WHEAT INFORMATION SERVICE

ISSN 0510-3517

No.77

November, 1993

WIS

Kihara Memorial
Yokohama Foundation for
the Advancement of Life Sciences
Yokohama, Japan

WHEAT INFORMATION SERVICE

Wheat Information Service (WIS) founded in 1954 is a biannual international journal on wheat genetics and its related fields, published by Kihara Memorial Yokohama Foundation for the Advancement of Life Science. WIS promotes the exchange of research information among wheat researchers all over the world.

Wheat Information Service publishes research articles, lists of genetics stocks, gene and chromosome nomenclature, records and announcement of meetings, and other information useful for wheat researches.

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   McIntosh RA, Hart GE and Gale MD (1991) Catalogue of gene symbols for wheat, 1991 Supplement. Wheat Inf Serv 73: 40 – 57.

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Wheat Information Service
Number 77: 1 – 6 (1993)

I. Review Article

Scientific contributions of Dr. Hitoshi Kihara to wheat studies — On the occasion of his centennial —

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The year 1993 is the centennial of Dr. Hitoshi Kihara, who was a founder of Wheat Information Service. He was born on October 21, 1893 in Tokyo, and died on July 27, 1987 in Yokohama. Since this 100 years coincide to the era of development of modern biological science, and since Dr. H. Kihara had established important concept and methodology in plant genetics and evolution during this era, it would be useful to review his scientific contributions for prospecting scientific development for the next century.

This article aims to introduce his contributions to wheat researches of genetics and breeding on the occasion of his centennial anniversary.

1. Study on chromosome of wheat and its relatives

The chromosome numbers of many cultivated plants including wheat were not identified until Sakamura revealed three kinds of chromosome number among wheat species in 1918. Kihara followed him by intensive studies on chromosome karyotypes of *Triticum*, *Aegilops*, *Secale*, *Avena*, and *Hordeum* species showing three levels of ploidy, that is, 2x, 4x and 6x in nature with their basic chromosome number of seven in 1924. Furthermore, from cytological observation of meiotic chromosome behaviours in these species and their hybrids, he developed the theory of polyploidy: Among polyploid species there are two types; one includes identical duplicated genomes, auto-polyploidy, and the other consists of different sets of genome, allo-polyploidy.

2. Study on interspecific hybrid

Soon after the discovery of three levels of chromosome number of *Triticum*, Kihara made a interspecific hybrid between a bread wheat (6x) and an emmer wheat (4x), called as pentaploid hybrid (2n = 5x = 35), on which progenies chromosome behaviors were traced. He found two categories among the progenies concerning their chromosome constitution; fertile combination and sterile combination. The latter is the group which showed low fertility and produced few progenies in the next generation. On the other hand, the former group was relatively fertile to produce next

generation. The fertile group included plants having chromosome numbers of 28 or 42, which are stable for fertility and chromosome number in their progenies. The other plants in this group also tended to converge to 28- or 42-chromosome individuals in their further generations. From these observations, he drew the conclusion that there must be an unit of inheritance, named as a genome, which assure a basic constitution of organism's lives, corresponding to seven chromosomes in the wheat species.

The concept of the genome was so established as a set of chromosomes containing all genes necessary to ensure a life (Kihara 1931). This concept was conflict either with Winkler's one (1920) which corresponded a haploid set of chromosomes, or with recent utilization for the term in molecular biology like 'genomic DNA' indicating nuclear DNA.

Recent advancement of molecular biology indicates that most of coding genes exist commonly in plant kingdom with the common fashion of their array along chromosomes. These facts suggest the importance of reviewing the concept of genome for understanding species differentiation and evolution.

3. Genome analysis in *Triticum* and *Aegilops*

Guided by the principles of genome homology, he and his colleagues developed the methodology for phylogenic classification of plant species, called as genome analysis. The genome analysis is mainly based on the degree of meiotic chromosome pairing in interspecific hybrids, in addition to karyotyping and comparative analysis of morphological characters between the concerned species. Kihara's studies were very systematic ones; he included always positive and negative controls when he conducted the experiments, that is, he used three diploid species as the analyzers whose genome had been known to be different each other to determine the genome constitution of the given material.

After systematic observations of chromosome pairing in interspecific hybrids, he concluded that a common wheat consists of three different kinds of genome, namely A, B, and D, and that emmer wheat had two common genomes, A and B, with common wheat. The genome formula of einkorn, *T. monococcum* and its wild species *T. boeoticum* were commonly designated as A. D was designated for *Ae. squarrosa* and the third genome of common wheat.

The genome analysis was conducted in the related species of wheat covering all *Triticum* and *Aegilops* species by him and his colleagues, revealing that these genera consisted of eight basic genomes and their modifiers; A, B, C, C^{u}(U), D, M, Mt, and S. Polyploid species were proved to be constructed from the combinations of these genomes. This study had been initiated in early 1930's and concluded in 1972. His conclusions and the designated genome formulas in *Triticum* and *Aegilops* were essentially accepted by further detail analyses with cytological, cytoplasmic and molecular examinations by recent investigators (see "Nuclear and organelar genomes of wheat species" edited by Sasakuma 1992 for the details).

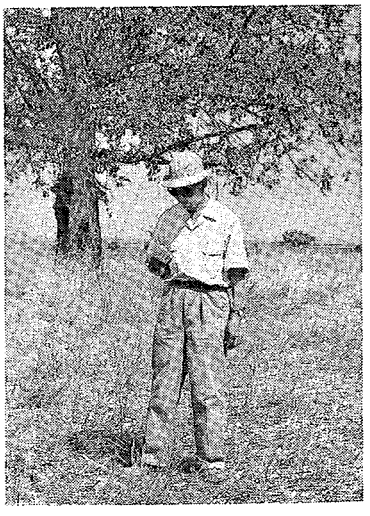
These discoveries led one of the important concepts of plant evolution; some plant species contain multiple differentiated genomes in their nucleus, that is, allo-polyploidy. This indicated

that these species had generated through interspecific hybridization and successive amphiploidization in plant evolution.

4. Disconvery of ancestral progenitors of common wheat

It was in 1945 just after the world war II, that Dr. Kihara become a world-wide famous geneticist as a discoverer of wheat ancestral progenitors, when American military mission visited his laboratory to search for scientific development during the war. He explained experimental and theoretical results that *Ae. squarrosa* should be a progenitor to D genome of hexaploid common wheat by means of genome analysis, as well as morphological analysis. He was noticed that the same conclusion had been independently achieved by Dr. Earnest R. Sears in University of Mioussouri, Colombia, USA at almost the same time (McFadden and Sears 1944). This coincidence is symbolic for the two big scientists in the wheat research.

Not only these analytical examinations, he employed two further methodologies to reach the conclusion. He made several hybridization experiment between emmer wheat and *squarrosa* accessions to produce ABD amphiploids called as synthetic wheats. These synthetic wheats were then crossed with conventional common wheats, and F_1 and F_2 progenies were cytologically and genetically examined. Since these synthetic wheats exhibited genomically identical to common wheat, it was sure that *squarrosa* is the D-genome progenitor to hexaploid common wheat. The thrid and final method was the ecological one. In 1954, he organized a plant expedition team (Kyoto University Scientific Expedition to Karakram Hindukush) to examine ecological distribution and habitat of *squarrosa* in Middle East. They found that *squarrosa* grew in the cultivated field of emmer wheat as a field weed, suggesting a possibility of natural hybridization to generate hexaploid wheat in nature. (See the picture in this page which shows the moment that Kihara found natural habitat of *squarrosa* in the suburbs of Gorgan, Iran in 1954.)



5. Study on nucleus-cytoplasm interactions

By successive backcrosses, nucleus and cytoplasm could be substituted between two species. This method was first applied for wheat and *Aegilops* species by Kihara in 1951, where *Ae. caudata* was successively backcrossed with *T. vulgare erythrospermum* as the recurrent male parent. This line showed male sterile with normal growth, that is the firstly developed strain of cytoplasmic male sterility in cultivated plants. This method has been widely applied for agronomic hybrid seed production in other crops and vegetables.

Kihara developed a series of cytoplasmic substitution lines of wheat, that is, alloplasmic lines of several 6x wheat nucleus having cytoplasm of various *Triticum* and *Aegilops*. Analyses of phenotipic traits including male fertility/sterility in these lines indicated that many plant characters were determined by interactions of nucleus and cytoplasmic genes. Furthermore, utilizing these lines, his colleagues compared overall characteristics of cytoplasmic genotypes of *Triticum-Aegilops* complex, and concluded possible cytoplasmic (maternal) progenitors of diploid species to polyploid ones (reviewed by Tsunewaki 1986).

Wheat is the only species in which comprehensive cytoplasmic substitution lines are available. This is due to another pioneering contribution by Kihara.

6. Other contribution to wheat research

Other contribution of Kihara to wheat research are listed as follows:

(1) Right- and left-handedness of wheat seedlings.
(2) Induction of haploid plant by delayed pollination in Einkorn.
(3) Cytological observation of haploid plants.
(4) Collection and conservation of wild species as genetic resources for wheat breeding.
(5) Stability of growth habitat in wheat species.
(6) Utilization of alloplasmic lines for plant breeding (NC-hybrid and NC-hetrosis).
(7) Origin of DARUMA: the parental variety of Norin 10.

As described above, Kihara made a great foundation of wheat genetics, on which modern wheat genetics and breeding base on. Before the development of molecular biology, this great scientist showed important evidences which are now alive in modern plant science from corss-hybridization experiment and cytological observation in wheat species. It is very important that he was a scientist who found not only experimental discoveries, but scientific concepts he established. Also, he was a pioneer who emphasized importance of conserving genetic strains as keys for biological research, and wild species as genetic resources for plant breeding. This is another coincidence to the case of Dr. E. R. Sears who recognized the importance of establishing genetic strains to develop a series of aneuploid lines, which were provided to world-wide wheat researchers for great deal of advancement of genetic reserach.

The concepts Kihara founded, and genetic strains he established, both would guarantee the

further development of wheat researches. In these senses, it is worthwhile to quote a motto Kihara described in an article in 1954:

The history of the earth
is recorded in the layers of its crust:
The history of all organisms
is inscribed in the chromosomes.

A list of main publication for Hitoshi Kihara

A. Main publications on wheat researches.

1924 Cytologische und genetische Studien bei wichtigen Getreidearten mit besonderer Rückischt auf das Verhalten der Chromosomen und die Sterilität in den Bastarden. Memoirs of the Coll of Sci, Kyoto Imp Univ, Series B. Vol. 1

1925 – 40 Weitere Untersuchungen über die pentaploiden *Triticum*-Bastarde. I-XII. Japan Journ Bot, Vol. 2-11.

1930 – 51 Genomanalyse bei *Triticum* und *Aegilops*. I-X. Cytologia, Vol. 3-16. (Coauthorship with I. Nishiyama, Y. Katayama or F. Lilienfeld).

1944 Discovery of DD-analyser, one of the ancestors of *Triticum vulgare* (in Japanese). Agr & Hort, Vol. 19.

1949 A new synthesized 6x-wheat. Proc. 8th Intern. Cong Genet, Hereditas, Suppl vol (Coauthorship with F. Lilienfeld).

1958 Fertility and morphological variation in the substitution and restoration backcrosses of the hybrids, *Triticum vulgare* × *Aegilops caudata*. Proc X Intern Genet Symp Vol. 1.

1965 Morphological, physiological, genetical and cytological studies in *Aegilops* and *Triticum* collected from Pakistan, Afghanistan and Iran. Result of the Kyoto Univ. Scientific Expedition to the Karakoram and Hindukush, 1955. Vol. 1. (Coauthorship with K. Yamashita & M. Tanaka).

1967 Cytoplasmic male sterility in relation to hybrid wheat breeding. Züchter, Vol. 37.

1970 Addendum to the classification of the genus *Aegilops* by means of genome-analysis. Wheat Inf Serv No. 22.

1975 Plant genetics in relation to plant breeding research. Seiken-Zihō Nos. 25-26.

1977 Spring wheats under the conditions of their old home, after their fifty year culture in Kyoto as winter crop. Wheat Inf Serv No. 44.

1979 Nucleo-cytoplasmic hybrids and nucleo-cytoplasmic heterosis. Seiken-Zihō Nos. 27-28.

1982 Importance of cytoplasm in plant genetics. Cytologia 47.

1983 Origin and history of DARUMA — a parental variety of Norin 10. Proc 6th Intern Wheat Genet Symp (Kyoto).

B. References

1) Wheat Studies — Retrospect and prospects. Kokahsha-Elsevier (1982).
2) Select Papers by H. Kihara. Kihara Foundation (1981).
3) Nuclear and Organellar Genomes of Wheat Species — Proceedings of Dr. H. Kihara Memorial International Symposium on Cytoplasmic Engineering in Wheat. Kihara Foundation (1992).
4) A complete list of publications by Hitoshi Kihara. Kihara Foundation (1993).

(References above are available by mail order from Kihara Foundation, Mutsukawa 3-122, Minami-ku Yokohama, Japan.)

Wheat Information Service
Number 77: 7 – 12 (1993)

II. Articles

Crossability of common wheat with *Aegilops squarrosa*

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Summary

Aegilops squarrosa, the D genome donor of common wheat, and rye, *Secale cereale* were crossed to eight common wheat cultivars, two sets of chromosome substitution lines of homoeologous group 5 chromosomes and their donor cultivars to reveal genetic relationship between the crossabilities of common wheat with *Ae. squarrosa* and rye. Wheat cultivars showing high and low crossabilities with rye also showed high and low crossabilities with *Ae. squarrosa*, respectively, suggesting that the crossability with *Ae. squarrosa* was controlled by the *Kr* alleles, which are known to control the crossability with rye and *Hordeum bulbosum*. Analysis by using chromosome substitution lines clarified that, as well as 5A and 5B, chromosome 5D carried genetic factor(s) controlling the crossability with *Ae. squarrosa*, which did not appeare clearly in the crossability tests with rye and *Hordeum bulbosum* in the previous investigations.

Introduction

Since *Aegilops squarrosa* (2n=2x=14, DD) is the most related diploid progenitor of common wheat, *Triticum aestivum* (2n=6x=42, AABBDD), it is expected to be one of the useful genetic resources for the improvement of common wheat. Recently, direct transfer of genetic variability of *Ae. squarrosa* to common wheat have been achieved by some workers (Thomas and Conner 1986, Gill and Raupp 1987, Cox et al. 1990). However, hybridization between common wheat and *Ae. squarrosa* is, so far, still difficult to obtain the tetraploid hybrids (ABDD). Systematic genetic analysis on the crossability of wheat with *Ae. squarrosa* would provide useful information not only for practical agriculture but also for genetics or evolution of wheat.

Crossability genes of common wheat, *Kr1* and *Kr2* located on chromosomes 5B and 5A, respectively, are known to inhibit the crossability with rye (Riley and Chapman 1967) and with *Hordeum bulbosum* (Snape et al. 1979, Falk and Kasha 1983). Investigations by Thomas et al. (1980) and Koba and Shimada (1992) showed that *Kr* alleles play an important role for the crossability of common wheat with wide range of alien species.

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We examined in the present study the relationship between the crossability of common wheat cultivars with *Aegilops squarrosa* and rye, *Secale cereale*, by using common wheat cultivars having high and low crossability with rye (Koba and Shimada 1992). It was also examined by using chromosome substitution lines whether the variation in crossability of common wheat with *Ae. squarrosa* was attributable to the factors located on the chromosomes of homoeologous group 5 of common wheat.

Materials and methods

Eight common wheat cultivars, six intervarietal chromosome substitution lines of cultivar Chinese Spring (CS) in which homoeologous group 5 chromosomes were substituted with those of Hope and Cheyenne, and their donor cultivars, as shown in Table 1 were crossed with *Aegilops squarrosa* var. *strangulata* (strain No. KU 20-9) and rye, *Secale cereale* cv. Petkus under greenhouse and field conditions. Wheat cultivars were chosen from those shown to have high and low crossability with rye in our previous study (Koba and Shimada 1992). Normal line of *Ae. squarrosa* was used in the greenhouse, while in the field an early mutant genotype of *Ae. squarrosa* which was isolated by Dr. T. Makino, National Agricultural Research Center, Tsukuba, Japan, was used for the crosses, except for the cross with Hope, because of its coincidence of the flowering period with those of the wheat lines.

CS/Hope and CS/Cheyenne chromosome substitution lines, rye cv. Petkus, and normal and mutant lines of *Ae. squarrosa* were kindly provided by late Dr. E. R. Sears, U.S.A., Kihara Institute for Biological Research, Laboratory of Plant Breeding, Tottori University and Dr. T. Makino, respectively.

In order to adjust the flowering period for the crosses in the greenhouse, seedlings of wheat, rye and *Ae. squarrosa* were kept in cold chamber at 2°C for at least one month for vernalization, then transferred periodically into the greenhouse and grown under long day photoperiod (15h) condition at 15°C and 25°C at night and day, respectively. Twenty to twenty-four florets of the first and second florets in a wheat spike were emasuculated two or three days prior to anthesis. Simultaneously, only for the crosses with *Ae. squarrosa*, a 100 mg/l 2,4-D was injected into upper one or two internodes of the wheat culms in order to accelerate the development of the hybrid embryos. The efficiency of treatment of 2,4-D for wide hybridization in common wheat was shown by Inagaki (1986) and Koba et al (1991). In the case of crosses with rye, fresh pollen grains were collected in a petri dish and a small brush was used for pollination. In the field, the same procedures were used for crossing.

At 15 to 20 days after pollination, all of the developed ovules were dissected and presence or absence of the hybrid embyros were examined in the case of common wheat × *Ae. squarrosa*, since the endosperm was not formed or incompletely formed and ovules were filled with liquid. Thus the crossability of this cross was estimated as the ratio of number of embryos formed to number of florets pollinated. In the case of common wheat × rye, number of seeds obtained in each cross was counted four weeks after the crosses and the ratios to number of florets pollinated were calculated.

Statistical analyses were carried out by using transformed values to angles of the percentages in individual spikes.

Results

Crossabilities of eight wheat cultivars with *Ae. squarrosa* and rye under greenhouse and field conditions are shown in Table 1. Significant differences between wheat cultivars in crossabilities with both *Ae. squarrosa* and rye were observed after analysis of variance in which variation between spikes within cultivars was regarded as error (Table 2). Although a difference between the crossabilities in the greenhouse and in the field was observed in each wheat cultivar, similar clear differences were observed in both conditions in both crosses with *Ae. squarrosa* and rye. Six wheat cultivars except Aobakomugi and Nanbukomugi showed relatively higher crossabilities with both *Ae. squarrosa* and rye, while Aobakomugi and Nanbukomugi showed lower crossabilities with both *Ae. squarrosa* and rye, although Aobakomugi showed rather higher crossability with *Ae. squarrosa* in the greenhouse than that in the field. These data indicate that crossabilities of common wheat cultivars with *Ae. squarrosa* and rye are controlled by the same genetic factor(s).

Six chromosome substitution lines of Chinese Spring in which a pair of each homoeologous group 5 chromosomes are substituted with their respective homologous chromosomes of cultivars Hope and Cheyenne, and their two donor cultivars were crossed with *Ae. squarrosa* and rye in the field (lower part in Table 1). In both crosses, significant differences were observed between the lines including Chinese Spring (lower part in Table 2). Donor cultivars of the substitution lines of homoeologous group 5 chromosomes, Hope and Cheyenne, showed significantly lower crossabilities than that of Chinese Spring with both *Ae. squarrosa* and rye, Hope being lower than Cheyenne, showing that Hope and Cheyenne possess genetic factors suppressing crossability not only with rye but also with *Ae. squarrosa*.

Among the six chromosome substitution lines, all of the lines showed significant reduction in their crossabilities with *Ae. squarrosa* from that of Chinese Spring under field condition at the 5% or 1% levels. Chromosome 5B's of both Hope and Cheyenne showed the greatest reduction among the homoeologous chromosomes. Chromosome 5D's also induced lower crossabilities than those of chromosome 5A's of Hope and Cheyenne, although no significant differences were observed among the six substitution lines after *t*-tests. These facts show that genetic factors controlling the crossability of wheat with *Ae. squarrosa* locate on all of the homoeologous group 5 chromosomes.

As to the crossabilities with rye, chromosome 5B's of Hope and Cheyenne showed greater reduction than chromosome 5A's which also showed significant differences from Chinese Spring. Chromosome 5D's of Hope and Cheyenne did not show any reduction in the crossability with rye as reported in the previous works (Snape et al. 1979, Falk and Kasha 1983), instead, 5D of Cheyenne showed higher crossability than that of Chinese Spring. The inefficiency of chromosome 5D's of Hope and Cheyenne on the reduction of the crossability of common wheat with rye was different from their responses with *Ae. squarrosa*.

Table 1. Crossabilities of common wheat cultivars and six chromosome substitution lines with *Aegilops squarrosa* var. *strangulata* and rye, *Secale cereale* cv. Petkus

Female parent (cv. or line)	*Ae. squarrosa*			Rye		
	No. florets pollinated	No. embryos formed	%	No. florets pollinated	No. seed set	%
Cultivar test:						
(in greenhouse)						
Fukuhokomugi	72	39	54.2	118	105	89.0
Norin 61	96	47	49.0	119	115	96.6
Shirodaruma	119	58	48.7	120	119	99.2
Shinchunaga	116	10	34.5	120	109	90.8
Nobeokabouzu	113	32	28.3	125	74	59.7
Chinese Spring (CS)	96	25	26.0	146	124	84.9
Aobakomugi	118	30	25.4	96	7	7.3
Nanbukomugi	74	0	0.0	120	0	0.0
(in field)						
Norin 61	120	84	70.0	120	82	68.3
Nobeokabouzu	120	72	60.0	122	116	95.1
Chinese Spring (CS)	120	79	65.8	126	88	73.3
Shinchunaga	119	67	56.3	120	81	67.5
Fukuhokomugi	117	50	42.7	120	47	39.2
Shirodaruma	118	44	37.3	120	106	88.3
Aobakomugi	118	4	3.4	116	20	17.2
Nanbukomugi	120	0	0.0	120	2	1.7
Substitution test:						
Hope	117	1	0.9**	84	4	4.8**
Cheyenne (Cnn)	116	13	11.2**	70	8	11.4**
CS (Hope 5A)	71	24	33.8**	60	22	36.7*
CS (Hope 5B)	72	1	1.4**	70	1	1.4**
CS (Hope 5D)	60	4	6.7**	72	60	83.3^{ns}
CS (Cnn 5A)	70	20	28.6*	71	18	25.4**
CS (Cnn 5B)	72	1	1.4**	72	8	11.1**
CS (Cnn 5D)	72	8	11.1**	72	71	98.6**

Note) Normal line and an early mutant line of *Ae. squarrosa* were used in the greenhouse and in the field, respectively, except in the cross with Hope in which the normal line was used in both conditions.
ns, * and **: Not significant, significantly different from Chinese Spring at the 5% and 1% levels, respectively.

Table 2. Analysis of variance of crossabilities of eight common wheat cultivars (upper), and six chromosome substitution lines and their recipient and donor cultivars (lower) with *Aegilops squarrosa* and rye, *Secale cereale*

Cross	Source of variance	df	MS	F
Cultivar test:				
Wheat cvs. × *Ae. squarrosa*	Between cultivars	7	758.68	9.06**
(in greenhouse)	Within cultivars	25	83.77	
Wheat cvs. × *Ae. squarrosa*	Between cultivars	7	2401.91	23.82**
(in field)	Within cultivars	32	100.84	
Wheat cvs. × Rye	Between cultivars	7	4912.84	66.62**
(in greenhouse)	Within cultivars	32	73.74	
Wheat cvs. × Rye	Between cultivars	7	2753.37	29.06**
(in field)	Within cultivars	31	94.76	
Substitution test:				
Wheat lines × *Ae. squarrosa*	Between lines	8	1266.45	12.56**
	Within lines	24	100.82	
Wheat lines × Rye	Between lines	8	2481.43	27.37**
	Within lines	20	90.67	

**: Significant at the 1% level.

Discussion

Genetic analyses on the crossabilities of common wheat with alein species have been done with respect to those with rye, *Secale cereale* (Lein 1943, Riley and Chapman 1967) and *Hordeum bulbosum* (Snape et al. 1979, Falk and Kasha 1981, 1983, Sitch and Snape 1989). In both cases, *Kr1* and *Kr2* alleles, located on chromosomes 5B and 5A, respectively, were shown to have major roles on the crossability of wheat. However, since Krowlow (1970) reported that chromosome 5D carried crossability gene *Kr3*, it has not been clearly shown that chromosome 5D had any effects on the crossabilities with rye or *H. bulbosum*, except that Fedak and Jui (1982) showed all of the homoeologous group 5 chromosomes, including 5D, had responsibility for the crossability of wheat with a cultivated barley Betzes, although they used wheat lines as male parents. In the present study, it was demonstrated that not only chromosomes 5B and 5A, but also chromosome 5D had responsibility in the crossability of wheat with *Ae. squarrosa*. Therefore, it is probable that the genetic factors controlling the crossability with *Ae. squarrosa* located on the chromosomes 5A, 5B and 5D correspond to *Kr2*, *Kr1* and *Kr3*, respectively.

Since *Ae. squarrosa* is the D genome donor of common wheat, it seems strange that the crossability of common wheat with *Ae. squarrosa* is suppressed by the genetic factor(s) located on the chromosome of the D genome itself. Riley and Chapman (1967) described the evolutional significance of the *Kr1* and *Kr2* alleles with respect to the relationship between wheat and rye that the dominant inhibitors of crossability arose by mutation and conferred evolutional and agricultural advantage upon wheat by preventing the production of sterile wheat-rye hybrids. Probably as in the case of *Kr1* and *Kr2*, dominant mutation would be occurred at a locus on chromosome 5D after the establishment of hexaploid wheat by hybridization between tetraploid wheat and *Ae. squarrosa*. Variation in the crossabilities of common wheat cultivars with *Ae. squarrosa* may be due to the combinations of the dominant cross-inhibiting factors located on the homoeologous group 5 chromosomes.

Since the genetic factor(s) located on chromosome 5D was found to be effective only for the inhibition of hybridization with *Ae. squarrosa*, not with rye, the factor(s) might be specific to prevent the production of wheat -*Ae. squarrosa* hybrid. More precise genetic characterization of the factors on the crossability with *Ae. squarrosa* will be necessary.

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Wheat Information Service
Number 77: 13 – 18 (1993)

Intermeiocyte connections and cytomixis in intergeneric hybrids. II. *Triticum aestivum* × *Psathyrostachys huashanica* Keng

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Summary

The intergeneric F1 hybrid of *Psathyrostachys huashanica* Keng with *Triticum aestivum* L. cv J-11 was produced and studied cytologically. Chromatin transfer through conjugation openings among microsporocytes was observed. The chromatin migration occurred at the chromonema stage of the prophase of meiotic PMCs and stage of resting nuclei of young pollen grain. The consequential, unusual nuclear behavior frequently occurred, such as coenocytism, high level chromosome multiplication, multipolar division, variation in size of pollen grain and appearance of aneuploid. These events could lead to the doubling of spontaneous chromosome number. The possible origin of autoallopolyploid and aneuploid plants by these processes is discussed in the paper.

Introduction

We had previously studied the intermeiocyte connections and cytomixis in intergeneric hybrids of *Roegneria ciliaris* (Trin.) Nevski with *Psathyrostachys huashanica* Keng. It was found that chromatin transferred through conjugation tube or conjugation opening before, during and after meiosis in the hybrid. Consequently, unusual nuclear behavior frequently observed included coenocytism, cell size variation and abnormal chromosome or nucleus number, non-synchronous or multipolar division, and delayed chromatin condensation (Yen et al. 1993).

In order to study biosystematic relationships between *Triticum aestivum* and *Psathyrostachys huashanica* Keng, we studied the microsporogenesis of their F1 hybrid. The variations in cell size and chromosome number per cell, the chromatin material migration among microsporocytes, and the formation of conjugation tube and opening were observed in *Roegneria ciliaris* × *Psathyrostachys huashanica*. In *Triticum aestivum* × *P. huashanica* F1 hybrid, all these phenomenona were also observed except the conjugation tube.

This paper reports descriptions of nuclear material transferring, coenocytism, chromosome number diminution and multiplication, and multipolar division in the F1 hybrids of *Psathyrosachys huashanica* with *T. aestivum*.

Materials and methods

Psathyrostachys huashanica Keng (2n=14, N^hN^h) used in this study was collected from the Huashan Mt., Shaanxi province, China. *Triticum aestivum L. cv.* J-11 (2n=42, AABBDD) is a

selected strain of a landrace native to Sichuan province.

Hybridization was made by pollinating hand-emasculated spikes of *T. aestivum* cv J-11 with pollen of *P. huashanica*. Immature hybrid embryos were cultured on N_6 and C_{17} media 16-17 days after pollination. The hybrid seedlings obtained were transplanted into soil pots when the seedlings reached the three leave stage.

For cytological observations, young spikes of the F_1 hybrid were fixed in Carnoy's fluid. Chromosome numbers were counted at metaphase I of the PMCs. Microsporogenesis was studied on slides prepared by standard acetocarmine squashing.

Results and discussion

The intergeneric F_1 hybrids of *P. huashanica* with *T. aestivum* cv. J-11 are theoretically expected to have 28 chromosomes. The majority of the PMCs observed met the expectation (Table 1, Fig. 1 (1)). The meiotic data of the normal F_1 hybrids and their parents indicate that *P. huashanica* shares no common genome with *T. aestivum* (Sun et al. 1992a). However, as shown in Table 1, unusual chromosome numbers were observed. The chromosome number was fewer than 28 in 18.8% of the PMCs observed; and it was more than 28 in 7.2% of the PMCs. The highest chromosome number was more than one hundred (Fig. 1 (8)).

Table 1. Chromosome number per cell and its frequency at MI of pollen mother cells of *Triticum aestivum* with *Psathyrostachys huashanica* F_1 hybrid

Chromosome number	No. cells observed (%)	Chromosome number	No. cells observed (%)
15	1 (0.37)	42	1 (0.37)
17	1 (0.37)	47	1 (0.37)
20	2 (0.75)	49	1 (0.37)
21	1 (0.37)	51	1 (0.37)
22	5 (1.89)	54	1 (0.37)
24	10 (3.77)	56	1 (0.37)
25	5 (1.89)	62	1 (0.37)
26	16 (6.04)	66	1 (0.37)
27	9 (3.39)	67	1 (0.37)
28	196 (73.96)	70	1 (0.37)
29	2 (0.75)	84	1 (0.37)
30	2 (0.75)	100	4 (1.51)
36	1 (0.37)		

Microspore formation was observed in intergeneric hybrids of *T. aestivum* with *P. huashanica*. Under certain circumstances, chromonemata were migrating from one PMC into immediate neighboring PMCs through small openings, which might be just common plasmodesmata reported

in many literatures. In some cases, chromonemata were seen passing from one PMC to another through a big opening (Fig. 1 (3)). If microsporocytes were arranged closely together, conjugation openings were formed at these conjoined points. The nucleus, chromatin mass or chromonemata (Fig. 1 (3, 5, 6)) could migrate through the opening into immediate neighbouring microsporocytes. The conjugation opening observed in this hybrid was similar to that in *Roegneria ciliaris* × *P. huashanica* hybrid (Yen et al. 1993). In that F_1 hybrid of *R. ciliaris* × *P. huashanica*, meiocytes were arranged very loosely. Outgrowth of bud-like structure came into contact with other pollen mother cells and became fused together, forming conjugation tube between cells (Yen et al. 1993). In this hybrid, meiocytes were arranged very closely. Thus, the cells came into contact with other so closely that there was no space for conjugation tube formation. A conjugation opening had the same function as a conjugation tube, but they differed in morphology (Yen et al. 1993). If the chromatin mass migrates through an opening as small as plasmodesma, this is cytomixis, which has been reported by many authors. In this hybrid, we observed that the chromatin material of pre-meiotic PMCs could migrate through the conjugation opening (Fig. 1 (2, 3)) and from coenocytes (Fig. 1 (7)). It has been observed that the chromatin of the pollen grains migrates through the conjugation opening after meiosis (Fig. 1 (4, 5, 6)). Fig. 1 (4) shows that the walls of young pollen grains (a) and (b) are dissolving, the nucleus of pollen grain (a) is elongating toward pollen grain (b), the young pollen grain walls of (c) and (d) have dissolved and formed a giant pollen grain. The nucleus migration is taking place between pollen grains (c) and (d), and the two nuclei are fused together.

Coenocytism in microsporogenesis is not rare in intergeneric hybrids in *Triticeae* (Kagawa 1929; Kihara and Lilienfeld 1934; Villax and Mota 1953; Nakajima 1954a, b). According to Price (1956), coenocytes were formed: i) by the failure of cytokinesis in the mitotic division preceding to meiosis, ii) through the passage of a nucleus from one PMC into another, and iii) through the fusion of PMCs as reported also by Mehra and Kalia (1973). Our observation showed that the coenocytes were formed through the nucleate materials transferring of PMCs at different stages of meiosis. Wang (1988) reported coenocytism in the *P. huashanica* × *Secale montanum* hybrids and observed an average of 4.44 nuclei, ranging from 2 to 25 per PMC. Yen et al. (1993) reported that 19.92% of the PMCs observed in the *R. ciliaris* × *P. huashanica* hybrids were found to be coenocytes containing 2 to 11 nuclei. In the present study, 52.0% of the PMCs observed were coenocytes containing 2 to 4 nuclei (Table 2).

Table 2. Coenocytes in *Triticum aestivum* with *Psathyrostachys huashanica* F_1 hybrids

Nuclei per cell	No. cell (%)
1	308 (48.0)
2	212 (33.1)
3	93 (14.5)
4	28 (4.4)

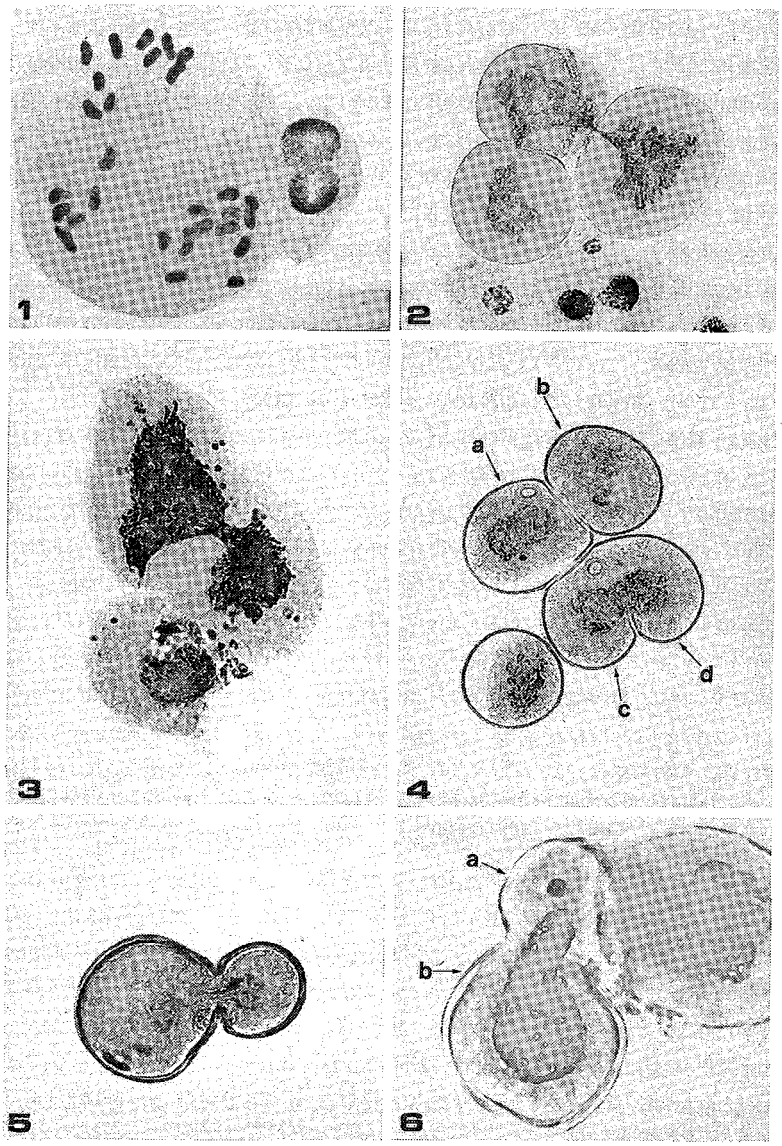
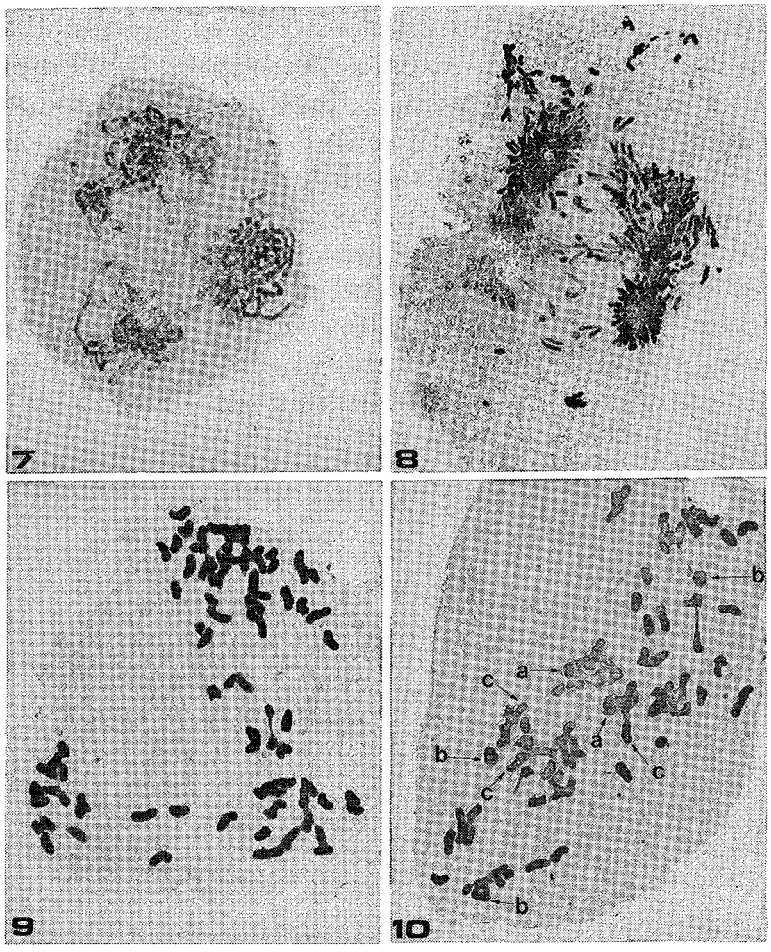


Fig. 1. PMCs of the *T. aestivum* × *P. huashanica* hybrid. (1) A normal PMCs of the *T. aestivum* × *P. huashanica* F_1 hybrid, showing 28 univalents. (2) The PMCs of the *T. aestivum* × *P. huashanica* hybrid, chromonemata migration among PMCs through a very small opening (maybe a normal plasmodesmata) (3) Chromonemata transfer through conjugation opening observed in the *T. aestivum* × *P. huashanica*. (4) Walls of young pollen grain (a) and (b) are dissolving, the nucleus in pollen grain (a) is elongating toward pollen grain (b), the young pollen grain walls of (c) and (d) have dissolved and formed a giant pollen grain, the nuclei migration are taking place between (c) and (d). (5) The choromatin is transferring between pollen grains through conjugation opening. (6) The nucleus of cell (a) is transferring into cell (b) through conjugation opening.



(7) Coenocytism with three synchronized nuclei. (8) A PMC contains probably more than one hundred chromosomes (their high density make an accurate count impossible) (9) A PMC contains more than 28 chromosomes, showing multipolar division and lagging chromosomes. (10) A PMC of the *T. aestivum* × *P. huashanica* F_1 hybrid, showing 2 quadrivalents (arrow a), 3 ring bivalents (arrow b), 3 rod bivalents (arrow c) and 64 univalents.

If a coenocytes has synchronized nuclei (Fig. 1 (7)), the chromosome number could be doubled or redoubled by nuclei fusion and a unified high level polyploid nucleus could be formed, although in some cases nuclei may not remain fused in coenocytes (Fig.1 (7)). PMCs that contained probably more than one hundred chromosomes (the high density of chromosomes made an accurate count impossible) were observed (Fig. 1 (8)). The decaploid PMC (Table 1) could form a pentaploid tetrad after meiosis. This might be a way in which spontaneous chromosome number doubling occurs. Thus, high level autoallopolyploid *Leymus* and *Elytrigia* species might have evolved by this mechanism.

If the transfer of a nucleus into a neighboring cell is not complete, aneuploid PMCs will appear. A loss or gain of one or more chromosomes has two obvious possibities: firstly extremely deficient gametes will not survive and they will be eliminated; and secondly, those gametes which contain chromosome numbers different from the normal are able to survive. The latter may be responsible for producing aneuploids. Fig. 1 (9) shows a 70-chromosome PMC. If the transfer of a nucleus into a neighboring cell is complete, chromosome number would double. Fig. 1 (10) shows a 84-chromosome PMC, which contains two quadrivalents (arrow a), three ring bivalents (arrow b), three rod bivalents (arrow c) and 64 univalents. This may explain the process of polyploid formation.

Multipolar division, which occurred in this hybrid (Fig. 1 (9)) might be caused by the formation of multipolar zones of synchronized nuclei in a coenocyte. We speculate that this kind of PMCs cannot form normal tetrads and has to disintegrate eventually. Conversely, synchronized nuclei in a few PMCs might form normal tetrads, following normal bipolar division (Yen et al. 1993). If this is true, the spontaneous chromosome number doubling and redoubling might have occurred. It might be one of the pathways of speciation in *Triticeae*. Such a pathway could lead to the origin of a high level autoallopolyploid such as *L. angustus*. We believe that the mechanism of chromatin transfer through conjugation tube or opening is a kind of variation of fertilization. According to our observation, chromatin material migration among cells has been found in all the intergeneric hybrids which derived from *Psathyrostachys huashanica* (Sun et al. 1992b; Yen et al. 1993; and the present study). We suggest that the N genome has a gene system for controlling this process.

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Wheat Information Service
Number 77: 19 – 22 (1993)

Detection of Quadrivalents in the Brazilian wheat 'Frondoso'

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Translocations have been detected in many wheat (*Triticum aestivum* L.) cultivars in comparison to the chromosome standard, 'Chinese Spring' (Baier et al. 1974; Vega and Lacadena 1982; Lange et al. 1987). Heterozygous reciprocal translocations might persist in wheat cultivars, even after generations of self-pollination, due to the compensation for deficient genes by genes on homoeologous chromosomes.

Primard et al. (1991) identified quadrivalents in the wheat cultivar 'Atlas 66' due to a heterozygous reciprocal translocation involving chromosome arms 2AL and 2DL. They indicated that the translocation had persisted through seven generations of self-pollination and that its origin was unknown.

Atlas 66 was developed in North Carolina, USA from the cross'Frondoso'//'Redhart 3'/'Noll 28' (Heyne 1958). Frondoso originated from Brazil (USDA, ARS, Germplasm Resources Information Network, Beltsville, Maryland, USA). Love (1951) examined 19 Brazilian wheat cultivars for meiotic instabilities. One of these cultivars, 'Frontana', a cultivar with the same pedigree as Frondoso, had an abnormal meiosis characterized by failure of pairing and lagging of bivalents at disjunction.

The purpose of this study was to examine the meiosis of Frondoso for quadrivalents. The existence of quadrivalents was hypothesized based on Frondoso's Brazilian origin, its use as a parent in the development of Atlas 66, and the prior identification of quadrivalents in Atlas 66.

Materials and methods

Seed of Frondoso was obtained from the USDA National Small Grains Collection. Frondoso is a red spring wheat cultivar developed from the cross 'Fronteira'/'Mentana' (USDA, ARS, Germplasm Resources Information Network, Beltsville, Maryland, USA).

Anthers, with pollen mother cells (PMCs) at metaphase I, were identified in temporary acetocarmine smears (Darlington and Lacour 1950) and fixed in a 3:1, 95% alcohol:glacial acetic acid mixture. Anthers, collected from 10 different plants grown in a glasshouse, were hydrolyzed in 1N HCl for 12 min, stained with Feulgen (Darlington and LaCour 1950), and smeared in propionic orcein. Slides were made permanent by mounting a coverslip with Canada Balsam after passing them through a 50:50, 100% tertiary butyl alcohol (TBA):glacial acetic acid mixture and two changes of 100% TBA.

Meiotic observations were made for 20 well-spread, complete cells from each plant sampled and configurations were recorded following the nomenclature of Kimber and Sears (1968).

Results

In PMCs from Frondoso, 21-bivalent configurations were observed, however, some had a ring or a chain quadrivalent (Fig. 1). Meiotic configurations, differing from a 21-bivalent configuration, were observed in at least one cell of eight of the 10 Frondoso plants analyzed (Table 1). In addition to bivalents, univalents and/or quadrivalents were observed in 37.5% of the cells. A quadrivalent was observed in at least one cell in seven of the 10 plants analyzed and a quadrivalent was observed to be present in 6% of the cells analyzed. Twenty-five percent of the quadrivalents were observed as chains and 75% as rings. Three of the plants were monosomic and two of these, had a ring and/ or chain quadrivalent along with a univalent in some cells (Table 1).

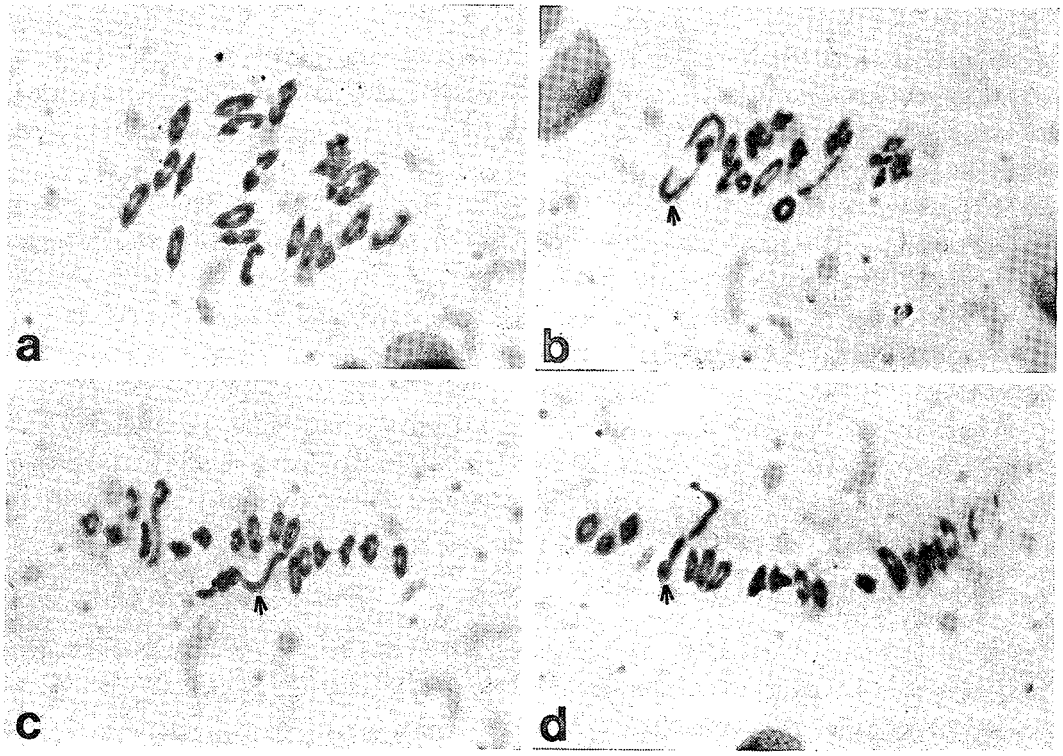

Fig. 1. Representative metaphase I meiotic configurations in PMCs from Frondoso (a-b).
(a) 21 bivalents, (b) 19 bivalents + 1 ring quadrivalent, (c) 19 bivalents + 1 chain quadrivalent, (d) 18 bivalents + 1 chain quadrivalent + 1 univalent (quadrivalents indicated by arrows).

Table 1. Metaphase I meiotic configurations in PMCs from Frondoso

	No. of cells with indicated configuration			
Plant No.	21"	20"+2'	19"+1^{IV} ring	19"+1^{IV} chain
1	20	–	–	–
2	20	–	–	–
3	14	4	2	–
4	17	2	–	1
5	18	–	2	–
6	17	–	3	–
7	19	–	–	1
Subtotal	125	6	7	2
Plant No.	20"+1'	18"+1'+1^{IV} ring		18"+1'+1^{IV} chain
8	20	–		–
9	18	1		1
10	19	1		–
Subtotal	57	2		1

Discussion

The presence of quadrivalents in Frondoso, at a frequency of 6%, is comparable to the 10.7% frequency reported by Primard et al. (1991) for Atlas 66. Love (1951) observed abnormal meiosis in Frontana, a Brazilian cultivar with the same pedigree as Frondoso, and Vega and Lacadena (1982) detected quadrivalents in hybrids produced from crossing Chinese Spring to Mentana, a parent of Frondoso.

It is possible that Frondoso is a genetically unstable cultivar of the type described by Suarez et al. (1988). They observed that some Argentinean wheat cultivars showed aneuploidy at a frequency as high as 27%. Ring and chain quadrivalents were common in these cultivars and it was suggested that aneuploids arose from an abnormal regrouping of chromosomes at telophase I of meiosis. In addition, depending on the orientation of a quadrivalent and the occurrence of crossovers during meiosis, duplicate-deficient gametes, indicated by a reduction in pollen fertility, can be produced in plants with a quadrivalent configuration (Burnham 1956). In the present study, no quantitative data was gathered on the pollen fertility of Frondoso; however, a number of spikes on various plants were observed to be infertile, possibly as a result of pollen sterility.

Because Frondoso is a parent of Atlas 66 and quadrivalents were observed to occur at a comparable frequency in both cultivars, it is possible that Atlas 66 inherited its translocation from Frondoso. Test crosses are being made to Frondoso to determine if quadrivalents result from a translocation involving the same chromosome arms as in Atlas 66.

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Wheat Information Service
Number 77: 23 – 24 (1993)

Characterization of hexaploid derivatives for *Ne1* and *Ne2* necrotic genes of wheat

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Summary

Three hexaploid derivatives D 525-2 (from CPAN 6051), D 3237-5 (from DWL 5023) and D 3542-6 (from CPAN 6073) identified meiotically from the F_2 population of the crosses between *Triticum durum* and *T. aestivum* were characterized for hybrid necrotic genes *Ne1* and *Ne2*. These derivatives in crosses with *T. aestivum* cvs. Spica (carrier of *Ne1*) and Kalyan Sona (carrier of *Ne2*) were evaluated in the field for necrosis. Derivative D525-2 carries *Ne2* and *Ne1* is present in D 3237-5 and D 3542-6. Being resistant to leaf rust of wheat the derivatives can be utilized in the breeding programmes.

Introduction

Transfer of useful traits in wheat through intervarietal crosses is mainly restricted by the action of dominant complementary hybrid necrotic genes, *Ne1* and *Ne2* (Hermsen 1963). *Ne1* is present in most of the durum wheats (Nishikawa 1967; Zeven 1981) and *Ne2* in 70% of aestivum wheats (McIntosh 1983). Classification of cultivars carrying these genes is very essential for the proper analyses and utilization of the breeding material in wheat improvement. Keeping this in view, the present investigations were carried out with the characterization of necrotic genes in three hexaploid derivatives.

Materials and methods

The derivatives were identified meiotically from the F_2 population of the crosses between *Triticum durum* cvs. CPAN 6051, DWL 5023 and CPAN 6073 and a *Triticum aestivum* cv. Agra Local. These derivatives were designated as D 525-2 (from CPAN 6051), D 3237-5 (from DWL 5023) and D 3542-6 (from CPAN 6073). Each derivative was crossed with *T. aestivum* cvs. Spica (carrier of *Ne1*) and Kalyan Sona (carrier of *Ne2*) to detect necrotic genes. F_1's were raised in 100 cms long rows spaced 50 cms apart in an open experimental area. The plants were observed throughout the wheat season at a weekly intervals to study the necrosis.

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Results and discussion

Results on hybrid necrosis on different cross combinations are summerised in Table 1. All the plants in a cross between D 525-2 and Spica were necrotic whereas in D 525-2 × Kalyan Sona cross were non-necrotic. This derivative when tested against 14 different Australian wheat leaf rust cultures, was found to carry *Lr13* along with *Lr23* (Saini 1987). The dominant complementary necrotic gene *Ne2* is linked with *Lr13* with a linkage distance 33.17 ± 4.12 mμ (McIntosh 1983; Anand et al. 1991). The cross between Spica and D 525-2 showed necrosis due to the presence of *Ne1* in Spica and *Lr13* - *Ne2* in D 525-2. The crosses of D 3237-5 and D 3542-6 with Spica were non-necrotic but with Kalyan Sona were necrotic. These observations indicate that hexaploid derivative D 525-2 carries dominant necrotic gene *Ne2* whereas D 3237-5 and D 3542-6 carry *Ne1*.

All the three derivatives confer seedling and adult plant resistance against different leaf rust races of wheat prevalent in India (Cupta et al. 1991, 1992), therefore, their characterization for necrotic genes *Ne1* and *Ne2* would help breeders to use them effectively in their wheat breeding programmes.

Table 1. Hybrid necrosis in the crosses of hexaploid derivatives with Spica and Kalyan Sona

Hexaploid derivative	Spica (*Ne1*)	Kalyan Sona (*Ne2*)
D 525-2 (From CPAN 6051)	+	–
D 3237-5 (From DWL 5023)	–	+
D 3542-6 (From CPAN 6073)	–	+

+ Presence of necrosis

– Absence of necrosis

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Wheat Information Service
Number 77: 25 – 28 (1993)

Monosomic analysis for total and sterile floret number per spike in the multispikelet line 10-A of common wheat

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Summary

Chromosome location of the genes for total and sterile floret number per spike in the common wheat was carried out by using multispikelet line 10-A and two sets of monosomic lines, Chinese Spring and Abbondanza. The large number of total florets per spike of 10-A was controlled by the chromosomes 5A, 7A, 1B, 2B, 2D and 6D, but the genes on the chromosomes 1B, 2B, 2D and 6D controlled mainly the high number of sterile florets per spike. The useful value of 10-A was discussed in wheat breeding of increasing grain number per spike as main objective.

Introduction

Yen et al. (1993) selected a common wheat, multispikelet line 10-A by using the genetic resources for large number of spikelets per spike from rye. The large number of florets per spike results entirely from increasing spikelet number per spike, and so this kind of germplasm undoubtedly is very useful ideotype of increasing the grain number per spike in wheat breeding (Zheng et al, 1992). Unfortunately, the number of the sterile florets per spike of "10-A" is much higher than that of the popular wheat varieties, resulting in giving rise to the less grain number of "10-A". This study aimed to locate the genes governing the total and sterile floret number per spike of 10-A on certain chromosome.

Materials and methods

The tested line 10-A was selected from the offsprings of backcrossing *Triticale* (8x) with common wheat by Yen et al. (1993). Two sets of monosomic lines, Chinese Spring and Abbondanza, were used in the monosomic analysis. From each monosomic line, two or three monosomic plants were pollinated with 10-A. Three monosomic and at least one disomic plants were mitotically selected from each F_1 hybrid. The selected F_1 plants were observed with respect to the total and sterile floret number per spike. Of the each set, 21 F_2 populations derived from monosomic F_1 hybrid for different chromosomes and one euploid F_2 population derived from disomic F_1 plants were included, and these two characters were investigated on 160 plants of each F_2 population.

In the statistic analysis of data, the number of total or sterile florets per spike was maximum selected from the 5-8 observed spikes of each sample plant. The significance of differences between the mean values were detected by t-test. F-test was adopted to detect the significance of the differences between the variances.

Results

Monosomic analysis for total floret number per spike

The large number of florets per spike of 10-A was found to be controlled by six pairs of genes, located on the chromosomes 5A, 7A, 1B, 2B, 2D and 6D (Table 1). However, it should be noteworthy that the three pairs of genes on the chromosomes 2B, 2D, 6D could have much stronger effects than other three pairs of genes on the chromosomes 5A, 7A and 1B in governing this

Table 1. The results of monosomic analysis for total floret number per spike of 10-A

Population	Chinese Spring series			Abbondanza series		
	F_1 mean ± SE	F_2 mean	F_2 variance	F_1 mean ± SE	F_2 mean	F_2 variance
1A	146 ± 3	115	288	140 ± 2	110	239
2A	143 ± 3	113	240	142 ± 3	111	239
3A	140 ± 3	109	277	139 ± 2	109	220
4A	141 ± 2	111	241	136 ± 3	105	229
5A	156 ± 3**	125**	291	152 ± 3**	122**	288
6A	141 ± 3	112	274	140 ± 2	108	275
7A	156 ± 3**	126**	247	160 ± 3**	129**	142**
1B	154 ± 2**	124*	270	150 ± 3**	119*	119**
2B	163 ± 3**	133**	133**	166 ± 3**	136**	120**
3B	143 ± 2	113	227	142 ± 3	111	245
4B	141 ± 2	110	230	143 ± 2	112	251
5B	142 ± 3	112	212	140 ± 2	109	219
6B	147 ± 3	117	231	142 ± 3	113	218
7B	143 ± 2	113	235	138 ± 2	107	255
1D	144 ± 2	114	228	139 ± 2	108	218
2D	168 ± 4**	138**	154*	160 ± 3**	131**	140*
3D	143 ± 2	111	237	144 ± 3	105	269
4D	143 ± 2	113	208	139 ± 3	110	221
5D	146 ± 2	116	283	140 ± 3	108	245
6D	164 ± 4**	135**	153*	161 ± 3**	131**	138*
7D	142 ± 2	112	269	139 ± 3	110	232
Disomic	144 ± 3	114	244	140 ± 3	110	218

* and ** represent significance at the 0.05 and 0.01 levels, respectively.

character. Chinese Spring, Abbondanza and 10-A had 114±2, 106±3 and 176±5 florets per spike of mean values, respectively, whereas the mean values of floret number per spike of the two F_1 disomic hybrids were 144 and 140 (Table 1), respectively, so the large number of florets per spike of 10-A should be controlled by the multiple nondominance genes.

Monosomic analysis for sterile floret number per spike

The genes controlling the high number of sterile florets per spike of 10-A were found to be carried on the chromosomes 1B, 2B, 2D and 6D (Table 2). Of these four pairs of genes, the genes on chromosomes 2B and 2D have much stronger effects than the gene on chromosome 1B which has stronger effect than the gene on chromosome 6D in this character. Chinese Spring, Abbondanza and 10-A had 33±4, 24±3 and 97±6 sterile florets per spike of mean values, respectively, but the two F_1 disomic hybrids had 55 and 41 sterile florets per spike of mean values (Table 2), respec-

Table 2. The results of monosomic analysis for sterile floret number per spike of 10-A

Population	Chinese Spring series			Abbondanza series		
	F_1 mean ± SE	F_2 mean	F_2 variance	F_1 mean ± SE	F_2 mean	F_2 variance
1A	53±5	45	226	42±3	30	178
2A	55±5	44	184	41±3	31	189
3A	60±4	40	211	38±4	29	193
4A	60±4	41	181	39±4	36	169
5A	51±5	41	236	40±5	29	188
6A	53±4	41	214	38±3	28	158
7A	53±4	40	186	39±4	29	148
1B	66±5**	49*	112*	53±4**	41**	90**
2B	80±6**	54*	73**	68±5**	47**	69**
3B	53±4	43	162	43±3	32	145
4B	56±5	40	143	42±3	32	157
5B	59±4	41	172	45±3	29	179
6B	57±5	42	169	43±4	33	217
7B	53±5	42	155	39±3	35	224
1D	54±3	44	183	39±3	34	171
2D	82±6**	59**	93**	74±4**	53**	67**
3D	53±4	41	226	44±3	36	170
4D	52±5	42	181	40±4	29	148
5D	59±5	46	223	41±3	34	145
6D	62±5	45	123*	49±3*	39*	97*
7D	53±4	42	186	38±4	34	139
Disomic	55±5	44	190	41±4	32	169

* and ** represent significance at the 0.05 and 0.01 levels, respectively.

tively, so the genes for the high number of sterile florets per spike of 10-A should be also multiple but partially recessive inheritance.

Discussion

The effect of chromosomes on the total floret number per spike of common wheat was not found to be reported in the past literatures, but the genes controlling the sterile floret number per spike of common wheat were located on the chromosomes of groups 2 and 6 (Sears 1954) and chromosome 4A (Driscoll 1975, Barlow and Driscoll 1981). In this experiment, the large number of total florets per spike of 10-A was found to be controlled by the chromosomes 5A, 7A, 1B, 2B, 2D and 6D, but the genes on chromosomes 1B, 2B, 2D and 6D might mainly control the high number of sterile florets per spike. In other words, these genes on chromosomes 1B, 2B, 2D and 6D could have pleiotropism. This is the obstacle to hardly overcome in the breeding projects of increasing grain number per spike. It was fortunate that the chromosomes 5A and 7A increasing the number of total florets per spike did not carry the genes governing the high number of sterile florets per spike, so the chromosomes 5A and 7A of 10-A could provide the favourable genetic resource for wheat breeding of increasing grain number per spike. In fact, some improved strains derived from 10-A have 150-160 florets per spike and only 20-30 sterile floret per spike, and 120-130 grains per spike which is very higher than that of the popular variety Mianyang-11 with 60-70 grains per spike (Zheng et al. 1992). From theoretical and practical aspects, it has been shown that 10-A is an excellent parent in wheat breeding projects of increasing grain number per spike.

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Wheat Information Service
Number 77: 29 – 32 (1993)

Studies on the male sterility in wheat (*Triticum aestivum*) induced by two new chemical hybridizing agents; EK and ES

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Summary

Experiments about the effect on male sterile (MS) induced by two chemical hybridizing agents (CHA) EK and ES have been made for successive six years. The results were as follows:

1. EK and ES were two ideal CHAs on wheat. 95 - 100% MS and 80% more seed set (SS) could be got by spraying of 7,000 ppm for EK or 6,000 ppm for ES, during the pollen mother cell stage to meiotic stage under the dosage of 1,350 kg/ha.

2. The two CHAs were two wide-spectrum gametocides. The average MS of 70 genotypes treated with them was over 95%, in which only several cultivars showed different results suggesting that different genotypes maybe have a different response.

3. The two CHAs have a side effect on the plant height as well as on the length of last internode, that is, shorting of them after spraying.

Introduction

Fourteen chemical hybridizing agents (CHAs) have been reported in nearly 30 years (Roell 1971, Tschahold 1988 and Liu 1990), but from the practial pointview they do not have the properties of low cost, no remnant poison, no air polution, good MS and good SS, etc, (Li 1989). So the hybrid developed by CHA has not been extensively used in wheat production (Johnston 1985). Hebei Hybrid Wheat Research Associated Team (HHWRAT) has started this work since 1987 during which two new CHAs, EK and ES were successfully developed, which gave very satisfied results in field. This paper discusses their utility value in order to open up a new approach of hybrid wheat.

Materials and methods

1. Experiment times and locations: Chemical experiments were carried out in our experimental farm (Hengshui, 37°44′ N, 115°42′ E) and field utilization was made in hybrid wheat seed production station in Louzi village, Zaoqiang county, from 1987 to 1992.
2. Sprayer: Gongnong-16 model.
3. Tested genotypes: All the genotypes used in this experiment were from our breeding nursery and from the Germplasm Research Group of our institute whose heading date are more similar, but other characters vary very much.
4. CHA: Chemicals (EK and ES) were from HHWRAT (Patent No. 92103773.2).

5. Spraying dosage and method: The dosage used in the whole test was 1,350 kg/ha and the spraying speed, 3.5 km/hr under which three replicated spraying was made. Equal amount of water was sprayed on check.

6. Plot area: The plots area of spraying time and concentration tests were 50 (10×5) m^2, others were 100 (20×5) m^2. Male plots were equal to the sprayed plots.

7. Sampling: Every ten heads from main stems were randomly collected to examine the spike differentiation stage under light microscope and calculated for the male sterility (MS) and seed set (SS) of the females. The heads of females were bagged after heading for MS counting. The formular used in this calculation was:

$$\text{MS/SS } \% = \frac{\sum \text{Seeds from basal floret}}{\sum \text{basal floret}} \times 100$$

Results and discussion

1. Spraying time identification: In 1988, 7,000 ppm for EK or 6,000 ppm for ES were sprayed on Jinfeng 1 at the shealth length of flag-leaf of 0, 2, 3, and 4 cm. Light microscope examination for young spike differentiation was made at same time. The effective spraying time for the two CHAs were from sporogenous to meiotic stage, it was flagging time in field. The average shealth length of flag-leaf was –2 to 2 cm. Monokaryon stage seems to be critical time for spraying and after that the MS decreased to 79% for both chemicals. The result is shown in Table 1.

Table 1. Sterility in different spraying times of CHAs, EK and ES in Jinfeng 1

Shealth length	Pollen developing stage	No. of spikes	Sterility %	
			EK	ES
0	sporogenous-mother cell	10	98.7	96.1
2	mother cell-meiosis	10	98.3	92.5
3	meiosis–monokaryon	10	96.2	92.0
4	monokaryon–dikaryon	10	79.3	78.6

Generally speaking, this stage will be last 4 to 5 days for a cultivar in field. The date of spraying could be selected according to the weather.

2. Identification of spraying concentration: in 1989, Jinfeng 1 used as female, Jimai 21, male, respectively. Concentration experiment was made on flagging time with the dosage of 1,350 kg/ha. The best MS and the best SS has got under the concentration of 7,000 ppm for EK and 6,000 ppm for ES, respectively. Results are show in Table 2.

Table 2. Sterility of different concentration on Jinfeng 1

CHA	Concentration (ppm)	No. of spikes	Sterility (%)	
			MS	SS
EK	3,000	10	54.5	78.7
	5,000	10	85.4	77.3
	7,000	10	93.6	79.8
	9,000	10	98.8	52.6
ES	2,000	10	35.5	72.0
	4,000	10	52.9	74.8
	6,000	10	96.3	78.5
	8,000	10	97.7	59.3
	10,000	10	98.2	54.2

Table 3. Effect of EK (7,000 ppm) on eleven cultivars

	Jimai 6-2	Jimai 21	87-3046	Jimai 9	Zaofeng 1	84-4152	C 659	Heng 500	Jian 61	Ji 86-680	Zi 88-4227
MS %	94.7	84.1	100	97.1	100	100	95.7	100	96.9	97.9	100
SS %	84.8	90.1	81.3	71.3	82.1	83.8	80.2	74.2	75.1	85.3	74.0

Table 4. Effect of ES (6,000 ppm) on eight cultivars

	Gan 86-5	Tan 87-299	87-1077	Jian 144	Jimai 16	Henong 215	87-6150	H 11
MS %	100	100	90.3	100	100	84.2	78.3	100
SS %	73.1	86.5	86.9	75.1	83.1	93.4	95.5	84.0

Table 5. Effect of two CHAs on eight cultivars

		C 41-1/0	87-7021	875-045	85-1	781-2	Han 83-16	Henong 215	Yuanzao 2
MS	EK %	100	100	100	100	96.7	84.6	91.9	95.4
	ES %	92.1	77.1	100	100	100	100	84.2	100
SS	EK %	80.7	74.7	49.8	71.1	82.7	73.8	78.8	83.4
	ES %	87.4	74.7	78.0	82.9	77.4	78.3	83.5	84.9

3. Comprehensive assessment to the two CHAs.

(1) The interaction between CHAs and cultivars: In 1990, the experiment about same CHA to different cultivars and about same cultivar to different CHAs were carried out. Results are shown in Tables 3 to 5.

In 1990, 70 cultivars which flagging time are relatively similar to each other was sprayed with EK and ES at flagging time. The characteristics analyzed are shown in Table 6.

Table 6. Responses of agronomic characters to EK and ES in 70 cultivars

	Plant height		Length of last internode (LLI)		LLI: Plant height		MS		SS	
	cm	t-test	cm	t-test	Proportion	t-test	%	t-test	%	t-test
EK	55.2	0.14	14.3	0.24	3.9:1	1.43	97.3	1.22	82.9	0.19
ES	55.5		14.4		3.8:1		95.8		83.4	
Control	90.0		32.4		2.8:1		0		100	

The average MS of 70 genotypes treated with them was over 95%, in which only several cultivars shown different suggest that different genotype maybe have a different response. The pre-testing should be made in order to get satisfied hybrid. The two CHAs have a side effect on plant height as well as on the length of last internode, that is, shortening of them after spraying. Generally speaking, the higher the plant is, the shorter it becomes by spraying. The decreasing extent was from 8.4 to 32.4 cm and from 7.1 to 32.1 cm for plant height and the length of last internode, respectively. The ratio of the latter to the formers was 1:2.8 before spraying, where it become 1:3.8 to 1:3.9 after spraying.

(2) Hybrid seed production. In 1992, EK was used to produce hybrid Huayou 9, 74197/888-1, in 0.53 ha in Louzi village. The females yield was 4,223 kg/ha. The male yield was 4,695 kg/ha, indicating only 472.5 kg/ha yield decreasing or 90% more male's yield.

(3) The main composition of the two CHAs was Ethrel, which is widely used both in crops and fruit production. Except the plant height decreasing after spraying, there were no another side effect like heading difficulty, spikelet aborting and green spike increasing caused by Ethrel mono-spraying. These CHAs have no air pollution, no remnant and their costs are low. The outcrossing rate varied from 71.33-86.49% for the female whose MS were over 95%, maybe the variation was caused by different flowing time of both male and female, the practical cross ability was satisfied had shown their utilizing potential.

(4) The length of last internode of plant is a heritable character. Differences have been observed among 70 cultivars. The proportion varies from 1:2.04 to 1:3.94. Genotypes being longer length of last internode is more suitable for female because it becomes shorter after spraying. On the other hand the outcrossing rate would be improved by selecting the synchronizing flowering parents and breeding good flowering habit parents.

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Wheat Information Service
Number 77: 33 – 38 (1993)

Wheat cultivation under saline irrigation

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Introduction

Wheat (*Triticum aestivum* L. emend. Thell) is one of the most important cereal crops of the world to nourish the mankind. It is grown in wide range of climatic zone and mostly in irrigated conditions. In the arid and semi-arid areas, saline ground water is a common feature. Irrigation with saline water throughout the growth period of crops resulted in deterimental affect on growth and yield potential of the crops. Bernstein (1964), Bhumbla et al. (1964), Kanwar and Kanwar (1969) and Tripathi and Pal (1979) have reported the reduction in yield of wheat with high saline irrigations. Besides, grain yield, crop growth and yield attributes are found to vary with sensitivity for salinity. Therefore, it will be of vital interest for scientist to try to overcome the salinity menace to predict the wheat crop growth development and yield potential with varying salinity of irrigation water on the basis of long term experimentation.

Material and methods

A field experiment in microplot size of 2.5 m × 2.5 m (net plot size 2 m × 2 m) was conducted during *rabi* seasons of 1972-73 to 1978-79 consecutively at the Research Farm, Raja Balwant Singh College, Bichpuri, Agra, India. The plots were separated by polythene sheets upto 0.9 m depth to prevent lateral movement of water and salt. The annual rainfall in the region is about 600-700 mm of which about 80% is received during July, August and September. The soil was alluvial, sandy loam (15% clay, 14% silt and 70% sand) in texture with 1.75 cm/hr hydraulic conductivity. The soil initially had ECe 3 dS/m, pH_2 8.6, SARe 15 and ESP 6 at surface (0-15 cm) depth.

Seven salinity levels of irrigation water with EC_{iw} (control), 2, 4, 6, 8, 12 and 16 dS/m were tried in Randomized Block Design with four replications. Artificially synthetic water were prepared from canal water by adding the salts of chlorides of sodium, calcium and magnesium and sulfates and bicarbonates of sodium keeping the ratio of Na:Mg:Ca as 60:25:15 and Cl:SO_4:HCO_3 as 2:1:1 as long as sulfates did not exceed 30 miliequivalent/litre and HCO_3 10 miliequivalent and excess of these ions were substituted by chloride ion. The composition of these irrigation waters are as per composition of the ground water of this locality. Under the Pearl Millet-Wheat crop rotation for consecutive 7 years on the same field, wheat (HD 1593) was sown in November and harvested in April in respective years. The crop was fertilized with the dose 120 Kg/ha N and 60 Kg/ha P_2O_5. Irrigation was adjusted at 6 cm CPE with ratio 1.0 of CPE/depth of irrigation. In all, 4-5 irrigations

were provided each year for wheat cultivation. The details of rainfall and water table depth are presented in Table 1.

Results and discussion

During wheat crop production, the salinity build up (ECe) has been recorded about 1.0 to 1.5 times to that of irrigation water (EC_{iw}). This increased ECe ultimately increased the soil osmotic potential, resulting reduced water intake by crop besides specific ion effect. Plants make adjustment when faced unfavourable conditions upto certain limit but beyond it, depressed plant growth happened.

The data pertaining to effect of varying saline irrigation on wheat crop growth and yield for seven years of experimentation are presented in Table 2 and 3. The germination performance of seed, which directly related to soil moisture content, revealed that it decreased progressively with salinity of water. However, the magnitude of reduction was more with high salinity. From EC_{iw}-6 to 8 dS/m it decreased about 1.2% with each unit of EC_{iw} and from EC_{iw}-8 to 10 dS/m the reduction per unit EC_{iw} was about 4%. The correlation between EC_{iw} and germinability ($r = -0.61$) was also found negative and significant with regression equation as $Y = -1.82 x + 65.62$.

The crop growth judged by plant height and number of tillers revealed that both these characters declined with salinity but only beyond EC_{iw}-8 dS/m. The $EC_{iw}12$ declined crop growth by about 10% while at $EC_{iw}16$ by about 30%. The correlation between EC_{iw} vs plant height ($r = -0.36$) and number of tillers ($r = -0.37$) were found negative and significant. The respective regression equations are $Y = -1.25 x + 87.5$ and $Y = -1.08 x + 69.4$.

The yield contributing character viz. ear length, number of grain per ear and 1000 grain weight were also studied. It has been observed that upto $EC_{iw}12$ dS/m ear length was not found affected and with 3.6% reduction only at $EC_{iw}16$ dS/m. Similarly, number of grain per ear was not found to be affected upto $EC_{iw}8$ and only with 5% reduction at $EC_{iw}12$ to 16 dS/m. 1000 grain weight was started to declined from $EC_{iw}2$ dS/m onwards progressively but with very low degree (Table 2). The correlation between EC_{iw} and these yield attributes was rated non-significant (Table 3).

The crop yield was found to decline with salinity of irrigation water. The drymatter yield declined only at $EC_{iw}12$ and 16 dS/m by 18 and 33% respectively. The remarkable reduction in grain yield started above $EC_{iw}8$ dS/m. With $EC_{iw}12$ and 16 dS/m the grain yield lowered by 21 and 37% respectively. Reduction in grain yield per unit EC of water from 8 to 16 dS/m was about 4%. Almost similar reduction in wheat yield was reported by Poonia et al. (1974) and Tripathi and Pal (1979). Mildy saline water ($EC_{iw}2$ to 5 dS/m) have shown the improvement in grain and drymatter yield (Tripathi et al. 1971). The EC_{iw} has been found to be significantly negative correlated with grain yield ($r = -0.50$) and drymatter yield ($r = -0.42$) with respective regression equation as $Y = -1.01 x + 43.49$ and $Y = -2.09 x + 103.02$.

Table 1. Rainfall and depth of water table in different years

Particulars	Years						
	1972-73	1973-74	1974-75	1975-76	1976-77	1977-78	1978-79
Total rainfall (mm)	293 (1972)	650 (1973)	512 (1974)	640 (1975)	750 (1976)	1044 (1977)	895 (1978)
Rainfall during kharif (mm)	272	558	388	504	653	958	816
Rainfall during cropping period (mm)	51	17	101	29	53	68	114
Water table depth during cropping period (mm)	–	–	3.3-4.8	4.9-5.4	3.9-4.4	1.2-2.1	1.3-2.2

Table 2. Effect of saline irrigation on growth and yield of crop (average 7 years)

Treatments ECiw (ds/m)	Germination count/metre row length	Number of tillers/metre row length	Plant height (cm)	Ear length (cm)	Number of grains/ear	1000 grain weight (gm)	Drymatter yield (q/ha)	Grain yield (q/ha)
ECiw-1	60.6 ± 9.1 (100.0)	65.0 ± 9.3 (100.0)	81.7 ± 10.6 (100.0)	8.4 ± 0.6 (100.0)	40.4 ± 6.2 (100.0)	34.4 ± 5.0 (100.0)	95.4 ± 13.4 (100.0)	40.4 ± 5.2 (100.0)
ECiw-2	60.1 ± 8.5 (99.2)	65.5 ± 8.5 (100.8)	82.9 ± 10.9 (101.5)	8.5 ± 0.7 (101.2)	41.7 ± 5.0 (103.2)	34.0 ± 4.7 (98.8)	95.8 ± 15.4 (100.4)	40.9 ± 6.4 (101.2)
ECiw-4	62.4 ± 8.6 (103.5)	67.8 ± 10.0 (104.3)	82.5 ± 9.9 (101.0)	8.6 ± 0.5 (102.4)	43.2 ± 4.6 (106.9)	32.5 ± 15.6 (94.5)	95.8 ± 15.3 (100.4)	39.5 ± 6.4 (97.8)
ECiw-6	55.2 ± 9.7 (91.1)	65.7 ± 10.8 (101.1)	82.2 ± 12.2 (100.6)	8.5 ± 0.7 (101.2)	41.0 ± 5.4 (101.5)	32.5 ± 5.2 (94.5)	97.0 ± 17.4 (101.7)	39.3 ± 3.4 (97.8)
ECiw-8	53.7 ± 8.8 (88.6)	65.8 ± 11.7 (101.2)	82.0 ± 11.9 (100.4)	8.8 ± 0.9 (104.8)	40.8 ± 5.8 (101.0)	31.0 ± 5.8 (90.1)	96.3 ± 18.3 (101.1)	39.3 ± 6.3 (98.7)
ECiw-12	43.3 ± 14.6 (71.5)	57.8 ± 15.1 (98.9)	73.6 ± 15.2 (90.1)	8.5 ± 1.3 (101.2)	38.4 ± 6.5 (95.1)	30.6 ± 6.4 (89.0)	78.6 ± 32.5 (82.4)	31.8 ± 11.4 (78.7)
ECiw-16	34.8 ± 17.9 (57.4)	44.7 ± 19.8 (68.8)	54.9 ± 20.1 (67.3)	8.1 ± 1.8 (96.4)	38.7 ± 8.8 (95.8)	28.8 ± 8.4 (83.7)	63.6 ± 32.2 (66.7)	25.4 ± 11.2 (62.9)
S.D.	± 9.5	± 7.5	± 9.5	± 0 .2	± 1.5	± 1.8	± 12.0	± 5.1

( ) Data in parentheses indicate percentage over control as100

± Standard deviation

Seed rate: 180~200 seeds/2.5 m row length.

Table 3. Correlation between salinity of irrigation water and crop characters

Characteristics	'r' value	Regression equation
EC_{iw} vs Germination	–0.61*	Y = –1.82 x + 65.62
vs No. of tillers	–0.37*	Y = –1.08 x + 69.40
vs Plant height	–0.36*	Y = –1.25 x + 87.51
vs Ear length	–0.09	—
vs No. of grains/ear	0.186	—
vs 1000 grain weight	–0.27	—
vs Drymatter	–0.42*	Y = –2.09 x + 103.02
vs Grain yield	–0.50*	Y = –1.01 x + 43.49

* Significant at 5% level

Table 4. Correlation studies between grain yield and different crop characters

Characteristics	'r' value	Regression equation
Grain yield vs Germination	0.70*	Y = 3.60 x – 153.92
vs No. of tillers	0.76*	Y = 0.53 x + 4.31
vs No. of effective tillers	0.16	—
vs Plant height	0.52*	Y = 0.50 x – 2.97
vs Ear length	0.02	—
vs No. of grains/ear	0.02	—
vs 1000 grain weight	0.11	—
vs Drymatter yield	0.95*	Y = 0.38 x + 2.83

* Significant at 5% level

Further, the relationship of different plant characters with grain yield under saline irrigations were also assessed and presented in Table 4. The figure No. 1 shows that germination performance is closely related with grain yield. Plant height and number of tillers also showed the trend similar to yield. The ear length and number of grain per ear had shown no resemblance with grain yield pattern. The correlation studies (Table 4) also showed that only germination, number of tillers and plant height were found to be significantly correlated with grain yield.

Thus, in light textured soils and semi arid climatic conditions, wheat can be grown upto EC_{iw}-8 dS/m comparable to control (canal water). The saline irrigation at EC_{iw}-12 and 16 dS/m reduced wheat yield by 21 and 37 per cent over control with negative significant correlation (r = –0.42). The reduction in yield mainly caused by poor germination and tillering, stunted growth and to some extent by low 1000 grain weight.

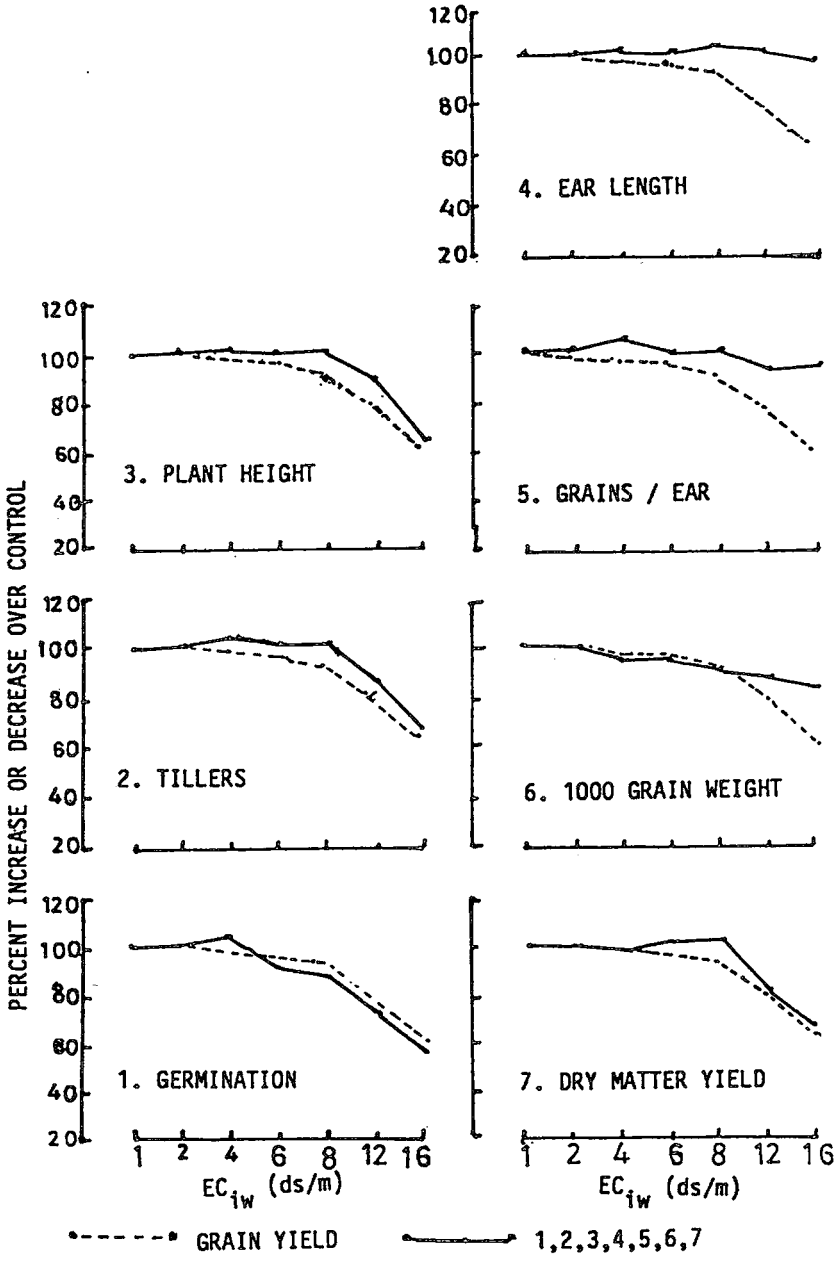

Fig. 1. Grain yield in relation to different plant characters of wheat under saline water irrigations. (7 years average)

Acknowledgement

The authors are very much thank to I.C.A.R. New Delhi for financial assistance, Principal, Raja Balwant Singh College, Agra for providing necessary facilities and to the staff who made this investigation a success.

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Wheat Information Service
Number 77: 39 – 45 (1993)

Telocentric mapping of α-amylase loci in wheat

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Summary

With the improved technique of electrophoresis the precise genetical analyses of α-amylase isozymes were realized with the following results;
Aka, a Japanese local variety is different from Chinese Spring in Band 20 coded by *α-Amy-A1*, which was located on the long arm apart from the centromere of chromosome 6A with recombination value of 3.7 ± 0.01(%). In comparison with Chinese Spring a common wheat cultivar, Jones Fife have Band 15 instead of Band 18, which is coded by the alleles of *α-Amy-B1*, and Band 1 which is deficient in Chinese Spring and coded by *α-Amy-B3*. As the results of three point analysis, centromere – *α-Amy-B3* – *α-Amy-B1* were mapped in this order with recombination values, 5.5 ± 1.7(%) and 9.3 ± 2.2(%), respectively. Several isozyme bands vary between *georgicum* and *durum* LD 222, and the telocentric mapping showed that the map distances between centromere – *α-Amy-B1*(*α-Amy-B5*) – *α-Amy-B4* were tentatively determined 13.2 ± 3.5(%) and 22.3 ± 4.6(%).

Introduction

With a limited number of morphological markers, the linkage map in wheat is still insufficient in comparison with some other crops such as corn, rice, barley and so on. Various kinds of aneuploid series are available in wheat, and telocentric mapping is distinguished for being able to determine the centromere position, and results in the reduced map distance (Nishikawa 1991). Hart et al. (1993) summarized linkage map of hexaploid wheat and *T. tauschii*. On the other hand, deletion mapping (Endo and Mukai, 1988; Tsujimoto and Noda, 1990), and *in situ* hybridization mapping (Mukai, 1991) are now developing.

It was in 1981 that Nishikawa et al. first reported genetic analyses of α-amylase loci, and thereafter with improved electrophoresis technique more precise analyses could be realized, which we will report in this paper.

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Materials and Methods

Chinese Spring ditelosomic lines of homoeologous group of 6 were used for identifying α-amylase isozyme bands and also for telocentric mapping. Aka, a Japanese local variety, and Jones Fife, each having the specific zymogram pattern, were also used. *Triticum turgidum* (L.) Thell.ssp *turgidum* conv. *durum* (Desf.) MK cv. LD 222 and ssp. *dicoccum* (Schrank) Thell. var. *georgicum* Dek. et Man. were AABB tetraploid used in this study. Ditelo 6BL-monotelo 6BS of LD 222 used for telocentric mapping in Emmer wheat carries telocentric chromosomes introduced from the corresponding Chinese Spring telosomic lines into LD 222 genetic background (Nishikawa unpublished).

α-amylase was extracted by homogenizing a germinating grain in 1 ml of 0.05M tris-HCl buffer (pH 7.0, containing 0.002 M $CaCl_2 \cdot 2H_2O$), followed by centrifugation at 25,000 × g for 10 minutes. α-amylase isozymes in the extract were separated by thin layer (19 × 14 × 0.5 cm) polyacrylamide (0.5%) gel isoelectrofocusing. Carrier ampholites (Pharmalyte: Pharmacia, Sweden) and electorode solutions used were shown in Table 1. Electrophoresis was performed by applying constant current (2.1 $w/cm^3 \cdot$ gel) from the constant power supply (SJ-1065, Atto Ltd., Tokyo) for three hours. The gel was soaked in 3% starch sol for 10 minutes, incubated at 38°C for 2 minutes and stained with Lugol's solution.

Table 1. Ampholite mixtures and electrode solutions for malt type α-amylase isozymes in germinating grain of wheat

Ampholite* mixture (v:v)		Electrode solution	
pH4.0-6.0	pH5.0-8.0	Cathode	Anode
1	27	0.5×10^{-3}M NaOH	0.3M glutamic acid in 0.5M H_3PO_4

* Pharmalyte (Pharmacia, Sweden)

Results and Discussion

It is well known that α-amylase isozymes in germinating grain are grouped into two types, Malt type and Green type, the former are encoded by the genes on the long arm of chromosomes of homoeologous group 6. This was reconfirmed in this study as shown in Fig. 1. Among some twenty bands detected, however, Bands 3, 10 and 14 remained unknown about the chromosome arms, on which the genes concerned are located. In addition, three added bands, 9, 13 and 23 occurred in ditelo 6DS, which was not detected in disomic. There is no definite explanation how these three bands appeared, but there are two possibilities; the long arm of 6D carries the inhibiting effect to these bands, and the other is that missing the major bands nearby, Bands 8, 12, and 24 enables to discover Bands 9, 13 and 23 which were masked by them. Out of 17 common wheat cultivars tested, Aka, a Japanese local variety, lacked Bands 20, 21 and 22, and had Bands 15 and 15', and

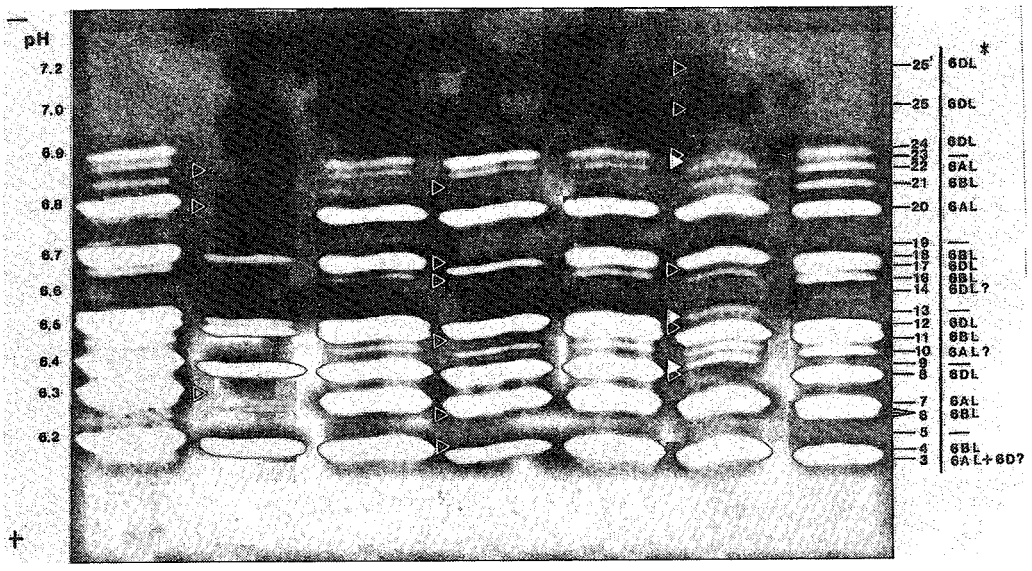

Fig. 1. Zymogram of malt type α-amylase in germinating grain of Chinese Spring (CS).
(left to right) ditelo-6AL, -6AS, -6BL, -6BS, -6DL, -6DS, disomic (▲ deficient, △ added).

Jones Fife lacked Bands 16 and 18 and had Bands 1, 1', 15 and 15', in comparison with Chinese Spring, respectively (Fig. 2-a,-b).

1) Band 20 (former Band 2, cf: Nishikawa et al. 1981)

Aka lacked Band 20 (Fig.2-a), which was known to be encoded by the gene on the long arm of chromosome 6A (Nishikawa et al. 1981), the allele for Band 20 being designated as *α-Amy-A1a*, and the one for missing Band 20 as *α-Amy-A1b*. Though not shown in Table 2, unexpected chromosome complements such as 40+t and 41 occurred among BC_1 plants. Because all the PMC's in F_1 monotelodisomic for 6AL formed a heteromorphic bivalent, and the missing chromosome is considered as one other than 6A, those plants with the aberrant chromosome number were treated as 41+t or 42 plants. With 8 crossover type in total 216 plant, the recombination value between *α-Amy-A1* and centromere was estimated as 3.8 ± 0.01(%), in other word, *α-Amy-A* is located on the

Table 2. Segregation of chromosome complements and Band 20 in BC_1 of (CS ditelo6AL × Aka) × Aka

2n	Band 20		Total
	Present	Absent	
42	5[1)]	94	99
41+t	114	3[1)]	117
Total	119	97	216

[1)] crossover type

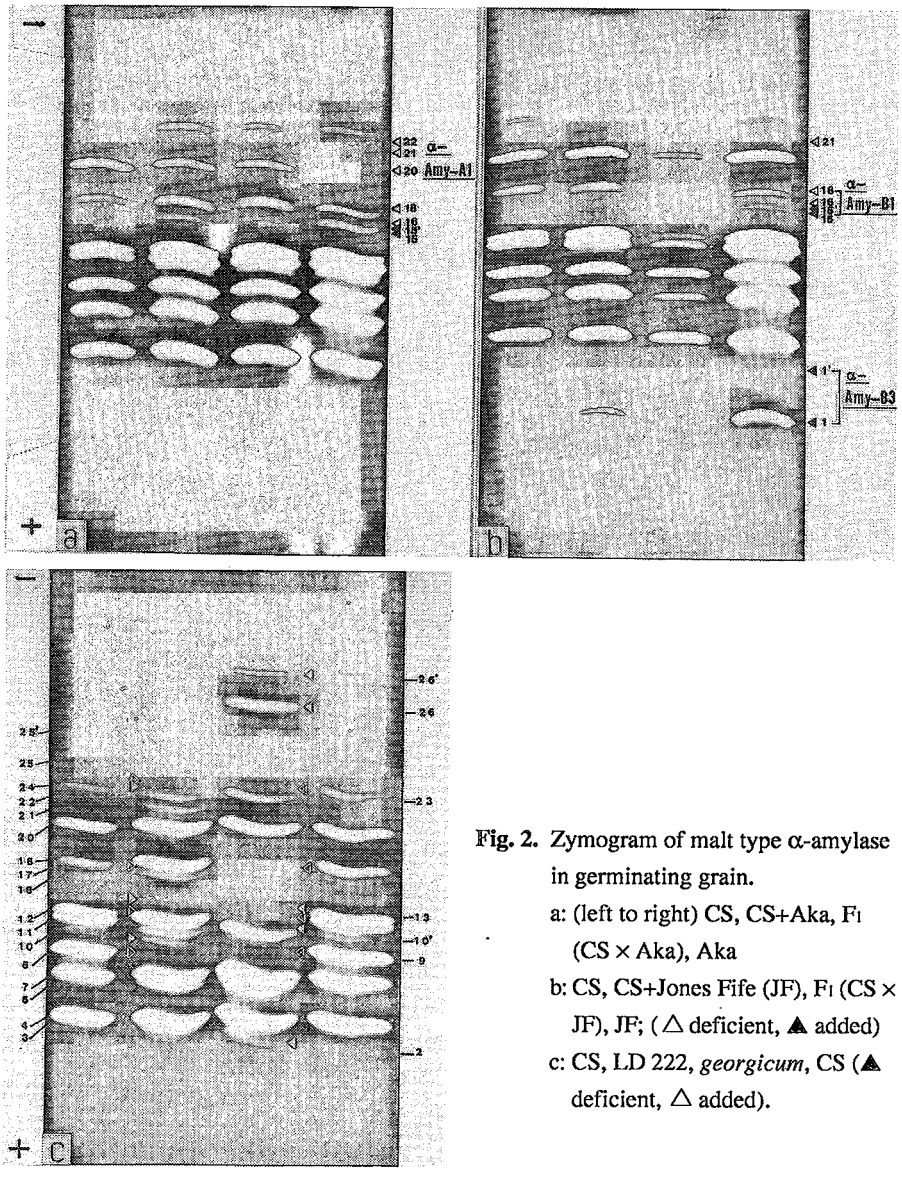

Fig. 2. Zymogram of malt type α-amylase in germinating grain.
a: (left to right) CS, CS+Aka, F_1 (CS × Aka), Aka
b: CS, CS+Jones Fife (JF), F_1 (CS × JF), JF; (△ deficient, ▲ added)
c: CS, LD 222, *georgicum*, CS (▲ deficient, △ added).

long arm of 6A apart from the centromere with the distance of 3.8 ± 0.01(%) (Fig. 3-a).
2) Band 18 (former Band 3) vs. 15 (former Band 4'), and Band 1 (former Band 10) vs. its absent. Jones Fife is different from Chinese Spring in α-amylase zymogram pattern, i.e. lacking Bands 16, 18 and 21, and having added Bands 1, 1', 15 and 15' (Fig. 2-b). Bands 18 and 15 have been known to be allelic, coded by *α-Amy-B1a* and *α-Amy-B1b*, respectively. Whereas Band 1 vs. its absent are controlled by *α-Amy-B3a* and *α-Amy-B3b*. Chromosome complements and presence or absence of the respective bands were scored on individual seed basis in BC_1 of (CS ditelo 6BL × Jones Fife) ×

CS (Table 3). Though four plants with the unexpected chromosome complements, 41 and 40+t, two plants each, occurred, these were treated as 42 and 41+t, respectively, taking chromosome pairing at F_1 meiosis into consideration as in the previous case of Aka. From the results shown in Table 3, recombination values between centromere and two loci were estimated as follows:

Centromere – *α-Amy-B1* $13.8 \pm 2.6(\%)$

Centromere – *α-Amy-B3* $5.5 \pm 1.7(\%)$

α-Amy-B1 – *α-Amy-B3* $9.3 \pm 2.2(\%)$

Thus, these loci are located as shown in Fig. 3-b.

Table 3. Segregation of chromosome complements, Band 1 vs. absent and Band 15 vs. 18 in BC_1 of (CS ditelo 6BL × Jones Fife) × CS

2n	Band				Total
	1	1	–	–	
	15/18	–/18	15/18	–/18	
42	$94^{0)}$	$2^{3)}$	$1^{2)}$	$6^{1)}$	103
41+t	$3^{1)}$	$0^{2)}$	$14^{3)}$	$62^{0)}$	79
Total	97	2	15	68	182

–: absent, $^{0)}$ non-crossover(co) type, $^{1)}$ co in region 1, $^{2)}$ co in region 2, $^{3)}$ double co in regions 1 and 2

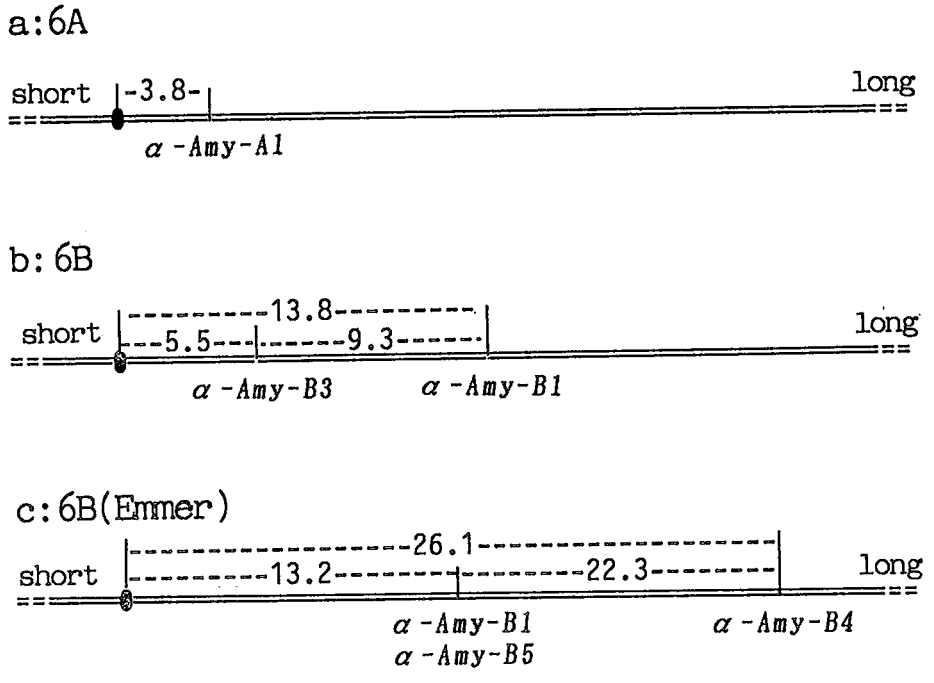

Fig. 3. Chromosome map.

a and b: 6A and 6B in common wheat, c: 6B in Emmer wheat (tentative).

Gale et al. (1983) and Ainsworth (1985) reported one compound locus of α-amylase isozymes on the long arm of each chromosome belonging to homoeologous groups 6 and 7. In this study, however, we confirmed evidently two loci of α-amylase as previously reported by Nishikawa et al. (1981), and this agreed completely with Mukai (1991), who clearly showed by *in situ* hybridization technique two loci of α-amylase gene on the long arm of chromosome 6B. It seems evident that the signal on proximal segment corresponds to *α-Amy-B3*, and the signal on distal segment to *α-Amy-B1*.

3) α-amylase loci in AABB tetraploid wheat.

Comparing with Chinese Spring, tetraploid wheat lacked, as expected, those bands known to be controlled by the genes on chromosomes 6D and 7D. Ssp. *georgicum* once classified as species of Timopheevi group, carried its specific bands 2, 10', 26 and 26' on one hand, and lacked Bands 9 and 23 in comparison with *durum* LD 222, our standard strain of AABB tetraploid. Moreover, major bands, 11, 16, 18 and 21 in LD 222, occurred as minor bands in *georgicum* (Fig. 2-c).

From the experiment using LD 222 doubleditelosomic for A and B genome chromosomes, developed by the senior author, α-amylase isozyme variation given above became evident to be attributable to the genes on chromosome 6B, with an exception for Band 9, which seems to be coded by the gene on 6A. In F_2 plants between LD222 and *georgicum*, recombination occurred neither between Bands 2, 26 and 26', nor between Bands 11, 16 and 21. Then, these bands are treated tentatively as controlled by the respective compound loci. Because Band 18 is coded by *α-Amy-B1* in common wheat, the compound locus for Bands 16, 18 and 21 is designated as *a-Amy-B1*, though there is no direct evidence for their homology, and the one for Bands 2, 26 and 26' as *α-Amy-B5*. The gene for Band 10' which is designated as *α-amy-B4* was also linked with 6BL.

Table 4. Segregation of chromosome complements and α-amylase isozyme bands in F_2 from the cross (doubleditelo6B of LD 222 × *georgicum*)

Band			2n			Total
26	18	10'	28	27+tL+ts	26+2(tl+ts)	
+	±	+	18	3	1	22
+	±	−	0	0	0	0
+	+	+	6	30	0	36
+	+	−	2	22	0	24
−	+	+	0	0	1	1
−	+	−	0	1	17	18
−	±	+	0	0	0	0
−	±	−	0	0	0	0
Total			26	56	19	101

+: present, ±:minor, −: absent

F_2 segregations of chromosome complements and α-amylase isozyme bands are shown in Table 4, from which recombination values between markers are estimated.

α-Amy-B1 – *α-Amy-B5*	less than 1%
α-Amy-B1 – *α-Amy-B4*	22.3 ± 4.6%
centromere – *α-Amy-B1*	13.2 ± 3.5%
centromere – *α-Amy-B5*	2.1 ± 1.1%
centromere – *α-Amy-B4*	26.1 ± 5.0%

There are considerable discrepancies among the recombination values calculated, which seem due to too small population size, especially to obtain double recessive segregants from F_1 hybrid in a repulsion phase. That is, the recombination values between *α-Amy-B1* and *α-Amy-B4*, and also between centromere and *α-Amy-B5* seem to be considerably underestimated, because some of crossover types were deficient. Taking these conditions into consideration we drew the tentative map as shown in Fig. 3-c.

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III. Report

A report on the 8th International Wheat Genetics Symposium (Beijing, China)

Shouyi Chen
Secretary general of the 8 IWGS, Director of the Institute of Genetics, Chinese Academy of Sciences, Bd no. 917, Datum Road, Andingmenwai, Chaoyang, Beijing, 100101, China

The 8th International Wheat Genetics Symposium was successfully held in Beijing, July 20-25, 1993. Over 500 participants from 38 countries and areas attended at the symposium and 334 papers were presented either as oral demonstrations or as posters on the seven topics; 1. Evolutionary genome relationships of Triticeae, 2. Cytogenetics, transfer of alien genetic material and genetic resources, 3. Molecular genetics and biotechnology, 4. General genetic analysis, gene mapping and marker system, 5. Genetics of resistance to pathogens and pests, 6. Genetics of tolerance to environmental stresses, and 7. Genetical approaches to breeding and the application of new breeding technologies.

New members of the international committee for organizing the 9th IWGS were elected. They are Li Zhensheng (China), B. S. Gill (USA), E. Kerber (Canada), J. W. Snape (UK), N. P. Ponia (Italy), A. B. Damania (India), P. Sharp (Australia), and T. R. Endo (Japan). Prof. Li Zhensheng was elected as the chairman of the 9th IWGS that will be held in Canada in 1998.

In the 8 IWGS, papers with good quality were contributed and included in the proceedings. This will be published in January 1994 at the costs of US $100.00. Scientists who are interested in this proceedings can subscribe it through the secretariat (Prof. Shouyi Chen, Institute of Genetics, Chinese Academy of Sciences, Beijing 100101, China, Fax: +86-014914896)

IV. Information

1. Plant genome II (January 24 - 27, 1994; San Diego, U.S.A.)

Plant genome II, the international conference on the status of research on the plant genome, will be held at Town & Country Hotel in San Diego, CA, USA. Secretariat: A Professional Conference Organizer, 11 Penn Plaza, Suite 1003, New York, NY 10001 U.S.A., Tel (212) 643-1750, Fax: (212) 643-1758.

2. Third International Triticale Symposium (June 13 - 16, 1994; Lisbon, Portugal)

Secretariat: Prof. Henrique Guedes-Pino, 3rd International Triticale Symposium, Theoretical and Applied Genetics Division, University of Tras-os-Montes and Alto Douro, Ap. 202,5001 VILA REAL Codex, Portugal. Fax: +351-59-74480, Phone +351-59-320595 or +351-59-320543.

3. Seventh International Symposium, Pre-harvest Sprouting in Cereals (July 2 - 7, 1995; Abashiri, Japan)

Specific topics will include: Physiology and molecular biology of grain development and germination; influence of environmental, physical and agronomic factors on sprouting; genetics and plant breeding; effects of sprouting damage on cereal end products. To receive a first announcement contact: Secretariat, 7th International Symposium on Preharvest Sprouting in Cereals, Kitami Agricultural Experiment Station, Kunneppu, Hokkaido 099-14, Japan; telephone 0157-47-2146, fax 0157-47-2774 or M. K. Walker-Simmons, USDA-ARS, 209 Johnson Hall, Washington State University, Pullman, WA 99164-6420; telephone 509-335-8696, fax 509-335-8674, e-mail simmons@wsuvml.edu.

* Please send information of international congresses, books, jobs, and anything concerning wheat genetics and the related field to WIS office.

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Bulgaria	2	2	4	Morocco	1	0	1
Brasil	0	1	1	New Zealand	4	1	5
Belorussiya (CIS)	1	1	2	Pakistan	10	1	11
Canada	14	4	18	Philippines	3	1	4
Chile	1	0	1	Poland	4	1	5
China	86	2	88	Portugal	7	1	8
Croatia	3	0	3	Rumania	3	0	3
Czech	1	1	2	Russia	4	1	5
Denmark	1	1	2	Slovakia	1	0	1
Egypt	6	0	6	Saudi Arabia	2	0	2
Finland	1	0	1	South Africa	8	1	9
France	9	3	12	Spain	4	0	4
Germany	11	5	16	Sweeden	9	4	13
Greece	2	0	2	Switzerland	0	2	2
Gruziya	1	0	1	Syria	4	1	5
Hungary	4	1	5	Taiwan	2	0	2
India	30	4	34	The Netherlands	2	3	5
Iran	3	0	3	Turkey	6	0	6
Iraq	4	1	5	USSA	0	1	1
Ireland	1	0	1	USA	85	19	104
Israel	10	2	12	UK	11	7	18
Italy	12	7	19	Yugoslavia	4	0	4
Japan	126	28	154				
Total	53 countrties				550	127	677

V. Editorial Remarks

We are glad to be able to publish the present issue in the centennial year of Dr. Hitoshi Kihara, who is the founder of Wheat Information Service. It was in 1953 on the occasion of the 9th International Congress of Genetics held at Bellagio, Italy, 26 geneticists, representatives of 19 counties, who were interested in wheat genetics, met to discuss several issues concerning wheat genetics with Dr. H. Kihara as chairperson including publication of an international journal and international wheat genetics symposium. Wheat Information Service was so born in 1954 that will cerebrate 40 year anniversary. This is very much indebted to Dr. Kihara for his initiative, as well as international cooperation.

But we are not free from problems for publishing WIS. The followings were some suggestion, proposal, or opinion which were sent to WIS during the last 8 IWGS at Beijing.

(1) The name of WIS should be changed to "Wheat Science", "Journal of Wheat Research" or other.

(2) WIS should accept such articles or reports as the other "leading" journals could not accept because of contents like biometrical data, characteristics of genetic stocks, or evaluation of genetic resources.

(3) WIS should be published more often, 3-4 volumes per year.

(4) Information from molecular analysis (DNA clones) should be included.

(5) Contributed articles could be reviewed internationally.

(6) Publication coast should be covered by subscribers. (Of course donation is very much welcome.)

(7) Continuous publication is the most important.

Thank you very much for these valuable suggestion.

Managing Staffs
Nishikawa, Sasakuma, Tsujimoto

Explanation of the picture on the cover

The monument of "The origin of wheat research" placed in the experimental field of Hokkaido University, where the original research on pentaploid hybrid in wheat were carried out in 1919 by Drs. Hitoshi Kihara and Toru Sakamura. See the article by T. Sasakuma for the details.

WIS No.77

編集 国際小麦研究連絡会議
西 川 浩 三

発行所 木原記念 横浜生命科学振興財団
〒232 横浜市南区六ツ川 3–122–20
Tel. (045) 721–0751

発行日 1993年 11月 11日

印刷 株式会社 野 毛 印 刷
Tel. (045) 252–2511

Wheat Information Service No. 77

Contents