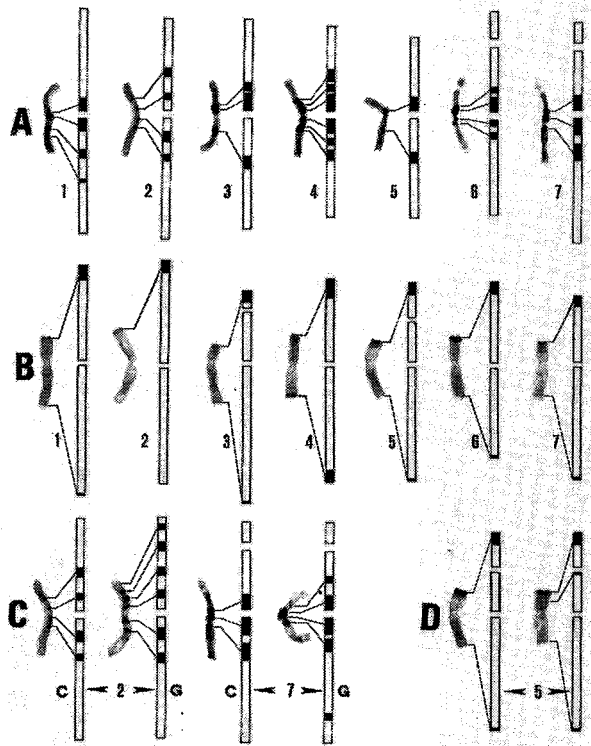


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I. Research Notes

Chromosome pairing in interspecific hybrids in genus *Aegilops*

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The purpose of this report is to communicate the observed amounts of chromosome pairing at metaphase I (MI) in hybrids obtained from several combinations of species in the genus *Aegilops*. Some of these hybrid combinations are reported for the first time; others have been reported previously but usually characterized only by ranges and modes of configurations instead of means.

Materials and Methods

Seed of the species used was obtained as indicated in Table 1 from the collections of the Plant Breeding Institute, Cambridge, England; Dept. of Plant Science, University of California, Riverside, USA; Agriculture Research Service, USDA, at the University of Missouri, Columbia, USA; and the USDA at Beltsville, Maryland, USA.

All plants were maintained and crosses were made under greenhouse conditions. Embryos were excised 14 days after pollination and cultured aseptically until the two-leaf stage on a modified (DVORÁK 1981) B5 medium. Spikes of hybrids were fixed in Carnoy's solution (6 : 3 : 1) and anthers were squashed in acetocamine. For each hybrid, pollen mother cells (PMCs) at MI were scored for chromosome configurations and these scores were averaged yielding a mean frequency per PMC for each configuration.

Genome symbols are those used by KIHARA (1982) except for U instead of C^u as proposed by CHENNAVEERAI AH (1960) and B instead of S as proposed by LÖVE (1982). The distinctness of the karyotype of *Ae. uniaristata* Vis. from that of *Ae. comosa* Sibth. et Smith (M genome) was noted by CHENNAVEERAI AH (1960) and its genome was given the symbol L by LÖVE (1982). This genome has been shown to be involved in the tetraploid species *Ae. ventricosa* Tausch by karyotype analysis (CHENNAVEERAI AH 1960), by synthesis of an amphiploid from a hybrid

Table 1. Source of accessions of *Aegilops* species used in crosses.

Species	Genome	Source
<i>Ae. longissima</i>	B	Cambridge, line A
<i>Ae. caudata</i>	C	Cambridge, line A
<i>Ae. umbellulata</i>	U	Cambridge, line A USDA, PI 776994 Riverside, G 629
<i>Ae. ventricosa</i>	DL	Cambridge, line A
<i>Ae. cylindrica</i>	CD	Cambridge, line A
<i>Ae. kotschyi</i>	BU	Riverside, G 813
<i>Ae. variabilis</i>	BU	Cambridge, line A
<i>Ae. triuncialis</i>	CU	Cambridge, line A
<i>Ae. geniculata</i>	MU	Riverside, G 418
<i>Ae. lorentii</i>	MU	Riverside, G 1013
<i>Ae. juvenalis</i>	DMU	Cambridge, line A
<i>Ae. recta</i>	MMU	Columbia, P 68-38-1 Cambridge, line A

between *Ae. tauschii* Coss. and *Ae. uniaristata* which resembled *Ae. ventricosa* (MATSUMOTO *et al.* 1957), and by chromosome pairing in a hybrid between *Ae. ventricosa* and *Ae. uniaristata* (KIMBER *et al.* 1983). Thus DL will be used here for the genomes of *Ae. ventricosa*.

Results and Discussion

The use of MI chromosome pairing data from hybrids for the purpose of genome analysis must accommodate two considerations. One is that a certain extent of relatedness exists between the chromosomes of any two genomes as a result of their descent from a diploid ancestor common to all taxa in the Triticeae. In this descent, chromosomes become differentiated structurally and nonstructurally from their ancestral homologues. There is evidence that nonstructural differentiation, presumably at the nucleotide sequence level, is the most important cause of the pairing failure observed in hybrids within species and between species (DVORÁK & MCGUIRE 1981; CROSSWAY & DVORÁK 1984; DVORÁK & CHEN 1984; KOTA *et al.* 1986). The other consideration is that most if not all polyploid *Aegilops* species possess an oppositional genetic system that regulates heterogenetic chromosome pairing to produce diploid-like, bivalent MI pairing in those species (MCGUIRE & DVORÁK 1982).

The single diploid hybrid reported here is *Ae. longissima* Schweinf. et Muschl. × *Ae. umbellulata* Zhuk (Table 2). A low level of pairing was observed with a mean of 2.00 bivalents, 0.36 trivalents, and 0.04 quadrivalents. KIHARA (1945) obtained a hybrid between these same two species and observed a similar level of pairing, reporting a range from zero to four bivalents with a mode of two, none of which were rings, and no or one trivalent. His conclusion, which the present data support, was that these two species do not have a common

Table 2. Observed pairing configuration frequencies in diploid, triploid and tetraploid hybrids.

Hybrid Combination	Genomes	No. of PMCs	Mean Chiasmata	Mean Observed Chromosome Pairing per PMC (Range)						
				Univ.	Rod biv.	Ring biv.	Triv.	Open quad.	Closed quad.	Quin.
<i>Aegilops longissima</i> × <i>Ae. umbellulata</i> G 629	BU	54	2.86 (0-7)	8.77 (4-14)	1.98 (0-4)	0.02 (0-1)	0.36 (0-3)	0.04 (0-1)	0.00 —	0.00 —
<i>Ae. ventricosa</i> × <i>Ae. umbellulata</i> G 629	DLU	32	3.66 (0-7)	14.09 (7-21)	2.94 (0-7)	0.00 —	0.22 (0-2)	0.09 (0-1)	0.00 —	0.00 —
<i>Ae. cylindrica</i> × <i>Ae. umbellulata</i> PI 776994	CDU	131	8.20 (1-14)	7.56 (2-15)	4.06 (1-8)	0.14 (0-2)	1.08 (0-4)	0.23 (0-2)	0.00 —	0.11* (0-2)
<i>Ae. kotschyi</i> × <i>Ae. umbellulata</i> A	BUU	53	10.28 (7-13)	7.42 (6-11)	2.91 (1-6)	2.62 (0-6)	0.02 (0-1)	0.24 (0-1)	0.34 (0-1)	0.02 (0-1)
<i>Ae. triuncialis</i> X <i>Ae. caudata</i>	CCU	37 36 33	10.82 11.57 10.51	5.65 5.10 5.79	3.65 3.06 3.67	2.68 2.89 2.39	0.86 1.11 1.03	0.03 0.17 0.00	0.00 0.00 0.00	0.00 0.00 0.00
<i>Ae. triuncialis</i> × <i>Ae. cylindrica</i>		Mean	10.97 (7-14)	5.51 (3-8)	3.46 (1-7)	2.65 (1-6)	1.00 (0-3)	0.07 (0-4)	0.00 —	0.00 —
<i>Ae. triuncialis</i> × <i>Ae. cylindrica</i>	CUCD	28	14.61 (11-18)	6.04 (2-11)	5.04 (2-7)	2.25 (0-4)	1.61 (0-4)	0.39 (0-2)	0.00 —	0.11** (0-1)

* Plus 0.03 (0-1) sexivalents, 0.03 (0-1) septivalents, and 0.03 (0-1) nonavalents.

** Plus 0.04 (0-1) septivalents.

genome.

Four triploid hybrids were obtained (Table 2). Three had been produced earlier by KIHARA (1937, 1945) and the fourth by KIMBER & ABU BAKAR (1981). For *Ae. ventricosa* × *Ae. umbellulata*, KIHARA (1937) reported a range from zero to five bivalents, with a mode of two, and no or one multivalent and concluded that the two species have no genome in common. The mean pairing reported here, 2.94 bivalents, 0.22 trivalents, 0.09 quadrivalents, is consistent with this conclusion. Two haploids of *Ae. ventricosa* (D and L genomes) were recently obtained by FEDAK (1983). Very little pairing with a mean of only 0.46 chiasmata per PMC was reported for the two plants. However, in the hybrid reported here, there was a chiasma frequency of 3.66. If as little pairing occurred between chromosomes of the D and L genomes in this hybrid as occurred in the haploid, then pairing in the hybrid must be between the chromosomes of the D and U genomes and the L and U genomes. This could account for the bivalents but not for the trivalents, as many as two of which were observed in some PMCs. A more likely explanation is that pairing was distributed equally among these three distinct genomes and that the extent was the result of promotion of heterogenetic pairing by this genotype of *Ae. umbellulata*.

For *Ae. cylindrica* Host × *Ae. umbellulata*, KIHARA (1937) reported ranges from six to eight bivalents, as many as two of which were rings, and zero to three multivalents. Reviewing this and other related data, KIHARA (1954) concluded that the U genome of *Ae. umbellulata* is a modified version of the C genome of *Ae. caudata* L. The pairing in this hybrid was assumed by KIHARA to be due to pairing between the chromosomes of the U and C genomes. However, the close relationship between these two genomes has been questioned by others (SEARS 1948; CHENNAVEERAI AH 1960) with recent analysis suggesting the two genomes are nonhomologous (KIMBER & ABU BAKAR 1981; MILLER 1981). The hybrid reported here had means of 4.20 bivalents, 1.08 trivalents, 0.23 quadrivalents, and 0.20 larger multivalents (Table 2).

The hybrid *Ae. kotschyi* Boiss. × *Ae. umbellulata* had an average of 5.53 bivalents, nearly three of which were rings, 0.02 trivalents, 0.58 quadrivalents, and 0.02 quinquevalents. The mean of 0.58 quadrivalents per PMC shows that the two U genomes differ by a translocation. KIMBER & ABU BAKAR (1981) earlier reported a hybrid between these two species which had similar pairing. However, they reported no quadrivalents which means that a polymorphism for a translocation must occur either in *Ae. umbellulata* or more likely in *Ae. kotschyi*. FURUTA (1981) has already shown the presence of such a polymorphism in his collections of *Ae. kotschyi*.

The karyotype of *Ae. umbellulata* has four markedly heterobrachial chromosomes (SENJANINOVA-KORCZAGINA 1932; CHENNAVEERAI AH 1960) that can be readily identified if they are involved in a multivalent configuration at MI. A heterobrachial chromosome was involved in only three of the thirty-three observed quadrivalents in *Ae. kotschyi* × *Ae. umbellulata*. Thus, the translocation does not involve any of the heterobrachial chromosomes of the U genome of *Ae. kotschyi*.

The fourth triploid hybrid, *Ae. triuncialis* L. × *Ae. caudata*, has an average chiasma

frequency similar to that of the previous hybrid and a mean of 6.11 bivalents, 1.00 trivalent, and 0.07 quadrivalents (Table 2). KIHARA (1945) reported for this hybrid combination a mode of seven bivalents, as many as six of which were rings, and zero to two multivalents. The pairing in a haploid reported by CHAPMAN & MILLER (1977), most likely derived from the same accession of *Ae. triuncialis* as that used here, indicates that at least two bivalents as well as a trivalent or quadrivalent in this hybrid may be accounted for by pairing between chromosomes of the U and C genomes. Even though KIHARA (1954) maintained that the C genome was present in an unmodified condition in *Ae. triuncialis*, there is evidence that modification has occurred. Both SENJANINOVA-KORCZAGINA (1932) and CHENNAVEERAI AH (1960) have shown that the karyotype of the presumed C genome in *Ae. triuncialis* is altered in some varieties. The pairing reported here for this triploid hybrid suggests that such modification has occurred in this accession of *Ae. triuncialis*.

The single tetraploid hybrid obtained was between *Ae. triuncialis* and *Ae. cylindrica*. Observed were an average of 7.29 bivalents, of which only 2.25 were rings, 1.16 trivalents, 0.39 quadrivalents, and 0.15 larger multivalents (Table 2). Higher bivalent frequencies were reported in earlier hybrids between these two species. PERCIVAL (1930) recorded a range from three to eleven bivalents of which five to six were rings. KIHARA & LILJENFELD (1932) reported zero to twelve bivalents with a mode of ten to eleven; three to six were rings. KAGAWA (1931, cited in KIHARA 1937) in the reciprocal combination reported six to eleven bivalents and no or one trivalent. The possible modification in the C genome of this accession of *Ae. triuncialis* discussed above could account for the apparent discrepancy between the pairing reported here for this tetraploid hybrid and that from earlier reports.

In the three pentaploid hybrid combinations, *Ae. recta* (Zhuk.) Chenn. was a common parent. The second parent in each case possessed the U genome in common with *Ae. recta*. Observed in *Ae. variabilis* Eig \times *Ae. recta* were means per PMC of 6.63 bivalents, 2.27 of which were rings, 1.19 trivalents, and 0.11 quadrivalents (Table 3). KIHARA (1945) reported seven to eleven bivalents, as many as four of which were rings, and zero to two multivalents. He concluded that the two species had only one genome (U) in common. The chromosomes of the B and U genomes were shown to be able to produce at least two bivalents in the diploid hybrid discussed above. This affinity may be reflected in this pentaploid by the frequencies of both rod bivalents and trivalents.

In addition to the U genome, the other pentaploid hybrid combinations supposedly have versions of the M genome in common. Evidence for this is indirect and in no case has an unmodified M genome from *Ae. comosa* been demonstrated in an *Aegilops* polyploid. In the case of *Ae. geniculata* Roth (= *Ae. ovata* auct.) evidence for a modified M genome is very indirect. In fact, the extent of pairing in hybrids of *Ae. geniculata* and *Ae. ventricosa* (e.g., KIHARA 1937) suggests that these two species have a genome in common, in which case the genome formula of *Ae. geniculata* should be LU. There is even less direct evidence for an M genome in *Ae. lorentii* Hoch. (= *Ae. biuncialis* Vis.). Based on karyotype analysis CHENNAVEERAI AH (1960) concluded that the second genome of *Ae. lorentii* might well be something other than a modified M.

Table 3. Observed pairing configuration frequencies in pentaploid, and hexaploid hybrids.

Hybrid Combination	Genomes	No. of PMCs	Mean Chiasmata	Mean Observed Chromosome Pairing per PMC (Range)						
				Univ.	Rod biv.	Ring biv.	Triv.	Open quad.	Closed quad.	Quin.
<i>Aegilops variabilis</i> × <i>Ae. recta</i> A	BUMMU	47	11.61 (5-16)	17.66 (12-22)	4.36 (1-8)	2.27 (0-3)	1.19 (0-3)	0.11 (0-1)	0.00	0.00
	MMUMU	10	15.80	12.00	5.70	3.40	1.20	0.30	0.00	0.00
		39	12.10	15.79	5.92	1.59	1.05	0.26	0.00	0.03
		24	15.57	11.25	6.75	3.29	1.04	0.08	0.00	0.04
<i>Ae. recta</i> P 68-38-1 × <i>Ae. lorenzii</i>	MMUM	Mean	14.55 (7-21)	13.01 (6-23)	6.12 (3-11)	2.76 (0-6)	1.10 (0-3)	0.21 (0-1)	0.00	0.02 (0-1)
		28	14.43	12.14	6.11	1.57	2.00	0.14	0.00	0.14*
		9	16.31	10.22	6.00	2.56	1.44	0.32	0.00	0.33
	12	14.17	13.17	5.58	2.00	1.92	0.25	0.00	0.00	0.00
<i>Ae. juvenalis</i> × <i>Ae. recta</i> A	DMUMMU	Mean	14.88 (9-20)	11.88 (7-19)	5.90 (2-10)	2.04 (0-4)	1.79 (0-4)	0.24 (0-2)	0.00	0.15** (0-1)
		27	14.25	19.19	5.59	1.19	2.48	0.44	0.00	0.00
		21	12.69	20.90	6.57	1.14	1.71	0.14	0.00	0.00
	Mean	13.47 (8-21)	20.05 (14-28)	6.08 (2-9)	1.17 (0-4)	2.10 (0-4)	0.29 (0-3)	0.00	0.00	0.00

* Plus 0.04 sexivalents.

** Plus 0.01 (0-1) sexivalents.

Aegilops recta × *Ae. geniculata* hybrids have not been reported before. The three plants reported here had means of 8.88 bivalents, 2.76 of which were rings, 1.10 trivalents, 0.21 open quadrivalents, and 0.02 quinquevalents (Table 3). In the *Ae. recta* × *Ae. lorentii* hybrids, means of 7.94 bivalents, 2.04 of which were rings, 1.79 trivalents, 0.24 open quadrivalents, 0.15 quinquevalents, and 0.01 sexivalents were observed (Table 3). KIHARA (1945) reported two hybrids from this parental combination. One had about nine bivalents, as many as five of which were rings, and some trivalents and quadrivalents. The other had a range of six to eleven bivalents, many of which were rings, and an occasional quinquevalent. These results for these two hybrid combinations provide evidence for no more than one genome in common in each case as was found for the *Ae. variabilis* × *Ae. recta* combination just discussed. In conjunction with the karyotypic evidence of CHENNAVEERAI AH (1960), this must be the U genome. Thus, the identity of the non-U genomes in these polyploids is questionable.

The hexaploid hybrid, *Ae. juvenalis* (Thell.) Eig × *Ae. recta*, is also a combination reported for the first time. In the two plants there were combined means per PMC of 7.25 bivalents, with 1.17 rings, 2.10 trivalents, and 0.29 quadrivalents. On the basis of these data, especially the low frequency of ring bivalents, one might question if one genome could be considered common to both species. However, other evidence has shown the presence of the U genome in both *Ae. juvenalis* (MCGINNIS 1956; KIHARA 1963; KIMBER & ABU 1981) and *Ae. recta* (KIHARA 1937, 1957).

None of the data suggested any definitive changes in the current understanding of the identity of the component genomes of the polyploid taxa considered here. However, there is enough uncertainty in the cases of the polyploid species that presumably have modified M genomes to warrant some direct genome analytical work particularly with the diploid species *Ae. comosa* and *Ae. uniaristata* as testers as was done recently with *Ae. uniaristata* and *Ae. ventricosa* (KIMBER *et al.* 1983). In the cases here where comparisons could be made with earlier hybrids, the discrepancies underscored the need for wider sampling within species to assess the extent of genome modification and of genetic variability for the regulation of heterogenetic pairing. In addition, the level of pairing in the *Ae. ventricosa* × *Ae. umbellulata* hybrid plant when compared with pairing reported in haploids of *Ae. ventricosa* (FEDAK 1983) suggested promotion of heterogenetic pairing by *Ae. umbellulata*.

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Giemsa C-banding karyotype identification of two *Hordeum vulgare* cultivars and one *Agropyron* species grown in Greece

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Chromosome morphology of common barley (*Hordeum vulgare* L.) has for long been studied both by conventional cytological and cytogenetical methods, as well as by C-banding techniques. Undoubtedly, the Giemsa C-banding procedure applied by LINDE-LAURSEN firstly in "Emir" barley and subsequently in a great number of barley lines and varieties (LINDE-LAURSEN 1975, 1978; LINDE-LAURSEN *et al.* 1982), by VOSA (1976) in ten distinct cultivars and, more recently by FINCH & BENNETT (1982) in TULEEN 346 barley, provided new and more definite insights towards identifying the particular members of the genome.

However, the problem has not as yet been thoroughly solved since the barley chromosome complement has always presented some ambiguous features due to: 1) The overlapping of chromosome parameters (relative length and arm ratio) manifested by the majority of genomic members (1 to 4), 2) subsequent chromosome rearrangements such as interchanges likely to occur in the numerous cultivars, and 3) the distribution pattern of heterochromatin resulting in C-banding polymorphism. That is why the normal, standard karyotype first designated by TJIO & HAGBER (1951) and substantially retained up to the present, has at times undergone partial revisions (TULEEN 1973; NODA & KASHA 1978, LINDE-LAURSEN 1978; COUCOLI *et al.* 1981) according to information obtained by using a broader spectrum of materials and new modifications of techniques. This study was undertaken to clarify the forementioned problems.

Materials and Methods

The two-rowed barley varieties used, namely CARINA and GEORGIA (GEORGIE) were introduced from West Germany (1972) and England (1974) respectively. CARINA's parental origin is Union x (WV x Viola) and GEORGIA's Vada x Zephyr. Both varieties have been successfully cultivated in Greece for more than ten years. The seed material was kindly provided by the Institute of Cereals (Thessaloniki, Greece). *Agropyron striatulum* material was collected from littoral Greek biotopes and voucher specimens are being retained at our Department of Botany (MOUSTAKAS & COUCOLI 1982).

Microscopic C-banding slides were prepared and the establishment of the corresponding karyotypes was made on mitotic metaphase cells of root-tips. The C-banding technique used was the one described by LINDE-LAURSEN (1975). In our studies we used mainly Leishman stain and partially Giemsa stain with some other minor modifications. The

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technique used for *Agropyron* was the one described by GUSTAFSON *et al.* (1976).

Fifteen complete metaphases from ten roots in average were studied in all three materials. C-banding positions were measured from photographs at least in 5 chromosomes per member-type and the mean positions were inserted on the corresponding idiograms as they were established from Feulgen preparations in GEORGIA barley (COUCOLI *et al.* 1980) and in *Agropyron striatulum* (MOUSTAKAS & COUCOLI 1982).

Results and Discussion

A. C-banding patterns of *Hordeum vulgare* CARINA

Numbering order of chromosomes was put according to the standard karyotype (TJIO & HAGBERG and subsequent workers). The C-banding pattern appears in Fig. 1A.

Chromosome 1. Each arm shows a centromeric band of equal size. In addition the long arm has two interstitial bands.

Chrom. 2. Both arms lack precise centromeric bands, yet each of them shows two bands in the corresponding proximal regions, the one quite near the centromere (pericentric).

Chrom. 3. Three bands were totally observed. Two of them were on the short arm, the one centromeric and larger. The position of the one band observed on the long arm was almost median.

Chrom. 4. It is a heavily banded chromosome, with three bands on each arm. The two centromeric bands appeared very large with the largest one on the short arm.

Chrom. 5. There was found evident difference between the two arms in banding pattern. The short arm (the shortest in the barley chromosome complement) showed a large centromeric band. The long arm possessed an almost medium-sized interstitial band.

Chrom. 6. Each arm is characterized by the presence of two bands, the one centromeric (very large on the short arm relatively small on the long one), and the second almost pericentric.

Chrom. 7. There were observed two large centromeric bands the larger on the long arm. The same arm possesses another evident band, rather proximal.

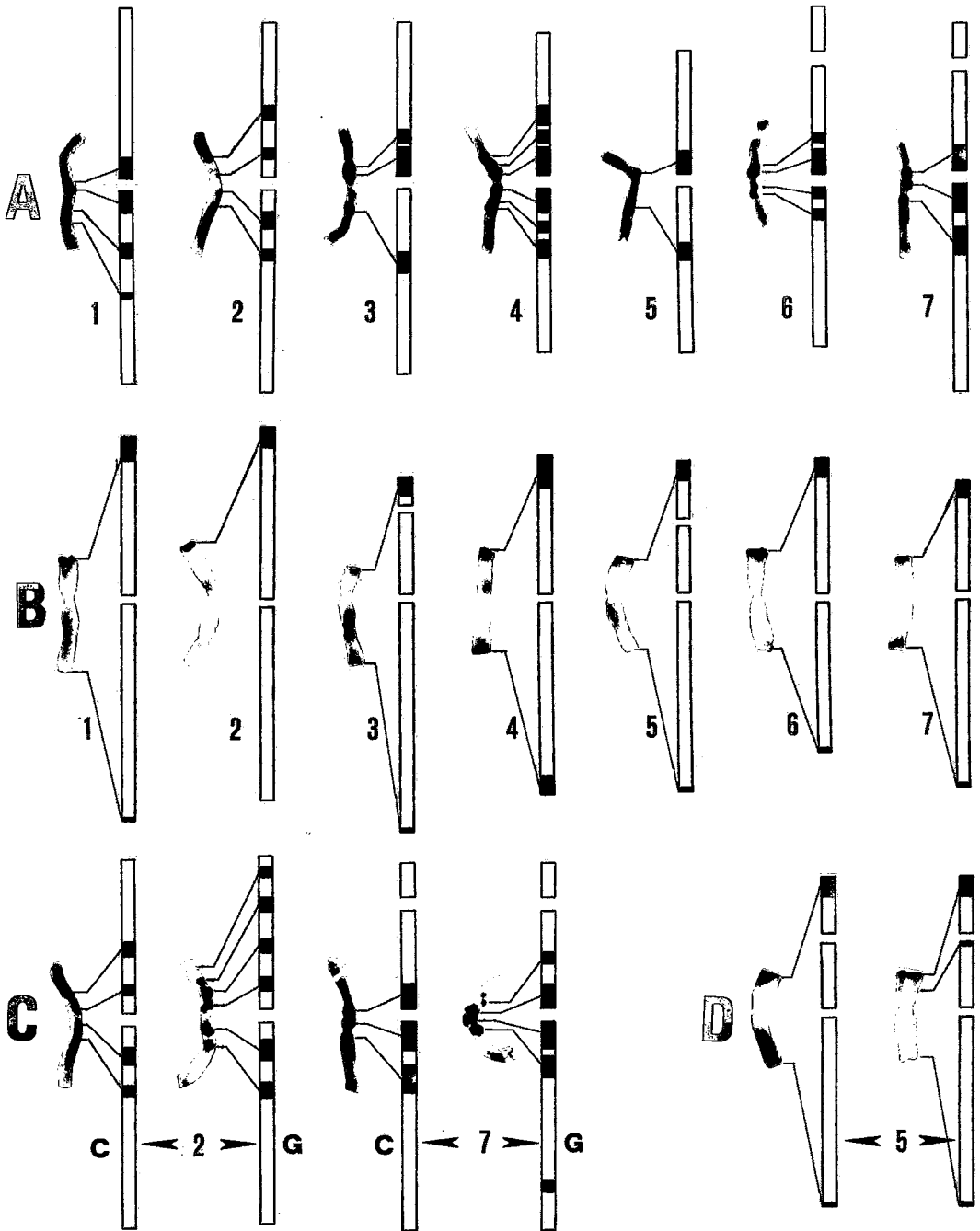
B. C-banding pattern of *Hordeum vulgare* GEORGIA

The basic banding pattern appeared to be the same with that of CARINA apart from chromosomes 2 and 7 (Fig. 1C).

In detail: On chromosome 2, two more bands were found, lying at the distal region of the short arm equilocally distributed. On chromosome 7, two additional bands, one per arm, were recognized. More concretely, on the short arm (the satellited) was observed a median-

Fig. 1. Chromosome idiograms

- A. Idiogram of the chromosomes of *H. vulgare* "CARINA" showing sizes and positions of the C-bands (Leishman stain)
- B. Idiogram of the chromosomes of *Agropyron striatulum* showing relative sizes and positions of C-bands (Leishman stain)
- C. C-banding pattern variants of chromosomes 2 and 7 of the barley varieties "CARINA" and "GEORGIA".
- D. C-banding pattern variants of chromosome 5 of *Agropyron striatulum*.



positioned band, fairly narrow, whereas on the long arm a narrow band was also detected, at very distal region. Thus, band polymorphism recognized on chromosomes 2 and 7 resulted in two banding pattern variants, not included in the polymorphic types presented by LINDE-LAURSEN *et al.* (1982). Comparatively with his results chromosome 7 variant observed by us could be attributed to a possible exchange of the long armed distal parts between chromosome 5 and chromosome 7. This suggestion of course, could be thoroughly verified only by meiotic studies.

Summarizing the above, the following conclusions could be drawn. 1) The majority of C-bands recognized in both varieties were centromeric or interstitial, the interstitial ones mostly proximal than distal. No telomeric bands were found at all. 2) In both varieties each chromosome of the complement showed a distinct C-banding pattern, allowing precise identification. 3) Each variety represents a single C-banded karyotype without evidence of major intravarietal polymorphism. 4) At the intervarietal level, the detected polymorphism seems to reflect the parental origin of the respective varieties. Thus CARINA barley including the genome of UNION (VOSA 1976) proved to be less banded, fitting partially the pattern provided by VOSA in TIBET and by NODA & KASHA (1978) in BETZES (paucity of conspicuous distally located or telomeric bands). GEORGIA a more banded modern cross-bred variety, showed some differences by comparing our results with those presented by LINDE-LAURSEN *et al.* (1982) in the same variety (different source and parallel breeding). The concrete differences regard 1) presence of bands at the secondary constrictions of chromosomes 6 and 7 (absent in our material) and 2) presence in general of telomeric bands (completely absent according to our data). The contradicting results forced us to examine the situation of a differential expression of the constitutive heterochromatic regions according to the application of different stains. Therefore we found out that when Giemsa stain was used instead of Leishman the disputable zones could be detected. The same holds for TULEEN's 346 barley (complete absence of telomeric C-bands in Leishman-stained chromosomes) as manifested by FINCH & BENNETT (1982).

C. C-banding patterns of *Agropyron striatum*

We report only preliminary results, that is one banding karyotype established by handling plants from two populations collected. The conventional karyogrammic phenotype suggested by MOUSTAKAS & COUCOLI (1982) represents a rather symmetrical chromosomal set with median or submedian members, including two satellited chromosomes (the one with ST centromere).

The C-banded karyotype (Fig. 1B) showed a uniform characteristic pattern, with rather gross telomeric bands, and complete absence of centromeric heterochromatic segments. The majority of chromosomes (1, 3, 4, 5, 6, 7) manifested telomeric bands in both arms, those observed in the short arms being evidently larger. Chromosome 5 in particular showed an additional satellited band exclusively in the material of one population. In both populations, we observed cells heteromorphic for chromosome 2. This means that one of the homologues in these cells was bandless.

Obviously, the "banding style" observed in *Agropyron* characterized of conspicuous

telomeric bands, irrespectively of the staining technique used, fits the typical pattern found in other cross-fertilizers, as Rye, *Ae speltooides*, maize (LINDE-LAURSEN 1978). Though the subject has not as yet been experimentally investigated, it seems likely that the clear opposite results observed so far in banding patterns between in- and outbreeders could be associated with chiasma frequency reported as higher in inbreeding systems (MACKEY 1970).

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A novel behavior of a ring chromosome in common wheat

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The ring chromosome produced by the free end fusion following the chromosome breakages is reported in several eukaryotes, *e.g.*, human, *Drosophila* and maize. In wheat, FRANKEL (1949) first reported a ring chromosome and proposed a mechanism of its production. The very unique behavior of a ring chromosome in somatic division was called the breakage-fusion-bridge cycle by McCLINTOCK (1941). She observed in maize, chromosome bridges formed by a ring chromosome in anaphase that produced two ring chromosomes of different sizes after breakage of the bridges and reunion of the free ends.

The author found a plant having a ring chromosome in the self-pollinated progeny of a monosomic plant of common wheat. The behavior of this ring chromosome, different from that reported by McCLINTOCK (1941), is described in this paper.

Materials and Methods

Monosomic series of a common wheat, *Triticum aestivum* (L.) Thell. cv. Chinese Spring produced by SEARS (1954) was provided by Dr. K. NISHIKAWA, Gifu University, Japan. A plant having the ring chromosome was found in the selfed progeny of mono-4B. Root tips of this plant and its progeny, which were pretreated in cold water (0°C) for 24 hrs, were fixed in 1:3 acetic alcohol. Acetocarmine squash method was applied for the cytological observation of their mitosis.

Results

In the routine work of chromosome checking for maintenance of monosomic series, a plant carrying 40 meta- or submetacentric and one ring chromosome, *i.e.*, $2n = 40 + 1^{\text{ring}}$, was obtained in a self-pollinated progeny of mono-4B (Fig. 1A). Morphology of this plant was similar to that of nulli-4B, by having short and slender culms with narrow leaves, and small and compact spikes with short awns due to deficiency of the *Hd* gene on the chromosome 4B. The plant was semi-sterile.

Karyotypes of ten plants in the self-pollinated progeny of this plant were observed. One, six and two plants carried 42, 41 and 40 meta- or submetacentric chromosomes, respectively. Only one plant had ring chromosomes in some cells. Two root tips of this plant were available for observation. In one root tip, 16 cells were observed, which had only 41 rod chromosomes in total. In the other root tip, 21 cells were observed, 17 of which carried one ring and 40 rod-shaped chromosomes. The remaining four cells had no ring but 41 rod chromosomes. No size difference was found among the ring chromosomes. The rod



Fig. 1. Root-tip mitoses of a plant carrying a ring chromosome that was found in the progeny of mono-4B.

A: Metaphase showing a ring chromosome. B: Anaphase showing O-shaped double size ring chromosome. C: Anaphase showing 8-shaped double size ring chromosome (Ring chromosome and bridges are indicated by arrow).

chromosomes did not show any visible aberration, and no telosomes or dicentric chromosomes were observed. Among 16 anaphase or telophase cells observed, 14 showed 1:1 separation of the equal-sized ring chromosomes, whereas two had chromosome bridges. Fig. 1B and C show two anaphase cells in which a double-sized ring chromosome formed bridges; one of them was elongated O-shaped and the other 8-shaped.

A single plant carrying 42 rod-shaped chromosomes derived from the original ring-chromosome carrier died before heading. Its sib plants having 41 rod-shaped chromosomes were similar to nulli-4B in morphology, like the parental ring-chromosome carrier.

Discussion

According to McCLINTOCK (1941), a dicentric, double-sized ring chromosome produced by sister chromatid exchange between replicated ring chromosomes forms chromosome bridges in mitotic anaphase. These bridges are broken and the resulted chromosomes produce new ring chromosomes by the fusion between active, free chromosome ends. The ring chromosomes successively produce new ring chromosomes of different sizes by the breakage-fusion-bridge cycle. TSUNEWAKI (1959) observed this cycle in *Agropyron glaucum*, a related species of wheat. TSUJIMOTO & TSUNEWAKI (1985) found ring chromosomes in the offspring of the gametocidal-gene carriers of common wheat, which also changed their size during successive root-tip mitoses.

Behavior of the present ring chromosome found in the offspring of mono-4B differed from those reported in the above cases. Although the present ring chromosome formed bridges in mitotic anaphase and was broken, the resulted rod-shaped chromosomes seemed not to produce new ring chromosomes by the fusion of broken chromosome ends. Occurrence of plants or cells carrying only the rod-shaped chromosomes in the offspring of the ring-chromosome carrier supports it.

The facts that the broken chromosome ends do not fuse and that no aberrant chromosomes are produced may indicate that the present ring chromosome has a point at which the chromosome breaks preferentially and the resulting free ends heal before fusion takes place.

Awnedness of this line shows deletion of a chromosome segment carrying the *Hd* gene that locates very close to the centromere ($7.7 \pm 3.7\%$, RAO 1981). Thus, the present ring chromosome seems to lack most part of the short arm of chromosome 4B. In fact, the ring-chromosome carrier and monosomic plants derived from it had a morphology similar to nulli-4B.

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Interactions between chromosome 1D of common wheat and *Aegilops uniaristata* cytoplasm

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By biological and biochemical investigations, all the cytoplasm of *Triticum* and *Aegilops* species were classified into 16 plasma types (TSUNEWAKI & TSUJIMOTO 1984). According to this classification, cytoplasm of *Ae. uniaristata* belongs to the plasma type M^u. This cytoplasm causes complete male sterility in three of the 12 common wheats which were used as the nucleus donor to the alloplasmic lines, but no alterations of the other morphological and physiological characters. The male sterility manifested in the three lines is controlled by a fertility-restoring gene, *Rfm1*, on the short arm of chromosome 1B (MUKAI 1983). In this paper we report a gene(s) on chromosome 1D that suppresses the seed shriveling of the alloplasmic lines having the *Ae. uniaristata* cytoplasm.

Materials and Methods

An alloplasmic line of common wheat cultivar Chinese Spring carrying *Aegilops uniaristata* cytoplasm was used in the present investigation. This line, abbreviated (*uniaristata*)-CS, was produced by more than four backcrosses of normal Chinese Spring (CS) as recurrent male parent to (*uniaristata*)-Selkirk produced by MAAN (1977). Ditelocentrics and nullitetrasonics (SEARS 1965, SEARS & SEARS 1978) of the first homoeologous-group chromosomes were used in the aneuploid analysis of the suppressor of seed shriveling caused by this cytoplasm. The cross combinations for the production of the alloplasmic aneuploid lines are mentioned in "Results and Discussion".

Pollen grains from anthers in the anthesis stage were mounted on microslides in a mixture (1:1) of acetocarmine and glycerine. Pollen fertility was estimated by the percent of fertile pollen grains having three developed nuclei. Selfed seed fertility was determined by recording the percentage of seed set in the first and second florets of spikelets of bagged spikes. The basal and apical spikelets were excluded from the determination.

Chromosome constitution in root tip cells and configuration in pollen mother cells were observed by usual acetocarmine squash and smear method, respectively.

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Table 1. Pollen and selfed-seed fertility (%) of disomic and aneuploid lines of *Triticum aestivum* cv. Chinese Spring having *Ae. uniariistata* cytoplasm.

Line	Chromosome constitution	Meiotic chromosome configuration	No. of plants exam.	Pollen fertility	Selfed seed fertility	% Shriveled seeds*
Disomic	42	21 ⁿ	3	98.7	93.1	0.0
Mono-tri 1B-1D	42	19 ⁿ +1 ^r (1B)+1 ^m (1D)	5	44.5	15.1	0.0
Monotelodi-1BL	41+t ¹	20 ⁿ +t1 ^m (1B-1BL)	5	60.0	36.5	0.0
Monotelodi-1BS	41+t ^s	20 ⁿ +t1 ^m (1B+1BS)	5	93.5	90.6	0.0
Mono-tri 1D-1A	42	19 ⁿ +1 ^r (1D)+1 ^m (1A)	4	50.2	72.7	59.1
Mono-tri 1D-1B	42	19 ⁿ +1 ^r (1D)+1 ^m (1B)	5	56.7	90.0	69.0
Mono-1D	41	20 ⁿ +1 ^r (1D)	3	52.1	54.9	62.8
Monotelodi-1DL	41+t ¹	20 ⁿ +t1 ^m (1D-1DL)	4	97.9	91.6	0.0
Monotelomono-1DL	40+t ¹	20 ⁿ +t ¹ (1DL)	2	46.1	30.2	70.0
Monotelomono-tri 1DL-1A	41+t ¹	19 ⁿ +t ¹ (1DL)+1 ^m (1A)	3	53.3	36.0	63.0
Monotelodi-tri 1DL-1A	42+t ¹	19 ⁿ +t1 ^m (1D-1DL)+1 ^m (1A)	1	95.1	93.5	0.0
Mono-tetra 1D-1A	43	19 ⁿ +1 ^r (1D)+1 ^m (1A)	1	47.9	41.9	72.0
Monotelodi-1DS	41+t ^s	20 ⁿ +t1 ^m (1D-1DS)	1	54.5	87.1	65.4

* Shriveled but viable seeds.

Results and Discussion

Fertility and seed shriveling of alloplasmic aneuploids carrying *Ae. uniaristata* cytoplasm

By crosses between (*uniaristata*)-CS as female and nulli-tetrasomic 1B-1D, 1D-1A and 1D-1B, alloplasmic mono-trisomic 1B-1D, 1D-1A and 1D-1B were produced. These mono-trisomics were self-pollinated or crossed as female to normal CS and ditelocentric 1BL, 1BS, 1DL and 1DS, and the various alloplasmic aneuploid lines listed in Table 1 were obtained. Chromosome constitution, meiotic chromosome configuration, and pollen and selfed seed fertility of the alloplasmic aneuploid lines are shown in Table 1.

The alloplasmic aneuploid lines having the short arm of chromosome 1B in the hemizygous state, *i.e.*, mono-trisomic 1B-1D and monotelodisomic 1BL, show low pollen and selfed seed fertility (Table 1). This finding supports a previous report (MUKAI 1983) that a major fertility-restoring gene, *Rfun1*, is located on the short arm of chromosome 1B. The lines having the long arm of chromosome 1D in the hemizygous state also show low pollen and seed fertility except selfed seed fertility of mono-trisomic 1D-1B and monotelodisomic 1DS. The remarkable point for these lines, is the production of many shriveled seeds by selfing (Table 1). On the contrary, no shriveled seed was produced by the hemizygotes of 1BS as well as 1BL or 1DS. These findings indicate that a gene(s) controlling seed shriveling is located on the long arm of chromosome 1D.

Chromosome constitution of the plants derived from the shriveled seeds

Table 2 shows the chromosome constitution of plants derived from the shriveled and plump seeds obtained by the self-pollination of alloplasmic monosomic 1D and monotelodisomic 1DS. The chromosome constitution is closely related to the seed morphology: All the plants derived from the shriveled seeds except one lacked a long arm of chromosome 1D, *i.e.*, they were monosomic 1D or monotelodisomic 1DS, whereas all plants from plump seeds except one had normal 42 chromosomes. This indicates that female gametes lacking chromosome arm 1DL produce shriveled seeds after fertilization. In other words, the long arm of chromosome 1D has a gene(s) that suppresses gametophytically seed shriveling caused

Table 2. Chromosome constitutions of the self-pollinated offspring of alloplasmic monosomic 1D and monotelodisomic 1DS having *Ae. uniaristata* cytoplasm.

Line	Seed morphology	No. of plants obs.	Chromosome constitution		
			41	41+t*	42
Mono-1D	Plump	12	1	0	11
	Shriveled	12	12	0	0
Monotelodi-1DS	Plump	12	0	0	12
	Shriveled	12	7*	4	1

* Including one plant having an acrosome carrying a satellite which is different from chromosome arm 1DS.

by the *Ae. uniaristata* cytoplasm. Shriveling of the seed from which the former exceptional plant having 42 chromosomes was obtained should have been due to some other cause than the deletion of 1DL arm. The latter exceptional plant having 41 chromosome which was produced from a plump seed seems to have a shifted monosome.

No plants lacking a pair of chromosome arm 1DL, *i.e.*, nullisomic 1D or ditelocentric 1DS were obtained. This suggests that pollen grains lacking 1DL become sterile. Low pollen fertility of the hemizygotes for chromosome arm 1DL supports it. Occurrence of monosomics in the progeny of the monotelodisomic 1DS must be attributed to univalent elimination following the partial asynapsis between chromosome 1D and telosome 1DS.

The present seed shriveling manifested by the combination of *Ae. uniaristata* cytoplasm and absence of chromosome 1D can be used for screening monosomic 1D without cytological observation.

Relationship between Rfun1 for fertility restoration on chromosome 1B and suppressor for seed shriveling on chromosome 1D

MAAN (1978) reported that an *Ae. uniaristata* chromosome was transmitted preferentially through recurrent backcrosses which were made in order to produce alloplasmic *durum* wheat having *Ae. uniaristata* cytoplasm, because the seeds not carrying this chromosome ($2n=28$) became shriveled and inviable. The shriveled seeds in the present study had viability in contrast to MAAN's results because they have a long arm of chromosome arm 1D transmitted from the pollen.

The short arm of chromosome 1B where *Rfun1* is located has fertility-restoring genes for many other cytoplasm: *Rf3*, *Rfu1*, *Rfv1*, *Rfo2* and *Rfm1* for G, C^u, S^v, M^o and Mt type cytoplasm, respectively (TAHIR & TSUNEWAKI 1969; TSUNEWAKI 1974; MUKAI & TSUNEWAKI 1979; TSUNEWAKI 1982; TSUJIMOTO & TSUNEWAKI 1984). The long arm of chromosome 1D has a gene for microgametophytic viability against the *Ae. squarrosa* cytoplasm, which was designated *Mgv* by TSUJI & KOKA (1983). Combining this and the above-mentioned MAAN's (1978) results, seed shriveling seems to be caused by the absence of *Mgv* in the egg cell having the *Ae. uniaristata* cytoplasm.

The results of isozyme and seed protein studies revealed that the short arm of chromosome 1B is homoeologous to the short arm of chromosome 1D (PAYNE *et al.* 1982; CHOJECKI & GALE 1982). Consequently, *Rf* genes on chromosome arm 1BS and *Mgv* on 1DL can not be homoeologous with each other although both suppress the inviability caused by some *Aegilops* cytoplasm. Hence, it is reasonable to distinguish the *Mgv* gene from *Rf* genes.

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Induction of chlorophyll and viable mutations in *Triticum aestivum* L.

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The main object of mutation breeding are (i) to enhance the frequency of mutations and (ii) to increase the mutation spectrum. Many reports on the induction of macromutations in diploid species have been presented earlier (AASTVEIT 1968; NILAN *et al.* 1977; TIWARI & SISODIA 1981), on the contrary, with polyploid species only comparatively few experiments have been conducted (LARIK & AL-SAHEAL 1986; WASHINGTON & SEARS 1970). With the use of chemical mutagens all sorts of chlorophyll mutations are obtained which helped in further understading of genetics of chlorophyll development.

The present study deals with the frequency of chlorophyll and viable mutations induced by EMS in two bread wheat cultivars extensively grown in Saudi Arabia.

Material and Methods

Dormant seeds of two hexaploid bread wheat cultivars namely ; Al-Samma and Maaya were presoaked in distilled water for 20 h, treated with freshly prepared 0.2%, 0.4% and 0.6% EMS solution for 7 h and 9 h duration at a constant room temperature $20 \pm 1^\circ\text{C}$. The EMS solutions were prepared using standard phosphate buffer of pH 7. The treated seeds, after thorough washing in running tap water for 30 min, were grrown in pots in replicates to obtain M_1 generation. All M_1 plants were harvested individually and M_2 generation was raised as row progenies. M_2 population was carefully screened for both chlorophyll and viable mutations throughout the life span of the crop.

Results and Discussion

The chlorophyll mutations in M_2 generation have been proved to be most dependable indices for evaluating the genetic effect of mutagenic treatments (TSUKUDA *et al.* 1977; TIWARI & SISODIA 1981). In present study mutation frequency was calculated in terms of (i) percentage of families segregating for mutations and (ii) percentage of mutant plants in M_2 population. Chlorophyll mutation frequency is summerized in Table 1. The highest and the lowest chlorophyll mutation frequency was observed under EMS 0.6% with 9 h and EMS 0.2% with 7h duration which was 23.53% and 13.63% on the basis of M_1 segregating families and 5.22% and 2.9% on the basis of M_2 population, recorded in cultivars Al-Samma and Maaya respectively. Four types of chlorophyll mutations were observed in the following order chlorina>tip-xantha>viridis > xantha. No chlorophyll mutants were observed in control. The chlorophyll mutations chlorina and viridis induced in hexaploid wheat with

Table 1. Frequency of chlorophyll mutations in M_2 generation of two hexaploid wheat cultivars following EMS-treatment.

Cultivar/ Treatment	Number of M_1 progenies	Number of M_2 plants	Chlorophyll mutations			
			Number of fam- ilies seg- regating	Number of muta- tions	Frequency	
					% segre- gating M_1 families	% of mutation in M_2 popula- tion
Al-Samma (Control)	50	280	—	—	—	—
EMS 0.2% 7 h dur.	50	270	7	8	14.00	2.96
EMS 0.2% 9 h dur.	38	265	8	9	21.05	3.39
EMS 0.4% 7 h dur.	40	258	7	10	17.50	3.87
EMS 0.4% 9 h dur.	35	248	6	8	17.14	3.22
EMS 0.6% 7 h dur.	30	240	5	9	16.66	3.75
EMS 0.6% 9 h dur.	34	230	8	12	23.53	5.21
Maaya (Control)	50	250	—	—	—	—
EMS 0.2% 7 h dur.	44	240	6	7	13.63	2.91
EMS 0.2% 9 h dur.	36	232	5	7	13.88	3.01
EMS 0.4% 7 h dur.	34	238	5	6	14.70	2.52
EMS 0.4% 9 h dur.	38	240	5	6	13.15	2.50
EMS 0.6% 7 h dur.	35	236	6	6	17.14	2.54
EMS 0.6% 9 h dur.	36	230	6	7	16.66	3.04

EMS are assumed to be point mutations rather than deficiencies. Evidence for this is found earlier (SHAMA RAO & SEARS 1964; WASHINGTON & SEARS 1970).

The frequency of viable mutations with respect to various populations is depicted in Table 2. The highest frequency of viable mutations was observed in cultivar Al-Samma under EMS 0.6% with 9 h duration, 41.17% on the basis of M_1 segregating families and 13.04% on the basis of M_2 population. The same cultivar displayed lowest frequency of viable mutations under EMS 0.2% with 7 h duration on the basis of M_1 segregating families, whereas the lowest frequency of viable mutations on the basis of M_2 population was shown by cultivar Maaya under EMS 0.2% with 9 h duration. Resistance of Maaya and sensitivity of Al-Samma in terms of recovery of viable mutations could partly be on account of their inherent genetic property. Such varietal differences in mutation yielding ability as been reported by LARIK (1985). Already there exists much evidence that genetic differences, even though they are as small as single gene difference, can produce significant changes in mutation expression (LARIK *et al.* 1984; LARIK & AL-SAHEAL 1986).

The spectrum of chlorophyll mutations show that some mutations like chlorina, tip-xantha, viridis and xantha are found relatively in sufficient number after EMS treatment. It is known that in hexaploid wheat many traits are controlled by triplicate genes. The fact that none of the nullisomics of hexaploid wheat is deficient in chlorophyll suggests that the chlorophyll development in this plant is controlled by several unlinked genes (SWAMINATHAN *et al.* 1962; WASHINGTON & SEARS 1970). This means that the induction of high rates of chlorophyll mutations might have been a multimutational event, or simultaneous deletion of

Table 2. Frequency of viable mutations in M_2 generation of two hexaploid wheat cultivars following EMS-treatment.

Cultivar/ Treatment	Number of M_1 progenies	Number of M_2 plants	Viable mutations			
			Number of fami- lies seg- regating	Number of muta- tions	Frequency	
					% serge- gating M_1 families	% of mutation in M_2 popula- tion
Al-Samma (Control)	50	280	—	—	—	—
EMS 0.2% 7 h dur.	50	270	9	15	18.00	5.55
EMS 0.2% 9 h dur.	38	265	10	25	26.31	9.43
EMS 0.4% 7 h dur.	40	258	8	16	20.00	6.20
EMS 0.4% 9 h dur.	35	248	9	20	25.71	8.06
EMS 0.6% 7 h dur.	30	240	7	18	23.33	7.50
EMS 0.6% 9 h dur.	34	230	14	30	47.17	13.04
Maaya (Control)	50	250	—	—	—	—
EMS 0.2% 7 h dur.	44	240	8	12	18.18	5.00
EMS 0.2% 9 h dur.	36	232	7	10	19.44	4.31
EMS 0.4% 7 h dur.	34	238	9	14	26.47	5.88
EMS 0.4% 9 h dur.	38	240	7	9	18.42	3.75
EMS 0.6% 7 h dur.	35	236	9	14	25.71	5.93
EMS 0.6% 9 h dur.	36	230	9	16	25.00	6.95

at least two different loci on homoeologous chromosomes, or some special phenomenon is involved due to specific action of the EMS. The experience in mutagenesis has shown the multimutations are frequently induced but are usually those involving the linked genes, or some cases pleiotropy may give an impression of multimutational event. Hence the possibility of simultaneous mutation of many unlinked genes or simultaneous deletion of different loci on homoeologous chromosomes though not totally excluded is a very rare event. In this context, it seems that some other phenomenon is involved in the induction of such mutations by EMS. One of the possibility is based upon the specificity of EMS to certain region of the chromosome *i.e.*, those regions which are carriers of genes for chlorophyll development. SWAMINATHAN *et al.* (1962) pointed out to the randomness in the action of physical mutagens and the specificity of EMS to some loci in barley and wheat. They suggested that in the evolution of the gene placement along the chromosome arms, it is likely that linkage groups constituted of genes without need for recombination are located near centromere where linkage is tight and recombination is restricted. As such genes for chlorophyll development are located near centromeres and also in the proximal segments of the chromosomes. However, it is not practically confirmed that the genes for chlorophyll production are concentrated near centromeres and these blocks are more vulnerable to EMS action (WASHINGTON & SEARS 1970). Therefore, the specificity of EMS to chromosome regions with genes for chlorophyll development and the antimorphic action due to the alteration in the function of the gene, are the main causes of high rate and wide spectrum of chlorophyll mutations in EMS treatment.

A broader induced viable mutation spectrum observed in present study, affected almost all parts of the plants. Some viable beneficial mutations observed at different frequency are (i) dwarf mutants (ii) increased spike length mutants (iii) increased spikelets and seeds per spike mutants (iv) increase grain weight mutants and (v) early mutants. These beneficial mutations transferred from one generation to the next show a direct quantitative improvement over parental cultivars.

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How to overcome hybrid necrosis in wheat ?

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Hybrid necrosis occurs in wheat due to the complementary gene interaction of dominant alleles of the two loci Ne_1 and Ne_2 (HERMSEN 1963). Of the two complementary necrotic genes, Ne_1 is widely regarded as typical of durum wheat. Bread wheat cultivars with Ne_1 gene are known to have derived their Ne_1 from *T. durum* through artificial crosses between the non-carrier bread wheat ($ne_1 ne_1 ne_2 ne_2$) and $Ne_1 Ne_1 ne_2 ne_2$ durum wheats. Hybrid necrosis restricts the gene flow between *T. durum* and *T. aestivum* wheat varieties with Ne_2 gene and even among *T. aestivum* varieties. In order to permit free gene flow amongst wheat and durum cultivars, it is very important to overcome the hybrid necrosis phenomenon.

Certain necrotic F_1 hybrid combinations were grown simultaneously in the off-season nursery in the summer, 1982 at Keylong (Himachal Pradesh) at a low temperature varying from 4 to 20°C as well as at Gurdaspur in the green house at a higher temperature ranging from 30-38°C. The F_1 hybrid combinations sown at Keylong died of hybrid necrosis, while the ones at Gurdaspur survived. It was, therefore, surmised that the hybrid necrosis is expressed only at low temperature. Attempts were made to ascertain the threshold temperature below which the hybrid necrosis appears.

Two necrotic hybrid combinations, one involving two *T. aestivum* cultivars viz. WL711 and C306 with Ne_2 and Ne_1 genes respectively (RANDHAWA, DHALIWAL & SHARMA, 1983) and the other involving *T. aestivum* cultivar WL711 with Ne_2 gene and *T. durum* variety PBW34 with Ne_1 gene, were grown in the field at weekly intervals throughout the growing season of wheat from November, 1983 to April, 1984. Under the field conditions neither of the necrotic hybrid combinations survived at any of the sowings. During this period highest minimum temperature of 24°C was observed in April, 1984. This indicated that the lowest threshold temperature for hybrid necrosis could still be higher than 24°C.

Subsequently the F_1 hybrid seed of the two necrotic crosses were grown at a constant temperature of 28°C in the growth chamber from August to November, 1984. The hybrid necrosis did not appear at 28°C in both the crosses. F_2 seeds were obtained from the F_1 hybrid WL711 × C306. The other cross WL711 × PBW34 failed to flower as it did not receive any of the required vernalization treatment. To circumvent hybrid necrosis in critical crosses in the breeding programmes the F_1 hybrids should preferably be grown under controlled conditions at a temperature between 28-35°C at which the hybrid necrosis does not appear and also a reasonable seed set is obtained.

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Magnitude of change induced through X-rays and fast neutrons in Triticale*

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Most important cereal crops used as food or feeding stuffs, were domesticated thousands of years ago and all have been improved by human beings from time to time. Yet these improvements were not enough to fulfil the needs of increasing population of the world. Therefore the search for high yielding varieties and new crops remained open for the research workers. Very recently an entirely new cereal grain crop—Triticale—has been produced, which appears to have the potential of producing more yield per unit area than all of the existing traditional cereals (MUNTZING 1979). However, the triticales now available have a narrow genetic base, because they were derived from a limited number of primary triticales (KALTSIKES 1974). Enlargement of this genetic variability is obviously needed, so that suitable plant types of this crop may be developed. It has been reported that different types of mutagens could be used to induce variability in quantitative characters in different crop plants (AARTVEIT 1968). Such attempts have also been made on triticales. VETTEL (1960) and RAMANATHA & JOSHI (1976) found that a greater variability could be produced through induced mutations in triticale rather than by hybridization technique. The present study was also designed to discuss the nature of quantitatively induced variations with a special reference to the genetic improvement of triticale mediated through the yield and various yield components.

Materials and Methods

Seed of a Canadian Triticale Spring Farm were subjected to different mutagenic treatments of X-rays (3 kR and 5 kR) and fast neutrons (1.5 N). At maturity the earheads were harvested from each treatment. These treated seeds were grown to obtain the M_2 population with untreated seeds as control. Thirty plants were selected at random from each of the treatment. Observations were recorded for straw length, number of spikes per plant, number of florets per spike, number of kernels per spike and spike fertility. Variances (Var), genetic variance (V_g) and broad sense heritability $h^2(bs)$ were calculated.

Results and Discussion

The data regarding means, ranges, variances, coefficient of variation and heritability for

* Present studies is part of the Ph. D. thesis presented in the Agricultural University of Norway.

Table 1. Ranges, means, difference \pm standard error, Variances (Var), Coefficient of Variation (c.v.) genetic Variance (Vg) and broad sense heritabilities (h^2 (b.s)).

Treatment	Ranges	Means and differences from control	Var.	C.V.	Vg	h^2 (b.S)
STRAW LENGTH						
Control	34 — 45	38.80 \pm 0.45	6.10	6.36	0	0
1.5 Neutron	12 — 45	-14.27** \pm 1.45	63.36**	32.45	57.26	0.90
3 kR, X-rays.	22 — 38	7.5** \pm 0.73	15.94**	12.76	9.97	0.60
5 kR, X-rays.	16 — 48	10.43** \pm 1.45	63.07**	27.99	56.97	0.90
NUMBER OF SPIKES PER PLANTA						
Control.	1 — 5	2.07 \pm 0.21	1.37	56.73	0	0
1.5 Neutron	1 — 3	0.84** \pm 0.09	0.25	40.87	0	0
3 kR, X-rays.	1 — 6	- 0.04 \pm 0.22	1.40	71.05	0.03	0.02
4 kR, X-rays.	1 — 8	0.09 \pm 0.39	4.49*	97.78	3.12	0.69
NUMBER OF FLORETS PER SPIKE						
Control.	43 — 112	76.56 \pm 3.02	309.59	22.98	0	0
1.5 Neutron	11 — 78	-31.53** \pm 2.75	279.53	37.13	0	0
3 kR, X-rays.	21 — 103	-17.66** \pm 1.90	264.24	27.61	0	0
5 kR, X-rays.	13 — 95	-27.81** \pm 1.86	246.56	32.21	0	0
NUMBER OF KERNELS PER SPIKE						
Control.	22 — 67	38.38 \pm 2.30	181.70	35.12	0	0
1.5 Neutron.	0 — 43	-29.08** \pm 1.80	118.77	117.22	0	0
3 kR, X-rays.	1 — 70	-13.24** \pm 2.03	305.13*	69.50	123.43	0.40
5 kR, X-rays.	0 — 64	-19.99** \pm 1.71	207.10	78.27	25.4	0.12
SEED SET						
Control.	26.04— 76.74	50.64 \pm 2.39	194.29	27.53	0	0
1.5 Neutron.	0 — 69.70	-32.17** \pm 3.12	360.16*	102.77	165.87	0.46
3 kR						
X-rays.	3.70— 91.89	10.76** \pm 2.50	460.90**	53.83	266.61	0.58
5 kR						
X-rays.	0 — 93.75	-14.49** \pm 2.77	544.23**	64.53	349.94	0.64

*, ** indicate significance at 5% and 1% level of probability respectively.

all the characters studied in the M_2 generation of triticale are given in Table 1.

Straw length being controlled by polygenes has an evolutionary significance (LARIK 1978). It is associated with the efficient utilization of nitrogen, lodging resistances and thus influence the crop yield (JOPPA 1973). The results obtained in respect to straw length (Table 1) reveal that the mean values decreased significantly ($p=0.01$) in response to the increased radiation doze in all the treatments as compared with control. These results are similar to those reported on wheat by various workers. For example, Gaul & AASTVEIT (1966) and BOROJEVIC & BOROJEVIC (1972) found that irradiation treatment resulted in the dwarfness of wheat plants. In particular, the dwarfness was more pronounced among the material treated with higher radiation doses. Furthermore, the occurrence of mutants with short culm, often accompanied by straw stiffness in irradiated wheat and barley has also been reported (BROCK

1967; SIDDIQUI 1972). Segregate in downward direction observed in the present triticale might be useful in producing high yielding dwarf types.

Heritability estimates regarding straw length (Table 1), show a highly significant increase in the genetic variation in treated population of triticale. The large variabilities observed in the present study may possibly offer better scope of selection in the further segregating generations.

Productive tillers make direct contribution to increase productivity per unit area. It may be adduced from the data presented in Table 1 that induced mutation has significant effect on reduction in spike number only when the material is treated with 1.5 Neutron. A significant increase in genetic variance and broad sense heritability in the productive tillers observed in the present study indicates the potential of the improvement of this character, that one could expect to achieve through mutations. These results are found to be in a close agreement with those reported by LARIK (1978) and support the hypothesis suggested by ARIAN & SIDDIQUI (1976).

Florets per spike, kernels per spike and seed set are also important yield components and are considered to be a reliable measure of the yielding ability of a crop (BOROJEVIC & BOROJEVIC 1972). The frequency of induced changes in subsequent generation depends on the number of seeds which transmit them (LARIK 1978). Mean values for above three quantitative characters were found to be significantly ($p=0.01$) reduced in triticale in response to both of the radiation sources (Table 1). The shift of mean values for these quantitative characters in the negative direction, supports the hypothesis of GAUL & AASTVEIT (1966), which suggests that the change in the mean values for the quantitative characters occurs both in positive or negative direction and is associated with reduced vitality independent of the genotype used. Radiation affects the vitality of individuals. Poor seed set is amongst other factors a manifestation of an impaired fertility, transmitted from the affiliated embryos, through organogenesis, with the ultimate depression in seed yield per inflorescence. Mean values for seed set character observed in the present studies (Table 1) did show a significant shift towards negative direction but exhibited an increase in the genotypic variation. These results indicate that this character could be transmitted to further generations and significant gain could possibly be achieved through selection in early generations (LARIK 1978). Practical difficulties with triticale mutation breeding might be encountered since the shift in the mean was mostly in the negative direction. However, the range indicated an enlargement of the variation in both directions from the mean. Thus, the variation observed in the M_2 generation for all the characters in triticale due to the mutagenic treatments clearly shows the potential usefulness of mutation breeding for improvement of triticale. Present investigations are preliminary in nature, and more extensive studies are required before sound conclusions could be made. Further studies in this respect show that mutation breeding which has produced useful strains in barley and other crop plants (MUNTZING 1972) should be used in triticale. RAMANATHA & JOSHI (1976), have also observed induced variation in triticale and recommended mutation as a method for improvement. The producers should be aimed at increasing the genetic base that is too narrow in the existing triticales.

This should lead to an acceleration of the improvement in this new crop.

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Genotypic differences in RuP₂carboxylase activities during ontogeny of × *Triticosecale* Witt.

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RuP₂ carboxylase (EC 4.1.1.39) is the fundamental carboxylating enzyme in C₃ photosynthesis and the correlation of RuP₂Case activity with photosynthetic rates were reported (BJORKMAN 1968 ; FREY & MOSS 1976 ; TREHARNE 1972). Photosynthetic CO₂ fixation is the ultimate source of plant dry matter and the role of RuP₂Case in this process has gained much importance in recent times. However little is known about the regulatory role of RuP₂Case as a rate limiting enzyme for crop improvement programmes. It would be of great interest to screen genotypes of economically important crops for genetic diversity in RuP₂Case activity for selection of plants to improve photosynthetic productivity.

The objective of present investigation was to screen genotypes of triticale for variations in RuP₂Case activity to understand the genetic diversity of this enzyme during different developmental stages.

Materials and Methods

Six American triticale lines-6A 1092 (Rosner+ +), 6A 1093 (Rosner- -) 6A 845, 6A 854, 801/1208, 801/1210 and a Poland line 'Salvo' were used in the present study.

Plants were grown in 30 cm clay pots under natural photoperiod during September-December, 1983. The day/night temperature regime was 30/20°C with the average photosynthetic photon flux density of 1,300 μE m⁻² sec⁻¹. Evaluations were made by random selection of leaves from the plants of individual pots. The excised leaves of each genotype were washed and cut into small pieces and the crude enzyme extract was prepared by grinding the leaf bits in a pre-chilled mortar with a pinch of sand in 50 mM tris-HCl buffer (pH 7.8) containing 5 mM dithiothreitol (DTT), 5 mM MgCl₂ and 1% PVP. The homogenate was filtered through cheese cloth and the filtrate was centrifuged at 10,000 rpm for 10 minutes. The enzyme was pre-activated in 5 mM NaHCO₃ and then assayed by measuring the fixation of ¹⁴C-bicarbonate. The reaction mixture contained 50 mM tris-HCl buffer (pH 8.0), 5 mM DTT, 10 mM MgCl₂, 5 mM NaHCO₃(¹⁴C), 0.5 mM RuP₂ and the enzyme extract. The reaction was initiated by adding RuP₂ and terminated with the addition of 3N HCl. The incorporated radioactivity was determined with liquid scintillation system. Chlorophyll was estimated according to ARNON (1949).

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Table 1. RuP₂Case activities (μ moles mg chl⁻¹hr⁻¹) at different developmental stages in seven triticale genotypes.

Genotype	Seedling	Flowering	Grain filling	Maturity
6 A-1092	93.02±5.15	156.69±5.71	200.92± 2.10	186.83±2.87
6 A-1093	99.02±1.44	180.10±7.48	295.87±10.27	271.05±6.91
6 A-854	86.28±0.96	152.82±4.58	199.98± 2.71	168.60±3.62
6 A-845	77.47±1.95	158.30±3.49	211.29± 6.30	179.07±4.61
801/1208	79.48±2.67	174.54±3.71	258.42± 7.53	201.97±4.87
801/1210	71.34±2.01	163.22±3.55	226.68±10.24	198.96±2.09
SALVO	82.34±3.33	165±98.7.16	216.58±11.75	178.39±4.65

Results and Discussion

Table 1 reveals a vast array of variation of RuP₂carboxylase activity both between genotypes and different developmental stages. RuP₂Case levels at the onset of grain filling were at the highest followed by maturity stage. 6A-1093 recorded the highest activity of the enzyme followed by 801/1208 and the lowest was in cultivar 6A-854. In all four stages studied, 6A-1093 exhibited maximal activity. The range of variation among the seven genotypes was not significant at seedling stage but the maximum was observed at grain filling stage. All the genotypes exhibited a unique performance of a gradual increase in RuP₂Case activity in the first three developmental stages and a steady decline from grain filling to maturity.

The present observations suggest that RuP₂Case activity in triticale was found to be associated with developmental stages. The enzyme activity in young seedlings was relatively constant in the seven genotypes and this may be due to beginning of leaf blade expansion prior to reaching the maximum polyribosome content associated with the synthesis of fraction-1 protein. The maximal activities of RuP₂Case observed at the grain filling stage indicate greater stimulation of photosynthetic rates, probably due to greater demand for photosynthates to reproductive structures and grains. The decline in maximum activity during the late seedset indicates low photosynthetic CO₂ assimilation rates and high partitioning of photosynthates during grain filling period (PEET *et al.* 1977). The sampling dates in each developmental stage did not vary greatly in light, temperature or moisture and hence the ontogenetic changes in RuP₂Case activity was probably not due to the environmental changes. Thus the enzyme activity during grain filling stage may be useful screening tool for improving photosynthetic productivity in triticale.

The developmental profile of RuP₂Case activity was significantly affected by genotype reflecting the differences in the proportion of carboxylase protein. Screening of genotypes for high RuP₂Case activity may be of great advantage in selection of varieties for carboxylation efficiency.

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Nitrate uptake and nitrate reductase activity in wheat (*Triticum aestivum*) seedlings

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Nitrate uptake pattern is characterised by slow initial rate and a subsequent accelerated rate occurs when wheat seedlings previously grown without nitrogen are first exposed to nitrate containing solution (MINNOTI *et al.* 1968). Similar results have been observed in my laboratory (DINESH 1980), the presence of Mo accelerated NO_3 uptake and addition of tungstate rather inhibited its absorption. JACKSON *et al.* (1972) observed that initial lag phase was observed only in case of NO_3^- uptake when corn seedlings raised earlier without NO_3^- and Cl^- and when exposed to both, nitrate induced nitrate reductase during the lag phase. Experiments were raised in this laboratory to understand the association of nitrate reductase activity and nitrate uptake in wheat seedlings.

Material and Methods

Wheat seeds of variety HD 2258 recently bred for high fertility conditions were rinsed for one min. in 5.25% NaOCl and washed in running tap water and rinsed thoroughly in deionised water. Seeds were germinated on 5 layers of germinating paper saturated with 1 mM CaSO_4 . After planting the seeds, the trays were covered with plastic food wrap, perforated to allow for air exchange and placed in dark chamber at about 24°C and high humidity. Germinating papers were constantly kept moist. Seven days later, the seedlings were removed (at this stage the endosperm was completely exhausted in the etiolated seedlings), and fixed in series of 1-litre pyrex beakers containing 1.0 mM $(\text{NH}_4)_2\text{SO}_4$, 1.1 mM K_2SO_4 . Trace elements were kept at 1/4 concentration of Hoagland solution (1950), four seedlings were kept in each beaker. Beakers were kept under natural light conditions in the glass house. Some of the seedlings were kept under one eighth normal molybdenum concentration. At the day 10, 15 and 20, uniform seedlings were selected and transferred in 1-litre beaker containing standard uptake solution consisted of 0.05 mM nitrate as $\text{Ca}(\text{NO}_3)_2$, 0.5 mM CaSO_4 and 20 μg of chloramphenicol per ml and pH 7 was regularly maintained (at this pH maximum NO_3 absorption was observed in one of four earlier experiments with various wheat genotypes). Each beaker carried two seedlings with 15 replications. Nitrate was assayed in the depleted solutions according to technique reported in the communication entitled "Soil Science" 6(1) 71-80 (1975). Nitrate reductase was assayed as described by HAGEMAN & HUCKELSBY (1971) at 12 and 24 hr after the transfer of seedlings.

Table 1. NO_3^- absorbed in 24 hour from the uptake solution by wheat seedlings transferred after 10, 15 and 20 day stay in the nutrient solution. Each beaker containing uptake nutrient solution carried two seedlings and 15 beakers were kept as replicates (Mean value of 15 replicates)

Treatment	$\mu\text{g NO}_3^-$ depleted from each beaker in the uptake solution	
	Without Mo in the uptake solution (Seedlings raised under 1/3 molybdenum concentration)	With 5 $\mu\text{g Mo}$ in the uptake solution (Seedlings raised under normal conditions)
10 Day stay in the nutrient solution	19.6	37.0
15 Day stay in the nutrient solution	31.2	49.8
20 Day stay in the nutrient solution	33.7	56.4
S.E.	4.8	7.3

Table 2. Effect of protein inhibition on NO_3^- uptake in 15 day old seedlings. Uptake solution included 5 μg of Mo (Mean value of 5 replicates)

1. Control	($\mu\text{g NO}_3^-$ depleted in 24 hr)= 45.6
2. 5-fluorodeoxy uridine	(10^{-6}M)= 21.3
3. 5-flourauracil	(10^{-6}M)= 19.2
4. Cyclohexamide	(2 $\mu\text{g ml}^{-1}$)= 10.0
5. Puromycin	(400 $\mu\text{g ml}^{-1}$)= 12.0

Results and Discussion

The presence of Mo in the test solution was helpful in the uptake of NO_3^- (Table 1). Similarly results were obtained earlier in my laboratory with different wheat genotypes raised with and without molybdenum and tungstate. The tungstate reduced nitrate absorption thus confirming that association of molybdenum was necessary for nitrate uptake. Since molybdenum is known to be the constituent of nitrate reductase protein, experiments therefore were raised to see that if the protein was in any way involved. The data obtained in this regard as shown in Table 2, indicated that 5-fluorodeoxyuridine and 5 flourouracil known to be RNA inhibitors, both of these reduced the nitrate absorption. Cyclohexamide an inhibitor of protein synthesis drastically inhibited nitrate uptake whereas puromycin which is presumed to compete with aminoacyl tRNA during polypeptide synthesis also restricted the NO_3^- uptake. These experiments therefore suggest that RNA and protein synthesis were also required for the process involved in the acceleration of nitrate absorption and molybdo-protein system may be working for the same.

Table 3. Nitrate reductase activity in roots after 12 and 24 hour period in the uptake solution carrying 5 ug Mo (Mean values of 5 replicates)

Treatment		$\mu\text{M NO}_2/\text{gm}^{-1} + \text{W}/\text{hr}^{-1}$		
		Root	Leaves	
10	Day stay in nutrient culture	12 hr in uptake solution	0.39	1.02
		24 "	0.32	1.16
15	Day stay in nutrient solution	12 hr "	0.29	1.96
		24 hr "	0.21	2.13
20	Day stay in the nutrient solution	12 hr "	0.23	2.23
		24 hr "	0.19	1.86
	Se		0.05	0.60
	Se		0.07	0.46

Since NR is a molybdoflavoprotein, the activity of this enzyme was estimated both in the roots as well as in the shoot (Table 3). Higher enzyme activity in the roots was observed in the seedlings which had 10 day stay in the nutrient solution whereas seedlings which were kept for 15 days and 20 days in the nutrient solution showed poor enzyme activity but no uptake as shown in Table 1 was higher. Virtually, no relationship in NO_3^- absorption and the enzyme activity in the root was noticed. However, the enzyme activity in the shoot was higher in 15 and 20 days nutrient culture seedlings, which were also showing higher NO_3^- absorption. Minimum NO_3^- absorption was observed in 10 days culture and simultaneously the NR activity in these seedlings was also comparatively less.

It may be concluded that NR in the roots may not be involved as such in NO_3^- absorption but may possibly working in the modified form. A mutant lacking in NR in *Arabidopsis* was reported to absorb nitrate (DODDEMA & OTTEN, 1979). Unlike in roots, higher enzyme activity in shoots and higher nitrate uptake as noticed in some of the treatments (Table 1 & 3) suggested the possibility of shoot activity and nitrate uptake. Various mechanism by which NO_3^- reduction in shoot controls the NO_3^- uptake by roots have been reported by BENZION *et al.* (1971) and FROST *et al.* (1978). They reported that nitrate arriving in the leaves undergoes a reduction, as in the root, the resulting increase in anion charge is transferred to carboxylate the K carboxylate may then return to root and may be metabolised to form bicarbonate which can be exchanged for more nitraee. BRETELER & HANISCH TENCATE (1978) concluded that Benzionis model is not universely valid. But the results obtained by KIRBY & ARMSTRONG (1980) which may be interpreted as providing direct evidence of nitrate uptake by roots regulated by nitrate uptake in the tops, the process being facilitated by the recirculation of K in the plant.

In conclusion, it may be reported that though molybdenum and protein in the root system may have a direct relationship in nitrate uptake, nitrate reductase activity in shoot too has its strong influence in this aspect. The possible association of both the systems is suggested.

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Inhibiting effects of peroxidase activity on dry matter accumulation in developing kernels of bread wheat

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In general, semidwarf wheats have low kernel weight in comparison to tall wheats (EPHRAT 1974). The possible reasons for the poor kernel weight in semi-dwarf wheats, include inadequate assimilation for filling of increased number of kernels, relatively higher respiratory losses or imbalanced activity of hormones during seed development. Our previous study (SINGHAL *et al.* 1979) had shown significant negative correlation between peroxidase activity in coleptile and kernel weight at maturity. The present study was planned to study the peroxidase activity in kernels during development and its relation with dry matter accumulation in kernels of wheat varieties.

Materials and Methods

Eight wheat genotypes differing in kernel weight and plant height were grown under high fertility condition (N.P.K. 100, 60, 40 kg/ha⁻¹). The ears were harvested at 10, 17, 24, 31 days after anthesis and at maturity. The kernels were removed and stored in liquid nitrogen before enzyme assay or immediately analysed. All varieties except Mex C.B. 116 and Olesen's Dwarf took 37-40 days from anthesis to maturity. Mex C.B. 116 and Olesen's Dwarf matured in shorter time (33-35 days) from anthesis. Matured grain samples were taken at 40 days after anthesis in all the varieties. Dry weight of 100 kernels was determined by oven drying at 100°C till constant weight.

Fresh seeds were hand-ground in 0.05 M Tris-HCl buffer (pH 6.0, 1 : 5 W/V) with chilled pestle and mortar at 4°C. The cell paste suspension was centrifuged at 10,000 × g for 15 min at 4°C. The supernatant obtained was used for peroxidase assay. Peroxidase was assayed according to the method of SHANNON *et al.* (1966). The activity has been expressed as change in absorbance per min per g fresh weight.

Results and Discussion

Substantial variation was observed in the pattern of dry matter accumulation in developing kernels. Low kernel weight varieties like Kalyansona, Max C.B. 116 and Olesen's Dwarf accumulated upto 39.7 to 48.6 per cent of mature kernel weight till day 17 after anthesis while bold seeded varieties HD 1944, NP 880, Sonalika, K. 65 and Pusa 5-3 could accumulate only 21.9 to 38.1 per cent (Table 1). After day 24 all the bold seeded varieties accumulated greater dry matter than low kernel weight varieties. The triple dwarf variety HD 1944 was similar

Table 1. Dry weight (g/100 kernel) of kernels of wheat varieties during development.

Variety	Plant Height at maturity (cms.)	Days after anthesis				
		10	17	24	31	Mature grain
Mex C.B. 116	53.8	0.593(18.5)	1.508(47.7)	2.360(73.7)	3.200(99.9)	3.203
Olesen's dwarf	47.8	0.345(14.5)	1.158(48.6)	1.484(62.3)	2.407(101.0)	2.382
Kalyansona	93.4	0.753(21.2)	1.410(39.7)	2.150(60.5)	2.737(77.0)	3.556
HD 1944	74.5	0.741(16.5)	1.311(29.2)	2.434(54.2)	4.214(93.9)	4.487
Sonalika	98.5	0.760(14.0)	1.530(28.2)	2.750(50.7)	4.230(78.0)	5.423
K 65	123.0	0.548(10.3)	1.627(30.6)	3.044(57.2)	4.447(83.6)	5.230
NP 880	126.6	0.648(11.9)	1.197(21.9)	3.040(55.6)	5.397(98.7)	5.467
Pusa 5-3	98.7	0.623(12.5)	1.908(38.1)	3.057(61.1)	4.680(91.9)	5.003

Values in paranthese indicate % of mature seed weight.

Table 2. Peroxidase activity (OD/g fresh weight) in developing kernels of wheat varieties

Variety	Day after anthesis				
	10	17	24	31	Mature grain
Mex C.B. 116	50.4	64.0	57.0	55.1	460.8
Olesen's dwarf	73.6	95.3	83.0	60.1	610.8
Kalyansona	62.8	65.2	52.8	55.3	450.8
HD 1944	62.6	80.3	61.5	38.8	333.9
Sonalika	49.4	69.9	50.4	42.2	312.5
K 65	50.7	64.9	39.0	36.0	378.6
NP 880	61.2	51.4	38.7	34.2	262.6
Pusa 5-3	66.2	50.1	41.4	37.1	285.7

to double dwarf variety Kalyansona in its dry matter accumulation in kernels upto day 17 but later on HD 1944 accumulated more matter than Kalyansona.

The variety Olesen's Dwarf had the highest peroxidase activity at all the stages of kernal development (Table 2). At maturity steep increase in peroxidase activity has been recorded in all the varieties. The correlation between peroxidase activity and kernel weight was highly significant negative at day 24, 31 and maturity (Table 3). At day 10 Sonalika and at day 17 Pusa 5-3 had accumulated the highest kernel weight and had the lowest peroxidase activity, while at the same time variety Olesen's Dwarf had accumulated the least kernel weight and showed the highest peroxidase activity. Pusa 5-3 from day 11 to 17 and NP 880 from day 18 to 31 accumulated higher kernel weight (1.28 and 4.20 g. respectively) and showed relatively lower peroxidase activity then others. The results, in general, indicate inhibiting effects of peroxidase towards the development of kernels.

The exact role of peroxidase in plants is not yet clear but it has been shown to be involved in growth and devopment by inactivating auxin (GALSTON *et al.* 1953). Accumula-

Table 3. Simple correlation coefficient of 100 kernel weight (g) with peroxidase activity (O.D/g fresh weight) at different stages of kernel development.

Days after anthesis	Correlation Coefficient
10	-0.420
17	-0.500
24	-0.941**
31	-0.964**
Mature grain	-0.929**

** Significant at 1% level.

tion of peroxidase in slow growing tissues and dwarf plants suggests a growth inhibitory activity of growth regulating enzyme, auxin. Single gene dwarf mutant when treated with gibberellin have shown a decrease in peroxidase activity and an increase in growth (McCUNE & GALSTON, 1959). Conversely, marked increase in peroxidase activity in normal plants with the application of compounds which prevent gibberellin biosynthesis has also been observed (GASPER & LACOPPE 1968). RAO *et al.* (1976) had also observed a positive correlation between peroxidase activity and degree of grain shrivelling in triticale. Peroxidase activity in coleoptile showed a negative relationship with plant height and kernel weight (SINGHAL *et al.* 1979) and plant height has been found to have relationship with kernel weight (EPHRAT 1974), further the present study extends the negative effects of peroxidase on dry matter accumulation at different stages of kernel development. An important question arises that how the development of a semi-dwarf wheat plant with higher kernel weight is possible. Our previous study (SINGHAL *et al.* 1979) showed considerable variation in the amount of peroxidase activity among the semi-dwarf wheats and a deviation from negative relationship and possibility of developing a dwarf plant type with well filled grain do exist. The critical examination of data from the present study showed that the triple dwarf variety HD 1944 had higher kernel weight at maturity and lower peroxidase activity than the double dwarf variety Kalyansona. Upto day 24 after anthesis, average kernel weight accumulation and peroxidase activity did not differ much between Kalyansona and HD 1944. The variety HD 1944 showed a substantial decrease in peroxidase activity from day 24 to day 31 at a period when substantial increase in its kernel weight (1.78 g/100 kernels) occurred. On the other hand in variety Kalyansona peroxidase activity did not change in this period, therefore, the increase in kernel weight was relatively low (0.587 g/100 kernels). At maturity HD 1944, possessed relatively lower peroxidase activity, higher grain weight and short plant height than variety Kalyansona. The present study indicates that a genotype with relatively higher peroxidase activity during early stages of plant growth would result in the dwarf plant type and decrease in peroxidase activity at later stages of kernel development as has been noticed in HD 1944, would result in the greater accumulation of grain weight.

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A new lethal combination in Triticale hybrids

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The phenomenon of hybrid lethality has been found to be common in bread wheat where the presence of Ne_1 and Ne_2 genes have been established to operate, but this manifestation of hybrid lethality in triticales has been of rare occurrence. The only reference of CVETKOV (1980) for necrotic F_1 's in crosses between octoploid triticales derived from wheat varieties carrying Ne_1 and Ne_2 genes does indicate that not sufficient crosses have been tried to establish the presence of hybrid lethality in octoploid triticales. The hybrid lethality is not expected in hexaploid triticale (ZEVEN, 1973) as the only Ne_1 allele are possible to exist since these are derived from tetraploid wheat \times *Secalecereals* crosses. However, more octoploid triticales combinations can be studied for the presence of Ne_1 and Ne_2 alleles in them.

Twenty hybrid seeds of each of two cross combinations viz. (C 306 \times Assam Rye) \times (Sonalika \times Russian Rye) and (C 306 \times Russian Rye) \times (WL 410 \times Russian Rye) and their reciprocals involving four octoploid primary triticales, were sown in pots. The parental forms of the four octoploid primary triticales viz. (C 306 \times Assam Rye), (Sonalika \times Russian Rye), (C 306 \times Russian Rye) and (WL 410 \times Russian Rye) were also sown for the purpose of comparison. The seedlings emerged, were quite normal. After three weeks, from the data of sowings, the hybrid seedlings in both the cross combinations and their reciprocals started showing hybrid lethality. The necrosis started at the tip of first leaf and proceeded gradually downwards towards the leaf base. This process was repeated on the remaining leaves and as a consequence all the hybrid seedlings died. The seedlings in the four parental forms did not show any sign of necrosis.

From the results it can be inferred that the rye (*Secale cereale*) component involved in the octoploid primary triticales has got no suppressing effect on the Ne -genes associated with the wheat component. As a result the Ne_1 gene found in one of the parents in both cross combinations carrying C 306 as hexaploid wheat component caused hybrid necrosis in combination with the octoploid primary triticales carrying Ne_2 genes in the wheat components Sonalika and WL 410.

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Genetic divergence in some triticales strains and their hybrids

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Extent of genetic diversity in parental stocks largely determines the inherent potential of a cross. Hybrids between highly diverse parents are expected to show high heterosis in F_1 and wide spectrum of variability in segregating generations. On the other hand, low pace of progress in triticales improvement programmes has been attributed to its narrow genetic base and unlike other cereals, improvement work in triticales has to be preceded by creating variability (MUNTZING 1979; BEHL *et al.* 1985). Therefore, quantitative assessment of degree of divergence among genotypes entering crosses and their hybrids is essential. However, such reports in triticales are scanty (SRIVASTAVA & ARUNACHALAM 1977; AHMAD *et al.* 1980; & BEHL *et al.* 1985). Present study was, therefore, conducted to determine genetic divergence among 72 F_1 hybrids and their 22 parents.

Materials and Methods

Twenty two strains of hexaploid triticales, selected on the basis of genetic divergence (BEHL *et al.* 1985), were crossed into line (female) × tester (male) matings using 18 lines and 4 tester to yield 72 F_1 hybrids. Ninety four genotypes (parents and hybrids) were evaluated in randomized block design with three replications. Observation on randomly selected five plants per plot in each replication were recorded on 14 characters related to plant morphology and components of grain yield and quality.

Mahalanobis's D^2 -statistic was used for assessing genetic divergence among genotypes. The original variables (X'S), which were inter correlated, were transformed into a set of mutually uncorrelated variables (Y'S, linear functions of X'S) by pivotal condensation method (RAO 1952). Then, the D^2 value between two strains is given by the simple sum of squares of differences in Y'S as shown by

$$D^2 = \sum_{i=1}^p (Y_{1i} - Y_{2i})^2$$

The genotypes were grouped into a number of clusters using generalized statistical distance $D = \sqrt{D^2}$ according to Tocher method (RAO 1952). The per cent contribution of a character towards genetic divergence was calculated as the percentage of combination in which the characters ranked first.

Results and Discussion

Analysis of variance revealed significant differences among parents, hybrids and parents

Table 1. Grouping pattern of 22 parents and 72 F₁ hybrids based on D²-analysis.

Group number	No. of Genotypes included	Genotypes
I	49	T 125, TL 37, TL 39, Chinnamon, TL-22 UPT 74535, T 130×ST 69-1, T 1 34×ST 69-1, TL 37×St 69-1, TL 49×St 69-1, TL 56× St 59-1, UPT 74418×St 69-1, UPT 74460× St 69-1, UPT 74536×St 69-1, Arm 147× St 69-1, Armadillo×St 69-1, T 135× 6 TA 204, TL 46×6 TA 204, UPT 4460× 6 TA 204, UPT 74536×6 TA 204, Koala× 6 TA 204, Cinnamon×6 TA 204, T 103× TL-22, T 125×TL-22, T 130×TL-22, T 134×TL-22, Tc1 3×TL 22, TL 37× TL-22, TL 39×TL-22, TL 46×TL 22, TL 56×TL 22, UPT 74364×TL-22, UPT 74428×TL-22, UPT 74460×TL-22, Armadillo×TL-22, Koala×TL-22, Chinnamon×T1-22, T 125×UPT 74535, T 130×UPT 74535, TL 37×UPT 74535, TL 46×UPT 74535, TL 56×UPT 74535, UPT 74460×UPT 74535, UPT 74536× UPT 74535, Arm 147×UPT 74535, Koala× UPT 74535 and Cinnamon×UPT 74535.
II	11	T 24×ST 69-1, T 24×6 TA 204, T 103× 6 TA 204, T 130×6 TA 204, Tc1 3× 6 TA 204, TL 39×6 TA 204, Arm 147×6 TA 204, Armadillo×6 TA 204, Arm 147×TL-22, T 134×UPT 74535 and TL 39×UPT 74535.
III	8	St 69-1, T 103×St 69-1, T 125×St 69-1, Tc1 3×ST 69-1, TL 39×St 69-2, T 125×6 TA 204, T 24×TL 22 and Armadillo×UPT 74535.
IV	8	UPT 74364, UPT 74536, 6 TA 204, UPT 74364× St 69-1, TL 56×6 TA 204, UPT 74536×TL 22, UPT 74364×UPT 74535 and UPT 74418× UPT 74535.
V	7	T 24, T 103, T 134, Tc 13, Arm 147, UPT- 74364×6 TA 204 and T 24×UPT 74535.
VI	4	TL 46, UPT 74460, Armadillo and Koala.
VII	2	T 130 and TL 56
VIII	2	UPT 74418 and Cinnamon×6 TA 204
IX	1	TL 37×6 TA 204
X	1	T 103×UPT 74535
XI	1	Tc 13×UPT 74535

Table 2. Intra and intercluster generalized distance (D^2)

Cluster Number	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
I	6.4	8.9	7.4	9.0	9.5	8.0	11.5	11.6	9.6	10.1	10.5
II		7.0	8.7	9.7	10.7	12.5	15.0	14.2	11.8	10.3	9.2
III			6.0	10.4	11.7	9.7	14.0	14.1	10.3	9.3	11.2
IV				6.0	9.8	10.2	11.1	10.8	10.0	9.0	10.5
V					6.7	11.4	8.7	15.2	13.9	10.1	9.8
VI						6.0	10.9	9.6	9.9	11.6	13.7
VII							5.7	13.5	14.6	12.0	13.3
VIII								6.1	10.6	15.0	16.6
IX									0	11.3	13.4
X										0	10.0
XI											0

vs hybrids, suggesting thereby sufficient amount of genetic variability. This was further substantiated by the fact that D^2 -values for 4371 combinations among 94 genotypes ranged from 5.5 between T 24 and Armadillo×6TA 204 to 326.4 between Tc13×St69-1, whereas, such a range among parental combinations was from 10.74 (T125) to 178.20 (UPT 74418). Thus, considerable increase in variation spectrum was added after hybridization between parental stocks.

On the basis of degree of divergence (D^2), 94 populations could be grouped into 11 clusters (Table 1). Cluster I and II were the largest and included 6 parents and 54 hybrids. Rest 16 parents and 18 hybrids scattered over 9 groups mainly added to the divergence. This corroborated the findings of SRIVASTAVA & ARUNACHALAM (1977), that only few hybrids could add substantial variation in the population. Groups IX, X and XI were monogenotypic and comprised of genotypes which were extraordinary for one or more characters. In general, intracluster distances (Table 2) were almost equal and lower than the intercluster distances. Thus, the genotypes included, within a cluster tended to diverge less from each other possibly due to large similarity in parentage or selection of genotypes. The inter cluster distances varied from 7.4 between group I and III to 16.6 between VIII and XI. Cluster VIII, in general, was more divergent from all other clusters because the genotypes included were very late in ear emergence, dwarfest in height and had maximum tillers per plant.

The cluster means showed appreciable differences for several characters among single as well as multigenotypic clusters. However, the differences were more clear for days to ear emergence, plant height, grains per spike, floret fertility, 1,000 grain weight and grain yield (Table 3). F_1 hybrid Tc 13×UPT 74535 included in cluster XI was good for 1,000 grain weight, grain crushing hardness, grain density and grain yield, while genotypes grouped in cluster VII were good for grains per spike, floret fertility and harvest index and in group II for protein content, biological yield per plant and grain yield. Inclusion of these genotypes in hybridization programme would, therefore, be worth while.

Most of the characters appeared to contribute almost equally to the total divergence.

Table 3. Cluster means for various characters.

Group NO.	Genotypes included	Characters													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
I	49	101.0	129.8	10.3	12.1	27.2	60.9	72.1	46.3	7.1	1.1	13.2	86.8	31.2	26.4
II	11	104.8	161.2	9.6	14.3	30.3	62.9	67.1	48.5	7.4	1.1	13.9	94.7	29.8	27.3
III	7	104.6	143.7	7.9	11.3	25.8	65.3	75.1	45.7	7.0	1.2	13.7	85.1	23.7	20.0
IV 8	8	111.2	138.2	8.7	14.4	32.8	62.1	63.9	41.4	7.1	1.0	13.3	76.4	27.0	20.6
V	8	99.0	140.2	8.8	12.5	27.2	64.9	76.1	50.0	7.0	1.1	13.2	88.0	30.4	27.0
VI	4	102.5	112.1	9.5	10.3	26.0	62.4	78.1	43.2	6.6	1.2	12.1	62.6	32.7	20.5
VII	2	103.0	112.7	9.9	10.7	25.4	70.8	80.9	43.7	5.9	1.1	13.8	77.5	33.6	25.9
VIII	2	114.0	90.1	12.2	13.7	29.5	59.2	64.2	37.2	6.4	1.0	13.1	81.8	28.1	23.0
IX	1	108.9	127.4	9.0	11.8	27.7	49.3	55.9	42.5	6.3	1.2	13.7	61.5	29.8	17.0
X	1	111.8	119.1	7.2	10.7	23.9	56.4	64.9	37.6	6.4	1.1	14.4	76.6	23.6	18.1
XI	1	110.6	154.8	11.1	14.1	27.5	61.4	70.1	48.4	9.2	1.3	15.1	90.2	28.2	25.4
% Contribution to total divergence.		8.6	10.9	6.1	9.0	6.3	6.9	6.4	8.6	5.0	5.1	6.6	7.2	7.6	5.7

where 1=Days to ear emergence, 2=Plant height (cm), 3=Number of tillers/plant, 4=Spike length(cm) 5=Number of spikelets/spike, 6=Number of grains/spike, 7=Floret fertility(%), 8=1000 grain weight(g), 9=Grain crushing hardness(kg/seed), 10=Grain density(g/cc), 11=protein content(%), 12=Biological yield/plant(g), 13=Harvest index(%), and 14=Grain yield/plant(g).

However, plant height (11.0%), spike length (9.0%), days to ear emergence (8.7%) and 1,000 grain weight (8.6%) appeared to contribute relatively more, while grain crushing hardness being the lowest (5.0%).

The clustering pattern of the hybrids is known to be influenced by their parentage because of close affinity between the parents and progeny (CHAUDHARY & SINGH 1975). In present study also, mainly three grouping trends were evident. Out of 72 hybrids, 34 were grouped in different clusters than both the parents. Such a grouping behaviour of F_1 hybrids may be explained on the basis of genic interactions, among parents. In other 32 cases, hybrids were found to be grouped with one of the parent which showed dominance in its favour. In rest 6 cases, F_1 's and their parents were clustered together. Such cross combinations depicted relatively low genetic divergence among parents.

The importance of genetic diversity among parents entering crosses has been duly emphasized (BHATT 1973). However, in present study, genetic divergence among parents did not reveal any consistent relationship with grain yield potential of their hybrids. Despite the large differences for D^2 -values among parents in cross T103×6TA204 (107.2) and Koala×TL-22 (15.6), the *per se* performance of both these F_1 hybrids was same (33.0 g/plant). It appeared that the genotypes with restricted genetic divergence and falling in the same clusters may also produce desirable hybrids provided they compliment the major weaknesses of each other as against those involving genotypes which fall in distant clusters and are supposed to have wide genetic divergence. In that context, four crosses; T130×6TA204, T103×6TA204, TL56×St69-1 and Koala×TL-22 figured important for further breeding programmes.

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Genetical analysis of grain yield and agronomic characters in hexaploid triticale

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The hexaploid triticales, compared with octoploid types, improved cytogenetic stability, fertility and yield potential, and renewed the interest in breeding of this species. The crossing of hexaploid triticales with octoploid triticales or hexaploid wheats presented many potentially useful plant types (QUALSET *et al.* 1973), while the rapid increase in yielding ability of hexaploid triticales was affected with the development of Armadillo strains in CIMMYT, Mexico (ZILLINSKY 1974). Under certain ecological conditions, the improved hexaploid triticales outyielded the best wheat and barley check cultivars (KROLOW 1977). The present paper, however, reports the results from early generations of crosses between hexaploid triticale strains. The main aim was to evaluate the prepotency of the parents, and to predict the genetic productivity of crosses for further isolation of superior homozygous genotypes in advanced generations based on information of gene action involved in expression of several agronomic traits.

Material and Methods

The generations P_1 , P_2 , F_1 , F_2 , B_1 ($P_1 \times F_1$) and B_2 ($P_2 \times F_1$) were evaluated from each of two hexaploid triticale crosses, namely UC 8825 \times TL 116 (cross 1) and Beagle \times 6T-70 (cross 2). The parental material was highly selected for meiotic stability, adaptability and fertility but genetically diversified for many other attributes contributing to productivity. Each cross was considered as a unit in the planting scheme. The planting arrangement was a completely randomized block design with three replications of single row plots. The rows were 150 cm long and 30 cm apart with 10 cm inter plant spacing. In each replication, 20 plants of parents and F_1 , 100 plants of F_2 and 60 plants of backcrosses were sampled for recording data on heading data, plant height, tillers per plant, spikelets and kernels per ear, 100-kernel weight and single plant yield. The data were analysed by analysis of variance. The heterosis was measured by the magnitude of the difference in mean performance between F_1 and better parent (P_1 or P_2) and expressed as per cent. In genetic model proposed by HAYMAN (1958) the generation means are expressed as the linear function of various gene effects. In the present study, the variation between generation means was partitioned into variation due to additive and dominance effects and that due to deviations from the additive-dominance model by fitting unweighted least square regression analysis to generation means. This permitted the test of the adequacy of additive-dominance model and evaluation of

importance of additive and dominance effects in their contribution to genetic variation.

Results and Discussion

Analysis of variance indicated significant differences existed between generations for all characters measured in both crosses. The parent UC8825 was higher performing than TL116 for all traits except kernel weight. Beagle was later in heading but possessed more tillers/plant, spikelets and kernels/ear and heavier kernels than 6T-70. The F₁ hybrids deviated significantly from the desirable parent in both crosses for heading date, number of spikelets and kernels, and kernel weight, and in cross-1 for plant height and grain yield. This heterotic expression of F₁ hybrids tended to indicate a certain degree of dominance for those traits. However, the F₁ mean value approximately equal to mid-parent value in either of cross for tiller number, indicating the minor importance of non-additive gene action for its genetic expression. In general, the degree of heterotic expression was higher in cross 1 than in cross 2.

The decline in the mean performance from F₁ to F₂ was noted for plant height, kernel weight and yield in cross 1 and 2 and spikelets/ear in cross 1. In almost all cases the means of F₂ populations appeared to be intermediate between parental means. While judging the

Table 1. Mean values and heterosis for grain yield and its components in two 6x triticales crosses

	Heading date	Plant height (cm)	Tillers/plant	Spikelets/ear	Kernels/ear	Kernel weight (g)	Yield/plant (g)
Cross 1							
P ₁ (UC 8825)	118.87	133.58	9.87	37.59	74.72	3.52	21.99
P ₂ (TL 116)	104.80	96.63	7.01	24.50	56.90	3.93	14.86
F ₁	113.20	132.34	9.39	32.77	56.99	5.25	27.93
F ₂	116.31	105.34	10.82	29.48	53.70	3.87	22.24
B ₁	113.74	117.68	9.89	32.06	56.44	3.94	22.30
B ₂	112.46	107.29	9.21	29.15	53.48	4.20	18.52
Mid-parent value	111.84	115.12	8.44	31.05	65.81	3.76	18.43
Heterosis(%)	8.02**	-39.96**	-4.86	-12.82**	-23.21**	33.59**	21.01**
LSD (0.05)	5.20	12.13	1.65	2.42	9.03	0.18	3.93
Cross 2							
P ₁ (Beagle)	113.31	133.58	10.59	32.25	75.59	4.45	26.36
P ₂ (6 T-70)	110.42	131.37	9.02	26.94	55.11	3.90	23.81
F ₁	101.34	135.02	10.09	28.90	60.82	5.39	27.40
F ₂	109.47	117.71	8.41	28.20	57.17	4.12	21.95
B ₁	108.62	123.65	9.49	30.36	61.12	4.46	22.75
B ₂	105.46	108.78	7.86	24.96	52.06	4.11	21.47
Mid-parent value	111.87	132.43	9.81	29.60	65.35	4.18	25.09
Heterosis (%)	-8.22**	2.78	-4.72	-11.56**	-19.54**	21.22**	3.95
LSD (0.05)	2.23	8.21	1.30	1.42	10.86	0.58	2.71

* Significance deviations of F₁ from better parent (P₁ or P₂) at P=0.01

Table 2. Analysis of generation means for two 6 x triticales crosses for yield and its component characters

Source of variation	D.F.	Headings date	Plant height	Tillers/plant	Spikelets/ear	Kernels/ear	Kernel weight	Yield/plant
Cross 1								
Generations	5	65.30**	684.81**	4.93**	53.38**	182.61**	1.02**	57.31**
Additive	1	245.39**	2131.44**	12.29**	253.87**	1424.13**	1.44**	97.63**
Dominance	1	10.10	328.39*	3.72	2.73	254.61**	2.80**	162.45**
Deviations	3	23.67	321.61**	2.88	10.10	78.10	0.29**	8.83
Error	10	8.17	44.39	0.82	1.76	24.60	0.01	4.65
Cross 2								
Generations	5	52.41**	319.64**	3.12**	19.61**	203.61**	0.84**	17.59**
Additive	1	23.98**	111.63*	6.83**	76.99**	750.60**	0.63**	12.21*
Dominance	1	216.08**	25.54	0.08	3.02	96.92	2.21**	1.49
Deviations	3	7.32*	486.92**	2.90	6.01**	56.85	0.45**	24.75**
Error	10	1.50	20.34	0.51	0.61	35.58	0.10	2.22

*, ** Significant at P=0.05 and 0.01, respectively

crosses for mid-parental values, cross 2 appeared to be superior to cross 1. From basic genetic considerations BAKER (1980) viewed that the use of mid-parent value should be an effective *a priori* method of selection among crosses even under severe type of epistasis.

Generation mean squares of crosses were partitioned into various genetic effects as shown in Table 2. Mean squares fitting due to additive gene effects were significant for all the traits in each cross, while mean squares fitting due to dominance gene effects were significant for plant height, number of kernels, kernel weight and yield in cross 1 and heading date and kernel weight in cross 2. With exception of yield in cross 1 the magnitude of additive mean squares was larger than that of dominance mean squares. It should be, however, noted that the estimate of dominance gene effects are effected by balancing of plus and minus values (ambidirectional dominance). Significant mean squares due to deviations from additive-dominance model indicated the role of epistasis for plant height, number of spikelets and kernel weight in both crosses and heading date and yield in cross 2. Since the magnitude of deviations mean squares approached significance for other characters, the epistatic gene action for them could not be ignored.

The present study, thus, indicated predominant additive nature of genetic effects in cross 1. This signifies the early generation selection in cross 1 can be made effective for bringing an improvement in several characters including yield. On other hand, non-additive genetic effects were frequently detected in cross 2, however, their contribution relative to additive effects was minor. Conventional selection in this cross should be delayed to later generations for a more tangible advance.

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Analysis of plant height promotion by chromosome 6D in common wheat

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Monosomic lines in the wheat variety Chinese Spring, developed by SEARS (1954), were used for producing aneuploid lines in an Indian wheat variety Pb. C591 (SWAMINATHAN *et al.* 1968). SINGH *et al.* (1970) reported the involvement of chromosome 6D of var. Pb. C591 for height character, where they observed that monosomic ($2n=41$) plants were about 30 cm shorter than disomic ($2n=42$) plants. Nullisomics in this line were still shorter (height of nullisomic 6D was observed to be about 70 cm). It was suggested that genes located on chromosome 6D promote height in variety Pb. C591. Effects were markedly noticeable even if one of the homologous chromosomes was missing.

Height reduction in monosomic ($2n=41$) line 6D of var. Pb. C591 was further investigated to ascertain the mode of reduction in height. Data were taken on the internode number, internode length and plant height on monosomic ($2n=41$) and disomic ($2n=42$) plants separately. Mean values were calculated and the data were subjected to statistical analysis to test the differences between means of internodes, internode length and total length of the plants of monosomics and disomics.

The internode distribution patterns of disomic ($2n=42$) and monosomic plants as seen from the Table 1, show that in disomic as well as in monosomic plants the basal internode is smallest in length and the successive internode have progressively increased lengths. The last internode that supports the spike is the longest and accounts for about 40% of the total culm length. Reduction in height in monosomic plants has been observed to be due to the shortening of all the internodes to a variable degree. The reduction in the absolute length of all the internodes was found in an order of 3.96 cm (16.90% of the total reduction) in Ist internode, 3.37 cm (14.38%) in IInd internode, 2.11 cm (9.00%) in IIIrd internode, 3.23 cm (13.78%) in IVth internode, 4.37 cm (18.65%) in Vth internode and 6.51 cm (27.78%) in the VIth internode.

It is therefore, concluded that the gene(s) located on chromosome 6D of variety Pb. C591 which possesses genes for promoting the total plant height in this variety, promotes height by way of increasing the length of all the internodes with variable degree. It is likely that this gene product utilizes the GA like substances or the gene product itself functions like GA for promoting the plant height in this variety.

Table 1. Data on mean length of internodes (cm), plant mean height (cm) on the plants obtained from disomics (2n=42) and monosomics (2n=41) for chromosome 6D of var. Pb. C 591.

Parameters	No. of plants	Internode						Total plant height
		Basal	2 nd	3 rd	4 th	5 th	6 th	
Disomics	43	5.91±0.28	11.72±0.19	14.29±0.25	19.84±0.12	27.58±0.25	48.60±0.41	127.96±0.55
Monosomics	83	1.95±0.15	8.35±0.15	12.18±0.19	16.61±0.20	23.21±0.23	42.09±0.33	104.53±0.53
CD 5 %		0.29	0.29	0.37	0.39	0.45	0.64	1.03
Absolute decrease in length		3.96	3.37	2.11	3.23	4.37	6.51	23.43
Total decrease in percent		16.90	14.38	9.00	13.78	18.65	27.78	—

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Heading date in the aneuploid lines of wheat and cause of variation

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We have observed that the flowering time of disomic plants ($2n=42$), in different monosomic lines in the aneuploid series of wheat variety Chinese Spring (SEARS 1954) and Pb. C591 (SWAMINATHAN *et al.* 1968) is significantly different. Within a line the disomic and the monosomic plants ($2n=41$) flower at the same time. Since the disomic plants of all the lines carry a full complement of chromosomes it is expected that they should not differ from each other in the expression of this character. Differences in the monosomic plants, as compared to control, could be expected due to the deficiency of a chromosome. In this note we report the variation in disomic plants belonging to different monosomic lines for the onset of flowering and analyse source of this variation.

Data on mean number of days for flowering in the monosomic and the disomic plants of 20 aneuploid lines of Pb. C591 were recorded. It was observed that in all the lines the monosomic and the disomic plants did not differ significantly in flowering date from each other and, therefore, the data of individual lines for flowering date was pooled up to obtain mean values (Table 1). The data show that monosomic and the disomic progenies of the line derived from mono-5B, which are earliest in flowering, head after 85 days of sowing and those of line 6B take 91 days to flower. Other lines fall in between this range.

What is the source of variation of disomic derivatives of monosomic lines? The time period available for identifying all the aneuploid lines of Chinese Spring and Pb. C591, in

Table 1. Mean number of days for heading taken by different aneuploid lines (monosomic or disomic plants) of var. Pb. C591

Hemoeologous	Genome	A	B	D
	M or D	M or D	M or D	M or D
1		87.6±0.3	89.8±0.3	87.1±0.5
2		89.8±0.2	86.6±0.3	87.0*
3		90.0±0.5	89.4±0.5	89.7±0.4
4		88.1±0.3	90.3±0.8	89.2±0.2
5		—	85.0±0.4	87.0±1.0
6		89.4±0.1	90.0±0.2	89.3±0.6
7		88.7±0.2	89.6±0.2	89.8±0.4

M=monosomic ($2n=41$); D=disomic ($2n=42$);

* Data recorded on one plant.

addition to other concomitant cytological analyses, is very short and the personnel are few, as such the identification of monosomic plants is started when the very first plant comes to analyzable stage. Due to this reason any spontaneous mutation for earliness would be selected in some lines. The derivatives of these lines then would become early as compared to other lines. Similarly, there is a possibility of selecting late mutations in some lines because it is attempted to prolong the time period of analysis of meiotic chromosomes and monosomic plants in some lines are identified late in the season.

KUSPIRA & UNRAU (1957) have shown, using substitution lines of Chinese Spring, that major genes for earliness are located on several chromosomes in the three varieties studied by them. Spontaneous mutations for this character are thus expected to occur in many aneuploid lines. Since the genes on the univalent of the monosomic plants are present in a hemizygous state, it is to be expected that the expression of mutations of genes on the univalent will be facilitated. This could effect homozygosity for newly arisen mutants.

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**The effect on gliadin allele composition of environmental selection
and selection for seed size in a population formed from
a multi-line cross of bread wheat varieties**

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Introduction

There are several methods of selection of the best genotypes available for the cereal breeding programmes. One of them involves growing a hybrid population for several generations in the field. Natural selection favours those genotypes which are most adapted to the particular field conditions and decreases or eliminates the less adaptive ones ¹⁾. Therefore the selective value of a character can be measured by determining the change in its frequency in the population before and after selection. This approach was successfully used in studies of hybrid populations in barley (2) and maize (3), where the polymorphism of certain enzymes was strongly affected by natural selection. We used the same approach and found differences in adaptive value of several alleles of Gld IB and Gld ID, two main complex loci of wheat controlling the synthesis of gliadin, the storage protein of the seed.

Methods

The initial population was created by a three-step hybridization of 8 varieties of spring wheat *T. aestivum*: Saratovskaya 210, Dalnevostochnaya, Kzyl Bas, Zarnitsa, Kirgizskaya Yubileinaya (all from USSR), Solo (FRG), Norrona (Norway), Siete Cerros 66 (Mexico). In step one, 4 pairs of parents were crossed and the resulting F₁ progeny were crossed with each other in step two. In the third step, the secondary hybrids were crossed, giving progeny which contained genes from all eight parents. At each step at least 30-40 maternal spikes and 50-80 paternal plants were used for each cross. The final hybrid material was propagated in a glasshouse (2 first generations of self-pollination) to obtain seeds of the initial population (IP). These seeds were sown in the field at the rate of 20 cm² for one plant, in the north forest-steppe of Novosibirsk, USSR. All plants of a harvest without any exception were thrashed together. 500-1,000 seeds (in different years) were randomly selected from the harvested grain and used for sowing.

There are two variant types of population originated from IP, the first having arisen only by environmental selection during 4 years (NS). The second is natural plus artificial selection for grain size and marketability being about 33% of all seeds (NAS). In the NAS variant the random sample for sowing was taken from the mass of seeds after artificial selection.

The extraction of gliadin with 70% ethanol and single-seed electrophoresis was performed as described earlier⁴⁾. Alleles in parental varieties were identified by analysis of F₂ seeds of the primary crosses (self-pollination of some F₁ plants). Gld 1B and Gld 1D are the main gliadin-coding loci localized on chromosomes 1B and 1D, respectively. This nomenclature and numeration of alleles are in accordance with the catalogue of blocks of gliadin components⁴⁾.

Results

The frequencies of alleles Gld 1B and Gld 1D in variants of population (IP, NS and NAS) are listed in Table 1. The comparison of variants IP and NS shows the effect of 4 years of natural selection: the frequencies of Gld 1B4 and Gld 1D3 increase, and of Gld 1B15 and Gld 1D6 decrease. These differences between the two populations are statistically significant ($F=10.8^{**}$, 7.3^{**} , 9.7^{**} , and 8.3^{**} , respectively). Consequently, both Gld 1B4 and Gld 1D3 are adaptive and in contrast, Gld 1B15 and Gld 1D6 both have some negative effects on the survival or grain production under the conditions of experiment. The changes in frequencies of other alleles are not statistically significant.

Table 1. The frequencies of alleles of gliadin-coding loci in different variants of hybrid population of spring wheat (in %%)

Vaeriant of population	Locus Gld NN alleles	1B					1D				
		4	1	17	15	2	3	5	6	±	± 0
IP		42.3	32.8	9.7	12.7	2.5	42.6	14.9	12.4	15.0	13.8
NS		55.1	27.4	9.2	5.5	2.8	53.1	12.5	6.0	17.7	9.1
NAS		48.7	37.6	8.6	4.9	0	61.0	17.0	11.4	9.7	1.1

It is known that selection can also operate at the level of twolocus combinations⁵⁻⁷⁾. We studied changes in frequencies of the most widespread alleles of one Gld locus in combinations with the different alleles of the second locus (Table 2). The comparison of IP and NS variants shows the strong influence of natural selection on some two-allele combinations. For example, in NS almost 98% of Gld 1D1 exists in genotypes either with Gld 1B4 or Gld 1B1. The combinations of Gld 1D3 with Gld 1B4 or Gld 1B1 are also favourable. In contrast, alleles Gld 1D5 and Gld 1B1 interact unfavorably.

The comparison of variants NS and NAS shows the influence of grain size selection. As one might expect, the effects of this 4-year-long selection on allele frequencies were stronger than those of environmental selection (Table 1). There are significant difference between NS and NAS in the frequency of 4 out of 5 Gld 1D alleles studied, as well as Gld 1B1 allele ($F=4.9^*$ for Gld 1D3; 10.7^{**} for Gld 1D1; 7.3 for Gld 1D6; 31.5^{***} for Gld 1D10; 9.6^{**} for Gld 1B1).

There are many changes in frequencies of two-allele genotype also (Table 2). Apparently it is possible to interpret the increase in Gld 1D3 frequency by favouring artificial selection for combination Gld 1B1-Gld 1D3. In NAS variant, Gld 1D5 exists only with Gld 1B4 or Gld

Table 2. The frequencies of alleles of one locus on the background of different alleles another locus.

1. Gld ID alleles on the different Gld IB background (in %%)							
Population	Background allele Gld	Gld ID alleles	3	5	1	6	10
IP	IB 4		43.2	13.8	17.4	13.8	11.8
IP	IB 1		39.6	15.3	14.5	13.9	16.6
NS	IB 4		54.6	13.8	22.0	6.1	3.2
NS	IB 1		49.1	9.1	19.7	3.2	19.6
NAS	IB 4		57.1	12.7	13.3	16.9	0
NAS	IB 1		59.6	28.0	1.4	7.0	2.8

2. Gld IB alleles on the different Gld ID background (in %%)							
Population	Background allele Gld	Gld IB alleles	4	1	17	15	2
IP	ID 3		42.7	30.4	10.9	14.6	1.5
IP	ID 1		48.8	31.5	4.2	9.5	6.0
IP	ID 5		37.4	32.2	11.5	14.9	4.0
NS	ID 3		56.5	25.2	8.9	7.0	2.3
NS	ID 1		68.4	29.4	1.4	0.7	0
NS	ID 5		56.5	18.5	13.0	0.9	11.6
NAS	ID 3		45.6	37.5	11.5	5.3	0.0
NAS	ID 1		72.4	6.1	12.3	9.2	0.0
NAS	ID 5		36.2	63.8	0.0	0.0	0.0

1B1, but never with three other Gld 1B alleles studied. In contrast to environmental selection, selection for seed size causes a several-fold increase in the frequency of the Gld 1B1-Gld 1D5 combination, but reduces the frequency of Gld 1B1-Gld 1D1 genotypes.

Discussion

This is the first report to our knowledge in which significant changes in Gld allele frequencies in a hybrid population of *T. aestivum* after several years of selection has been described. Different Gld alleles as well as genotypes are not equal in their adaptive values. Natural selection was the major force responsible for the patterns of genetic change which occurred in hybrid populations of barley (2), and maize (3), and for the genetic structure of wild populations of barley (6, 7) and *T. dicoccoides* (8). Very likely, prolamin-coding loci as well as some enzyme loci used in these studies do not have direct effects but serve as good genetical markers through gene linkage. These markers may be successfully exploited in selection programmes (9). For example, 56% of all modern spring wheat varieties of the USSR have Gld 1B4, and 72% have Gld 1D3 alleles (Metakovsky, unpublished), although there are more than 10 different alleles in each of these two loci (4). It is these alleles which were shown to be the most adaptive in our study.

Two homoeologous loci studied was shown to be different in their responses to the selection for grain size. One may suggest that this result reflects to some extent the special role of D genome in formation of bread wheat grain.

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Correlation and path studies in wheat under normal and saline conditions

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Improvement in grain yield is the sole aim of breeding for cereals under any agro-climatic or soil condition. However, yield being the complex out come of its components, selection based on yield alone would be misleading. Selection based on yield components would, therefore, be more rewarding. This requires information on nature and magnitude of variations in the base population, association of yield components with yield and among themselves; and the extent of environmental influence. Correlation coefficients, though bring out necessary information on nature and extent of various associations yet do not provide information on cause and effect relationship. Path coefficient analysis measures the direct influence of a variable on other and permits the partition of associations into components of direct and indirect influences (DEWEY & LU 1959). Reports on correlation and path coefficient analysis are many in wheat under normal condition. (BAKER *et al.* 1968 ; JAIMINI *et al.* 1974 ; KUMAR 1979), information on the same under salt stress conditions in crop plants as a whole (SINGH 1979, 1980) and wheat, in particular (GIRIRAJ *et al.* 1980) are quite deficient. Present study was, therefore, undertaken to compute correlation and path coefficients in 15 genotypes of wheat under normal and saline environments.

Material and Methods

In the winter season of 1979-80, a field plot study was conducted on sandy loam light textured soils (ECe .5, pH 8.0). Fifteen genetically diversified cultivars common wheat (WL-711, WH-157, WH-147, UP 241, UP 270, UP 368, HD 2122, HD 2160, HD 1593, HD 1982, K 7435, HP 1102, HUW-SDW-1 and K. 68) were field grown in the main plots separated by polythene sheets burried 90 cm deep to check lateral movement of salts. A split-plot design with three repeats was adopted. Levels of water salinity 2.1 (control) and 16.0 mmho/cm were adjusted to main plots whereas, varieties to 2.5 m long single rows in each main plot. Waters of desired salinity were prepared keeping in view the natural poor quality under ground water encountered in this locality which contained Na : Mg : Ca = 60 : 25 : 15 and Cl : SO₄ : HCO₃ = 2 : 1 : 1 as reported by KUMAR *et al.* (1981). Source of control water was a tube-well, possessing good quality water. In all 5 irrigations of 6 cm each were applied.

One month of sowing, 50 plants at a distance of 5 cm apart were spaced in each row. Germination of seeds was assessed and expressed as a percentage, whereas, data on number of tillers/plant, plant height (cm), number of grain/spike, 1,000-grain weight (g) and grain yield/plant (g) were recorded on 10 random plants for each treatment. Correlation

coefficients were computed at the phenotypic level. The path coefficient analysis of yield/plant with its five components were estimated following DEWAY & LU (1959).

Results and Discussion

Correlation coefficients : The association of grain yield with plant height and grains/spike was significant positive ; was however, significant negative with germination of seeds under normal conditions (Table 1). These associations signify that yield/plant was adversely affected due to plant density increased, following higher germination rate, high yielding genotypes on the other possessed more grains/spike and were rather tall in stature under normal environment. In saline environment, however, all the attributes excepting 1,000-grain weight possessed significant positive association with grain yield ; associations of plant height and tillers/plant were however highly significant. This underlines the importance of plant height and tillering ability in selecting high yielding genotypes of wheat under salt stress environment. These results corroborate the earlier findings of TORRES & BINGHAM (1973) on tillers ; and of GIRIRAJ *et al.* (1980) and KUMAR *et al.* (1981) on plant height that tillers and plant height are the seriously affected components under saline conditions in wheat.

There was a significant positive association of plant height with grains/spike and tillers/plant under saline environment which suggests the possibility of their simultaneous improvement, confirming findings of GIRIRAJ *et al.* (1980) in wheat. Plant height and grains/spike exhibited significant positive association with grain yield over the environments. Association of 1,000-grain weight was recorded significant negative with grains/spike whereas, was non significant negative with tillers/plant in both the environments. KUMAR (1979) also observed significant negative association between 1,000-grain weight and grains/spike in wheat under normal environment. The traits 1,000-grain weight and grains/spike may not therefore, be simultaneously improved in either of the two environments.

Path coefficient analysis : In normal environment plant height had maximum direct positive

Table 1. Genetic correlation coefficients among six attributes in wheat two environments.

	Tillers/ plant	Plant height	Grains/ spike	1000-grain weight	Grain yield/ plant
Germination of seeds	0.322 (0.306)	0.498 (0.190)	0.577* (-1.000)**	1.000** (-0.099)	-0.547* (0.558)*
Tillers/plant	—	0.007 (0.861)**	-0.209 (1.000)**	-0.304 (-0.175)	0.504 (1.000)**
Plant height	—	—	0.498 (1.000)**	0.795** (0.071)	0.595* (0.725)**
Grains/spike	—	—	—	-0.692* (-0.878)**	0.576* (0.568)*
1000-grain weight	—	—	—	—	0.048 (-0.052)

*, ** Significant at P=0.05 and P=0.01, respectively.
The values in parenthesis are of saline environment.

Table 2. Path coefficient analysis of genotypic correlation of five attributes with grain yield in wheat under two environments

Correlated Characters	Direct and indirect effects					correlati. with grain yield
	Germination of seeds	Tillers/plant	Plant height	Grains/spike	1000-grain weight	
Germination of seeds	<u>0.014</u> (0.417)	0.020 (0.294)	0.807 (-0.054)	-0.069 (-0.120)	-1.319 (0.021)	-0.547 (0.558)
Tillers/plant	0.005 (0.128)	<u>0.062</u> (0.961)	0.011 (-0.246)	0.025 (0.120)	0.401 (0.037)	0.504 (1.000)
Plant height	0.007 (0.079)	0.001 (0.827)	<u>1.62</u> (-0.286)	0.018 (0.120)	-1.049 (-0.015)	0.595 (0.725)
Grains/spike	0.008 (-0.417)	-0.013 (0.961)	-0.212 (-0.286)	-0.120 (0.120)	0.913 (0.190)	0.576 (0.568)
1000-grain weight	0.014 (-0.041)	-0.018 (-0.168)	1.288 (-0.020)	0.083 (-0.106)	-1.319 (-0.217)	0.048 (-0.052)

Figures underlined denote direct effects; values in paranthesis pertain to saline environment.

Residual effects for normal environment = 0.380,
and for saline environment = 0.417.

effect with grain yield (1.62); whereas grains/spike and 1,000-grain weight had the strong negative direct effects (-0.120 and -1.319 , respectively) with grain yield (Table 2). GIRIRAJ *et al.* (1980) also reported highest direct positive effect of plant height on grain yield in wheat under normal conditions.

Notwithstanding, direct negative effect of grains/spike with grain yield, their association was significant positive in normal conditions (Table 1). This association might therefore, be due to high indirect influence of grains/spike via 1,000-grain weight. Even though, association of germination of seeds with grain yield was significant negative in normal environment, the direct influence of former was negligible. This association was thus, due to indirect negative influence of germination of seeds via 1,000-grain weight and grains/spike.

In saline environment, tillers/plant showed maximum direct positive effects on grain yield (0.961), followed by germination of seeds (0.417) and grains/spike (0.120). Our results on tillers/plant are in confirmity with those of GIRIRAJ *et al.* (1980) under saline environment. Grains/spike under salinity which possessed significant positive association with grain yield influenced it mainly indirectly via 1,000-grain weight. Even though, plant height possessed significant positive association with grain yield, direct effect was negative (-0.286), this association was therefore, mainly indirectly via tillers/plant and grains/spike.

It is worth mentioning that under normal environment germination of seeds and 1,000-grains weight exhibited more indirect effects via plant height. On the contrary, in saline environment per cent seed germination, plant height and grains/spike showed more indirect effects via tillers/plant. Higher values for residual path ways under saline conditions indicate that traits other than included in the study also played an appreciable role. In saline environment thus tillers/plant followed by per cent seed germination add grains/spike appear chief components.

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Correlation and path analysis in wheat under high temperature and moisture stress conditions

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Rainfed wheat in India is generally sown in later part of October to avoid high temperature at the early growth stage (HOWARD 1924) while monsoon recedes by later part of September. During this interim period, the soil loses moisture which adversely affects germination resulting drastic reduction in yield. In rainfed situations early growth and ripening both occurs under high temperature.

Effect of temperature on the early growth of wheat has been studied under controlled conditions (FRIEND *et al.* 1965 ; FRIEND 1966, ASANA 1974) as well as under field conditions (SISODIA 1977 ; SISODIA *et al.* 1978). In these studies, information on the nature and magnitude of association of yield components is not available.

Presently, there is dearth of suitable genotypes which can make satisfactory early growth if exposed to high temperature by advancing the date of sowing from late October to late September or early October to provide favourable soil moisture status for better germinating stand. Realising the situation, breeding wheat for high temperature tolerance has become increasingly important to get quantum jump in rainfed wheat yield, which requires information on correlation and path analysis to know the nature, extent and direction of selection criteria (DEWEY & LU 1959),

This study, therefore was undertaken to determine the components of yield in wheat under high temperature and moisture stress conditions and to suggest suitable parameters for selection under such stress conditions.

Materials and Methods

The material of this study consisted of 15 diverse genotypes (Table 2). These genotypes were planted on 7. 10. 1982, at Zonal Agricultural Research Station, Powarkheda, M.P., India, in a randomised block design with four replications, having a net plot size of 5 m × 1.20 m (4 rows/30 cm apart) In each variety and in each replication 10 random plants were selected for recording observations on plant height, number of effective tillers per plant, number of spikelets per Spike, ear length, grain weight per ear and grain yield per plant. Genotypes were exposed to 34.5°C average temperature at the early growth stages by sowing during early October and grown on conserved moisture of the preceding monsoon. No water was applied from sowing to maturity of the crop.

Genotypic and Phenotypic correlations were estimated as per MILLER *et al.* (1958) Path coefficient was calculated by the technique outlined by DEWEY & LU (1959).

Table 1. Summary of average temperatures(°C) during September to March at Powarkheda (Normal, 1982-83)

Month	Normal *		1982-83	
	Maximum	Minimum	Maximum	Minimum
September	33.5	22.2	31.5	23.2
October	34.8	19.1	34.5	20.9
November	31.8	13.3	29.1	16.3
December	26.6	9.7	28.4	12.7
January	28.0	9.5	26.4	10.1
February	30.3	11.2	28.1	11.6
March	36.2	15.7	34.2	15.5

* Average of 10 years

Results and Discussion

Temperature data :

Maximum temperature was found some what lower than normal during the month of September (31.5°C), November (29.1°C), January (26.4°C) and Febraury (28.1°C) whereas found close to normal during the month of October (34.5°C) and comparatively higher in December (28.4°C) and March (34.2°C). Table 1 shows that even normal temperatures of these months are not suitable for the normal development of wheat plant, though this Zone is traditionally wheat growing areas.

Rainfed wheat is generally planted after 15th October, which flowers in mid January and matures by mid March. The early growth and ripening both occurs under comparatively higher temperature conditions.

Temperature above 25°C decrease relative growth rate of wheat through their influence on leaf growth and net assimilation rate (FRINED *et al.* 1965). Increasing the temperature from 10-30°C increased the rate of elongation of developing spikes resulting smaller Spikes (FRIEND 1966). According to ASANA (1972), higher temperature after germination hasten differentiation and reduced tillering (as quoted by SISODIA *et al.* 1978).

ASANA (1976) studying the effect of temperature under controlled conditions (range 25°C to 31°C) On grain development in 2 Australian cultivars 'Ridley' and 'Diadem' and 3 Indian cultivars 'NP 824' 'NP830' and 'Pbc 281', observed that 6°C rise in day temperature decreased the mean grain weight by 16%.

In this study, genotypes were exposed to approximately 9°C higher temperature than the normal requirements (25°C) of wheat plant during early growth stages and found relatively tolerant to high temperature.

Correlation :

Highly significant difference for all the traits under study indicated wide gentic diversity among the genotypes (Table 2).

In general, results revealed comparatively higher magnitude of genetic correlations than

Table 2. Mean performance of different genotypes for various characters.

	Plant height (cm)	No. of effective tillers/plant	Ear length (cm)	No. of spikelets spike	Grain weight/ ear (gm)	Yield/plant (gm)
1. ASW 003	75.65	12.15	9.75	18.75	0.83	11.65
2. ASW 009	78.00	14.05	9.50	20.75	0.97	13.34
3. ASW 011	85.00	12.60	8.25	19.00	1.14	14.23
4. ASW 026	73.95	12.37	10.00	21.00	1.10	13.42
5. ASW 032	70.95	12.84	9.00	20.00	1.07	16.02
6. ASW 034	76.82	14.88	10.50	21.00	1.08	17.38
7. ASW 037	86.42	11.47	10.25	17.50	1.27	13.57
8. ASW 037	71.35	11.57	8.50	16.25	1.02	11.68
9. ASM 006	68.00	10.24	9.00	19.00	0.76	8.66
10. ASM 008/5	67.25	10.89	8.50	18.75	0.81	7.79
11. ASM 009/1	78.25	10.75	8.50	18.75	1.03	10.64
12. ASM 009/3	72.25	6.12	8.50	18.25	0.86	5.52
13. ASM 009/6	72.75	11.50	9.00	20.50	1.10	12.43
14. ASM 010/3	80.75	10.07	10.75	21.75	1.53	15.06
15. Sujata(Standare variety)	96.48	9.74	11.00	19.50	2.18	19.94
C.D.C. 01)	5.12	3.92	1.16	2.79	0.22	6.68

Table 3. Genotypic (rg) and Phenotypic (rp) correlations among six characters in wheat.

Character	Correlation	No. of effective tillers/plant.	No. of spikelets/spike	Ear length	Grain weight/ear	Yield/Plant
Plant height	rg	-0.063	0.072	0.616**	0.852**	0.740**
	rp	0.088	0.052	0.472**	0.684**	0.610**
No. of effective tillers/plant	rg		0.430**	0.244	-0.094	0.439**
	rp		0.214	0.080	-0.152	0.656**
No. of spikelets/spike	rg			0.538**	0.271	0.441**
	rp			0.422**	0.154	0.453**
Earlength	rg				0.707**	0.614**
	rp				0.584**	0.868**
Grain weight/ear	rg					0.882**
	rp					0.661**

* P=0.05, ** P=0.01

Table 4. Path coefficients of the components of yield

Character	Plant height	No. of effective tillers/plant	No. of spikelets/spike	Earlength	Grain weight/ear	Genotypic correlation with grainyield
Plant height	-0.014	-0.040	-0.006	-0.289	1.077	0.740
No. of effective tillers/plant	0.001	0.638	0.033	-0.114	-0.119	0.439
No. of spikelets/spike	-0.001	0.274	0.077	-0.252	0.342	0.441
Earlength	-0.008	0.156	0.041	-0.468	0.893	0.614
Grain weight/ear	-0.012	-0.060	0.021	0.331	1.264	0.882

The bold figures denote direct effects.

Phenotypic correlations (Table 3) indicating that selection for genetically associated characters could give better response in yield than would be expected on the basis of Phenotypic association (ROBINSON *et al.* 1951). At the genotypic level grain yield per plant had strong and highly significant positive correlations with grain weight per ear (.882**) . Plant height (.740**) and ear length (.614**). Grain weight per ear seemed to be most important character, due to its high correlation coefficients. Suggesting that an increase in grain weight per ear may considerably increase the plant yield under stress conditions (SIKKA & MAINI, 1962 ; SRIVASTAVA *et al.* 1980).

Path coefficient analysis :

Direct and indirect effects of yield components based on genotypic and Phenotypic correlations revealed almost similar results (SAHU & PATNAIK 1979). Hence, results based on genotypic correlations are only presented (Table 4). Grain weight per ear had the largest direct effect (1.264) on plant yield followed by number of effective tillers per plant (.638). Direct effect of number of spikelets per spike was trivial (.077). Ear length and plant height had negative direct effect (-0.468 and -0.014 respectively), though they have shown positive correlation with effects yield (Table 3) which were mainly due to their positive indirect via grain weight per ear (Table 4). This suggests that selection merely on the basis of simple correlation will be misleading (V. SINGH 1972). The high positive correlation of grain weight per ear was due to its direct and indirect effects via each other.

The direct contribution of grain weight per ear and its indirect importance from plant height and ear length distinctly emphasized the value of this character for selection of genotypes for breeding wheat under high temperature and moisture stress conditions. PATHAK & NEMA (1983) also reported direct bearing of this trait on plant yield under such conditions.

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Diallel analysis for combining ability over environments in wheat

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Phenotypic expression of quantitative characters is highly influenced by environmental fluctuations. Genotype \times environment interaction, depending upon their nature and magnitude, leads to bias in the estimates of gene effects and combining ability for various characters sensitive to environmental modulations. Such traits are less amenable to selection. It is, therefore, necessary to assess the sensitivity of estimates of gene effects under variable environmental conditions so as to ensure better prediction and gain under selection. Present study deals with such an endeavour.

Materials and Methods

The experimental material consisted of parental and F_1 generations of a 9×9 diallel set (excluding reciprocals) of spring wheat (*Triticum aestivum* L. em. Thell). The experimental material was laid out in a randomized block design with three replications in two environments, namely normal (irrigated) and stress (rainfed). The nine parents included were WL 711, NP 846, WG 377, HD 1981, UP 262, HD 1925, HD 2122, Raj 821 and Sonalika. Single seeds were sown in 3 m rows and at 30×15 cm row to row and plant to plant distance, respectively. From each entry (parent and F_1) five competitive plants were randomly selected from each replication in both the environments for recording observations on characters days to heading, plant height, tiller number, total biomass, number of grains/ear, 1,000-grain weight and grain yield/plant. Pooled analysis for combining ability was carried out following Method 2, Model 1 of GRIFFING (1956) as extended by SINGH (1973).

Results and Discussion

Pooled analysis of variance over the environments (Table 1) revealed highly significant differences amongst them. So was true for genotype \times environment interactions.

The pooled analysis of variance for combining ability reflected that both the general combining ability (gca) and specific combining ability (sca) mean squares were significant. Thus, both kinds of gene effects figured important in controlling inheritance of all the characters studied. Both gca \times environments as well as sca \times environments interactions were significant for all the characters except sca \times environments for days to heading, indicating thereby the sensitivity of both kinds of gene effects to the environmental variations. However, relatively higher magnitude of gca \times environments interactions as compared to sca \times environments interactions suggested a higher sensitivity of gca to environments than that of sca. Similar results were obtained by PARODA & JOSHI 1970a, b; PARODA & HAYS

Table 1. Pooled analysis of variance

Source	d.f.	Mean squares							
		Days to heading	Plant height	Tiller number	Total biomass	No. of grains/ear	1000-grain weight	Grain yield/plant	
Layout									
Environments	1	32148.30**	155395.10**	3583.22**	236823.66**	2270.03**	660.21**	7047.10**	
Genotypes	44	182.74**	780.40**	5.44**	308.52**	198.38**	95.88**	26.01**	
G × E	44	9.80**	99.14**	3.66**	231.83**	54.90**	11.59**	19.82**	
Error	176	3.88	6.74	0.88	27.20	8.39	2.66	1.94	
Combining ability									
gca	8	305.40**	1326.66**	3.62**	272.43**	307.30**	148.84**	12.04**	
sca	36	6.59**	23.14**	1.41**	65.16**	12.54**	5.99**	7.92**	
gca × environments	8	9.78**	132.99**	1.45**	85.29**	33.15**	8.88**	9.06**	
sca × environments	36	1.83	10.85**	1.17**	75.50**	15.01**	2.75**	6.06**	
Error	176	1.29	2.25	0.29	9.07	2.80	0.89	0.65	
gCa/sca ratio		5.22	5.76	0.27	0.43	2.84	2.64	0.14	

** Significant at 1% level of probability.

1971 and SHARMA & SINGH 1982. Perhaps the heterozygosity *per se* and physiological advantages attached hitherto by virtue of heterosis or enhanced metabolic rates (SINHA & KHANNA 1975) have contributed to lower sensitivity of sca to environmental fluctuations as compared to gca.

The gca/sca ratio (based on equivalent component of mean squares) in the pooled analysis indicated that gca effects were predominant and played a more important role than the sca effects in exercising genetic control for days to heading, plant height, number of grains/ear and 1,000-grain weight hence pedigree method of selection can be used for the improvement of these characters. Contrary to it, characters like tiller number, total biomass and grain yield were mainly under the control of non-additive gene action, though they also showed considerable amount of additive genetic variance. Improvements of such characters warrants for a breeding methodology which can capitalize additive as well as non-additive genetic variance. In this situation biparental mating offers good promise to increase the frequency of genetic recombination and hasten the rate of genetic improvement (GILL *et al.* 1972 and SRIVASTAVA *et al.* 1980). Inclusion of F₁ hybrids showing stable sca and having parents with good gca, less altered by changes to environmental variations into multiple crosses, could also prove a worthwhile approach.

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Studies on biological yield and harvest index in durum wheat*

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The biological yield refers to the total dry matter accumulation of a plant system. Improved harvest index represents increased physiological capacity to mobilize photosynthates and translocate them into organs having economic yield. Since economic yield is only a fraction of dry matter produced, the harvest index forms a useful measure of yield potential. Accordingly, the present study was taken up to study the biological yield and harvest index in durum wheat over three environments.

Material and Methods

The present study was conducted on 45 diverse genotypes of durum wheat (*Triticum durum* Desf.). All the genotypes were grown in randomized block design consisting of three replications in three different environments. The environments were, i) Normal sown, high fertility and irrigated (E_1), ii) Medium fertility and restricted irrigations (E_2) and iii) Rainfed and low fertility (E_3). The data were recorded for various characters and the correlation and path coefficients were obtained according to the standard formulae.

Results and Discussion

From the analysis of variance, the mean squares due to genotypes were found highly significant for all the eleven characters studied (flag leaf area, awn length, days to earing, plant height, tiller number, biological yield, grain yield, harvest index, grains per ear, spikelets per spike and 1,000 grain weight) indicating sufficient genetic variation among genotypes for all these characters. Considering the mean performance of genotypes for different characters studied in the three environments, it appeared that genotype V 45, R 6009, R 6011, R 6029, R 6032, CPAN 6048, CPAN 6035, WH 822, V 41, V 43 were good for grain yield in all the environments. These genotypes also showed expression of component characters viz., harvest index, tiller number and biological yield.

Of the various component characters of grain yield, a few which may be positively associated with yield, often prove to be useful in selection. Hence the knowledge of such associations is valuable in planning effective and successful breeding programme. In the present study (Table 1), grain yield showed highly significant and positive correlations with biological yield, tiller number and harvest index (except in E_3) and are in accordance with earlier reports in wheat. (KALTSIKES & LEE 1971; DE PACE *et al.* 1978; SIDU *et al.* 1976). Grain yield appeared to be weakly but positively correlated with plant height, grains and

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Table 1. Correlation coefficients between grain yield and other component characters in durum wheat in 3 environments

Character	Biological yield			Grain yield			Harvest index		
	E 1	E 2	E 3	E 1	E 2	E 3	E 1	E 2	E 3
Flag leaf area	0.045	0.168	0.058	-0.095	0.103	0.032	-0.355*	-0.289	-0.113
Awn length	0.107	0.165	0.031	0.076	0.091	-0.011	-0.062	-0.347*	-0.198
Days to earing	-0.038	-0.016	0.162	-0.069	-0.006	0.178	-0.072	-0.004	0.048
Plant height	0.276	0.232	0.269	-0.084	0.266	0.261	-0.598**	-0.053	-0.029
Tiller number	0.643**	0.745**	0.745**	0.633**	0.737**	0.727**	0.128	0.200	-0.070
Biological yield	-	-	-	0.904**	0.980**	0.961**	-0.001	0.247	-0.116
Grain yield	0.984**	0.980**	0.961**	-	-	-	0.408**	0.420**	0.147
Harvest index	-0.001	0.247	-0.116	0.408**	0.420**	0.147	-	-	-
Grain/ear	0.151	0.272	0.247	0.147	0.282	0.293	0.004	0.162	0.179
Spikelets/spike	0.065	0.304	0.177	0.070	0.317	0.229	0.016	0.184	0.187
1000-grain weight	0.063	0.228	0.183	-0.107	0.216	0.187	-0.224	0.017	-0.007

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

Table 2. Path coefficients of grain yield vs other characters in durum wheat in three environments

Character	Direct effect			Indirect effect through		
	E 1	E 2	E 3	E 1	E 2	E 3
Flag leaf area	0.008	0.000	0.003	HI (-0.142)	By (0.154)	-
Awn length	0.006	0.008	0.005	-	By (0.152)	-
Days to earing	-0.004	0.007	-0.001	-	Earing (-0.105)	By (0.157)
Plant height	-0.021	-0.101	0.003	By (0.249), HI (-0.240)	By (0.213)	By (0.260)
Tiller number	0.005	0.016	0.024	By (0.581)	By (0.685)	By (0.721)
Biological yield	0.903	0.920	0.968	-	-	-
Harvest index	0.402	0.192	0.260	-	By (0.227)	By (-0.112)
Grain/ear	0.016	-0.007	-0.003	By (0.136)	By (0.250)	By (0.239)
Spikelets/spike	-0.012	0.004	0.017	-	By (0.280)	By (0.171)
1000-grain weight	0.009	0.005	0.010	-	By (0.209)	By (0.177)

* By denotes biological yield; HI to harvest index and earing to days to earing.

spikelets per spike and grain weight. Positive association between grain yield and grains per ear has also been reported by KALTSIKES & LEE (1971) and others in durum wheat.

There was highly significant and positive correlation between biological yield and tiller number. This revealed that increase in tiller number will increase biological yield vis-a-vis the grain yield. A positive but weak association of biological yield with plant height, grains per ear, spikelets per spike and grain weight was also noticed. CHOWDHURY *et al.* (1988) observed total biological yield to be the best selection criteria with highest genetic advance and good heritability. For increasing total dry matter they had suggested to make efforts for horizontal increase *i.e.* increase in tillers per unit area and size of spike and grain. Similar conclusion can be made from the results obtained during this investigation.

The path coefficient analysis using yield as dependent variable and other characters as independent variables was carried out (Table 2). Harvest index showed considerable direct and positive effect in all the three environments. It also had considerable positive effects through biological yield in E_2 and E_3 . High and positive direct effect of harvest index was also reported by SIDHU *et al.* (1976). Biological yield had a very high positive direct effect on grain yield. Its value was almost equal to its correlation coefficient. Its indirect effects through other traits were unimportant. This indicates that the majority of the variation in grain yield was accounted for by its association with biological yield. These results are in agreement with earlier study by SIDHU *et al.* (1976).

While concluding it appears that there was a high and consistent positive correlation of grain yield with tiller number, biological yield and harvest index (except in E_3) in all the three environments. Path coefficient analysis further revealed that biological yield and harvest index had high positive direct effects on grain yield. Tiller number was another character which had sufficient indirect effect through biological yield. Thus these characters should be given due importance while breeding for higher grain yield. Since, the observations on biological yield and harvest index are difficult to make and also become possible only after harvesting, hence selection may be based on high tillering which may avoid these problems.

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II. Records

Catalogue of gene symbols for wheat 1985 supplement

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The following updated list for enzymes was prepared by Drs. G.E. Hart (U.S.A.) and M. D. Gale (U.K.). Because of the many additions and certain revisions, this section is presented in full.

New codes to stock lists: v: hexaploid wheat, tv: tetraploid wheat, dv: diploid wheat, ad: alien addition line, su: alien (homoeologous) chromosome substitution line, s: intercultivaral (homologous) chromosome substitution line, tr: alien translocation line.

Response to Photoperiod

<i>ppd1</i>	2D(482), 2DL(540).	s: CS/Ciano 2D(540).
<i>ppd2</i>	2BS(482, 539, 540).	s: CS/Marquis 2B(539); CS/Timstein 2B(540).
<i>ppd3</i>	2A(213), 2AL(540).	

Proteins

Enzymes

1. Acid phosphatase

<i>AcpH-A1</i> .	[<i>AcpH 4</i> , <i>AcpH 8</i> (133)].	4A β (544, 133).	v: CS.
<i>AcpH-B1</i> .	[<i>AcpH 2</i> , <i>AcpH 3</i> (133)].	4BS(544, 133).	v: CS.
<i>AcpH-D1</i> .	[<i>AcpH 5</i> , <i>AcpH 6</i> (133)].	4DL(544, 133).	v: CS.
<i>AcpH-H1</i> (565).		4H(565).	ad: CS/Betzes.
<i>AcpH-R1</i> .		7R(437); 7RS(546).	ad: CS/Imperial.

2. Alcohol dehydrogenase

<i>Adh-A1</i> (544).	[<i>Adh_a</i> (128), <i>Adh_A</i> (129)].	4A(129), 4A α (544, 133).	v: CS.
<i>Adh-A1a</i> (523).	[<i>Adh_a¹</i> (128)].		v: CS.
			tv: PI 226951(128); Malavika(523).
<i>Adh-A1b</i> (523).	[<i>Adh_a²</i> (128)].		tv: CI 4013(128); Bijaga Yellow (523).
<i>Adh-B1</i> (544).	[<i>Adh_B</i> (129)].	4B(129); 4BL(544, 133).	v: CS.

<i>Adh-D1</i> (544).	[<i>Adh_D</i> (129)].	4D(129) ; 4DS(544, 133).	v : CS.
<i>Adh-E1</i> (520).		4ES(520).	ad : CS/ <i>E. elongata</i> .
<i>Adh-E¹1</i> .		L4(591).	ad : Vilmorin/ <i>Ag. intermedium</i> .
		0(591).	ad : Caribo/ <i>Ag. intermedium</i> .
<i>Adh-H1</i> (562).		4H(562).	ad : CS/Betzes.
<i>Adh-R1</i> (437).	[<i>Adh_{R2}</i> (564)].	4R(564, 437) ; 4RS (546).	ad : Holdfast/king II(564) ; CS/Imperial (437, 546).

Adh-A1b was the only variant *Adh-1* allele detected in study of a large number of *T. aestivum* and *T. turgidum* accessions (545).

<i>Adh-A2</i> (521).		5AL(521).	v : CS.
<i>Adh-A2a</i> .			v : CS and 133 other accessions(521).
<i>Adh-A2b</i> .			v : <i>T. spelta</i> K-24696 and 11 other accessions (521).
<i>Adh-B2</i> (521).		5BL(521).	v : CS.
<i>Adh-D2</i> (521).		5DL(521).	v : CS.
<i>Adh-E2</i> (521).		5EL(520).	ad : CS/ <i>E. elongata</i> .
<i>Adh-A3</i> (553).		6A(590) ; 6AL(553).	v : CS(553) ; Carola(590).
<i>Adh-B3</i> (553).		6B(590) ; 6BL(553).	v : CS(553) ; Carola (590).
<i>Adh-D3</i> (553).		6D(590) ; 6DL(553).	v : CS(553) ; Carola(590).
<i>Adh-E3</i> (520).		6E β (520)	ad : CS/ <i>E. elongata</i>
3. <i>Aminopeptidase</i>			
<i>Amp-A1</i> (544).		6AS(544, 133).	v : CS.
<i>Amp-B1</i> (544).		6BS(544, 133).	v : CS.
<i>Amp-D1</i> (544).		6DS(544, 133).	v : CS.
<i>Amp-E1</i> (520).		6E α (520).	ad : CS/ <i>E. elongata</i> .
<i>Amp-H1</i> (562).		6H(562).	ad : CS/Betzes.
<i>Amp-R1</i> (437).		6R(437).	ad : CS/Imperial.
4. <i>α-amylase</i>			
<i>α-Amy-A1</i> (576). [<i>Amy 6A</i> (310)].		6AL(310, 569).	v : CS.
<i>α-Amy-A1a</i> (576). [<i>Amy 6A1</i> (568)].			v : CS.

<i>α-Amy-A1b</i> (576).		v: Bezostaya 1; Kavkaz.
<i>α-Amy-A1c</i> . [Amy 6A1 ^m (568)].		v: Aka.
	<i>α-Amy-A1b</i> may be the same allele as <i>α-Amy-A1c</i> .	
<i>α-Amy-B1</i> (576). [Amy 6B(310)].	6AL(310, 569).	v: CS.
<i>α-Amy-B1a</i> (576). [Amy 4, Amy 6B1, Amy 6B2 [°] (568)].		v: CS(576). Rare.
<i>α-Amy-B1b</i> (576). [Amy 4 ^m , Amy 6B1 [°] , Amy 6B2(568)].		v: Mara(576).
<i>α-Amy-B1c</i> (576). [Amy 4, Amy 6B1, Amy 6B2(568)].		v: Sava (576). Rare.
<i>α-Amy-B1d</i> (576). [Amy 4 ^m , Amy 6B1 [°] , Amy 6B2 [°] (568)].		v: Sicco (576). Rare.
<i>α-Amy-B1e</i> (576). [Amy 4 ^m , Amy 6B1 ⁴ , Amy 6B2 [°] (568)].		v: Cappelle-Desprez (576).
<i>α-Amy-B1f</i> (576). [Amy 4, Amy 6B1 ⁴ , Amy 6B2 [°] (568)].		v: Sappo(576).
<i>α-Amy-B1g</i> (576). [Amy 4, Amy 6B1 ⁴ , Amy 6B2 [°] (568)].		v: Cheyenne (576).
<i>α-Amy-B1h</i> (576). [Amy 4, Amy 6B1 [°] , Amy 6B2 [°] (568)].		v: <i>T. macha</i> (576). Rare.

Two types of nomenclature have been assigned to the genes encoding the α -AMY-1 isozymes. In one, allelic states are defined for individual isozymes (568) while in the other several isozymes are considered to be the products of compound loci (569, 576). This listing shows the 'alleles' described in (568) which are assumed in (576) to be synonymous with the *α-Amy-B1a* through *α-Amy-B1h* nomenclature. *Amy 4* and *Amy 4'* are unmapped alternatives (568) which appear to be identical to zymogram bands [bands 9 and 9b (576) forming part of the *α-Amy-B1* phenotype. *Amy 6B1* [with forms *Amy 6B1[°]*, and *Amy 6B1⁴*, considered to be mutually exclusive (568)] and *Amy 6B2* [with forms *Amy 6B2* and *6B2[°]* (568)] described further aspects of *α-Amy-B1* (576). See *α-Amy1* below for further consideration of *Amy 6B2* (568).

<i>α-Amy-D1</i> (576). [Amy 6D,(310)]	6DL(310, 569)	v: CS.
<i>α-Amy-D1a</i> (576). [Amy 6D1, Amy 6D2(568)].		v: CS.
<i>α-Amy-D1b</i> (576). [Amy 6D1, Amy 6D2(568)].		v: Prelude (310); Capelle Desprez (576).
<i>α-Amy-D1c</i> [Amy 6D1 ^m , Amy 6D2(568)].		v: <i>T. spelta</i> var. <i>duhamelianum</i> .
<i>α-Amy H1</i> . [<i>α-Amy 2</i> (568)].	6H(578).	ad: CS/Betzes.
<i>α-Amy-A2</i> (576). [Amy _{7A} (310)].	7AL(310, 569).	v: CS.
<i>α-Amy-B2</i> (576). [Amy _{7B} (310)].	7BL(310, 569).	v: CS.
<i>α-Amy-B2a</i> (569). [Amy 7B1, Amy 7B2(568)].		v: CS.
<i>α-Amy-B2b</i> (569). [Amy 7B1, Amy 7B2 ^m (568)].		v: Hope.

The alternative states of *Amy-7B2*, namely, *Amy 7B2* and *Amy 7B2^m* (568), are identical to the variation in band 2 (569). The complete description of the α -*Amy-B2* variation also includes variation in band 11 (569).

<i>α-Amy-D2</i>	[<i>Amy 7D</i> (310)]	7DL(310, 569).	v: CS.
<i>α-Amy-D2a</i> (569).	[<i>Amy 7D1</i> (568)].		v: CS.
<i>α-Amy-D2b</i> (577).	[<i>Amy 7D1'</i> (568)].		v: VPM 1(577), Sears' Synthetic (576); Largo (576).
<i>α-Amy-H2</i>	[<i>α Amy I</i> (578)].	7H(578).	ad: CS/Betzes.

Three other α -*Amy* loci, namely, *Amy 6B2*, *Amy 6D2*, and *Amy 7B2*, are reported (568). No variation was observed for the products of *Amy 6D2* and *Amy 7B2*, although nullisomic analysis located the genes in 6DL and 7B, respectively. In accordance with the Guidelines, these genes are assumed to be part of the α -*Amy-D1* and α -*Amy-B2* loci, respectively. *Amy 6B2* was observed to produce alternative phenotypes (568). In a test of the segregation of these phenotypes relative to two alternative products of *Amy 6B1*, the two loci were found to be linked with a recombination frequency of 20.6% (568). However, an attempt to confirm the presence of more than one α -*Amy* locus in 6BL was unsuccessful (576).

<i>α-Amy1</i>	[<i>Amy 6B2</i> (568)].	6BL(568).	v: CS.
5. <i>β-Amylase</i>			
<i>β-Amy-A1</i> (518).		4A, β (555,518).	v: CS.
<i>β-Amy-A1a</i> (518).			v: CS.
<i>β-Amy-A1b</i> (518)			v: Ciano 67.
<i>β-Amy-D1</i> (518).		4DL(555, 518).	v: CS.
<i>β-Amy-D1a</i> (518).			v: CS.
<i>β-Amy-D1b</i> (518).			v: Bersee.
<i>β-Amy-D1c</i> (518).			v: Sears' Synthetic. Rare.
<i>β-Amy-D1d</i> (518).			v: Ciano 67.
<i>β-Amy-D1e</i> (518).			v: Mara. Rare.
<i>β-Amy-H1</i> .		4H(565).	ad: CS/Betzes.
<i>β-Amy-A2</i> (518).		5AL(518, 579).	v: CS(518). s: CS/Federation (579).
<i>β-Amy-A2a</i> (518).			v: CS.
<i>β-Amy-A2b</i> (518).			v: Koga II.
<i>β-Amy-A2c</i> (518).			v: <i>T. macha</i> . Rare.
<i>β-Amy-A2d</i> (518).			v: Holdfast. Rare.
<i>β-Amy-A2e</i> (518).			v: Bezostaya I.
<i>β-Amy-B2</i> (518).		5BL(518).	s: CS/Synthetic.

β -Amy-B2a (518).		v: CS.
β -Amy-B2b (518).		v: Sears' Synthetic. Rare.
β -AmyE ⁺ 1.	L4(580).	ad: Vilmorin/ <i>Ag. intermedium</i> .
β -AmyR1	5R(582); 5RL (581).	ad: FEC 28/Petkus 5R(582) CS/Imperial 5RL, Holdfast/King II 5R, Kharkov/Dakold 5R (581).

6. Endopeptidase

<i>Ep-A1</i> (133).		7AL(133).	v: CS.
<i>Ep-B1</i> (133).	[<i>Ep-B1</i> , <i>EpI</i> (133)].	7BL(133).	v: CS.
<i>Ep-D1</i> (133).		7DL(133).	v: CS.
<i>Ep-E1</i> (520).		7EL(520).	ad: CS/ <i>E. elongata</i> .
<i>Ep-H1</i> (562).		7HL(562).	ad: CS/Betztes.

7. Esterases

<i>Est-A1</i> .	[<i>EstA</i> (522)]	3AS(556).	v: CS.
<i>Est-B1</i> .	[<i>EstB</i> (522)].	3B(556); 3BS(557).	v: CS.
<i>Est-D1</i> .	[<i>EstD</i> (522)].	3D(556); 3DS(557).	v: CS.
<i>Est-E1</i> (520).		3ES(520).	ad: CS/ <i>E. elongata</i> .
<i>Est-R1</i> .	[<i>EstR</i> (522)]	3R(556).	ad: CS/Imperial.

Each of 208 hexaploid accessions carried the same *Est-1* alleles except accessions of *T. compactum* var. *rubriceps*, each of which carried an *Est-B1* or *Est-D1* electrophoretic mobility variant (560).

<i>Est-A2</i> .	[<i>Est-2A</i> (560)].	3A(560).	v: CS.
<i>Est-B2</i> .	[<i>Est-2B</i> (560)].	3BL(560).	v: CS.
<i>Est-D2</i> .	[<i>Est-2D</i> (560)].	3DL(560).	v: CS.

Among 208 hexaploid accessions, an apparent *Est-B2* null allele occurred frequently in accessions of *T. macha* and *T. sphaerococcum* and occasionally in accessions of *T. compactum*.. The allele was not observed in *T. aestivum* and *T. spelta* accessions (560).

<i>Est-B3</i> .	[<i>Est-3B</i> (560)]	7BS(560).	v: CS.
<i>Est-D3</i> .	[<i>Est-3D</i> (560)].	7DS(560).	v: CS.

One accession carrying an apparent *Est-B3* null allele and one carrying an apparent *Est-D3* null allele were found among 208 hexaploid accessions (560).

A 7AS locus encoding three esterase isozymes in immature grains has been reported (566).

<i>Est-A4</i> .	[<i>Est-4A</i> (560)].	6AL(524, 560).	v: CS.
<i>Est-B4</i> .	[<i>Est-4B</i> (560)].	6BL(524, 560).	v: CS.

<i>Est-D4</i> .	[<i>Est-4D</i> (560)].	6DL(524, 560).	v : CS.
Probable <i>Est-A4</i> and <i>Est-D4</i> null alleles were detected in several accessions of <i>T. compactum</i> var. <i>rubriceps</i> (560) ; otherwise, no <i>Est-4</i> variant occurred among 208 hexaploid accessions (560).			
<i>Est-A5</i> (566).		3AL(524, 566).	v : CS.
<i>Est-A5a</i> (566).			v : CS.
<i>Est-A5b</i> (566).			v : Kalyansona.
<i>Est-B5</i> (566).		3BL(524, 560).	v : CS.
<i>Est-A5a</i> (566).			v : CS.
<i>Est-A5b</i> (566).			v : Big Club.
<i>Est-A5c</i> (566).			v : Timstein.
<i>Est-B5d</i> (566).			v : Sears' Synthetic.
<i>Est-D5</i> (566).		3DL(566).	v : CS.
<i>Est-D5a</i> (566).			v : CS.
<i>Est-D5b</i> (566).			v : <i>T. macha</i> .
<i>Est-D5c</i> (566).			v : Hobbit's.'
<i>Est-D5d</i> (566).			v : Sears' Synthetic.
8. <i>Glucosephosphate Isomerase</i>			
<i>Gpi-A1</i> (548).		1AL(548, 59).	v : CS.
<i>Gpi-B1</i> (548).		1BS(548, 59).	v : CS.
<i>Gpi-D1</i> (548).		1DS(548, 59).	v : CS.
<i>Gpi-D1a</i> (59).			v : CS.
<i>Gpi-D1b</i> (59).			v : CS variant and certain CS aneuploids. Rare.
<i>Gpi-E1</i> (520).		1ES(520).	ad : CS/ <i>E. elongata</i> .
<i>Gpi-H1</i> (565).		1HS(565).	ad : CS/Betzes.
<i>Gpi-H^{ch}1</i> (59).		1H ^{ch} (59).	ad : CS/ <i>H. chilense</i> .
<i>Gpi-R1</i> (59).		1R(59).	ad : CS/King II.
<i>Gpi-R^m1</i> (59).		1R ^m (59).	ad : CS/ <i>S. montanum</i> .
<i>Gpi-U1</i> (59).		1U(59).	su : CS/ <i>A. umbellulata</i> .
9. <i>Glutamic oxaloacetic transaminase</i>			
<i>Got-A1</i> (131)		6AS(131).	v : CS.
<i>Got-B1</i> (131).		6BS(131).	v : CS.
<i>Got-D1</i> (131).		6DS(131).	v : CS.
<i>Got-A2</i> (131).		6AL(131).	v : CS.
<i>Got-B2</i> (131).		6BL(131).	v : CS.

<i>Got-D2</i> (131).	6DL(131).	v : CS.
<i>Got-E2</i> (520).	6E β (520).	ad : CS/ <i>E. elongata</i> .
<i>Got-H2</i> (562).	6H(562).	ad : CS/Betzes.
<i>Got-R2</i> (437).	6R(437).	ad : CS/Imperial.
<i>Got-A3</i> (131).	3AL(131).	v : CS.
<i>Got-B3</i> (131).	3BL(131).	v : CS.
<i>Got-D3</i> (131).	3DL(131).	v : CS.
<i>Got-Ag3</i> (134).	3AgL(134).	ad : CS/TAP67 ; su : CS/TAP67 ; tr : Certain CS 3D/Ag lines.
<i>Got-E3</i> (520).	3EL(520).	ad : CS/ <i>E. elongata</i> .
<i>Got-R3</i> (437).	3R(437).	ad : CS/Imperial.
10. <i>Hexokinase</i>		
<i>Hk-B1</i> (512).	1BS(512).	v : CS.
<i>Hk-D1</i> (512).	1DS(512).	v : CS.
<i>Hk-B2</i> (512).	3BS(512).	v : CS.
<i>Hk-E2</i> (512).	3ES(512).	ad : CS/ <i>E. elongata</i> .
Allelic variation was observed in three of 55 hexaploid accessions (512).		
11. <i>Lipoxygenase</i>		
<i>Lpx-A1</i> (133).	4A α (133).	v : CS.
<i>Lpx-B1</i> (133).	4BL(133).	v : CS.
<i>Lpx-D1</i> (133).	4DS(133).	v : CS.
<i>Lpx-E1</i> (520).	4ES(520).	ad : CS. <i>E. elongata</i> .
<i>Lpx-A2</i> (133).	5AL(133).	v : CS.
<i>Lpx-B2</i> (133).	5BL(133).	v : CS.
<i>Lpx-D2</i> (133).	5DL(133).	v : CS.
<i>Lpx-E2</i> (520).	5EL(520).	ad : CS/ <i>E. elongata</i> .
12. <i>Malate dehydrogenase</i>		
<i>Mdh-A1</i> . [<i>Mdh2A</i> (571)].	1AL(571).	v : CS.
<i>Mdh-B1</i> . [<i>Mdh2B</i> (571)].	1BL(584, 571).	v : CS.
<i>Mdh-D1</i> . [<i>Mdh2D</i> (571)].	1DL(571).	v : CS.
<i>Mdh-H1</i> (565).	1HL(565).	ad : CS/Betzes.
13. <i>Peroxidase</i>		
<i>Per-B1</i> (572).	1BS(524, 572)	v : CS.
<i>Per-D1</i> (572).	1DS(524, 572)	v : CS.
<i>Per-D1a</i> (572).		v : CS.
<i>Per-D1b</i> (572).		v : Sears' Synthetic.
<i>Per-H^{ch} 1</i> (572).	1H ^{ch} (572)	ad : CS/ <i>H. chilense</i> .

<i>Per-R1</i> (572).		1RS(572)	ad: CS/King II. tr: Veery S.
<i>Per1.</i>		7D(573) ; 7DS(574, 585).	v: CS.
<i>Per2.</i>		4B(573) ; 4BL(574, 585).	v: CS.
<i>Per3.</i>		7A(573) ; 7AS(574, 585).	v: CS.
<i>Per4</i>		3BL(585).	v: CS.
<i>Per5.</i>		3DL(585).	v: CS.
<i>PerAg1.</i>		7AgS(574).	tr: Certain CS7D/ 7Ag lines.
14. <i>Phosphodiesterase</i>			
<i>Pde-A1.</i>	[<i>Pde-A3</i> (487)].	3A(487) ; 3AS(547).	v: CS.
<i>Pde-B1.</i>	[<i>Pde-B3</i> (487)].	3B(487) ; 3BS(547).	v: CS.
<i>Pde-D1.</i>	[<i>Pde-D3</i> (487)].	3DS(487).	v: CS.
<i>Pde-S¹1.</i>		3S ¹ S(563).	ad: CS/T. <i>longissimum.</i>
15. <i>Phosphogluconate dehydrogenase</i>			
<i>PgdR1.</i>		4RL(586).	ad: CS/Imperial ; Holdfast/King II.
<i>PgdR2.</i>		6RL(586).	ad: CS/Imperial ; Holdfast/King II.
16. <i>Phosphoglucomutase</i>			
<i>Pgm-B1</i> (587).		4BL(587).	v: CS.
<i>Pgm-D1</i> (587).		4DS(587).	v: CS.
17. <i>Shikimate dehydrogenase</i>			
<i>Skdh-A1</i> (195, 549).		5AS(195, 549).	v: CS.
<i>Skdh-B1</i> (195, 549).		5BS(195, 549).	v: CS.
<i>Skdh-D1</i> (195, 549).		5DS (195, 549).	v: CS.
<i>Skdh-R1</i> (195).		5RS(195).	ad: CS/Imperial. tr: CS 4A α /5RL ; CS 5BL/5RL.
<i>SKdh-U1.</i>		5U(195).	ad: CS/ <i>A. umbellulata.</i>
18. <i>Superoxide dismutase</i>			
<i>Sod-A1</i> (588).		2AL(588).	v: CS.
<i>Sod-B1</i> (588).		2BL(588).	v: CS.
<i>Sod-D1</i> (588).		2DL(588).	v: CS.

<i>Sod-R1</i> (588).	[<i>Sod-2</i> (589)].	2R(589).	ad : Hexaploid wheat/ <i>S. cereale</i> .
19. <i>Triosephosphate isomerase</i>			
<i>Tpi-A1</i> (561).		3AS(561).	v : CS.
<i>Tpi-B1</i> (561).		3BS(561).	v : CS.
<i>Tpi-D1</i> (561).		3DS(561).	v : CS.
<i>Tpi-E1</i> (561).		3E(561).	ad : CS/ <i>E. elongata</i> .
<i>Tpi-H1</i> (561).		3H(561).	ad : CS/Betzes.
<i>Tpi-R1</i> (561).		3R(561).	ad : CS/Imperial, Kharkov/ Dakold.
<i>Tpi-S¹1</i> (561).		3S ¹ (561).	ad : CS/ <i>T. longissium</i> .
<i>Tpi-A2</i> (561).		5AL(561).	v : CS.
<i>Tpi-B2</i> (561).		5BL(561).	v : CS.
<i>Tpi-D2</i> (561).		5DL(561).	v : CS.
<i>Tpi-H2</i> (561).		5H(561).	ad : CS/Betzes.
<i>Tpi-R2</i> (561).		5R(561).	ad : CS/Imperial, Kharkov/ Dakold.
<i>Tpi-S¹1</i> (561).		5S ¹ (561).	ad : CS/ <i>T. longissium</i> .
<i>Tpi-U2</i> (561).		5U(561).	ad : CS/ <i>T. umbellulatum</i> .

Endosperm Storage Proteins

Glutenin

Glu-R1(558). 1RL(588). tr : CS/1DS-1RL.

Ribosomal RNA

Nor1(543). 1BS(543). v : Most wheats.
Nor2(543). 6BS(559). v : Chinese Spring.

Reaction to *Erysiphe graminis*

Pm1. v : Anfield(541).
Pm2. v : Crossbow *Pm6 Mli*(541).
Pm4b. v : Mission(541).
Pm6. v : Timgalen(541). Crossbow *Pm2 Mli*(541).
Pm8. v : Hammer(541) ; Stetson(541).
Mli. v : Crossbow *Pm2 Pm6* (541).

Reaction to *Puccinia graminis*

Sr5. v : Juna (567). Amika *Sr31* (567) ; Istra *Sr31* (567) ; Solaris *Sr31* (567)

Sr8a(597). *Sr8*.
Sr8b(597). *SrBB*.

v: Barleta Benvenuto (597); Klein Titan (597). Klein Cometa *Sr30*(597).

Sr29.
Sr31.

v: Hela(567); slavia(567); Vala(567).
v: Amika (heterogeneous) *Sr5*(567); Istra *Sr5*(567); Solaris *Sr5*(567).

Reaction to *Puccinia recondita*

Lr3.

v: Ilyitchovaka(570); Juna (570); Odra(570); Yubileynaya(570).
Amika *Lr26* (567); Istra *Lr26*(567); Solaris *Lr26*(567).

Lr18.

v: Reference(598) replaces(249). Timvera Derivative (598). Certain WYR accessions (598).

Lr26.

v: Amika(heterogeneous) *Lr3*(567); Istra *Lr3*(567); Iris (570); Sabina (570); Solaris *Lr3* (567).

Lr27 (596). *LrGt*, *A* (595). 3BS (596). One of two complementary genes; the second gene, *Lr31*, is located in chromosome 4A β .

Wheats with *Lr27* + *Lr31*:

s: CS*6/Ciano 3B(595); CS*6/Ciano 5B(595); CS*6/Hope 3B(595).

v: Gatcher (595). SUN27A *Lr1 Lr2a*(595). Tingalen *Lr3 Lr10*(595).

Wheats with *Lr27* + *lr31*: Most wheats with *Sr2* (595).

Lr31(596). *B*(595). 4A β (596). One of two complementary genes; the second gene, *Lr27*, is located in chromosome 3BS.

Wheats with *Lr31*+*Lr27*: See *Lr27*.

Wheats with *Lr31*+*lr27*:

v: Chinese Spring (595).

Reaction to *Puccinia striiformis*

Yr1

v: Dalee(542); Galahad(542); Virtue (542). Stetson *Yr9* (542) Longbow *Yr2 Yr6* (542).

Yr2

v: Brigand (542). Rapier *Yr4*(542). Norman *Yr6*(542). Longbow *Yr1 Yr6* (542).

Yr4 allele not designated.

v: Rapier *Yr2*(542).

Yr6

v: Norman *Yr2*(542). Longbow *Yr1 Yr2* (542).

Yr7

v: Brock(542); Renard(542); Tommy(542).

Yr9

v: Baron(542); Hammer(542); Stuart(542). Stetson *Yr1* (542).

Genetic Linkages

Chromosome 1B

1BS	<i>Gli-B1-rf3</i>	22.1 ± 6.4%	594
	<i>Gli-B1-Gli1</i>	28.1 ± 5.8cM	593
	<i>Gli-B1-nor1</i>	36.8 ± 13.5%	594
	<i>Gli-B1-centromere</i>	41.6 ± 2.5%	593
	<i>Gli-B1-Glu-B1</i>	Independent	593
		30.8 ± 7.4%	594
	<i>Gli-Glu-B1</i>	25.5 ± 5.4cM	593
	<i>rf3-nor1</i>	22.6 ± 9.2%	594
	<i>rf3-Glu-B1</i>	34.1 ± 8.5%	594
	<i>nor1-Glu-B1</i>	22cM	543
		22.5 ± 9.3%	594

Gene order *Nor1-Hk-B1-Per-B1-centromere* (572).

Chromosome 1R

1RL	<i>Glu-R1-centromere</i>	4.65 ± 1.04cM	558
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Chromosome 2B

	<i>ppd2-Sr9g</i>	Independent	539
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Chromosome 3B

3BS	<i>Lr27-centromere</i>	33.6 ± 4.1% and Independent	596
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Chromosome 5A

5AL	<i>Q-centromere</i>	Independent	583
	<i>β-Amy-A1-Vrn1</i>	37%	518

Chromosome 5B

5BL	<i>Lr18-centromere</i>	Independent	598
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Chromosome 6B

6BS	<i>Gli-B2-C-Band</i>	10.2 ± 4.3cM	559
	<i>Gli-B2-nor2</i>	20%	559
	<i>Gli-B2-centromere</i>	20.0 ± 5.3cM	559
	<i>C-Band-centromere</i>	12.2 ± 4.6cM	559
	<i>nor2-centromere</i>	0 (at P=0.05, r < 6.1cM)	559

Chromosome 7B

7BS	<i>Vrn5-LrMod</i>	25.5 ± 4.6%	569
	<i>LrMod-Pc</i>	10.5 ± 3.7%	569
	<i>Pc-centromere</i>	22.8 ± 5.3%	569
7BL	<i>centromere-α-Amy-B2</i>	5.9 ± 5.5%	569
	<i>α-Amy-B2-Pm5</i>	44.4 ± 5.1%	569
	<i>Pm5-Lr14a</i>	30.1 ± 4.5%	569

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III. Editorial Remarks

Announcement for Future Issues

WIS Nos. 61 and 62 are published in a bound volume because of troubles in business office.

WIS No. 63 will be planned for publication in September, 1986, Manuscripts for this issue are most welcome and accepted any time, not later than July 31, 1986.

WIS is open to all contributions regarding methods, materials and stocks, ideas and research results related to genetics, breeding and cytology of *Triticum*, *Aegilops*, *Seeale*, *Haynaldia* and related genera. List of stock and record data are most welcome. Manuscripts should be typewritten (double-space) in English, and submitted with duplicates. One article should not exceed five printed pages, including two textfigures (smaller than 7×7 cm²). 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 :

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Explanation of the Figure on the Cover

Chromosome idiograms

- A. Idiogram of the chromosomes of *H. vulgare* "CARINA" showing sizes and positions of the C-bands (Leishman)
 - B. Idiogram of the chromosomes of *Agropyron striatulum* showing relative sizes and positions of C-bands (Leishman stain)
 - C. C-banding pattern variants of chromosomes 2 and 7 of the barley varieties "CARINA" and "GEORGIA".
 - D. C-banding pattern variants of chromosome 5 of *Agropyron striatulum*.
- See the text article by GEORGIU for the details.
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