distribution of n-alkanes isolated respectively from waxes of the following types: (A) Chinese Spring, 1A-S, 1A-L, 2A-S, 3A-S, 3A-L, 4A-α, 5A-L, 6A-α, 7A-S, 1B-L 3B-L, 4B-L, 5B-L, 6B-S, 7B-S, 1D-L, 2D-α, 3D-α, 3D-β, 4D-L, 5D-L, 6D-α 6D-β and 7D-S. (B) 1B-S, 2B-L, 6B-L and 7B-L. (C) 7A-L.

730 and 720 cm^{-1}.

The gas chromatograms were taken on a Carlo Erba mod. 2400 FID type attached with a glass column (2 m×3 mm) packed with 100–120 mesh GCP coated with 1% silicone OV1, 5°C/minute programmed temperature from 160°C to 270°C and 30 ml/minute flow rate of

from plants of Chinese Spring wheat and its 29 ditelosomic lines

3B-L	4B-L	5B-L	6B-S	6B-L	7B-S	7B-L	1D-L	2D-α	3D-α	3D-β	4D-L	5D-L	6D-α	6D-β	7D-S
tr.	tr.	tr.	tr.	1.8	tr.	1.3	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.
tr.	tr.	tr.	tr.	3.1	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.
3.2	3.0	5.3	4.4	8.0	3.0	3.5	3.0	3.7	3.2	4.4	2.8	3.1	6.5	3.7	0.8
tr.	tr.	tr.	tr.	3.7	tr.	1.1	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.
4.1	5.5	5.9	5.4	7.8	4.4	5.3	4.7	6.2	4.3	7.3	4.5	5.1	6.4	5.8	1.5
tr.	tr.	tr.	tr.	2.7	tr.	1.5	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	0.1
15.8	18.4	16.8	18.9	15.4	14.2	14.7	18.9	21.9	14.1	18.1	18.3	19.2	19.0	15.4	6.2
0.1	1.7	2.3	2.8	0.1	1.2	1.8	0.1	2.2	1.7	2.8	1.2	1.5	0.1	1.6	0.2
52.0	48.1	41.6	43.7	34.0	38.1	46.5	50.1	40.9	47.9	44.9	46.2	43.1	46.7	45.0	58.2
tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	0.1
21.0	21.0	22.2	19.8	19.6	29.1	20.8	19.5	19.6	24.0	19.3	21.1	21.7	18.0	23.9	29.2
—	—	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.	tr.
3.8	2.3	5.9	5.0	3.8	10.0	3.5	3.7	5.5	4.8	3.2	5.9	6.3	3.3	4.6	3.7

N_2 carrier gas. Authentic samples of alkanes were used as standards.

Results and Discussion

The n-alkane compositions of the waxes of Chinese Spring and of the 29 ditelosomic lines are shown in Table 1.

Although, as found previously by several authors, the dominant homologue chains are the common C_{27}, C_{29} and C_{31}, the data obtained allow to gather the lines studied in three groups according to the distribution on n-alkanes. The first group whose n-alkane distribution is shown in Figure 1 (A), comprises the Chinese Spring and 24 ditelosomic lines. The spectrum describing the per cent composition in n-alkane homologues is typical; that is C_{27}, C_{29} and C_{31} predominate and only a 1.4% of n-octacosane with traces of other even number homologues are present.

In the case of Chinese Spring n-alkanes also a small amount of short chain homologues, namely C_{14} (0.4%), C_{16} (3.7%), C_{18} (2.2%), C_{20} (0.9%) was found. Although traces of n-alkanes with chain lengths in this range are frequently detected in waxes of several plants, two points are of relevance: first the relatively high percentage of these homologues, second the even number chains.

The second group comprising 1B-S, 2B-L, 6B-L and 7B-L shows a significant increase in even carbon chains which, in fact, reaches an averaged value of 6.0% of the total (Figure 1 (B)).

Figure 1 (C) shows the very unusual distribution of chain lengths composing the n-alkanes of 7A-L wax. The percentage of even number carbon chains is exceptionally high (24.1%) for this cereal and in sharp contrast with the composition of the other lines analyzed.

Apart from the relevant biochemical aspects regarding the biosynthesis of alkanes which will be discussed in a forthcoming paper (BIANCHI *et. al.*) we believe that the present approach is the most promising in order to obtain information on the genetical control of the wax production. It seems very promising to be able to associate the absence of an arm of the chromosome with chemical composition, class by class, of wax and distribution of homologous chains within each class of compounds.

At this preliminary stage of our research it appears evident the superior validity of this approach compared with simple visual observations. The latter approach, in fact, could have failed in distinguishing between almost all the lines studied here. The chemical analyses, although limited to the alkanes, allow to relate the presence of well defined effect, at chemical composition level, with certain chromosomes.

Thus, the phenotypic characters, glaucousness-non glaucousness (waxiness-waxless or more precisely scarcity in wax production) are explained in terms of wax chemical composition.

Acknowledgment

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Choice of the most representative structural characters of the wheat kernel

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The breeding improvement of the cereals grain structure requires detailed studies of many features of caryopsis. One should include here both morphological and anatomical characters, as well as the chemism of kernel. The investigations of this type were made for many pure lines of *T. aestivum* var. *vulgare*, some species of *Triticum* genus as well as their hybrids of F_2 generation (KOSINA 1978). In *T. aestivum* var. *vulgare*, *T. turgidum* var. *durum* and var. *polonicum* the presence of interesting anatomical characters, considerably increasing the quality of kernels, was observed (KOSINA unpubl.). To analyse many various characters of caryopsis, one has to evaluate the usefulness of the parameters for the characterization of the investigated material. The parameters which repeat the information should be removed. The present report is devoted to this problem.

Materials

For big, random sample of kernels the nineteen characters of a single caryopsis were analysed: 1-width, 2-thickness, 3-length, 4-weight, 5-depth of the crease, 6-width of the crease, 7-length of the endosperm cavity arms, 8-height of the cavity, 9-thickness of the fruit and seed coat, 10-thickness of the aleurone layer, 11-thickness of the high-protein sub-aleurone endosperm layer, 12-specific gravity, 13-empirical volume of the kernel, 14-the maximum theoretical volume, 15-degree of filling of the kernel, 16-shape of the kernel, 17-coefficient of the endosperm yield from caryopsis, 18-coefficient of the endosperm quality, 19-quality of caryopsis (the microDBC-parameter). The above mentioned quantitative characters were grouped in three sets: I. — characters no. 10, 11, 12, 18, 19 (the set of parameters characterizing the "quality of caryopsis"), II — characters no. 1, 2, 3, 4, 13, 14, 15 (the set of parameters describing the "shapeliness of caryopsis", an important component of yield), III — characters no. 5, 6, 7, 8, 9, 16, 17 (the set characterizing the "quantity of endosperm in a single kernel"). The choice of the representative characters was made within each set. The information about the examined characters is important for the processing of grain (cleaning, descication, milling and baking). The representative characters were chosen for some populations of pure lines and hybrids of F_2 generation of spring wheat: *T. aestivum* var. *vulgare* cv. Opolska (01), *T. aestivum* var. *spelta* (Sp), Nagradowicka × Capega (N×C1), Capega × Ostka Popularna (C3×OP4), Oktawia × Capega (Ok2×C2), *T. aestivum* var. *spelta* × *T. aestivum* var. *sphaerococcum* (Sp × S1), Opolska × *T. turgidum*

var. *polonicum* (01×P). N, C1, C3, OP4, Ok2, C2, O1 are the pure lines of common wheat varieties.

Statistical Background (BARTKOWIAK 1974, 1978)

The study of the interdependence of characters in the below case is based on the analysis of regression. From the (p-character)-set r characters with the maximum information about the remaining p-r characters were extracted. All possible (r-character)-subsets from the initial set are analysed. Then the calculation for the linear functions of the 2, 3, 4 as well as (5-element)-sets of representatives were made in turn. The set of parameters $W=1, \cdots, p$ was divided each time into the regression set of representatives $R=i_1, \cdots, i_r$ as well as the NR set of rejected variables. For each set of parameters $R=i_1, \cdots, i_r$ the function

$X_{i_r+k}=a_0+a_1x_{i_1}+ \cdots +a_rx_{i_r}$ at $k=1, \cdots, p-r$ were calculated. The measure of goodness of approximation is $RV=1-R^2$ statistic, RV-residual variation, R^2-coefficient of determination (the square of multiple correlation coefficient). The calculation of RV was made for all variables with i_{r+k} indices belonging to NR-set. RV=max is remembered as the maximum loss of information about one of the rejected characters. From all (r-character)-subsets of the W-set the smallest maximum residual variation was extracted. The calculation was made in the Institute of Informatics Wrocław University on the Odra–1204 computer.

Results

The synthetical results are given in Table 1. Set I includes the characters each of which includes a great amount of information. The max R^2 value indicates the presence of a certain amount of information in the, last, rejected fifth character. For some populations, it is the eleventh character, for others, the eighteenth. For the Ok2×C2 hybrid the eleventh character has a great information value (max $R^2=0.805$) while for the spelta form, considerably smaller (max $R^2=0.161$). For the forms C3×OP4, Sp×S1, O1×P, the character no. 18 has an intermediate information value (max $R^2=0.256$–0.410). For all populations, we lose too much information while chosing the four representative characters. The max R^2 value at the choice for each population in succession 1,2,3 or 4 representative parameters also indicates the great losses of information and, therefore, the information importance of all five characters. For set no. II, the information value of the characters is, as a rule, exhausted with the three (01, Sp) or the four (N × C1, C3 × OP4, Ok2×C2, Sp × S1, O1 × P) representatives. In the first case one may not measure the width and thickenss of kernel, its weight, volume or degree of filling. In the second case it is most frequently the weight and the empirical volume of caryopsis. These characters can be removed from the complex of parameters characterizing the kernel, but their measurements are important for the information about the specific gravity of caryopsis, its shape or filling. In set no. III, just as in no. I, we lose much information in disregarding some characters.

Table 1. The analysis of representation of kernel characters in certain pure lines and hybrids of spring wheat

Number of representatives		01		Sp		N × Cl		C3 × OP4	
		No. of character	Max R^2	No. of character	Max R^2	No. of character	Max R^2	No. of character	Max R^2
I	1	10	914	18	966	11	998	19	932
	2	10, 19	849	12, 18	914	11, 12	952	12, 18	780
	3	12, 18, 19	701	10, 11, 12	718	10, 11, 12	888	10, 11, 12	738
	4	10, 12, 18, 19	502	10, 12, 18, 19	161	10, 12, 18, 19	431	10, 11, 12, 19	340
II	1	13	672	13	936	13	799	4	764
	2	4, 14	330	4, 14	331	4, 14	455	14, 15	243
	3	3, 14, 15	070	3, 13, 14	091	3, 14, 15	169	3, 14, 15	128
	4	1, 2, 3, 15	028	1, 2, 3, 15	015	2, 3, 14, 15	030	1, 2, 3, 15	020
	5	1, 2, 3, 4, 15	006	1, 2, 3, 13, 15	003	1, 2, 3, 4, 15	007	1, 2, 3, 4, 15	007
III	1	5	970	16	988	5	975	9	989
	2	16, 17	841	8, 16	912	5, 8	841	5, 8	878
	3	8, 16, 17	629	8, 16, 17	835	5, 8, 16	710	7, 9, 17	833
	4	6, 7, 8, 9	565	5, 6, 7, 9	757	6, 8, 9, 16	495	7, 8, 9, 17	478
	5	7, 8, 9, 16, 17	239	5, 6, 8, 9, 16	531	7, 8, 9, 16, 17	342	5, 7, 8, 9, 17	357
		Ok2 × C2		Sp × S1		O1 × P			
I	1	11	966	18	901	10	984		
	2	18, 19	933	12, 18	844	18, 19	869		
	3	10, 12, 18	855	10, 18, 19	748	12, 18, 19	542		
	4	10, 12, 18, 19	805	10, 11, 12, 19	410	10, 11, 12, 19	256		
II	1	4	893	1	903	4	662		
	2	4, 14	407	14, 15	325	13, 14	434		
	3	3, 13, 14	127	1, 13, 14	173	1, 13, 15	151		
	4	1, 2, 3, 15	030	1, 3, 14, 15	090	1, 3, 14, 15	062		
	5	1, 2, 3, 4, 15	007	1, 2, 3, 4, 15	015	1, 2, 3, 4, 15	015		
III	1	6	853	6	992	6	984		
	2	6, 9	714	7, 17	910	5, 16	878		
	3	7, 8, 9	561	7, 8, 17	833	9, 16, 17	718		
	4	8, 9, 16, 17	287	8, 9, 16, 17	779	8, 9, 16, 17	401		
	5	5, 8, 9, 16, 17	220	6, 8, 9, 16, 17	494	5, 7, 9, 16, 17	234		

$R^2 \times 10^3$ value of the coefficient of determination was given. Max R^2 means the maximum loss of information caused by the reduction in the number of representatives in comparison with the initial set of parameters.

With 5 representatives, the max R^2=0.220–0.531. The characters which are most frequently rejected with this number of representatives, are the dimensions of crease and cavity as well as the coefficient of endosperm yield or the shape of caryopsis. As the anatomical observations showed (KOSINA unpubl.), the parameters of crease and cavity can be of essential importance for the evaluation of the use value of caryopsis. The mentioned information value also indicates this. The data in Table 1, also indicate the most informative characters in the three considered sets, in case of the necessity of use of 1, 2, 3 and other representatives, as well as the information value of rejected characters in individual cases.

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Monosomic analysis in wheat (*Triticum aestivum* L. *em.* THELL.): Study of glume pubescence and awn colour*

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Studies on the nature of inheritance of qualitative characters in wheat species have been numerous but inconclusive. Aneuploid analysis was suggested in polyploid species like hexaploid wheat where several duplicate loci make the conventional genetic analysis difficult. But still, with only a few markers the monosomic analysis demands considerable labour. Therefore with an idea of establishing gene chromosome markers, two qualitative characters glume pubescence and awn colour were studied by monsomic F_2 analysis method whose results are presented in this paper.

Glume pubsscene is one of the good markers and genetic studies have indicated single dominant gene controlling this character (PAL *et al.*, 1956; SIKKA and RAO, 1957; SUVA *et al.*, 1958 and SRINIVASAN, 1962). Allelic series *Hg*, *hg* and hg_2 conditioning glume pubescence was proposed by SHEYBANI and JENKINS (1961). *Hg* is a dominant gene for pubescence; glabrous condition, *hg*, is recessive to *Hg* but dominant to hg_2 for pubescence. Chromosome 1A has been found to carry a gene for glume pubescence in varieties Sonora (KUSPIRA and UNRAU, 1960), Loro (ANDERSON and MCGINNIS, 1960), Prelude and Fife (TSUNEWAKI, 1961).

Black awn colour has been found to be dominant over white (KHAN, 1956) and linkage is noticed between the genes controlling awn colour and glume pubescence with a cross over value of 12.33±2.16 (SIKKA *et al.*, 1961). Epistatic (SUVA *et al.*, 1958) and complementary (ASLAM, 1958) gene actions have also been proposed to explain awn colour inheritance.

Material and Methods

The material for the present study comprised of one disomic and nineteen monosomic F_2 populations of the crosses between disomic and nineteen monosomic lines of Pb. C591 (except 1A and 4A) with UP 301 pollen. Monosomic condition was identified before making the cross and also in the F_1 by chromosome counting in mitosis and meiosis. The material was sown in a randomised block design with three replications in the Botany Garden, Agriculture College, Dharwar during October 1976. Glume pubescence and awn colour of individual F_2 plants were recorded by visual observation at the time of maturity. Chi-Square test was applied to test the goodness of fit of the assumed phenotypic ratios. In critical lines, where the assumed ratios showed a strong deviation, expected frequencies of

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different phenotypic classes were calculated, assuming the presence of genes under study on those chromosomes, and Chi-Square test was again applied to confirm the assumption.

Results and Discussion

Segregation pattern in one disomic and nineteen monosomic F_2 populations of the crosses of the disomic and monosomic lines of pubescent variety Pb. C591 with glabrous variety UP 301 are presented in Table 1. When a 3 pubescent: 1 glabrous glume ratio

Table 1. Segregation pattern for glume pubescence in monsomic F_2 populations

F_2 population or line	Pubescent glume		Glabrous glume		Total	χ^2 (189: 67)
	Observed	Expected	Observed	Expected		
2A	77	78	29	28	106	0.05
3A	140	150	63	53	203	2.56
5A	77	83	36	30	113	1.63
6A	0	49	67	18	67	very high**
7A	157	166	68	59	225	1.86
1B	99	98	34	35	133	0.04
2B	67	67	24	24	91	0.00
3B	47	41	9	15	56	3.28
4B	105	105	37	37	142	0.00
5B	101	100	35	36	136	0.04
6B	46	44	14	16	60	0.34
7B	102	99	32	35	134	0.35
1D	67	60	14	21	81	3.15
2D	54	58	25	21	779	1.04
3D	95	90	27	32	122	1.06
4D	123	124	45	44	168	0.03
5D	118	114	36	40	154	0.54
6D	91	103 (98)	48	36 (41)	139	5.40*
7D	49	57 (54)	28	20 (23)	77	4.32*
Total (except critical lines)	1475	1479	528	524	2003	0.04

Pb. C591 – pubescent glumes UP 301 – glabrous glumes
* and ** indicate significant deviations at 5 per cent and 1 per cent levels respectively.
Figures in the parenthesis represent the expected frequencies calculated assuming the genes responsbile for glabrousness are carried by these chromosomes.

was applied, several monosomic populations showed significant deviations. Therefore, 189:67 ratio which is very close to 3:1 ratio was applied to all the populations. Only three crosses involving chromosomes 6A, 6D and 7D of UP 301 showed significant deviation indicating the presence of gene/s for glabrousness on these chromosomes. This ratio results from the interaction of four genes, of which one is basic gene for pubescence and other three are complementary duplicate genes to the basic gene. Supposing that *A* is the basic gene for pubescent glume and genes *B*, *C* and *D* are complementary duplicate genes to *A*, then the ratio can be explained as follows.

Pb. C 591 – *AA BB CC DD* – Pubescent glumes
UP 301 – *aa bb cc dd* – Glabrous glumes
Disomic F_1 – *Aa Bb Cc Dd* – Pubescent glumes
Disomic F_2:

Frequency	*Genotype*	*Phenotype*	*Frequency*	*Genotype*	*Phenotype*
81	*ABCD*	pubescent glumes	9	*BC*	glabrous glumes
27	*ABC*	pubescent glumes	9	*BD*	glabrous glumes
27	*ABD*	pubescent glumes	9	*CD*	glabrous glumes
27	*ACD*	pubescent glumes	3	*A*	glabrous glumes
27	*BCD*	glabrous glumes	3	*B*	glabrous glumes
9	*AB*	pubescent glumes	3	*C*	glabrous glumes
9	*AC*	pubescent glumes	3	*D*	glabrous glumes
9	*AD*	pubescent glumes	1	*abcd*	glabrous glumes

In the critical cross involving gene *a* from UP 301 we should expect all the plants to be of glabrous phenotype since the basic gene for pubescent glumes is in recessive condition. This was found to be so in the monosomic population for chromosome 6A where all 67 plants showed glabrous phenotype. F_1's between the monosomic line 6A and UP 301 had glabrous glumes. Therefore the basic gene for glabrous condition in UP 301 was found to be associated with chromosome 6A.

In the critical cross involving gene *b* from UP 301 only the class 9*AB* showing pubescent phenotype in other crosses will show glabrous phenotype, while the rest of the classes will be unaltered in phenotype. Thus instead of 189:67 ratio, a ratio of 180:76 will be seen. Similarly in critical crosses involving other two complementary recessive genes *c* and *d* 180:76 ratio will be noticed. In monosomic popultions 6D and 7D the ratio of 180: 76 fitted well $\chi^2=1.7$ and 1.55 respectively, thereby confirming the presence of complementary recessive genes on 6D and 7D of UP 301. However, the third complementary recessive gene of UP 301 was not detected in the present study, but it may be present on one of the chromosomes 1A or 4A which were unfortunately missing. Thus the present investigation does not agree with the findings of earlier workers which reported a single dominant gene on chromosome 1A controlling this trait (TSUNEWAKI, 1961, KUSPIRA and UNRAU, 1960, ANDERSON and MCGINNIS, 1960) but detected a recessive gene for glabrousness on chromosome 6A of UP 301, in addition to two recessive complementary genes for glabrousness on chromosomes 6D and 7D of UP 301.

Segregation pattern for awn colour in one disomic and nineteen monosomic F_2 populations is presented in Table 2. The female parent Pb. C591 has black awns as against UP 301 which has brown awns. In the disomic F_2 population 57 brown: 7 black awn ratio was found to fit well. When this ratio was applied for all the monosomic F_2 populations, populations monosomic for chromosomes 6A, 2B and 1D showed highly significant deviations while those of 3B and 5B registered significance at five per cent level only. Here one independent and two complementary genes were assumed to control brown awns. In the F_2, segregation will occur in various populations as indicated below.

Table 2. Segregation pattern for awn colour in monosomic F_2 populations

Line	Brown awns		Black awns		Total	χ^2 (57 : 7)
	Observed	Expected	Observed	Expected		
2A	98	96	10	12	108	0.37
3A	183	183	23	23	206	0.00
5A	103	104	14	13	117	0.09
6A	69	61 (69)	0	8 (0)	69	9.05** (0)
7A	209	204	20	25	229	1.12
1B	118	120	17	15	135	0.30
2B	90	82 (86)	2	10 (6)	92	7.18** (2.85)
3B	59	54	2	7	61	4.03*
4B	122	128	22	16	144	2.53
5B	114	123	24	15	138	6.06*
6B	52	54	9	7	61	0.65
7B	120	120	15	15	135	0.00
1D	60	74 (62)	23	9 (21)	83	24.27** (0.25)
2D	73	70	6	9	79	1.13
3D	111	110	13	14	124	0.08
4D	151	151	19	19	170	0.00
5D	133	137	21	17	154	1.06
6D	135	128	9	16	144	1.76
7D	85	83	8	10	93	0.45
Total (excluding critical lines)	1693	1691	206	208	1899	0.02

Pb. C591: black awns UP 301: Brown awns

Figures in the parentheses indicate the expected frequencies calculated assuming the presence of genes for awn colour.

* Significant at 5 per cent level. ** Significant at 1 per cent level.

Genotype	Phenotype			
	Disomic and non-critical crosses	Critical cross involving		
		A	*B*	*C*
27 *ABC*	brown	brown	brown	brown
9 *AB*	brown	brown	brown	brown
9 *AC*	brown	brown	brown	brown
9 *BC*	brown	brown	brown	black
3 *A*	brown	brown	brown	brown
3 *B*	black	brown	black	black
3 *C*	black	black	brown	black
1 *abc*	black	black	black	black
Phenotypic ratio	57 : 7	64 : 0	60 : 4 or 15 : 1	48 : 16 or 3 : 1

In the cross involving chromosome 6A of UP 301 all the plants had brown awns which confirmed presence of independently dominant gene *A* for brown coloured awns on chromosome 6A of UP 301.

The F_2 population monosomic for chromosome 2B showed a good fit for 60 brown: 4 black awns (χ^2=2.85) indicating the presence of a dominant complementary gene, *B* on chromosome 2B of UP 301.

The critical population monosomic for chromosome 1D of UP 301 was found to agree with 3 brown: 1 black awns ratio (χ^2=0.25) which proved the presence of a recessive allele of the complementary gene *C* for brown coloured awns.

The other two populations viz., 3B and 5B which were critical at 5 per cent level of probability are thought to carry minor modifying factors which cause slight deviation in the phenotypic frequency.

As no reports are available on the cytogenetic analysis of awn colour, the present finding is only tentative. However, an indirect evidence can be derived. SIKKA *et al.* (1961) found linkage between genes controlling glume pubescence and awn colour. In the present investigation a basic gene for glabrous glume and an independent dominant gene for brown awns were found to be located on chromosome 6A of UP 301 which is an indication of linkage between the genes for glume pubescence and awn colour.

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Monosomic analyses of the culm length and length of the spike in wheat cultivar Sava

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Introduction

The use of monosomic analyses for the chromosomal location of the qualitative genes is as precise as the use of substitution lines. The use of monosomic analyses for the chromosomal location of the quantitative genes is not so precise since it is not possible to distinguish the effects due to chromosome dosage from the effects due to allelic differences (LAW and WORLAND, 1972).

The genes controlling quantitative characters have been located in specific chromosomes using substitution lines precisely (KUSPIRA and UNRAU, 1957; HERMSEN, 1963; LAW, 1967; and others). However, this method requires many backcrosses besides other disadvantages. Because the monosomic analyses is somewhat easier many authors have used it (ALLAN and VOGEL, 1963, 1964; SHARMA and BHOWAL, 1973; MAYSTRENKO and CHERNYKH, 1973; BAIER *et al.*, 1974; BARAS and KOSNER, 1974 and others). The results obtained using monosomic analyses were similar to the results obtained using substitution lines. Both methods show that more chromosomes are involved in the determination of any character and very often critical chromosomes were the same ones.

This paper presents the results of monosomic analyses carried out to locate genes for culm length and length of the spike in the hexaploid wheat variety Sava and to compare the results obtained using F_1 and F_2 monosomic analyses with the results obtained using Sava monosomics.

Material and Methods

Chinese Spring monosomic lines were crossed to hexaploid wheat cultivar Sava and also backcrossed to Sava five times. Chromosome counts for the Chinese Spring monosomics all F_1 plants and Sava monosomics were made in root-tip cells using the Feulgen squash method and also most of the monosomics and F_1 plants were checked during meiosis.

The F_1 plants and the Sava monosomics were grown in the glasshouse but in different years. The F_2 populations from F_1 monosomics, F_2 populations from F_1 disomics and parents were grown in field in space sowing 10×20 cm.

Culm length was measured from the crown to the base of the spike of the longest tiller of each plant and length of the spike was measured on the same tiller. Averages for F_1, F_2 and Sava monosomics were determined for both characters by means of frequency

distribution and the averages for each of the monosomic lines, or monosomic progenies were compared to normal F_1, F_2 and Sava using the Student's test (t test).

Results and Discussion

Culm length: Variety Sava had the average culm length about 65 cm (Tab. 1). The differences in that character between plants grown in glasshouse or in field, even in different years, were not high but the differences in culm length between Sava and F_1 or F_2 disomics were highly significant. None of the F_1 monosomics or F_2 populations from F_1 monosomics were significantly longer than normal F_1 or F_2 plants. The lines involving chromosomes belonging to group 2 and 4 (except 4A) and 3B chromosomes had average culm length smaller than corresponding disomics and the differences were highly significant. The differences in culm length between Sava monosomics and normal Sava were significant for most of the monosomics (Tab. 1, Graph. 1).

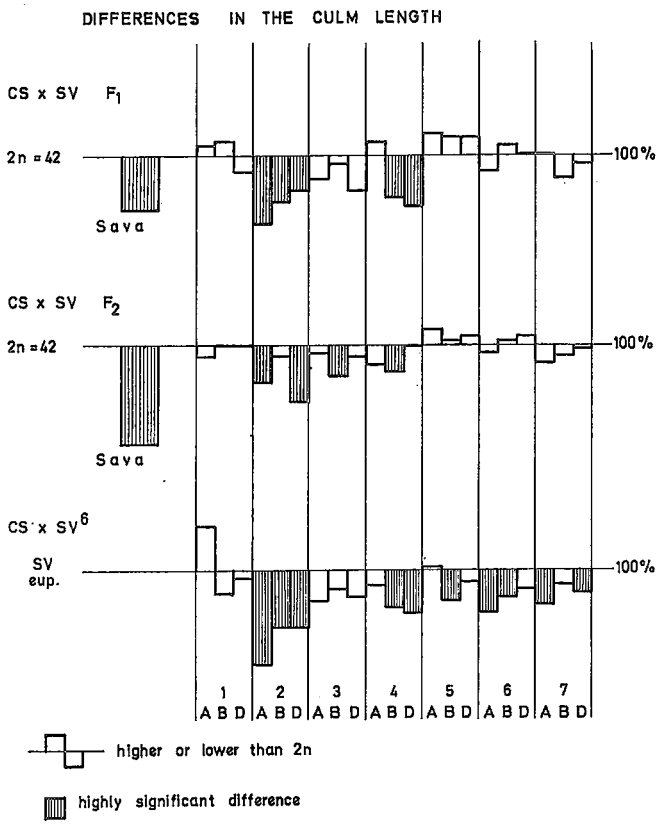
Table 1. Average culm length (in cm)

Chromosome	Chinese Spring × Sava		CS × Sava[6] monosomic
	F_1 mono.	F_2 pop.*	
1A	76, 5	88, 6	73, 0+
1B	76, 8	91, 6	61, 4
1D	70, 9	91, 6	64, 0
2A	61, 0−−	82, 7−−	49, 0−−
2B	65, 3−−	88, 4	55, 8−−
2D	67, 2−−	77, 8−−	55, 8−−
3A	69, 3	89, 3	60, 0−
3B	72, 4	84, 3−−	62, 3
3D	67, 6−	88, 8	60, 8−
4A	77, 0	86, 5−	62, 4
4B	65, 7−−	84, 6−−	58, 6−−
4D	64, 7−−	91, 5	57, 8−−
5A	78, 3	94, 8	65, 8
5B	77, 5	92, 0	59, 9−−
5D	77, 8	92, 9	63, 2
6A	71, 3	89, 4	58, 0−−
6B	76, 3	92, 4	60, 6−−
6D	74, 3	93, 3	62, 3−
7A	73, 7	87, 1	59, 4−−
7B	69, 5	88, 9	62, 8
7D	72, 4	90, 6	61, 2−−
2n=42	74, 0	91, 4	—
Sava	64, 0−−	67, 5−−	65, 3

* F_2 pop. from F_1 mono. grown in field; monosomics grown in the glasshouse.

Length of the Spike: Variety Sava had spike length about 9 cm and spike length means of normal F_1 and F_2 were slightly smaller. Significant differences were found between spike length means of the F_1 monosomics and normal F_1 for chromosomes 4B (shorter) and 5A and 6D (longer). Besides 5A and 5D chromosomes in F_2 population all three members of homoeologous group 1 and chromosomes 6B and 7B had significantly longer spikes and only

Graph 1



for 4B and 3D shorter (Tab. 2). Spike length means of several Sava monosomics are significantly smaller than normal Sava and none of them significantly longer (Graph. 2).

* * *

Each character is controlled by the genes located on several chromosomes and for different character different chromosomes are critical ones.

The effects observed for critical chromosomes were mainly in decreasing the mean values. The mean values for critical lines are mainly the results of the effects due to the chromosome missing.

According to LARSON (1959) the F_2 monosomic analyses of quantitative characters is the most effective in identifying critical chromosomes of the monosomic donor parent. In the present study variety Chinese Spring was the monosomic donor parent and that might be the reason that the results obtained were rather parallel to the results presented by SEARS (1954).

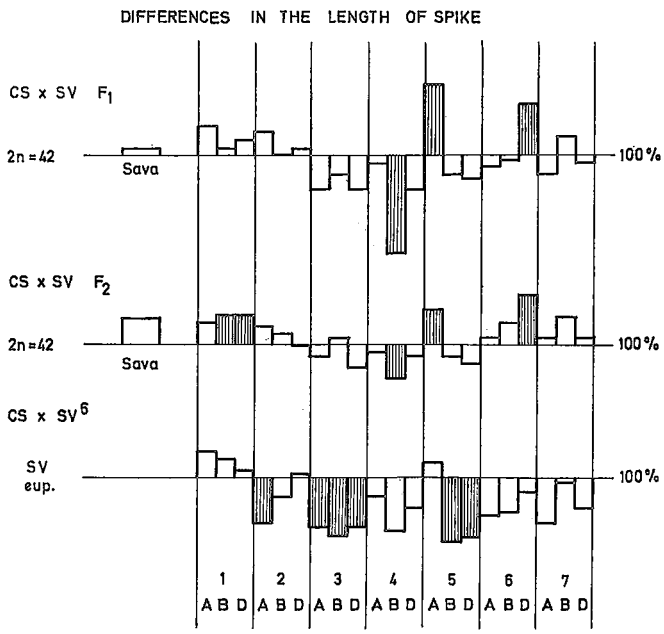
Finally, the use of F_1, F_2 monosomic analyses is not the best way for the chromosomal location of the quantitative genes and some other methods should be used.

Table 2. Average length of spike (in cm)

Chromosome	Chinese Spring × Sava		CS × Sava[6] monosomic
	F_1 mono.	F_2 pop.*	
1A	9, 5	9, 2+	10, 0
1B	9, 0	9, 4++	9, 8
1D	9, 1	9, 4++	9, 5
2A	9, 3	9, 1	8, 2−−
2B	8, 8	8, 9	8, 9
2D	9, 0	8, 7	9, 4
3A	8, 0	8, 4	8, 1−−
3B	8, 4	8, 8	7, 9−−
3D	8, 0	8, 1−	8, 1−−
4A	8, 6	8, 5	8, 9
4B	6, 5−−	7, 9−−	8, 0−
4D	8, 0	8, 4	8, 6−
5A	10, 5++	9, 4++	9, 7
5B	8, 3	8, 4	7, 7−−
5D	8, 2	8, 3	7, 8−−
6A	8, 5	8, 9	8, 4
6B	8, 7	9, 2+	8, 5
6D	10, 0++	9, 8++	9, 0
7A	8, 3	8, 8	8, 2−
7B	9, 2	9, 3+	9, 2
7D	8, 6	8, 9	8, 6
2n=42	8, 8	8, 7	—
Sava	9, 0	9, 3+	9, 3

* F_2 pop. from F_1 mono. grown in field; monosomics grown in the glasshouse.

Graph. 2



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Meiotic associations in a *Triticum aestivum* L. *em.* THELL. × *Agropyron distichum* (THUNB.) BEAUV. hybrid

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The first wheat-*Agropyron* hybrids were produced fifty years ago by SANDO and TSITSIN. Since then many crosses between the different wheat and *Agropyron* species were made in various countries in order to produce perennial wheat or to transfer the resistance to a number of pathogens from the *Agropyron* species to wheat (ARMSTRONG & MCLENNAN 1944; CAUDERON, 1966a; CAUDERON & SAIGNE, 1961; ELLIOT, 1957; KNOTT, 1961, 1964, 1968; KNOTT *et al.* 1977; POPE & LOVE, 1952; RILEY & KIMBER, 1966; SCHMIDT *et al.* 1956; SCHULZ-SCHAEFFER, 1970; TSITSIN, 1962; WIENHUES, 1968, 1973; a.o.). None of these crosses included *Agropyron distichum* (THUNB.) BEAUV.

A. distichum is indigenous to the Cape Province, South Africa, where it grows just above the high tide level along the southern and south western coast. As a rhizomatous, semi-xerophytic perennial which is 50–80 cm tall, it is a good binder of the saline sand along these coasts. It flowers during November and produces large (15–20 cm) wheat-like ears with 12 to 18 spikelets, each of which contains 8 to 12 florets. Its chromosome number is 2n=28 (PIENAAR, 1955).

All the initial wheat × *A. distichum* crosses failed, but in November 1976, the first successful cross was made with the hexaploid wheat cultivar Chinese Spring (PIENAAR *et al*, 1977). More crosses with other hexaploid and tetraploid wheats were therefore made. During 1977 some 2394 florets on 18 different hexaploid wheat entries, as well as 744 durum wheat florets on 5 cultivars were crossed with *A. distichum*.

None of these latter crosses yielded any filled kernels. Only two endospermless kernels were produced; one kernel was set on the hexaploid bread wheat cultivar Inia 66, and the other on the North Dakotan durum wheat line D6647 which was recently released in South Africa as the cultivar Nordum. Both these kernels contained an embryo (half normal size) at 18 days after pollination. The embryos were excised and cultured on sterile Difco Orchid Agar in McCarthney bottles. After the embryos had grown to the three leaf stage they were transplanted to pots in a growth chamber. Unfortunately, the D6647 × *A. distichum* hybrid died shortly after transplantation, but the Inia 66 × *A. distichum* hybrid grew vigorously and was cloned to produce 13 plants. Ten of these were treated with colchicine to induce chromosome doubling, and the other three were kept for meiotic and fertility studies on the F_1 hybrid.

The chromosome number in root tip cells of the hybrid is 2n=35. Since the chromosome number of the hexaploid wheats is 2n=42, and that of *A. distichum* 2n=28, the hybrid nature of the plant obtained from their cross was proved.

Young ears of the hybrid were fixed in Carnoy's acetic alcohol fixative. The pollen mother cells (PMC's) were stained according to the Feulgen procedure and squashed in aceto-carmine. The chromosome associations at the first meiotic metaphase were studied in 300 PMC's. The results given in Table 1 show that a mean of 11, 2 chromosomes per PMC associate in bivalents, trivalents and quadrivalents, and these associations have a mean chiasma frequency of 6,59. As much as 31, 6 percent of the PMC's have 14 or more chromosomes associated in bivalents, trivalents and quadrivalents.

Table 1. Mean chromosome associations at first meiotic metaphase in the PMC's of the F_1 hybrid of Inia 66 × *A. distichum* (ranges in parentheses)

No. of PMC's examined	Metaphase I chromosome associations							Chiasmata per PMC	
	Univalents	Bivalents			Multivalent			Total	Terminal
		Rod	Ring	Total	III	IV	V-X		
300	23, 78 (15-35)	4, 05 (0-9)	0, 06 (0-4)	4, 65 (0-10)	0, 44 (0-2)	0, 15 (0-1)	0 0	6, 59 (0-12)	6, 41 (0-12)

These results are similar to the levels of chromosome association that have been reported in other wheat × polyploid *Agropyron* hybrids by MATSUMURA & MURAMATSU (1956) and POPE & LOVE (1952). When these high levels of chromosome association in the Inia 66 × *A. distichum* hybrid are compared with the meiotic associations found in polyhaploid wheat by KIMBER & RILEY (1963), MARTIN & CHAPMAN (1977), and MILLAR & RILEY (1972), it is evident that in the hybrid only one or two bivalents may result from the autosyndetic associations of the homoeologous chromosomes in the three wheat genomes. The high incidence of associated chromosomes in the hybrid must therefore be due to one or more of the following:

a. India 66 and *A. distichum* have one genome in common, or the homoeology of many chromosomes of these two species are so close that allosyndetic associations occur readily.
b. *A. distichum* is an autopolyploid or segmental-allopolyploid and as such its two genomes in the hybrid are able to produce autosyndetic associations. It is known from the investigations of CAUDERON (1966), and SCHULZ-SCHAEFFER & ALLERDICE (1966), that many *Agropyron* species are indeed auto-allopolyploids or segmental-allopolyploids.
d. The *A. distichum* genotype like those of *T. speltoides* (*Ae. speltoides*) and *T. tripsacoides* (*Ae. mutica*) (RILEY, 1966; RILEY & KIMBER, 1966) suppresses the diploidising activity of the *Ph* gene of hexaploid wheat, with the result that in its hybrids with wheat a number of allo- and autosyndetic associations can take place between the homoeologues of the five genomes.

Investigations to determine which of the above alternatives are operative, are continued.

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Evaluation of wheat mutants for yield and yield components

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Introduction

Bread wheat, *Triticum aestivum* L. (2n=6x=42=AABBDD) being a polyploid, offers many opportunities of exploitation of mutations, recombinations and of increasing genetic variability in quantitatively inherited characters (SIDDIQUI, 1972; LARIK, 1975a, b). The presence of many triplicated and duplicated loci in wheat (SEARS, 1969) allows a large number of induced changes to be preserved and transmitted to the next generation. Also, with the advent of so-called green revolution interest in the induction of directed changes has considerably increased for redesigning ideotypes suitable for various agricultural environments. Induced mutations are also useful when it is desired to improve one or two easily identifiable characters in an otherwise well adopted variety (SIGURBJORNSSON, 1970).

In breeding programme, estimates of heritability, genetic advance and genotypic variance provide guideline for developing an appropriate variety (LARIK, 1978). The present paper is concerned with an evaluation of phenotypically stable wheat mutants isolated from one locally bred cultivar and two cultivars of Mexican origin. Such evaluations are important for studying the spectrum and magnitude of change and for directing the induced mutations in a breeding programme.

Material and Methods

The material originated from different doses of gamma rays (20, 25 and 35 kR) and ethyle methane sulphonate (EMS) of varieties C–591 (locally bred), Nayab and Indus–66 (Mexican origin) of bread wheat *Triticum aestivum* L. Phenotypically stable mutants were evaluated for yield and yield components in M_9 generation grown in the field in Tandojam during Rabi 1977–78. The seeds of these genotypes were procured from the Department of Botany and Plant Breeding, Sind Agricultural University, Tandojam, Pakistan. Homogeneous seed of mutants and cultivars was drilled in single rows each 3.1 m long with 30.5 cm interrow distance with path ways 1.0 m wide between blocks of a plot in randomized block design with four replications. After maturity 30 cm at each end of a plot was removed and remaining plot of 2.5 m was harvested and the weight of clean grain was recorded in g/plot. Observations were recorded on 5 randomly selected plants from each row for yield components. Thus 50 plants were studied from each mutant genotype and cultivars respectively. The mean values for the mutant population for each character were compared with the control mean by using *t* tests.

To make efficient and effective use of mutant genotypes in advanced generations through selection, estimates of broad sense heritability and expected genetic advance with a selection intensity of five per cent have been computed for yield components.

The broad sense heritability (h) of a character was estimated (LARIK, 1978) as under:

$$\%h = \frac{\sigma^2 g}{\sigma^2 t} \times 100$$

where $\sigma^2 g$=induced genetic variance and $\sigma^2 t$ is the total phenotypic variance calculated from mutant population.

The estimates of genetic advance (GA) at 5% selection intensity was based on the relation suggested by LARIK (1978) and computed by the following formula:

$$GA = (K)(\sigma p)(H)$$

where σp=phenotypic standard deviation of the mean performance of mutant population, H=heritability coefficient and K=2.06 constant for selection differential.

Results and Discussion

Mean yield (g/plot) of mutant strains were compared by LSD method, which indicated that considerable genetic variability had been achieved through mutation (Table 1). The yield data reveal that most of mutant strains from C–591 and Indus–66 cultivars were low yielding compared with their respective controls. In Nayab both high and low yielding mutant strains were obtained. Similar results were obtained by GAUL (1965), SIDDIQUI and GHAFOOR (1974), LARIK (1975a, b). These authors also observed a decrease in the mean values and increase in genotypic variance in mutant populations concomitant with a high frequency of plants having values on the negative side of the control mean. In present studies two mutants (Nos. 44 and 27) derived from Nayab were the highest yielding among all mutants included in the experiment. Mutant–44 is significantly higher yielding compared with Nayab control when judged by LSD method. However, two mutant strains (Nos. 13 and 37) were significantly low yielding compared with Indus–66 control.

Table 1. Mean yield (g/plot) of mutant srtains against their respective control

Sr. No.	Strain No.	Strain/Treatment/Origin	Mean yield (g/plot)
1.	43	C–591 (Control)	450.20
2.	38	C–591 EMS 7 hr.	440.00
3.	7	C–591 EMS 7 hr.	425.60
4.	28	C–591 EMS 7 hr.	398.00*
5.	32	Nayab (Control)	455.00
6.	44	Nayab 25 KR	605.50**
7.	10	Nayab 20 KR	335.50**
8.	27	Nayab 35 KR	465.10
9.	2	Indus–66 (Control)	412.80
10.	13	Indus–66 20 KR	340.00*
11.	37	Indus–66 20 KR	300.50**

*, ** Mutant strain significantly different from respective control by LSD method. (P≥0.05 and 0.01 respectively).

Among C–591 mutants, although all strains were low yielding than C–591 control, but one strain (No. 28) was significantly different from the parent strain.

Response to selection for quantitative characters (i.e. yield components) is directly proportional to the function of its heritability and its genetic variance. Heritability enables a plant breeder to recognise the genetic differences among strains and genetic variance indicates the potential for the improvement of a population. Keeping in view these points, the estimates such as genotypic co-efficient of variation, heritability and genetic gain expected from selection were obtained separately from each quantitative character and are presented in Tables 2 and 3.

Table 2. Estimates of mean values, genotypic co-efficient of variation, heritability and expected genetic advance with selection intensity (K)* of five percent for spike length (cm) and spikelets per spike of hexaploid wheat cultivar and mutant strains

Genotype	Mean	C.V. (P) %	C.V. (g) %	Heritability %	Genetic advance % of means
		Spike length			
C–591 (Control)	12.80	11.84	—	—	—
M–7	15.50**	12.66	11.54	83.58	21.70
M–28	15.25**	12.25	11.08	82.11	20.67
M–38	15.72**	11.09	9.81	79.00	17.95
Nayab (Control)	10.60	9.08	—	—	—
M–10	8.82*	11.89	8.92	51.07	12.68
M–27	10.85	14.46	15.33	73.25	23.46
M–44	14.12**	12.96	12.14	88.25	27.92
Indus–66 (Control)	10.57	14.24	—	—	—
M–13	10.50	18.75	16.50	54.58	34.58
M–37	13.92**	21.22	20.55	85.15	41.06
		Spikelets per spike			
C–591 (Control)	17.36	12.71	—	—	—
M–7	16.00**	15.94	9.30	34.04	11.17
M–28	16.04**	14.75	5.91	17.36	16.30
M–38	15.90**	15.90	15.20	26.65	18.33
Nayab (Control)	15.10	11.95	—	—	—
M–10	13.50**	17.50	8.87	25.85	9.29
M–27	14.80*	18.40	12.20	44.10	16.68
M–44	15.76**	19.30	12.55	42.42	16.84
Indus–66 (Control)	14.00	10.85	—	—	—
M–13	14.96	20.50	11.80	46.94	25.15
M–37	16.16	15.60	20.96	48.75	27.04

(K)*=5%=2.06 *, ** Significant at 5% and 1% level of probability respectively.

Spike length in mutant strains derived from different cultivars significantly enhanced as compared to their respective controls, except mutant strain No. 10 of Nayab in which spike length is signfiicantly ($P \geq 0.05$) reduced whereas, in mutant No. 13 of Indus–66 spike length was non-significantly decreased. Mean spike length of mutant strains derived from C–591 cultivar were reasonably homogenoeous. Similar significant shifts in mean values for spike length was also observed by LARIK (1975a, b), SIDDIQUI and GHAFOOR (1974).

For spike length, the mutant strains derived from mutagenic treatments of Indus–66

Table 3. Estimates of mean values, genotypic co-efficient of variation, heritability and expected genetic advance with selection intensity (K)* of five percent for seeds per spike and seed index (1000-seed weight) of hexaploid wheat cultivar and mutant strains

Genotype	Mean	C.V. (P) %	C.V. (g) %	Heritability %	Genetic advance % of means.
		Seeds per spike			
C–591 (Control)	52.08	16.89	—	—	—
M–7	51.35	16.99	5.32	9.80	5.42
M–28	52.24	21.28	10.20	24.50	15.52
M–38	48.20**	19.68	7.32	13.83	7.70
Nayab (Control)	50.90	10.92	—	—	—
M–10	45.50	17.74	8.52	23.15	10.84
M–27	52.44	20.86	12.46	28.10	15.33
M–44	55.32**	20.27	14.25	35.70	24.80
Indus–66 (Control)	52.58	16.81	—	—	—
M–13	55.10*	25.26	15.20	30.26	20.03
M–37	45.20**	24.14	14.33	25.04	17.52
		Seed index (1000-Seed weight in gm)			
C–591 (Control)	45.60	4.75	—	—	—
M–7	42.61**	8.90	4.81	70.01	14.80
M–28	41.50**	7.85	3.70	75.20	12.90
M–38	44.10	8.00	4.00	70.50	13.90
Nayab (Control)	44.00	5.95	—	—	—
M–10	38.50**	10.10	5.50	65.63	8.48
M–27	45.00*	7.25	4.10	67.88	8.95
M–44	50.20**	12.50	7.85	73.46	12.35
Indus–66 (Control)	42.10	10.50	—	—	—
M–13	39.14**	19.40	9.95	70.80	17.56
M–37	35.20**	20.45	10.20	75.78	19.45

(K)=5%=2.06 *, ** Significant at 5% and 1% level of probability respectively.

cultivar exhibited an increase of genetic variance as compared to all other mutant strains, this could be due to low yielding mutant strains (Table 2). Similar conclusions have also been drawn by GAUL *et al.* (1966) and SIDDIQUI and GHAFOOR ARAIN (1974). The heritability and genetic gain expected from selection also showed same tendency as the genetic variance. These estimates were of higher magnitude for the mutant strains of Indus–66 cultivar compared with C–591 and Nayab control. Thus indicated greater gains from selection for spike length are anticipated among the strains of Indus–66 (GHAFOOR ARAIN, 1973).

Spikelets per spike, seeds per spike and seed index (1000-seed wt.) are important yield components and are considered a reliable measure of yielding ability BOROJEVIĆ and BOROJEVIĆ (1972) as the frequency of induced changes in next generation depends on the number of seeds which transmit them (LARIK, 1978). The best criteria for the evaluation of superior genotypes is a comparison of its 1000-seed weight with the mother variety (GUSTAFFSON *et al*, 1971). Mean values for these quantitative characters were significantly ($P \geq 0.01$ and 0.05) reduced, except mutant strain No. 44 and 37 of Nayab and Indus–66 for spikelets per spike, mutant No. 44 and 13 of Nayab and Indus–66 for seeds per spike and mutants No. 27 and 44 of Nayab for seed index. These mutant strains displayed significant

($P \geq 0.01$, 0.05) increase for these quantitative characters over their respective controls. In the present study, the shift of mean values for these quantitative characters is mostly in negative direction, it provides support for the hypothesis of GAUL and AASTVEIT (1966) which states that the change in the mean values for the quantitative characters occurs both in positive and negative direction and is associated with reduced vitality independent of the genotype used.

Spike length of mutant–13 of Indus–66 and seeds per spike of mutant–7 and 28 and mutant–27 of C–591 and Nayab respectively were not significantly alterd from that of their respective controls. The non-significant shift in mean values of these characters is in agreement with findings of GHAFOOR ARAIN and SHEPHERD (1977) in wheat and OKA *et al.* (1958) in rice.

Highest genotypic co-efficient of variation was given by mutant strains No. 37 of Indus–66 for spikelets per spike, seeds per spike and seed index, indicates the potential for the improvement of these characters in the mutant populations. Heritability and genetic advance were of higher magnitude for the mutant strain No. 37 of Indus–66 for spikelets per spike and seed index and mutant No. 44 of Nayab for seeds per spike. This indicates that greater gains from selection for these characters are anticipated among the strains of Indus–66 and Nayab.

The present studies conclude that selection for superior genotypes for yield and yield components having low heritability values and low genetic advance is very difficult. It is therefore imperative from the breeders point of view to select those attributes displaying high heritability values among the mutant strains. The present studies have provided an evidence on the induction of genetic variability connected with yield and yield components of wheat crop. Thus, induced genetic variability can effectively be exploited for evolving mutant strains possessing desirable attributes.

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Suggestive information on an interspecific cross-incompatibility system in *Triticum*

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Failure of interspecific crosses in plants is usually induced by sexual barriers in pre-fertilization, resulting in non-fusion of the male and female nucleus or in post-fertilization, resulting in ceasing of the development of embryo and endosperm. Recently, Nishiyama and Yabuno (1978) have well interpreted a mechanism of hybrid seed failure in *Avena* in terms of a new hypothesis 'polar-nuclei activation' which is based on an idea that the triple fusion of the polar nuclei can play a major role in the abortion of hybrid seeds. That is, the intensity of activating action of the male nucleus and the reaction of the female nucleus at double fertilization are indicated as 'activating value (AV)' and 'response value (RV)', respectively. The seed development is closely related to the activation index (AI) of the polar nuclei, AV/2RV (or $\times$ 100) but not to that of the egg nucleus, AV/RV (or $\times$ 100). In a selfed plant the activation index of the polar nuclei is always 1/2=0.5 (or 50%) where the polar nuclei could be harmoniously activated for the normal development of the endosperm or the seed. The activating value which would be governed by a gene or genes may vary according to different species and roughly show additive effects in doubling the genome number. Then the activation index often deviates from 50% in distant crosses and the balanced activation may be disturbed, probably because of hyper- or hypoactivating action of the male nucleus. Such unbalanced activation may cause disturbance of the physiology of embryogeneis and result in the formation of deformed seeds or inviable seeds, following mainly the extent of defective endosperm development.

The present paper deals with a further application of the hypothesis to the interspecific hybridizations in *Triticum* which were previously reported by certain authors (Kihara, Wakakuwa and NISHIYAMA 1929, KATAYAMA 1934, LILIENFELD and KIHARA 1934, WAKAKUWA 1934, DHALIWAL 1977). The results are arranged in a model of the diallel cross using three diploid, five tetraploid and two hexaploid species (Table 1).

Based on the degree of abnormality of the hybrid seed relative activating values of the 10 species are arbitrarily assigned from 0.5 in *T. urartu* (2x) to 3 in *T. aestivum* (6x) where a standard value of 1 is adopted for *T. boeoticum* (2x) (Table 1). Table 1 further lists four seed development types, seed germination (%) and activation index of the polar nuclei (%) in most of 58 reciprocal crosses. According to the degree of seed development the hybrid seeds are grouped into four types, N-type, nearly normal seed, W-type, weakly developed seed, sometimes slightly wrinkled, Ps-type, partially shrivelled seed, and E-type, shrivelled-empty seed. The activation indices widely vary from 15 to 150% compared with a standard of 50% in selfed plants.

Table 1. Relationships between development and germination (%) of hybrid seeds, and polar-nuclei activation index (%) in interspecific crosses of *Triticum*

♀ RV \ ♂ AV	*urar.* 0.5	*mono.* 0.9	*boeo.* 1.0	*Timo.* 1.5	*pyra.* 1.6	*dic.-des* 1.7	*dico.* 1.7	*duru.* 1.75	*spel.* 2.9	*aest.* 3.0
urartu 0.5		Ps* 45 90.0	E 0 100.0							
monococcum 0.9	W 100 27.8		N 100 55.6	— — 83.3		Ps 50 94.4	Ps 9 94.4			
boeoticum 1.0	W 100 25.0	N 100 45.0		Ps 22 75.0	Ps 42 80.0	Ps 89 85.0	Ps 78 85.0	Ps 84 87.5	E 0 145.0	E 0 150.0
Timopheevi 1.5		— — 30.0	N 94 33.3		N 94 53.3		— 95 56.7	N 94 58.3		E 0 100.0
pyramidale 1.6			N 89 31.3	— 94 46.9				N 90 54.7		Ps 7 93.8
dicoccoides 1.7		— — 26.5	— 84 29.4		— — 47.1		N 78 50.0	N 80 51.5		— — 88.2
dicoccum 1.7		W 89 26.5	W 100 29.4		— — 47.1	N 100 50.0		N 92 51.5	— 86 85.3	— 94 88.2
durum 1.75		— — 25.7	W 100 28.6	N 89 42.9	N 95 45.7	N 100 48.6	N 100 48.6		— 100 82.9	Ps 29 85.7
spelta 2.9		— — 15.5	Ps 46 17.2	— — 25.9			W 91 29.3	W 100 30.2		N 100 51.7
aestivum 3.0		— — 15.0			W 91 26.7		W 100 28.3	W 100 29.2	N 100 48.3	

* Top: Seed-development type, W weakly developed seed, N nearly normal seed, Ps somewhat shrivelled seed, E empty-shrivelled seed. Middle: Mean seed-germination percentage. Bottom: Activation index of the polar nuclei (%).

The data are simply summarized in a diagramatic illustration showing the frequency distribution of the activation indices of the 58 crosses (Fig. 1). It is also indicated that the grouping of activation index series, 15–30, 30–60, 75–95 and 100–160% closely agrees with the grouping of W-, N-, Ps- and E- types, respectively, including mean percentages of the seed germination. It is of interest that the germination of Ps-type seeds greatly varied from 7 to 100% though 57% in an average. Such a variability appears to be attributed to the degree of abnormal seed development where environmental conditions or modified factors if present might be more effective in the other seed types.

As discussed at length the polar- nuclei activation hypothesis is very well applicable for understanding of seed failure in interspecific crosses of *Triticum*. The supplement of some appropriate crossing data would assist the establishing of a more perfect cross-incompatibility system in the genus *Triticum*.

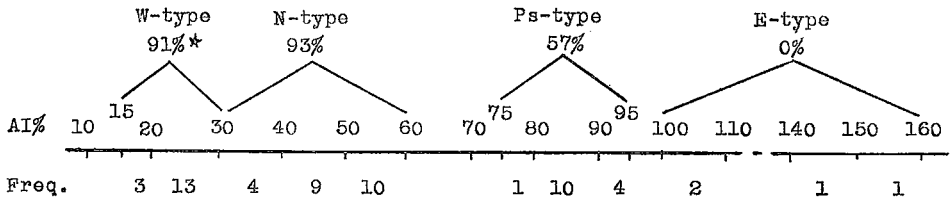

Fig. 1 Diagramatic illustration of the development and germination of hybrid seeds, and the frequency distribution of interspecific crosses in relation to the activation index of polar nuclei. * Mean seed germination (%).

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Transfer of the fertility-restoring genes of *Triticum macha* into a common wheat cultivar

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Large scale cultivation of hybrid wheats is not yet established apart from maize, sorghum and other crops 20 years after the discovery of cytoplasmic male sterility (KIHARA, 1951), although small scale cultivations are done at some limited areas in U.S.A., using the seeds commercially released by a few seed companies. This is mainly due to the difficulties to breed restorer lines which makes the respective hybrids to show stable fertilites under various climatic conditions. Therefore, the most important aim in the present program of hybrid wheat breeding is to obtain *Rf* genes having stable and strong fertility restoration ability.

KIHARA and TSUNEWAKI (1966) reported that *Triticum macha* var. *subletschchumicum* has a fertility restoring gene(s) to *timopheevi* cytoplasm, which could be utilized in hybrid wheat program. However, *T. macha* has a hybrid chlorosis gene *Ch*1 on chromosome 2A (Hermsen and Waninge 1972, Tsunewaki 1975), while most of common wheat cultivars have *Ch*2 on chromosome 3D (TSUNEWAKI and KIHARA 1961). Therefore, it is difficult to transfer a restorer gene(s) directly from *T. macha* to common wheat through crossing due to the hybrid chlorosis caused by the complementary gene action between the *Ch*1 and *Ch*2. Accordingly, *T. macha* has not yet been utilized as a source of restorer gene.

The present experiment was aimed to transfer fertility-restoring gene from *T. macha* to a common wheat cultivar by a bridging cross.

Materials and Methods

A procedure illustrated in Fig. 1, assuming that a single dominant gene (*Rf*) restores fertility, was adopted for the transfer of the *Rf* gene of *Triticum macha* to a common wheat. A strain, NIG–2 (by TSUNEWAKI 1975) free from both the complementary chlorosis genes, was employed as the bridging parent in the present investigation. NIG–2 was first employed as the female parent in a cross with *T. macha* var. *subletschchumicum* (abbreviated as *T. macha*). The F_1 plants at Step 1 (Fig. 1) should therefore have *Rf* and *Ch*1 in heterozygous condition. To separate *Rf* from *Ch*1, the F_1 plants were used as the male parents in the crosses with Chinese Spring having *timopheevi* cytoplasm (abbrevaited as (*timopheevi*)-CS), which has all *rf*, *ch*1 and *Ch*2 genes in homozygous state. Highly fertile segregants selected at Step 3 (Fig. 1) were selfed and their progenies were examined to determine the number of *Rf* gene involved. At the same time, those fertile plants were crossed with other Japanese cultivars as the secondary donors of the restorer gene(s).

Selfed seed fertility of each individual was estimated from two ears covered with parafin paper bag in green house. The plants of selfed seed fertilities lower than 20% were classified as sterile, and those higher than 21% as fertile.

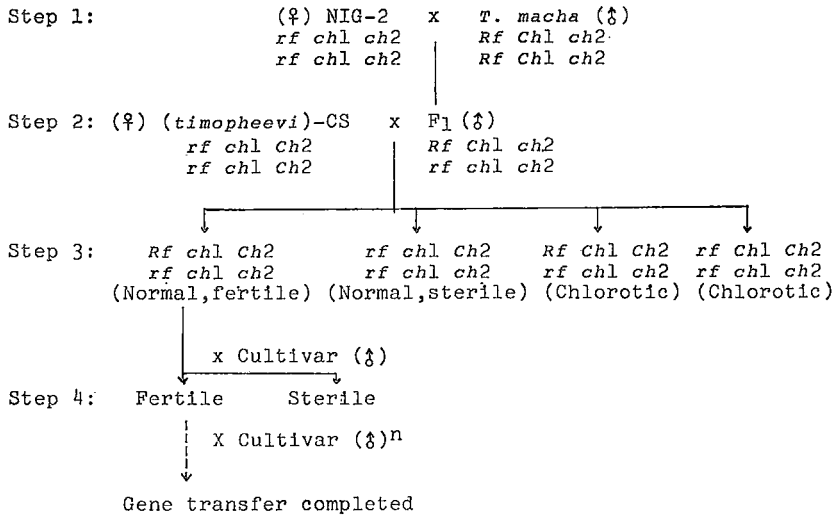

Fig. 1. A procedure for transferring a fertility-restoring gene(s) from *T. macha* to a common wheat cultivar.
(n: Repeated backcrosses to the fertile segregants.)

Results and Discussions

The fertilities observed at Step 3 are shown in Table 1. There were 13 chlorotic plants in addition to 23 normal plants classified as sterile (four) and as fertile (19). This gregation fits 1:3 ratio (X^2=0.710, d.f.=1) but not 1:1 ratio (X^2=9.783, d.f.=1), suggesting that *T. macha* carries two dominant *Rf* genes against the *timopheevi* cytoplasm.

In order to verify two gene control system, four fertile plants obtained were selfed to examine their progenies on the segregation pattern of fertilities. The results are summarized in Table 2. Three of the four lines (#1, #3 and #4) satisfactorily fit 1 (sterile): 3 (fertile) ratio (X^2=0.029, 0.017 and 1.127, respectively), suggesting that the parents of these lines had only one of the two *Rf* genes of *T. macha*. On the other hand, line #2 significantly deviated from 1:3 ratio (X^2=5.839), but rather fitted 1:15 ratio (X^2=3.007). Therefore, the parent of line #2 might have received both of the *Rf* genes of *T. macha*.

In the present experiment, lines #1, #3 and #4 as well as #2 showed similar range of selfed seed fertility. The plant which showed the highest fertility in line #2 was selfed and backcrossed to Chinese Spring to test the restoration ability of the *Rf* gene. The results obtained in the F_3 and B_1F_1 generations are shown in Table 3. It is clearly demonstrated that line #2-S1 (F_3) is homozygous for the *Rf* genes, and most of them showed higher than 80% of selfed seed fertility. While, the B_1F_1 plants showed wide range

Table 1. Segregation of chlorosis and male fertility from the cross of (*timopheevi*)-CS//NIG-2/*T. macha* (Step 3 in Fig. 1)

Phenotype	Selfed seed fertility (%)	No. of plants
Chlorotic		13
Normal		
Male sterile	0.0- 3.0	4
Male fertile	21.0-40.0	6
〃	40.1-60.0	7
〃	60.1-80.0	6
Total		36

Table 2. Segregation of male sterile and fertile plants in the selfed progenies of four fertile plants obtained at Step 3 in Fig. 1.

Line	Number of plants			Range of selfed seed fertility*	1:3 ratio		1:15 ratio	
	Total	Sterile	Fertile		χ^2-value	P value	χ^2-value	P value
#1	46	12	34	27.8-92.4%	0.029	0.75-0.90	27.219	-0.01
#2	66	8	58	21.9-92.1	5.839	0.01-0.05	3.007	0.05-0.10
#3	78	20	58	22.1-92.9	0.017	0.75-0.90	46.418	-0.01
#4	58	11	47	20.7-87.7	1.127	0.25-0.50	14.100	-0.01

*: The range observed among the fertile plants.

Table 3. Distribution of selfed seed fertility in F_3 and B_1F_1 plants from the line #2

Line	Generation	Total	Selfed seed fertility (%)										
			1	10	20	30	40	50	60	70	80	90	100
#2-B1	B_1F_1	14				1	2	1	2	3	3	2	
#2-S1	F_3	30									3	11	16

in selfed seed fertility similar to those in F_2 (about 20 to 90%). MILLER *et al.* (1974) reported that a common wheat cultivar Primépi has two fertility-restoring genes against *timopheevi* cytoplasm, and complete fertility restoration was ensured when both genes were present, either in the homozygous or heterozygous condition. The heterozygote or homozygote alone of either of the two genes was incompletely fertile. The data in the present experiment showed that the single *Rf* gene from *T. macha* can restore almost complete fertility in homozygous state and also in some of the heterozygotes.

In other heterozygotes, however, the *Rf* gene showed instability in fertility. This may be partly due to the gene interaction between *Rf* gene and background genes. FUJIGAKI and TSUNEWAKI (1976) reported that the *timopheevi* cytoplasm increased the inter-plant variation on four growth characters of common wheat. Therefore, the variation found on selfed seed fertility may be partly due to the increased developmental instability caused by the *timopheevi* cytoplasm.

In this study, *Rf* genes were transfered into a common wheat cultivar from *T. macha*. However, instability of gene expression of *Rf* gene in heterozygous condition is a problem

which should be resolved either through an appropriate combination of *Rf* genes or in breeding an easy restoration background.

Conclusion

An investigation was carried out on *Rf* genes of *Triticum macha* var. *subletschchumicum* against *timopheevi* cytoplasm and these genes were transfered into a common wheat cultivar. Since *T. macha* has *Ch*1 gene for hybrid chlorosis, and most of common wheat cultivars have *Ch*2, their F_1 hybrids become lethal due to chlorosis. Therefore, *T. macha* was first crossed to NIG–2 which has neither *Ch*1 nor *Ch*2 gene. The F_1 plants were crossed to (*timopheevi*)-Chinese Spring to select the plants having the *Rf* genes of *T. macha*, but free from the *Ch*1 gene. From these crosses, 13 chlorotic, four sterile and 19 fertile plants were segregated, which suggested that *T. macha* has two dominant fertility-restoring genes.

From these fertile plants, four lines were selected, and their progenies were tested for the segregation of fertility. The data indicated that line #2 has two *Rf* genes, the other three have only one gene for fertility restoration. The plant which showed highest fertility in line #2 was selfed and backcrossed to Chinese Spring. The line #2–S1 (F_3) is homozygous for the *Rf* genes and most of them showed more than 80% of selfed seed fertility. While, the B_1F_1 plants showed wide range in selfed seed fertility like in F_2.

These *Rf* genes of *T. macha* may be useful for breeding restorer lines against *tiompheevi* cytoplasm.

Acknowledgement

The author wishes to express his appreciation to Dr. K. TSUNEWAKI who kindly provided the strain NIG–2 used in the present investigation and read this manuscript critically. The author also thanks to Professor M. KAMANOI and Dr. T. SASAKUMA for their kind advices, discussions and supports.

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Catalogue of gene symbols for wheat, 1979 supplement

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Reprints of the original Catalogue (1973) and some of the Annual Supplements are available. A consolidation of the first five Annual Supplements will appear in the Proceedings of the Fifth International Wheat Genetics Symposium. Supplementary lists appear annually in Cereal Research Communications, Wheat Information Service and Wheat Newsletter.

Gross Morphology:

s1 3DL (127AA). Note that this location is not consistent with 212B.

Hairy Glume:

Hg 1AS (169E)

Hardness of Grain:

Ha (136B) s: CS (Cheyenne 5D) (159A);
: CS (Hope 5D) (136B) 5DS (136B)

The relationship of *Ha* to that described in 237B or those in 21A is unknown.

Chinese Spring genotype *ha*.

Pairing Homoeologous:

ph1a (301) v: Mutant 10/13 (301) 5BL (301)

ph1b v: Sears' High Pairing Mutant (243B) 5BL (243B)

ph2 v: Sears' Intermediate Pairing Mutant (243B)

Chinese Spring genotype *Ph1 Ph2*

Protein in Seeds:

Pro1 (136B) s: CS (Hope 5D) (136A) 5DL (136A)

Pro1 may be identical with *Vrn3* (136A)

Pro2 (136B) s: CS (Hope 5D) (136B) 5DS (136B)

Reaction to *Erysiphe graminis*:

Pm3a 1AS (169E)

Pm4a (278B) *Pm4* (30) 2AL (278A)

Pm4b (278B) *Mle* (315C) i: Federation*7/*T. carthlicum* W804 (278B) 2AL (19A, 278A)
v: ELS (315C); Maris Halberd; S–25 (19A);
S–28 (19A); TP–229 (106, 315C);
Weihenstephan M1 (315C).
Rang *Pm1* (19A).
Solo *Pm1** *Pm2* (19A)

* In Solo *Pm1* has been translocated from chromosome 7A to 7D (19A)

Pm7	v: Derivatives of Petuks rye-see *Yr10*	1B
Reaction to *Puccinia graminis*:		
Sr31	v: Derivatives of Petkus rye – see *Yr10*	1B
Sr32	v: *Triticum spelotides* derivatives produced by Dr. E.R. Sears.	2A
Reaction to *Puccinia recondita*:		
Lr22b	v: Canthatch, Thatcher.	2Dα
Lr26	v: Derivatives of Petkus rye – see *Yr10*	1B
Reaction to *Cochliobolus sativus*:		
	Disease: *Cochliobolus* root rot.	
Crr	approved for a recessive gene for resistance	5BL
Reaction to *Mayetiola destructor*:		
H3		5A (74A, 196A)
H6	v: Purdue 4835 A4–6 (196A)	5A (74A)

Genetic linkages:

1AS				
	Hg	– centromere	Independent	(169E)
	Pm3a	– 〃	〃	(169E)
2AL				
	Sr21	– centromere	2.4±0.9%	(278A)
	Pm4b	– centromere	Independent	(278A)
	Sr21	– *Pm4a*	37.5±1.7%	(278A)
2BL				
	Sr28	– centromere	34.6±2.8%	(162A)
	Sr28	– *Sr16* (or allele)	38.2±1.9%	(162A)
	〃	– 〃	29.2±4.2%	(162A)
	Sr*16* (or allele)	– centromere	Independent	(162A)
	〃	– *Sr9b*	〃	(162A)
	Lr23	– *Sr9b*	22.3±2.4%	(162A)
	〃	– 〃	24.1±2.2%	(162A)
	Lr23	– *Sr28*	28.5±2.8%	(162A)
	Sr9b	– *Sr28*	16.8±2.1%	(162A)
3DL				
	s1	– centromere	5.0±2.0%	(127AA)
	ch2	– centromere	36.1±4.0%	(127AA)

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Editorial Remarks

Announcement for Future Issues

WIS No. 50 (*25th Anniversary Number*) will be planned for publication in December 1979, possibly as a double page issue. Manuscripts for this issue are most welcome and accepted any time, not later than September 30, 1979.

WIS is open to all contributions regarding methods, materials and stocks, ideas and research results related to genetics, breeding and cytology of *Triticum*, *Aegiolops*, *Secale*, *Haynaldia* and related genera. Manuscripts should be typewriten in English, and submitted with duplicates. One article should not exceed five printed pages, including one textfigure (smaller than 7×7 cm^2). Lists of stocks are exempted from this page limit. Authors receive 50 reprints of their contributions free of charge. Extra copies are printed by order at cost price. Communications regarding editorial matters should be addressed to:

Kosuke YAMASHITA
Wheat Information Service,
Kihara Institute for Biological Research,
Mutsugawa 3–122, Minami-ku,
Yokohama 232, Japan

Membership Fee

Yearly Membership Fee has been raised up to ¥ 1,000 for foreign as well as Japanese members from the fiscal year beginning April 1978. The money should be paid by the Foreign Postal Money Order, otherwise considerable loss is caused due to the bank charges. Back numbers are available.

Acknowledgement

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The Managing Editor

Explanation of the Figure on the Cover

Cf. text figure in page 22 of an article by S. PETROVIĆ.

WIS No. 49

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