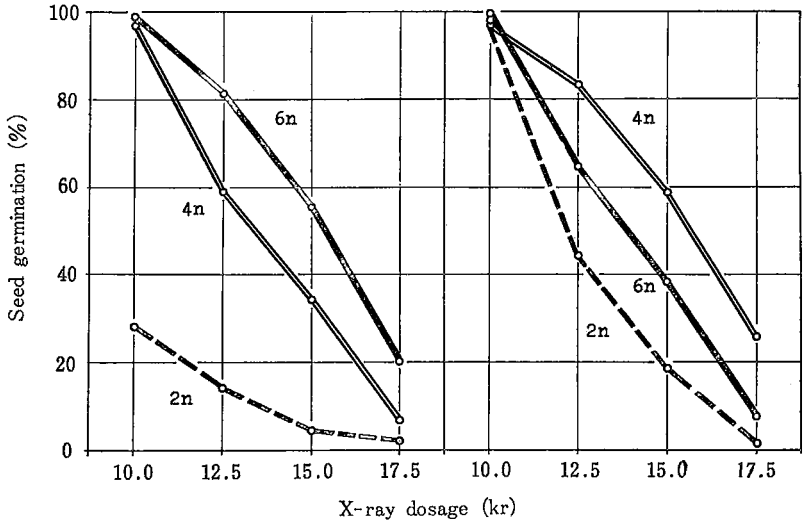
WHEAT INFORMATION SERVICE



No. 30 **March, 1970**

Wheat Information Service
Biological Laboratory, Kyoto University
Kyoto, Japan

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I. Research Notes

Addendum to the classification of the genus *Aegilops* by means of genome-analysis

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Classification of the genus *Aegilops* on the basis of genome-analysis was published in 1954 and 1957. At that time a Palestinian hexaploid species, *Ae. vavilovii* (ZHUK.) CHENN., was not studied, due to lack of living material. At first it was classified as belonging to *Ae. crassa* (var. *vavilovii* ZHUKOVSKY or var. *palaestina* EIG). Collected by YAMASHITA and others in Jordan (1959), it was studied morphologically and genome-analytically by TANAKA (cf. KIHARA 1963) and it became soon clear that it should be separated from *Ae. crassa* as an independent species [*Ae. vavilovii* (ZHUK.) CHENN.]. Therefore it might be worthwhile to have the whole list of genome-types of the genus (Table 1).

With the increase of our knowledge of the relationship of the two genera, *Aegilops* and *Triticum*, we need a complete revision of the genome symbols. However the situation is still uncertain. So we must be satisfied at present with the old symbols.

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—— 1957. Completion of genome-analysis of three 6x species of *Aegilops*. Seiken Zihô **8** : 3.

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Table 1. A classification of the genus *Aegilops* by means of genome analysis

Section	Species	Genome type
Polyeides	*Ae. umbellulata* ZHUK.	C^u
	Ae. ovata L.	C^uM^o
	Ae. triaristata WILLD. 4x	C^uM^t
	Ae. triaristata WILLD. 6x	$C^uM^tM^{t_2}$
	Ae. columnaris ZHUK.	C^uM^c
	Ae. biuncialis VIS.	C^uM^b
	Ae. variabilis EIG (incl. *Ae. kotschyi* BOISS.)	C^uS^v
	Ae. triuncialis L.	C^uC
Cylindropyrum	*Ae. caudata* L.	C
	Ae. cylindrica HOST	CD
Comopyrum	*Ae. comosa* SIBTH. et SM. (incl. *Ae. heldreichii* HOLZM.)	M
	Ae. uniaristata VIS.	M^u
Amblyopyrum	*Ae. mutica* BOISS.	Mt
Sitopsis	*Ae. speltoides* TAUSCH. (incl. *Ae. aucheri* BOISS.)	S
	Ae. longissima SCHWEINF. et MUSCHL. (incl. *Ae. sharonensis* EIG)	S^l
	Ae. bicornis (FORSK.) JAUB. et Sp.	S^b
Vertebrata	*Ae. squarrosa* L.	D
	Ae. crassa BOISS. 4x	DM^{cr}
	Ae. crassa BOISS. 6x	DD^2M^{cr}
	Ae. vavilovii (ZHUK.) CHENN.	$DM^{cr}S^p$
	Ae. ventricosa TAUSCH.	DM^v
	Ae. juvenalis (THELL.) EIG	DC^uM^j

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A proposal for the designation of nucleus-substitution lines and fertility-restoring genes in wheat

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Since the discovery of cytoplasmic male sterility of wheat caused by *Aegilops caudata* cytoplasm (KIHARA 1951), a large number of alien cytoplasms have been successfully transferred to emmer and/or common wheat, most of them being found to induce male sterility. Their list is given in Table 1. In many institutions, nucleus-substitution work to introduce

nuclei of various wheat cultivars into those cytoplasms is extensively carried out. Along with this, number of fertility-restoring genes, which have been factorially analyzed and located on specific chromosomes, is rapidly increasing. It seems, therefore, urgently needed to establish common rules for the designation of nucleus-substitution lines as well as fertility-restoring genes: I will propose here the following rules for their designation.

Table 1. List of alien cytoplasms introduced into emmer and common wheat

Donor of cytoplasm		Recipient wheat	Reference
Species	Genome constitution		
Ae. caudata	C	Common wheat	KIHARA (1951)
〃	〃	Emmer wheat	KIHARA and TSUNEWAKI (1961)
Ae. speltoides	S	〃	SUEMOTO (1969)
Ae. umbellulata	C^u	Common wheat	MURAMATSU (1965)
Ae. ovata	C^uM^o	〃	FUKASAWA (1959)
〃	〃	Emmer wheat	〃 (1953)
Ae. ventricosa	DM^v	Common wheat	OEHLER and INGOLD (1966)
T. boeoticum	A	〃	MAAN and LUCKEN (1969)
〃	〃	Emmer wheat	〃 (1967)
T. monococcum	〃	Common wheat	〃 (1969)
T. araraticum	AG	〃	〃 (〃)
T. timopheevi	〃	〃	WILSON and ROSS (1962)
〃	〃	Emmer wheat	KIHARA (1959)
T. zhukovskyi	AAG	Common wheat	MAAN and LUCKEN (1967)

Designation of nucleus-substitution lines

Rule 1. Name of the cytoplasm donor in italics to be shown in parantheses.

Rule 2. Name of nucleus donor is given after the name of the cytoplasm donor, with a hypen between them.

Example: (*timopheevi*)-Bison indicates a nucleus-substitution line of *Triticum aestivum* cv. Bison with the cytoplasm of *T. timopheevi*.

Rule 3. The number of crosses made with the backcross parent is indicated, if necessary, by a superscript to the name of the nucleus donor.

Example: (*ovata*)-Norin 26^{16} indicates the 14th backcross generation of *T. aestivum* cv. Norin 26 with the cytoplasm of *Ae. ovata*.

Designation of fertility-restoring genes

Rule 4. As the common, basic symbol, *Rf* meaning restored fertility, to be used.

Rule 5. A third letter indicating the name of the cytoplasm, in which the designated gene functions as a restorer, is added after the common symbol.

Example: A restoring gene to *Ae. caudata* cytoplasm is designated by *Rfc*.

As already pointed out by KIHARA and TSUNEWAKI (1967), the function of a fertility-restoring gene is, in general, specific to a certain cytoplasm, and an effective gene for

one cytoplasm does not necessarily function in other cytoplasms, unless they are related. Therefore, in designating the restoring gene, the name of cytoplasm, in which the gene functions, must be indicated.

However, we should retain the symbol, *Rf*, for restoring genes in *T. timopheevi* cytoplasm, because three restoring genes for it have been already designated by this symbol (LIVERS 1964, TAHIR and TSUNEWAKI 1969).

Rule 6. Non-allelic genes to the same cytoplasm are distinguished from each other by Arabic numerals given as subscripts to the symbol. Serial numbers starting from 1 should be given in the order of discovery.

Example: Non-allelic, restoring genes to *T. timopheevi* cytoplasm are designated by Rf_1, Rf_2, Rf_3, and so forth, in the order of discovery.

Rule 7. When the same gene functions as a restorer to more than one cytoplasm, the symbol first given is retained.

Applying these rules, the known restoring genes on a factorial basis will be designated as shown in Table 2.

Table 2. Proposed symbols for fertility-restoring genes in common wheat

Symbol	Location (chromosome)	Source	Male sterile cytoplasm	Reference
Rf_1	1A	*T. timopheevi*	*T. timopheevi*	LIVERS (1964), ROBERTSON and CURTIS (1967)
Rf_2	7D	〃	〃	LIVERS (1964), MAAN and LUCKEN (unpubl.)
Rf_3	1B	*T. spelta* var. *duh.*	〃	TAHIR and TSUNEWAKI (1969)
Rfc_1	1C	*Ae. caudata*	*Ae. caudata* and *Ae. ovata*	KIHARA (1951), KIHARA and TSUNEWAKI (1965)
Rfc_2	?	*T. compactum* cv. No. 44	*Ae. caudata*	TSUNEWAKI (1963)
Rfo_1	?	*T. aestivum* cv. Chinese Spring	*Ae. ovata*	(our unpubl. data)
Rfu_1	?	*T. aestivum* cv. Jones Fife	*Ae. umbellulata*	(our unpubl. data)

? : Chromosomal location unknown

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Nuclear conditions in the meristems of resting seeds of *Triticum durum*

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DNA labelling with ^{3}H-thymidine and DNA cytophotometry of Feulgen stained material have been used to study the sequential development of meristems in the embryo of *Triticum durum*: caryopses have been collected at different intervals during the last three weeks of development up to maturity (field grown plants) (AVANZI *et al.* 1969).

It has been found that the embryonic shoot apex completes its development at *ca.* 63% water content in the seed; other meristems-apices of primary root and the seminal roots of the first and second pair, primordia of leaves 1, 2 and 3-complete their development at 47~48% seed water content, or lower. At seed maturity, the shoot apex, the leaf primordia 1, 2 and 3 and most apices of the second pair roots consist exclusively of cells with a 2C nuclear DNA content, corresponding to the G_1 phase of the nuclear cycle in meristem cells. On the contrary, the meristems of the primary root and of the first pair roots contain different proportions of cells with 4C nuclei (G_2 phase of the nuclear cycle) in addition to 2C cells (Table 1).

Table 1. Frequency of nuclei with 2C and 4C DNA contents in meristems of five embryos excised from resting (mature) caryopses of *Triticum durum* (data from AVANZI *et al.* 1969)

Embryos / Meristems	No. 1		No. 2		No. 3		No. 4		No. 5	
	2C	4C	2C	4C	2C	4C	2C	4C	2C	4C
Primary root	77	23	86	14	61	39	72	28	80	20
I pair root	90	10	91	9	95	5	94	6	92	8
II 〃	100	0	100	0	92	8	100	0	100	0
I leaf	100	0	100	0	100	0	100	0	100	0
II 〃	100	0	100	0	100	0	100	0	100	0
III 〃	50	0	50	0	50	0	50	0	50	0
Shoot	30	0	30	0	30	0	30	0	30	0

An analysis of the labelling index (percentage of labelled interphases after feeding with ^{3}H-thymidine) and mitotic index (cells in mitosis in percent of cells scored) in the meristems of the embryos has shown that, at late stages of embryo development, DNA synthesis is stopped earlier than mitosis; but the interval between the inhibition of DNA synthesis and the inhibition of mitosis is different in different meristems. Consequently, in some meristems - leaf primordia, apices of most seminal roots of the second pair - mitotic activity lasts

long enough to deplete completely the meristems of 4C (G_2) cells; in the remaining root meristems, this "depletion phase" is less efficient, the degree of this efficiency decreasing progressively in the succession: roots of second pair→roots of first pair→primary root (this meristem contains the highest proportion of 4C relative to 2C cells).

If mature seeds are germinated in water containing ^{3}H-thymidine and the first mitotic cycle is observed in primary root apices, it is found that the nuclei first entering mitosis are unlabelled (nuclei in G_2 in the resting seed); to these labelled mitoses follow (nuclei in G_1 in the resting seed) (AVANZI *et al.* 1963).

As to the implications of these findings in studies on chromosome breakage and on developmental processes reference is made to our original papers.

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Association of homoeologous group 6 aneuploids with leaf necrosis in hexaploid wheat varieties[1),2)]

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SEARS (1954) first reported that Chinese Spring wheat plants nullisomic for chromosome 6B had necrotic patches on the leaves in some seasons, and that a telocentric for the short arm suppressed the necrotic condition. LATER (1966 and personal communication), he assigned the symbol *co* (corroded) to a locus on the short arm of 6B which was derived from some atom-bombed material provided by Luther SMITH. Because of its origin, SEARS considered the *co* locus to be a deficiency. If this is so, the necrotic phenotype in both materials

1) Cooperative investigations of the Department of Agronomy, University of Nebraska, Lincoln, Nebraska, and the Crops Research Division, Agricultural Research Service, U.S. Department of Agriculture, Lincoln, Nebraska. Published with the approval of the Director as Paper No. 2711, Journal Series, Nebraska Agr. Exp. Sta., U.S.A.

2) This study was supported in part by the Agricultural Research Service, U.S. Department of Agriculture, Cooperative Agreement No. 12-14-100-8425(34), administered by the Crops Research Division, Beltsville, Maryland, U.S.A.

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is due to the absence of a gene concerned with normal leaf development.

In the course of developing monosomic and other aneuploid conditions in the hard red winter wheat varieties, Wichita and Cheyenne, we have observed leaf necrosis involving the group 6 chromosomes. The necrosis occurred on seedlings in the greenhouse in the winter during the 7-week vernalization period at 4.4～7.2°C during the night and sometimes warming to a maximum of 13°C with sunlight during the day. No artificial lights were used during this period, so that only 8 to 10 hours of low-intensity daylight were available.

Some plants monosomic for 6A, 6B or 6D in both varieties had leaf necrosis which was evident at the one- to two-leaf stage. The only other aneuploid type in Cheyenne was a plant having one complete 6B chromosome and a telocentric for the long arm which usually formed a heteromorphic bivalent. This plant was necrotic and would be monosomic for the short arm.

In the variety Wichita, we have obtained nullisomics for all the group 6 chromosomes. Seeds for 6A nullisomics were kindly supplied by Dr. A. Mochizuki, Kobe University, Japan. Leaf necrosis was observed on 45 nullisomics for 6B, 4 nullisomics for 6A, and 11 out of 13 nullisomics for 6D. A monotelosomic for 6A was necrotic. One monoisosomic for 6D also was necrotic, but monotelosomics, ditelosomics, and a monoisosomic for 6D derived from a different misdivision event showed no evidence of necrosis. These results suggest that opposite arms of 6D are involved in the two situations, and that one arm contains a necrosis-suppressing gene. For 6B, the following aneuploids besides the nullisomics have been obtained: monotelosomic, ditelosomic and monoisosomic for the short arm (all of which had normal leaves except for one monotelosomic which was slightly necrotic); ditelosomic and di-isosomic for the long arm (all of which showed some leaf necrosis). These observations agree with those of Sears for Chinese Spring that the short arm of 6B is needed to suppress necrosis. We also have observed plants with a heteromorphic bivalent for 6B, where the telocentric involved the long arm. Some of these plants displayed leaf necrosis.

It may be that, with the low temperatures and low-intensity lighting under which the seedlings of these aneuploids were grown, the hemizygous condition of the genes for normal development cannot always prevent necrosis. However, there is less consistency of effect than in the case of nullisomics, where the normal genes are completely absent.

These observations suggest that one arm of each of the group 6 chromosomes has a gene(s) which suppresses leaf necrosis but that one dose of the gene is not always sufficient.

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A male sterile mutant in *Triticum aestivum*

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Genic male sterility has been reported in *T. durum* by BOZZINI and in *T. aestivum* by PUGSLEY and KRUPNOV. In these three cases, the first male sterile plants were observed in F_3 or F_4 of intervarietal crosses.

Seeds of the winter variety Probus were irradiated in 1966 with X-rays at a dosis of 24 kR and planted in the nursery. One ear of each M_1 plant was bagged, each ear giving a M_2 progeny. Among the 300 M_2 progenies, one segregated eight fertile to four sterile plants. The sterile plants were morphologically quite similar to the fertile ones but the florets remained broadly open at flowering. The anthers were typically thin and slightly curved. A microscopical examination showed only empty pollen grains. The sterile M_2 plants were discovered rather late at flowering and were therefore left open pollinated by the surrounding plants.

From each M_2 plant, a M_3 progeny was sown. These M_3 progenies segregated as follows:

Table 1. Segregation for fertility/sterility in M_3

M_2 plants		M_3 progenies Number of plants		χ^2 3 : 1	P.
Plant No.	Fertility	Total	Sterile		
1	fertile	20	0	—	
2	〃	28	0	—	
3	〃	27	0	—	
4	〃	30	0	—	
5	〃	18	5	0.0740	0.70～0.80
6	〃	18	4	0.0740	0.70～0.80
7	〃	29	9	0.5632	0.30～0.50
8	〃	29	7	0.0114	0.90～0.95
9	male sterile	60	5	8.8888	0.01～0.001
10	〃	51	0	—	
11	〃	145	0	—	
12	〃	81	3	19.5925	<0.001

The small number of progenies from M_2 fertile plants does not allow to check the ratio of segregating to not segregating progenies. Within the segregating progenies, the observed ratios fit a theoretical 3 : 1.

The segregation within progenies from M_2 sterile plants does not fit the 3 : 1 ratio. This can be explained as follows:

Going from the hypothesis of a single recessive gene for male sterility, the four M_2 sterile plants could have been pollinated by three types of plants:

1. normal fertile plants of neighbouring progenies
2. fertile plants of the same progeny homozygous for the dominant allele, like plants No. 1 to 4
3. fertile plants of the same progeny heterozygous for this allele like plants No. 5 to 8.

The cases 1 and 2 will give only fertile M_3 plants while the case 3 will segregate 1: 1. The observed ratios have to be considered as a mixture of these three possibilities.

At the same time, a M_3 composed of three ears-progenies from each M_2 plant was grown during the winter 1968~69 in a greenhouse at the Research Station for Agronomy, Zurich-Reckenholz. One ear of each M_3 plant was bagged. The average seed set was very low. It was therefore impossible to carry out a statistical analysis.

The M_4 from these bagged M_3 ears was grown in a greenhouse at Nyon in the spring 1969. Following segregations have been observed:

Table 2. Segregation for fertility/sterility in M_4

M_3 plants		M_3 progenies No.	M_4 progenies Number of plants		χ^2 3 : 1	P.
plant No.	fertility		Total	Sterile		
9	male sterile	9.1	39	9	0.0769	0.70~0.80
		9.2	43	10	0.0697	0.70~0.80
		9.3	73	15	0.7716	0.30~0.50
10	〃	10.1	22	4	0.5454	0.30~0.50
		10.2	55	9	2.1878	0.10~0.20
		10.3	102	29	0.6405	0.30~0.50
11	〃	11.1	60	17	0.3555	0.50~0.70
		11.2	32	7	0.1666	0.50~0.70
		11.3	32	5	1.5000	0.20~0.30
12	〃	12.1	26	7	0.0512	0.80~0.90
		12.2	43	14	1.3100	0.20~0.30
		12.3	33	7	0.2525	0.50~0.70
Total	–	–	560	133	0.4660	0.30~0.50

The homogeneity test gives a value of $\chi^2=7.46$.

These results indicate that male sterility is determined by a single recessive gene. At this stage, this conclusion only applies to the genotype of the variety Probus. Further investigations are needed for studying the expression of this gene in other genotypes. For this gene, we propose the designation ms^{a1} for male sterile *aestivum* 1.

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Wheat chromosomes controlling regular bipolar segregation of homologous chromosomes and integrity of the centromere

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The monosomic series of wheat varieties Chinese Spring and Pb. C591 are being maintained at the Division of Genetics, Indian Agricultural Research Institute, New Delhi (210 metres above sea level) and the Wheat Breeding Station, Simla (2120 metres above sea level). In the present study data were compiled on the number of different types of plants that are recovered from among the progenies of monosomics and their crosses from

Table 1. Frequency in wheat of disomes and a spectrum of aneuploids in the progenies of monosomic series of Chinese Spring and Pb. C591 and their crosses with other varieties, at tow locations

Location and Strain	Data based on (years)	1 D	2 M	3 DM	4 OA	Total
Delhi :						
Pb. C591 M	5	198	280	3	5	486
Chinese M	8	218	236	3	9	466
Pb. C591 M × E6160 D	1	18	23	0	2	43
Chinese M × Pb. C591 × Chinese M	2	16	19	0	2	37
〃 × E5883 D	2	12	11	0	1	24
〃 × E5008 D	2	34	42	1	10	87
〃 × Pb. C591 D	3	52	69	8	3	132
Pb.C591M × E6032 D	1	27	22	0	2	51
〃 × Sonora 64 D	1	18	8	0	0	26
Chinese M × *T. macha* D	1	8	7	0	0	15
Pb. C591 M × 〃	1	18	16	0	2	36
Simla :						
Chinese M	2	40	35	2	1	78
Chinese M × E5883 D	1	15	25	2	6	48
〃 × *T. macha* D	1	18	12	0	1	31

D=disome (21_{II}), M=monosome ($20_{II}+1_I$), DM=double monosome ($19_{II}+2_I$), OA=other aneuploids, Chinese=Chinese Spring.

the year 1961 to 1968. These data are presented in Table 1. Column 4, denoting other aneuploids, includes plants with isochromosomes and telocentric chromosomes in addition to the background chromosome complement of 42, 41, 40 and other aneuploid numbers.

Frequency of double monosomics:

In the crosses involving Chinese Spring monosomics and varieties Pb. C591 (Delhi) and E5883 (Simla) the frequency of double monosomes has been recorded as 6.1 and 4.1 percent respectively (Table 1). These frequencies are significantly higher than those obtained by selfing Chinese Spring and Pb. C591 monosomes under the same experimental conditions. From different year's data it has been observed that a majority of double monosomes (54 percent) originate from monosomics for chromosomes 1B, 4B and 6B. Significantly, out of these chromosomes 1B and 6B are satellited.

Frequency of other aneuploids:

It is observed from the table that the progenies of Chinese Spring and Pb. C591 monosomics which possess isochromosomes and telocentric chromosomes have a much lower frequency (range 1.0 to 1.9 percent) than the segregates derived from the crosses of these monosomic series (range 2.2 to 12.5 percent) with other varieties of wheat. It was noted that 84.6 percent plants which showed isochromosomes and telocentrics were derived from monosomic lines for chromosomes 1B, 4B, 2D and 4D.

The data presented reveal that chromosomes 1B, 4B and 6B of Chinese Spring and Pb. C591 control regular bipolar segregation of homologous chromosomes in each of the bivalent. In the absence of single dose (hemizygous state) of these chromosomes more double monosomes are produced. It is expected that the chances of "univalent shift" in the monosomic plants for these chromosomes would be higher.

Regarding the production of plants possessing isochromosomes/telocentrics it has been observed that chromosomes 1B, 4B, 2D and 4D are involved in maintaining the integrity of chromosome at the centromere. Their absence in one dose promotes misdivision of the centromere, leading to the formation of isochromosomes or telocentrics. Significantly, absence of chromosomes 1B and 4B promotes the production of both the double monosomes and that of isochromosomes and telocentrics.

Results of this study suggest that the regular bipolar segregation of homologous chromosomes and the integrity of the centromere are under genetic control and that chromosomes 1B, 4B, 6B, 2D and 4D are involved in these processes.

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On the location of the asynaptic gene in wheats[1)]

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In several previous studies it was found that the same asynaptic gene as of Chinese Spring of bread wheat (OKAMOTO 1957) is located on each chromosome 5B of two cultivars of bread wheat, Holdfast (RILEY and CHAPMAN 1958, 1960) and Poso (DRISCOLL and QUINN 1968), and of one of durum wheat, Stewart (MOCHIZUKI and KAWATA 1968).

F_1 plants between monosomic 5B F_1s of five Japanese cultivars with Chinese Spring and an inbred rye, strain 10, were grown at 15 to 28°C in the greenhouse and PMCs of them were cytologically examined. The results of an observation on the meiotic chromosome associations of 27- and 28-chromosome hybrids (Table 1) show that each chromosome 5B of five Japanese cultivars has the same 5B effect as of Chinese Spring.

Table 1. Mean chromosome associations and chiasmata at metaphase I of meiosis of five F_1 hybrid lines of the cross (monosomic 5B of Chinese Spring × Japanese cultivar) F_1 × inbred rye, with and without chromosome 5B (50 cells per line)

Cultivar	No. of chromosomes	No. of plants examined	Frequency per cell of								
			I*	II			III	IV	V	VI	chiasmata
				rod	ring	total					
Jujokomugi	28	1	27.52	0.24	0.00	0.24					0.24
Asozairai	27	2	10.72	2.94	2.54	5.48	1.32	0.28	0.02	0.02	11.68
Aburakomugi	27	1	14.42	2.60	1.86	4.46	1.34	0.12	0.02		9.44
Jujokomugi	27	5	9.50	3.12	2.00	5.12	1.34	0.24	0.10	0.02	11.00
Mubochinko	27	2	12.64	3.92	1.06	4.98	1.26	0.20	0.06		9.40
Akabungo	27	2	7.30	3.10	1.34	4.44	1.28	0.20	0.04		9.10

* I, II, III, IV, V and VI indicate univalent, bivalent, trivalent, tetravalent, pentavalent and hexavalent, respectively.

Out of five Japanese cultivars examined, only one cultivar, Asozairai, has a major reciprocal translocation concerning with chromosome 5B in relation to Chinese Spring (unpublished). By the meiotic observation of chromosome associations in the F_1 plants between monosomic 5A, 5B and 5D of Chinese Spring and Asozairai it is suggested that the translocated segment of chromosome 5B of Asozairai is larger than that of Poso and that there is one more minor translocation of defficiency-duplication type in addition to the reciprocal one between those two cultivars (Table 2).

1) This work has been supported by a grant from the Japan Society for the Promotion of Science as part of the Japan-U.S. Cooparative Science Programe.

Table 2. The frequency of chromosome associations per cell at metaphase I of meiosis in disomic and monosomic F_1 plants between monosomic 5A, 5B and 5D of Chinese Spring and Asozairai

Line	No. of chromosomes	No. of cells observed	Frequency per cell of						
			I*	II	III	IV			VI
						chain	ring	total	
disomic F_1	42	50	0.54	19.78	0.10	0.40	0.08	0.48	0.02
mono-5A F_1	41	50	1.22	19.18	0.00	0.22	0.12	0.34	
〃 -5B F_1	41	50	0.86	19.12	0.62	0.02	0.00	0.02	
〃 -5D F_1	41	50	1.36	18.78	0.02	0.38	0.12	0.50	
Poso F_1**	42	71	0.77	20.39	0.01	0.11	0.08	0.20	

* I, II, III, IV and VI indicate univalent, bivalent, trivalent, tetravalent and hexavalent, respectively.

** Calculated from the data by DRISCOLL and QUINN (1968).

It is, therefore, quite probable that the asynaptic gene is basically located on chromosome 5B of both emmer and common wheat, but on the proximal part of the long arm.

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Induction of earliness and grain color mutation in wheat variety Nadadores

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Nadadores, a hexaploid wheat variety, introduced in India from Mexico, has outyielded all other Indian and Mexican wheat varieties in yield trials conducted in the districts of Kinnaur and Pangi of Himachal Pradesh, at an altitude of about 2420 metres above the sea level, during 1966～68. This two gene dwarf wheat possesses all the desirable attributes of a variety suited to the higher hills, except the red color of its grain, which is disliked by the consumers.

Fig. 1. Early maturing amber grained mutant of Nadadores (left) and a row of parental strain (right).

Seeds of Nadadores were irradiated with gamma rays, and in the M_1 generation an earhead showed amber colored seeds in the material, which was treated with 30 kilo rads of gamma rays. In the M_2 generation, the progeny of this earhead bred true and the plants resembled parental Nadadores in all their morphological characters, except for the amber color of the grains and early maturity of plants by about 30 days (Fig. 1). Nadadores could not be grown in the plains of India due to its late maturity. The isolation of an amber grained mutant with early maturity could enlarge its area of cultivation from the hills to the plains of India. The seeds of this mutant are being multiplied for large scale trials.

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The RBE of 14.1 MeV fast neutrons and ^{137}Cs gamma rays in the pre-soaked seeds of *Triticum boeoticum* and its autotetraploid

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Seeds of *Triticum boeoticum* Boiss. (KU 101–1), a diploid wheat species having A genome, and of its autotetraploid (KU 201–1) were soaked for 14 hours at 20°C and were irradiated acutely with 14.1 MeV fast neutrons or with ^{137}Cs gamma rays at the National Institute of Genetics, Misima. The ranges of fast neutron doses applied were 121 to 502 rads and 207 to 753 rads for the diploid and autotetraploid, respectively, and those of gamma-ray doses were 291 to 1164 rads and 437 to 1746 rads, respectively. The number of seeds

employed for each dose was 30 or 60. The treated and control seeds were immediately carried back to Kyoto in a wet condition and were sown in wooden flats. Plants were grown in a greenhouse.

Measurements of seedling height and dry weight were performed 31 and 49 days after irradiaion, respectively, and the effects of fast neutrons and gamma rays were compared. It was found that fast neutrons caused more growth inhibition than gamma rays. Values of the Relative Biological Effectiveness (RBE) of 14.1 MeV fast neutrons to reduce seedling height as compared with ^{137}Cs gamma rays were calculated to be 3.12 and 2.66 for *T. boeoticum* and its autotetraploid, respectively. The RBE values in reducing dry weight were 3.52 and 2.74 for the diploid and autotetraploid, respectively.

The RBEs in the pre-soaked seeds determined in the present study are evidently much lower than those usually obtained from higher plants with 14.1 MeV fast neutrons (*ca.* 10 to 25), 0.43 to 4.7 MeV fast neutrons (*ca.* 10 to 100), or other heavy particles (*ca.* 10 to 50). Considering that most of the earlier high RBEs have been obtained from irradiation of dry seeds containing a small amount of water (*ca.* 10 to 15 percent), it seems to be reasonable to interprete that water content does modify RBE value. It is well known that gamma or X rays are less effective in causing damages in the case of irradiation of dry seeds than in the case of irradiation of wet systems such as growing plants, while the effectiveness of neutrons is changed only slightly by water content. The above interpretation that water content modifies RBE is supported by the author's recent data from *Tradescantia* stamen hairs (ICHIKAWA, in press). (Supported partly by the grant from the Ministry of Education, No. 96014, 1968).

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The relations between radiation susceptibility, mutation frequency, and level of ploidy in the genus *Triticum*

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Introduction

An extensive work has been done during the past decades concerning the relations between radiation susceptibility and level of ploidy in the genus *Triticum*, but the problem is not yet solved. Numerous contradictions can be found in the literature and it is possible to confirm each hypothesis theoretically conceivable by empirical findings. Many authors found an increasing radiation susceptibility of the diploid species in comparison to the polyploid ones (FRÖIER 1941, FRÖIER and GUSTAFSSON 1941, NATARAJAN, SIKKA and

SWAMINATHAN 1958, MATSUMURA and NEZU 1960, BHASKARAN and SWAMINATHAN 1961). In contradiction to this, some varieties of the diploid *Triticum monococcum* studied by SMITH (1946) turned out to be more resistant than the tetra- and hexaploid material. Divergent findings were also obtained by comparing tetra- and hexaploid species. In some cases, no clear differences were found (FRÖIER, GELIN and GUSTAFSSON 1941, SMITH 1946, NATARAJAN, SIKKA and SWAMINATHAN 1958, BHASKARAN and SWAMINATHAN 1961). Different authors, however, observed an increased radiation resistance of the tetraploid material in comparison to the hexaploid one (MATSUMURA, FUJII and KONDO 1957, MOHAMED 1962). The opposite behaviour was found by MATSUMURA and NEZU (1960) with regard to *T. durum* and *T. vulgare*. Finally, certain investigations show a differing susceptibility of species or varieties belonging to the same level of ploidy (FRÖIER 1946, MATSUMURA and FUJII 1955, MATSUMURA 1956, SARIC 1958, SCARASCIA *et al.* 1960). The heterogenious findings obtained are easily understandable if one assumes, that not the degree of ploidy, but the genotypic composition of a species, subspecies or variety is responsible for its reaction to radiation. In order to prove this hypothesis, several species and varieties of each of the three ploid groups of the genus were used studying their radiobiological and radiogenetic behaviour.

Material

The following varieties were used for our investigations:

Triticum	*monococcum*	var.	*macedonicum*	2n
〃	*boeoticum*	var.	*rufinigrum*	2n
〃	*dicoccum*	var.	*hybridum*	4n
〃	〃	var.	*krausei*	4n
〃	〃	var.	*tragi*	4n
〃	*durum*	var.	*valenciae*	4n
〃	〃	var.	*africanum*	4n
〃	*carthlicum*	var.	*fuliginosum*	4n
〃	*polonicum*	var.	*rubrovesticum*	4n
〃	〃	var.	*nigrobarbatum*	4n
〃	〃	var.	*velutinum*	4n
〃	*aestivum* ssp.	*vulgare*	var. *tschermakianum*	6n
〃	〃	〃	〃 *lutescens*	6n

Dry seeds were irradiated with 10, 12.5, 15, 17.5, 25 and 32.5 kr X-rays. A dosage of 17.5 kr was lethal for most of the varieties used. Different criteria showing the radiobiological response were studied in X_1-plants grown in the field. The mutation frequency of the X_2-generation was preferably studied in the greenhouse by evaluation of chlorophyll mutations.

Results

1. Radiobiological investigations

The following criteria of the irradiated material and of the X_1-plants were studied:

—the germination of the treated seeds,

—the number and length of culms,

—the number of caryopses per plant,

—the germination of the seeds of the X_1-plants.

Let us first consider the situation within the same level of ploidy. There are great differences in the response of the diploid species *T. boeoticum* and *T. monococcum* preferably after having used relatively low dosages. The variety *rufinigrum* of *T. boeoticum* turned out to be much more susceptible than *T. monococcum* var. *macedonicum* considering seed germination after irradiation. Corresponding observations were also made within the tetra- and hexaploid group. *T. durum* var. *valenciae* for instance showed a markedly less susceptibility as compared with *T. durum* var. *africanum* and *T. polonicum* var. *rubrovesticum*. That means, that there are not only differences within the same group but already within the same species. Analogous findings were obtained by MATSUMURA and FUJII (1955) and by MATSUMURA (1956) studying different varieties of the diploid *T. monococcum*.

According to these findings we cannot expect to obtain a generally valid relation if we consider the response of species or varieties belonging to groups having different chromosome numbers. This can clearly be seen from Figure on the cover. In the left-hand part of this figure, *T. boeoticum* var. *rufinigrum* (2n), *T. polonicum* var. *rubrovesticum* (4n) and *T. aestivum* ssp. *vulgare* var. *lutescens* (6n) are compared with one another as far as the relations between seed germination and X-ray dosage are concerned. An increasing resistance with increasing degree of ploidy was found. But the opposite situation is illustrated in the right-hand part of the figure. The tetraploid *T. durum* var. *valenciae* is more resistant than the hexaploid variety *tschermakianum* of *T. aestivum*. Moreover, the variety *macedonicum* of the diploid *T. monococcum* does not show the high susceptibility from the diploid material; on the contrary, it is nearly comparable with the hexaploid variety used for this comparison. These findings were confirmed in a second series of investigations.

In general, it can be stated that the varieties *valenciae* of *T. durum* (4n) and *lutescens* of *T. aestivum* (6n) behaved more resistant to X-rays than all other varieties proved. This regularity became also discernible with regard to the degree of tillering and the culm length in relation to the X-ray dosage. Moreover, the X_1-plants of these two varieties showed a less reduction of their seed production after irradiation than the other ones. Their relatively small susceptibility was also revealed in the low proportion of completely sterile X_1-plants. Finally, the same tendency could be observed with regard to the germination power of the seeds of the X_1-plants.

2. Radiogenetic investigations

In total, 278 chlorophyll mutations were obtained in our X-ray treatments. Furthermore, some other mutants were selected; details can be seen in a previously published paper (GOTTSCHALK and IMAM 1965). It was not our intension to perform a quantitative analysis

Table 1. Survey on the mutation frequency of the varieties used in our X-ray treatments related to the number of ear progenies

Level of ploidy	Variety	10 kr		17.5~32.5 kr		Total		
		Number of mutant genes	Mutation frequency in %	Number of mutant genes	Mutation frequency in %	Number of ear progenies	Number of mutant genes	Mutation frequency in %
2n	*T. monococcum*							
	var. *macedonicum*	53	6.4	2	6.9	854	55	6.4
4n	*T. dicoccum*							
	var. *hybridum*	10	8.8	0	—	137	10	7.3
	var. *krausei*	18	13.6	3	3.0	232	21	9.1
	var. *tragi*	22	8.8	4	6.7	310	26	8.4
	T. durum							
	var. *valenciae*	85	12.8	35	6.6	1196	120	10.0
	var. *africanum*	7	2.8	3	5.4	311	10	3.2
	T. carthlicum							
	var. *fuliginosum*	12	3.4	2	11.8	373	14	3.8
	T. polonicum							
	var. *rubrovesticum*	7	1.9	0	—	411	7	1.7
	var. *nigrobarbatum*	8	3.8	not treated		209	8	3.8
	var. *velutinum*	5	3.6	〃		140	5	3.6
Total of the tetraploids		174	7.0	47	5.6	3319	221	6.7
6n	*T. aestivum*							
	var. *tschermakianum*	0	—	0	—	470	0	—
	var. *lutescens*	1	0.3	1	0.2	754	2	0.3
Total of the hexaploids		1	0.2	1	0.2	1224	2	0.2
Grand Total		228		50		5397	278	5.2

of the mutations induced, but to compare the mutation frequency of the different varieties using chlorophyll deficiencies as a well discernible criterion of gene action. The results are listed in Table 1. The values of the dosages between 17.5 and 32.5 kr are summarized and compared with the mutagenic action of 10 kr. The mutation frequency was related to the number of ear progenies of the X_1-plants. In total, 5397 progenies were evaluated.

Only one diploid variety could be used for this purpose; its mutation frequency was 6.4%. A broad spectrum of varieties of different tetraploid species was studied. Some of them showed marked differences in their mutation frequency. The variety *rubrovesticum*

of *T. polonicum* for instance showed an extremely low number of mutations (1.7%); the opposite situation was found in *T. durum* var. *valenciae* (10.0%). These differences could likewise be confirmed in a second treatment. The unexpected high mutation frequency of *valenciae* is in contrast to its strikingly high resistance to X-rays as far as its radiobiological response is concerned. The mutation frequency of the hexaploid varieties was extremely low. The values obtained are approximately adequate to the 40th part of the corresponding rates of the diploid and tetraploid material.

Discussion

It is well known, that the action of radiation can be influenced by specific physiological or physical peculiarities of the seeds such as water content, pH-value, nucleus volume, chromosome size etc. But the results described in this paper seem to be due to specific genetic differences of the varieties used. An increased radiosensitivity of a distinct strain of *T. monococcum* was interpreted to be due to the presence of an "X-ray susceptible factor" (SMITH 1942). A corresponding concept was given by YAMASHITA (1956) likewise for *T. monococcum*. It is our opinion, that there is a close relation between the degree of radiosensitivity and the genetic composition of a variety. Not the number of genomes present but specific genes or gene combinations of the genomes could be responsible for the intensity of the reaction to irradiation, while the physiological criteria just mentioned have only a modifying action.

It is very complicated to give a plausible explanation of the divergent mutation frequencies observed in our experiments. If we consider the voluminous literature concerning this problem, all relations conceivable between the level of ploidy and the mutation frequency can be found. A detailed discussion of the findings existing was given by GOTTSCHALK and IMAM (1965). One of the main problems for understanding these contradictory findings is obviously the clarification of the question, whether the amphidiploid character of the hexaploid wheats resulted in a reduction of the allelism of originally homologous genes. Therefore, a detailed comparison of the mutational behaviour of auto- and allopolyploid species would be of great interest.

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DNA content per nucleus in *Aegilops* species

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Genus *Aegilops* includes about 20 species that have been thoroughly investigated from the cytogenetical viewpoint. In order to enhance further understanding of the phylogenetic relationships among these species, their nuclear DNA content was measured microspectrophotometrically, using the pollen tetrad nuclei stained by Feulgen's method (NISHIKAWA and FURUTA 1969, Jap. J. Genet. 44).

The results obtained are shown in Table 1, together with chromosome number and genome constitution. Analysis of variance revealed that the difference between nine diploid species (11 strains) was significant. DNA content per nucleus of *Ae. bicornis* was apparently the highest among all diploid species. No significant difference was found among *Ae. longissima*, *Ae. mutica*, *Ae. uniaristata* and *Ae. comosa*, between *Ae. umbellulata* and *Ae. squarrosa* var. *meyeri*, and among *Ae. squarrosa* var. *meyeri*, var. *strangulata* and *Ae. caudata*, respectively, while the difference was significant among all other species combinations. Moreover, *Ae. squarrosa* var. *typica* showed the lowest amount of nuclear DNA among 11 diploid strains.

In the tetraploids, no significant difference was found among two subspecies of *Ae. triuncialis* (amphidiploid between *Ae. caudata* and *Ae. umbellulata*) and the sum of its two analysers. On the other hand, a statistically significant difference was noted among five species, *Ae. variabilis*, *Ae. ovata*, *Ae. columnaris*, *Ae. biuncialis* and *Ae. triaristata* 4x which belong to Polyeides section. DNA content of *Ae. cylindrica* was approximate to the total of those of *Ae. caudata*, donor of C genome and *Ae. squarrosa* var. *meyeri* or var. *strangulata* (but not

Table 1. DNA content per nucleus in *Aegilops* species (in arbitrary unit). Relative DNA content of other species, taking *Ae. speltoides* as a standard is also shown

Species	2n	Genome	DNA content/Nucleus	
			$\bar{x}\pm s$	Ratio
Ae. speltoides TAUSCH	14	S	202±21	1.00
Ae. bicornis (FORSK.) JAUB. *et* Sp.	14	S^b	255±34	1.26
Ae. longissima SCHW. *et* MUSCH.	14	S^l	224±18	1.11
Ae. caudata L.	14	C	161±23	0.80
Ae. umbellulata ZHUK.	14	C^u	176±19	0.87
Ae. comosa SIBTH. *et* SM.	14	M	215±25	1.06
Ae. uniaristata VIS.	14	M^u	219±27	1.08
Ae. mutica BOISS.	14	Mt	219±23	1.08
Ae. squarrosa L.	14	D		
ssp. *eu-squarrosa* EIG				
var. *typica* L.			126±12	0.62
var. *meyeri* GRISEB.			171±24	0.85
ssp. *strangulata* EIG				
var. *strangulata* EIG				
Ae. cylindrica HOST	28	CD	162±24	0.80
Ae. triuncialis L.	28	C^uC	337±21	1.67
ssp. *eu-triuncialis* EIG				
var. *typica* L.			365±38	1.81
ssp. *orientalis* EIG				
var. *persica* (BOISS.) EIG			329±42	1.63
Ae. variabilis EIG	28	C^uS^v	479±53	2.37
Ae. ovata L.	28	C^uM^o	321±38	1.59
Ae. columnaris ZHUK.	28	C^uM^s	365±40	1.81
Ae. biuncialis VIS.	28	C^uM^b	393±43	1.95
Ae. triaristata WILLD. 4x	28	C^uM^t	539±35	2.67
// 6x	42	$C^uM^tM^{t2}$	752±76	3.72
Ae. ventricosa TAUSCH	28	DM^v	341±28	1.69
Ae. crassa BOISS. 4x	28	DM^{cr}	364±41	1.80
// 6x	42	DD^2M^{cr}	546±50	2.70
Ae. vavilovii (ZHUK.) CHENN.	42	DS^lM^{cr}	638±80	3.16
Ae. juvenalis (THELL.) EIG	42	DC^uM^J	654±55	3.24

var. *typica*), a D genome donor. This result is contradictory to that of JOHNSON (1967, Nature 216) obtained by protein electrophoresis which suggested *Ae. squarrosa* var. *typica* as the possible D genome donor to *Ae. cylindrica*. No difference was observed between *Ae. crassa* 4x and *Ae. ventricosa*, both of which had DNA content almost comparable to the sum of *Ae. comosa* or *Ae. uniaristata* and *Ae. squarrosa*. As to the hexaploid species, *Ae. triaristata* 6x showed DNA content that is equivalent to the sum of *Ae. triaristata* 4x and *Ae. comosa* or *Ae. uniaristata*. *Ae. crassa* 6x and *Ae. vavilovii* also showed an additive relation-

ship between their ancestries, that is, these hexaploids had DNA content nearly equal to the sum of *Ae. crassa* 4x and *Ae. squarrosa* and *Ae. crassa* 4x and *Ae. longissima*, respectively. In another hexaploid species, *Ae. juvenalis*, the observed value was higher than the expected one based on its putative ancestry.

In general, actual DNA content of polyploid species was comparable to that expected from their genome constitution. (Details of the results and discussion will be presented elsewhere.)

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Nucleic acid synthesis and adaptation in wheat

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Intervarietal differences in adaptability, generally tested through multilocation yield trials, are known to exist in wheat as in other crops. The present study was planned to determine some of the possible cytological and metabolic characteristics of wheat varieties, which have been found to differ significantly in their adaptability, through such tests. One of the characters for which these varieties have been tested is the turnover of DNA and RNA in their root tip cells at three different temperatures.

Six Indian commercial varieties of wheat—C 303, C 306, NP 824, NP 823, NP 825 and NP 798 formed the experimental material. Of these C 306 is known to be highly adapted, while NP 823 and 825 show very poor adaptability. The other varieties show an average type of adaptability.

The autoradiographic techniques was employed to study the synthesis of DNA and RNA in the root tip cells of the six varieties at temperatures of 20°C, 30°C and 38°C. The seeds were germinated at these different temperatures and the root tips, when about 1 cm long, were fed with tritium labelled thymidine in one case, and thymdine in the other. The thymidine (2C/ml, specific activity 3C/m Mol.) incorporation was allowed for a period of 10 hours while uridine (5C/ml, specific activity 2.24C/m Mol.) was fed for a period of 4 hours.

A quantitative study of incorporation of thymidine was made by counting the silver grains formed over chromosomes of nearly 30 metaphase cells in each of a number of root tips. In the case of RNA synthesis, 29 interphase cells showing well spread silver grains were scored in five or more root tips of each variety. These observations on grain count are presented in Figures 1 and 2.

It has been found that, in general, the DNA synthesis in the cells of a variety varies greatly with temperature. An important finding is that the variety C 306, known for its

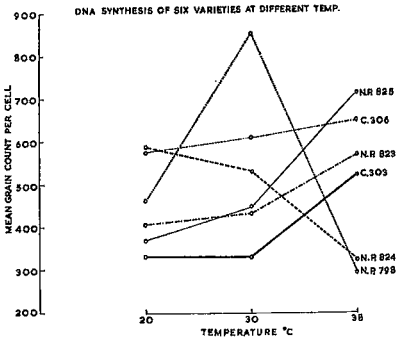

Fig. 1

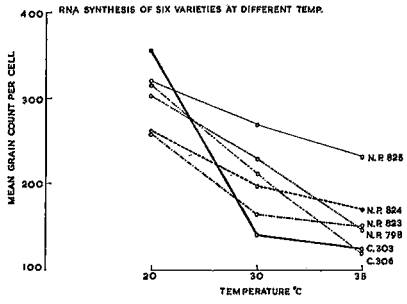

Fig. 2

high adaptability, is relatively constant in its DNA synthesis at different temperatures. It will also be seen that all the six varieties show variation in RNA synthesis with change in temperature. C 306 and C 303 show the largest variation in RNA synthesis, in contrast to the poorly adapted varieties like NP 897.

The above observations would suggest that constancy in DNA and plasticity in RNA synthesis under different environmental conditions may be important attributes of a well adapted genotype. That stability in the synthesis of DNA, the genetic material, should contribute to adaptability is understandable. It is possible that the capacity to vary the synthesis of RNA, the material closely associated with gene action, in response to changing environmental conditions also confers an adaptive advantage.

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Production of male-sterile and restoration lines of Pakistani wheat varieties with *Ae. ovata* and *T. timopheevi* cytoplasms[1)]

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A new chapter in wheat breeding was opened with the discovery of cytoplasmic male-sterility (KIHARA 1951); in almost all the progressive countries, work to develop hybrid wheat was started vigorously by establishing male sterile and their counterpart restoration lines of commercial varieties. The present work of nucleus substitution to produce male sterile and their counterpart restoration lines of Pakistani wheat varieties with *Ae. ovata* and *T. timopheevi* cytoplasms was initiated in 1966, and the first crosses were practised in the spring of 1967 by using the following four nucleus substitution lines having *Ae. ovata* or *T. timopheevi* cytoplasm, as female parents:

1) The work has been supported by a scholarship from the Ministry of Education, Japan.

I. (*ovata*)-Norin 26: Male-sterile line.

II. (*ovata*)-P168: Fertility restorer line.

III. (*timopheevi*)-Bison: Male-sterile line.

IV. (*timopheevi*) *T. spelta duhamelianum*: Fertility restorer line.

In the start five *T. aestivum* varieties, namely, C273, C271, C591, C518 and Mexi-Pak 65 and one strain of *T. sphaerococcum*, Pak Kohni, were used as pollinators to the above-mentioned nucleus substitution lines, and in the later years five more varieties of *T. aestivum*, i.e., C228, AU49, AU44, Dirk and H-68 were included in the project.

To accomplish the nucleus substitution work on accelerated pace two crops every year were raised, i.e., a greenhouse crop in winter (begining of September—middle of January) and a field crop in spring (end of January~middle of June). Every time the pollinators were grown in four repeats at one week interval to ensure the availability of pollen at the time of flowering for making subsequent backcrosses. Only, completely male sterile plants were utilized to develop sterile lines, and the plants exhibiting maximum pollen fertility were employed to establish restorer lines.

Nucleus substitution lines with *Ae. ovata* cytoplasm

Male-steriles: In all the 11 varieties pollen fertilities (percentage of good pollen grains) and selfed seed fertilities (estimated from the seed set in the first and second florets) in F_1

Table 1. Fertilities of nucleus substitution lines with *Ae. ovata* cytoplasm

Nucleus donor	Fertilities in the backcross generation (%)							
	Male sterile lines				Fertility-restorer lines			
	F_1	SB_1	SB_2	SB_3	F_1	SB_1	SB_2	SB_3
C273	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	81.8 (52.1)	87.9 (95.4)		
C271	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	82.2 (65.3)	80.4 (75.0)	73.4 (25.0)	11.2 (0.0)
C591	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	61.7 (45.0)	69.8 (41.7)	88.7 (93.7)	
Pak Kohni	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	81.5 (63.1)	81.3 (77.1)	84.8 (70.8)	
Mexi-Pak 65	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	
C228	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)		91.6 (82.1)	0.0 (0.0)	0.0 (0.0)	
AU49	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)		84.2 (58.3)	90.2 (62.5)		
AU44	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)		97.0 (97.9)	100.0 (100.0)	98.5 (98.6)	
Dirk	0.0 (0.0)	0.0 (0.0)			56.6 (6.3)	0.0 (0.0)		
H-68	0.0 (0.0)	0.0 (0.0)			10.0 (0.0)	15.4 (29.2)		

Upper and lower figures indicate pollen and selfed seed fertility, respectively.

and the following backcross generations were checked. All the varieties exhibited complete absence of good pollen and no seed fertility (0.0%) in the F_1 as well as in the subsequent backcross generations, with the exception of Pak Kohni. In this particular strain of *T. sphaerococcum*, out of 13 plants of the first substitution-backcross generation (SB_1) two plants exhibited partial pollen (31.7%) and seed fertilities (8.3%). The selfed seeds from those two plants were sown to check restoring genes, and again out of 21 plants, three plants showed partial seed fertility (6.5%). All the varieties of *T. aestivum* do not carry any restorer genes for *Ae. ovata* cytoplasm and complete sterility was induced.

Fertility-restorer lines: To develop the counterpart restorer lines for the male-steriles, all the varieties were crossed to (*ovata*)-P168, an established restorer line of P168 having *Ae. ovata* cytoplasm. Their F_1 hybrids exhibited varying degrees of pollen and seed fertilities, with the exception of Mexi-Pak 65 which showed complete male sterility in the F_1 and also in the backcross generations (Table 1). Varieties C273, C591, Pak Kohni, AU49 and AU44 exhibited fairly high fertilities in all the generations, whereas in variety C271 the fertilities went on diminishing with the advancement of nucleus substitution, exhibiting 11.2% pollen and 0.0% selfed seed fertilities in SB_3. Varieties C228 and Dirk became completely sterile from SB_1 generation onward; H-68 also showed very low fertilities in F_1 and SB_1 generations.

Table 2. Fertilities of nucleus substitution lines having *T. timopheevi* cytoplasm

Nucleus donor	Fertilities in the backcross generations (%)							
	Male-sterile lines				Fertility-restorer lines			
	F_1	SB_1	SB_2	SB_3	F_1	SB_1	SB_2	SB_3
C273	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	88.9 (68.6)	97.2 (93.8)	95.6 (69.4)	87.7 (53.1)
C271	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	87.9 (88.9)	81.3 (86.9)	82.6 (57.9)	41.7 (11.6)
C591	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	87.2 (90.3)	79.6 (90.3)	63.5 (59.7)	77.8 (88.3)
Pak Kohni	0.0 (0.0)	0.0 (0.6)	0.0 (0.0)	0.0 (0.0)	97.2 (93.8)	83.4 (91.6)	65.5 (20.9)	32.5 (6.0)
Mexi-Pak 65	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	95.5 (98.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
C228	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)		94.5 (96.9)	95.8 (89.8)		
AU49	0.0 (0.0)	12.8 (2.1)	0.0 (0.0)		95.8 (98.6)	97.9 (95.8)		
AU44	0.0 (0.0)	0.0 (4.8)	0.0 (0.0)		100.0 (100.0)	95.5 (82.3)		
Dirk	0.0 (0.0)	0.0 (0.0)			78.5 (87.5)	0.0 (0.0)		
H-68	0.0 (0.0)	0.0 (0.0)			86.4 (94.8)	85.7 (76.3)		

Upper and lower figures indicate pollen and selfed seed fertility, respectively.

Complete lack of fertility in Mexi-Pak 65, C228 and Dirk indicates that the restorer gene(s) of P168 does not restore fertility in these varieties in heterozyhgous condition. It will be necessary to seek new sources of restoring genes for those varieties.

Nucleus substitution lines with *T. timopheevi* cytoplasm

Male-sterile lines: Estimation of pollen and selfed seed fertilities in the F_1 and subsequent backcross generations revealed that none of the 11 varieties carry effective restoring genes, as all the lines became completely male sterile in the advanced backcross generations (Table 2).

Fertility-restoration lines: All the varieties exhibited very high pollen as well as selfed seed fertility in the F_1 generation (*timopheevi-T. spelta duhamelianum* × Pakistani varieties), indicating the strong fertility-restoring capability of *spelta*'s restorer gene, Rf_3, for *T. timopheevi* cytoplasm (Table 2). Varieties Mexi-Pak 65 and Dirk exhibited complete sterility in their backcross generations; whereas the rest of the varieties showed fairly high fertilities even in their most advanced backcross generations.

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The *Triticum* × *Agropyron* hybridization project at Montana State University[1)]

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The possible value of derivatives from *Triticum* × *Agropyron* hybridization has been recognized since the first successful crosses were reported by Tsitsin in 1933. Many such projects have explored the possibilities of wheat improvement, but the project reported here is oriented towards improvement of intermediate wheatgrass, *Agropyron intermedium* (Host.) Beauv., as a forage crop.

During the period from 1923 to 1935, Sando established hybrids between species of *Triticum* and *Agropyron* (Vinall and Hein 1937, USDA, 1958). Two of the hybrid combinations were *T. durum* Desf. (2n=28)×*A. intermedium* (2n=42) and *T. durum* (2n=28)× *A. trichophorum* (Link) Richt. (2n=42). Derivatives of these two crosses were distributed to several agricultural experiment stations, and were observed for possible usage in both wheat and forage grass breeding programs. In 1953, F_4 and F_5 seed of several of these hybrids was received for testing at the Montana Agricultural Experiment Station by Mr. R. F. Eslick. Chromosome counts of this material in 1958 revealed 2n numbers from 58 to 74 with an average number of 2n=65, demonstrating that the material was amphidiploid

1) Contribution of the Montana Agricultural Experiment Station, Bozeman, Montana, U.S.A. Paper No. 125, Journal Series, Montana Agr. Exp. Sta., published with approval of Director.

(AD).

The theoretical chromosome number of the amphidiploid is 2n=70. The author assumes that the missing bivalents were from the *Agropyron* parent since they were foreign to the cytoplasm of the female *Triticum* parent and may have been eliminated as laggards in meiotic divisions.

Induced chromosome doubling has not been reported for this material and amphidiploidy must have arisen by the fortuitous union of unreduced compatible gametes. LOVE and SUNESON in 1945 described the progeny of 2 hybrid seeds of *T. durum*×*A. trichophorum* which had been sent to them by Mr. W. J. SANDO in 1938. Both F_1 plants had the expected 2n number of 35 chromosomes. From the 35 F_1 seeds harvested only 11 F_2 plants were established. Cytological investigations of 4 of these F_2 plants revealed 2n=35 in one, 2n =56 in another and 2n=70 chromosomes in 2 plants. It appears clear therefore, that amphidiploid formation occurs naturally in this material through the union of partially reduced or unreduced gametes.

Chromosome pairing of *Triticum*×*Agropyron* in the very early generations was not as expected. However, LARTER and ELLIOTT (1956) reported regular chromosome pairing of 2n=56 derivatives of *Triticum*×*Agropyron* hybrids in the F_6 and F_7 generations. They consistantly observed 28 bivalents at metaphase I.

The SANDO amphidiploid *Agrotricum* material had meiotic instability as shown by the number of micronuclei in the microspores (Table 1). On the average, 50% of the microspores contained micronuclei in 28 plants. Micronuclei result from lagging chromosomes which were not included in the daughter nuclei and thus are lost to the gametes. Such chromosome loss may have caused chromosome numbers with less than 2n=70 in this amphidiploid material.

Table 1. Plant to plant ranges and average percentages of microspores having from 0 to 5 micronuclei in 28 plants of amphidiploid *T. durum*×*A. intermedium*

% of spores with micronuclei	Number of micronuclei per spore						% of microspores with micronuclei
	0	1	2	3	4	5	
Plant to plant range	20~98	2~42	0~28	0~18	0~10	0~6	2~80
Average percentage	50	26	15	6	2	1	50

Several new hybrids between different *Triticum* and *Agropyron* species were established at Bozeman in 1961 (SCHULZ-SCHAEFFER 1963). None of these had the perennial habit coupled with success in winter survival which is typical of the SANDO *Agrotricum* hybrids presently under study at Montana State University. Constant selection in the SANDO material for winter hardiness under Montana conditions for the last 16 years has resulted in strains superior in this respect.

The difficulty of recovering recombinations of the perennial habit of *A. intermedium*

with the large seed size of *T. durum* indicates close linkage of the small seed size of *A. intermedium* with its perennial habit. Although there exists a barrier to natural chromosome recombination in these intergeneric hybrids, it is possible by means of irradiation to induce an exchange between *Triticum* and *Agropyron* chromosome segments carrying genes for certain desirable agronomic characters. In order to obtain such segmental exchange, seeds of 3 strains of the *Agrotricum* material (strains AD 5a-2, AD 5a-3, and AD 7–2/3) were irradiated with X-ray dosages of 14, 15 and 16 thousand r units. Selfed seed of the X_1 generation served as parental material in the backcross program described below.

In 1960, the amphidiploid *Agrotricum* material was backcrossed with *A. intermedium* and with *A. trichophorum*. Table 2 compares the results of the first backcross with similar attempts at Washington State University (MARKARIAN 1958).

Table 2. Backcrossing of *Triticum* × *Agropyron* to *A. intermedium* (=SB_1)

Station	Year	Florets emasculated	SB_1 seeds	Percentage seed set
Washington	1955	3680	42	1.14
Montana	1960	5990	40	0.67

Out of 40 seeds obtained in the Montana crossing shown in Table 2, 32 vegetatively propagated first substitution backcross lines (SB_1)[1] were established in 1963. These lines show very distinct morphological differences in the degree of rhizome formation, the width, rigidity and color of leaves, and number of seed stalks. Additionally, differences in establishment and survival of plants were observed among these strains. Plant survival ranged from 30% in lines SB_1-16, SB_1-23 and SB_1-27 to 100% in line SB_1-1.

The backcross nature of this material has been verified cytologically in 22 SB_1 lines. Disregarding chromosome loss in the amphidiploid parent, the expected chromosome number would be 2n=56. Theoretically, 21 *Agropyron* bivalents and 14 *Triticum* univalents are expected in meiosis. The average chromosome number in these 22 lines was 2n=49 with a range from 33 to 54. The average bivalent number was 13 (range 5~21) and the average univalent number was 23 (range 9~37). The low total number may be due to chromosome loss in the amphidiploid parent. The high average number of univalents indicates a tendency for partial asynapsis. In some instances asynapsis is considerable in this material. If for instance only 10 chromosomes pair, there would be about 75% asynapsis. One would expect that there should be no fewer than 14 univalents, however, the chromosomes of the A and B genomes of *T. durum* can pair allosyndetically, accounting for fewer univalents. Cytological observations of the SB_1 strains have been reported

1) The term "substitution backcross" (SB) has been adopted from KIHARA (1951). It implies that in a series of backcrosses with the male parent to an original interspecific or intergeneric hybrid, the genomes of this male parent can be imbedded into a foreign cytoplasm, namely that of the female parent.

(SCHULZ-SCHAEFFER and FENBERT 1969) and will be further discussed in a following paper.

The SB_1 material was backcrossed with *A. intermedium* in 1965. Seed set was 0.77% which was similar to that after the first backcrossing. A pronounced shift of cytoplasmic male sterility was observed in the amphidiploids (AD), first substitution backcross (SB_1) and second substitution backcross generations (SB_2). Average pollen sterility estimates were 53% in the AD, 84% in the SB_1 and 97% in the SB_2. Sixty-nine percent of all SB_2 plants were 99~100% pollen sterile (SCHULZ-SCHAEFFER 1970). These data demonstrate that cytoplasmic male sterility can be obtained in intermediate wheatgrass after a few generations. This approach will be used in developing a hybrid intermediate wheatgrass.

Another aspect of this project is the development of chromosome substitution lines in intermediate wheatgrass. The SB_1 material has been selfed twice and selfing and backcrossing will be continued for several generations. This procedure will result in pairing of homologous *Triticum* chromosomes contributed by male and female gametes. Since the number of *Agropyron* bivalents in this material is less than 21, the establishment of chromosome substitution lines with *Triticum* bivalents should be possible. Five out of 330 (SB_1) S_1 plants showed increased seed set. Selection for high seed set will continue.

Line SB_1-33 had outstanding vigor and was taller than 'Oahe' intermediate wheatgrass, a well adapted variety. If increased seed set can be combined with these vigorous growth characteristics, a promising forage grass can be expected.

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Anther size and pollen longevity in wheat/rye addition lines

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The development of hybrid wheat requires the solution of many problems in addition to those associated with the exploitation of heterosis. It would, for example, be advantageous to use, as male parents, lines which had large numbers of pollen grains, or lines that extruded their anthers prior to dehiscence, or lines with pollen of extended longevity.

BITZER and PATTERSON (1967) have reported that seed set in wheat is directly related to the amount of wind-borne pollen. The amount of windborne pollen has been shown to be related to anther extrusion and anther size (JOPPA, MCNEAL and BERG 1968), whilst CAHN (1925) indicated that anther size may be simply inherited and directly related to the number of pollen grains per anther. Therefore, it is possible that increases of these parameters (anther size, anther extrusion and pollen longevity) may assist in the development of hybrid wheat.

Variation in these characters is uncommon, possibly due to the fact that *Triticum aestivum* is usually self fertilized. A possible source of variation may be found in a related out-pollinating species such as rye. This note reports investigations of pollen longevity, anther size and extrusion in wheat, rye, a wheat/rye amphiploid and six addition lines derived from the amphiploid.

The material, which was provided by Dr. E. R. SEARS, consisted of *T. aestivum* var. Chinese Spring, *Secale cereale* var. Imperial, the amphiploid of these species, and six of the seven possible addition lines, each with 21 pairs of wheat chromosomes and a single pair of rye chromosomes, except line E which had only one rye chromosome, designated 5R, 2R, C, D, E and 3R.

Table 1. Length of anthers in millimeters

Plant	Plant number				
	1	2	3	4	Mean
T. aestivum	3.40	3.41	3.50	3.49	3.45
S. cereale	8.25	8.48	8.13	8.14	8.25
Amphiploid	3.90	3.80	3.70	3.80	3.80
Addition 5R	2.88	2.73	2.86	2.83	2.82
〃 2R	3.95	3.63	3.90	3.84	3.83
〃 C	3.83	3.69	3.90	3.89	3.83
〃 D	2.82	2.94	2.88	2.80	2.86
〃 E	3.53	3.38	3.65	3.48	3.51
〃 3R	2.99	2.90	2.79	2.85	2.88

In the investigations of anther size the length of mature anthers selected just prior to dehiscence from the primary floret of the middle spikelet on the first tiller was taken as proportional to anther volume. Four anthers, fixed in Carnoy's solution, were measured from each of four plants of the types listed above. The mean of the sixteen measurements on the four plants of each line was taken as the mean anther size of that line.

From Table 1, where these measurements are listed, it is clear that rye has anthers approximately twice as long as wheat. The length of the anthers of addition lines 5R, D and 3R were significantly smaller than the anthers of all other addition lines. None of the other addition lines (2R, C and E) or the amphiploid had anthers that were significantly larger than *T. aestivum*. The anthers of rye were significantly larger than those of any other lines. This indicates that the small anther size of *T. aestivum* is epistatic in these lines to the larger anther size of *S. cereale*.

The pollen longevity of the material was estimated by observing the number of seed recovered on emasculated spikes of *T. aestivum* var. Chinese Spring after pollination with pollen stored (under greenhouse conditions) for various periods of time.

Anthers about to dehisce were tapped onto clean microslides, and the pollen was collected with a brush and transferred to the stigmas of the emasculated plants of Chinese Spring. Pollinations were made with the pollen from the microslides after zero, five, ten, fifteen, thirty and sixty minutes. Approximately 30 florets were pollinated for each storage time in each line. The percentage of seed set is shown in Table 2. Some rye pollen was

Table 2. Seed set (per cent) on *T. aestivum* after pollination at different times with pollen from wheat, rye and wheat/rye derivatives

Pollen Parent	Time (Minutes)					
	0	5	10	15	30	60
T. aestivum	72.0	0.0	0.0	0.0	0.0	0.0
S. cereale	80.0	53.1	24.0	13.3	13.3	0.0
Amphiploid	40.0	6.7	0.0	0.0	0.0	0.0
Addition 5 R	20.0	0.0	0.0	0.0	0.0	0.0
〃 2 R	23.3	0.0	0.0	0.0	0.0	0.0
〃 C	62.5	0.0	0.0	0.0	0.0	0.0
〃 D	25.0	0.0	0.0	0.0	0.0	0.0
〃 E	56.0	0.0	0.0	0.0	0.0	0.0
〃 3 R	42.3	0.0	0.0	0.0	0.0	0.0

still viable following storage for 30 minutes whilst no sets were obtained from the florets pollinated with wheat pollen stored for only five minutes. None of the addition lines had any viable pollen after five minutes storage also but some seed was set with pollen from the amphiploid after this period of time.

It is possible that pollen longevity is controlled by several factors; however, it is clear

that even if simply inherited, the extended pollen longevity of rye is not fully epistatic to the short viability period found in wheat. It is possible, also, that significant differences in pollen longevity in periods of time of less than five minutes may be observed. Experiments are being made to investigate this possibility.

In a visual comparison of the extrusion of anthers in these lines the estimated length of the anther visible outside the floral parts at the time of dehiscence was taken as an index of extrusion. In rye the entire anther was extruded prior to anthesis; however, no difference was observed in the extrusion of anthers between wheat, the amphiploid or any of the addition lines. Again it is probable that the anther extrusion of rye is not epistatic to the closed pollination mechanism of wheat.

From the results obtained in these preliminary studies it would appear that it may be impracticable to attempt the cytogenetic transfer of these desirable characters from rye to wheat for utilization in hybrid-wheat-breeding programs. It is possible that these characters of large anther size, anther extrusion and pollen longevity which are found in other members of the Triticinae may be controlled by genetic mechanisms that would allow their introduction into *T. aestivum*. Some of these possibilities are being examined.

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(Received March 3, 1970)

II. News

The Program of the Botanical Expedition to the Northern Highland of Mesopotamia (B.E.M.), Kyoto University, Japan, 1970

B.E.M. Committee, Kyoto University, Kyoto, Japan

During 1955～1968, Kyoto University has organized several scientific expeditions including four wheat and *Aegilops* expeditions*, namely KUSE 1955, BMUK 1959, BEC 1966 and KUSES 1967～1968. By these four expeditions, most of the important areas for the studies on the origin of wheat in Pakistan, Afghanistan, Iran, Caucasia, Turkey, Greece, Italy, Syria, Lebanon, Jordan, Egypt and Ethiopia have been explored. The areas of the present project are the remaining very important places for the survey of wheat and *Aegilops*.

Dr. H. KIHARA, Emeritus Professor of Kyoto University, and others have established the origin of Common Wheat or Dinkel (2n=42) that *Aegilops squarrosa* is one of its ancestors and the place of origin is the Transcaucasia. While, the origin of Emmer Wheat is still indefinite.

In recent years, *T. dicoccum*, an oldest variety of Emmer Wheat (2n=28), was found in the archeological excavations at Jarmo in the North of Baghdad, which suggests the origin of this species as old as B.C. 7000. Two important wild species are known in Emmer Wheat, namely *T. dicoccoides* and *T. araraticum*; the former was found in the skirt area of Mt. Hermon, Syria by BMUK 1959 and the latter was found in the Highland of Armenia by BEC 1966. These two wild species and Einkorn Wheat (2n=14), *T. aegilopoides* and *T. monococcum*, will occur together with *Ae. speltoides*, which is most likely one of the ancestors of Emmer Wheat, in the range between the above two regions, named as "Fertile Crescent". Hence, many important materials for furthering the studies on the origin of Emmer Wheat will be collected by the present expedition. From mountainous regions many endemic varieties will be also collected as a part of the world program of gene introduction and preservation.

The present program will be carried out under co-operation with FAO and respective Governmental Organizations of Iraq, Syria and Turkey.

*KUSE : Kyoto University Scientific Expedition to the Karakoram and Hindukush, 1955.
*BMUK : Botanical Mission of Kyoto University to the Eastern Mediterranean Countries, 1959.
*BEC : Botanical Expedition to the Caucasia, Kyoto University, 1966.
*KUSES : Kyoto University Scientific Expedition to the Sahara and its Surrounding Areas, 1967～1968.

The party will leave Tokyo around May 11 and return around July 25, 1970. Detailed schedule will be arranged according to the local situations.

Members

Kosuke YAMASHITA : Dr. Ag., Professor, School of Liberal Arts & Sciences, Kyoto University, (Leader) Botanist & Geneticist

Masatake TANAKA : Dr. Ag., Assistant Professor, Faculty of Agriculture, Kyoto University, Agronomist & Geneticist

Sadao SAKAMOTO : Dr. Ag., Researcher, National Institute of Genetics, Botanist & Geneticist

Three junior members will join the party.

The Death of Dr. Isamu UCHIKAWA

It is really regretable to report that Dr. Isamu UCHIKAWA, Emeritus Professor, Ehime University, Matsuyama, Japan, passed away due to the softening of the brain on January 14, 1970.

He made considerable contributions to WIS, as one of the members of the Co-ordinating Committee. His death means certainly a serious loss to the world of science. (K.Y.)

Correction

WIS No. 29: In an article "Telocentric mapping of a second gene for grass-clump dwarfism" by R.A. McINTOSH and E.P. BAKER, the following correction should be noted.

Page 7, Line 6: For "McINTOSH and BAKER (1968) located D2"
read "McINTOSH and BAKER (1968) located D1"

III. Editorial Remarks

Announcement for future issues

WIS No. 31 will be planned for publication in August 1970. Manuscripts for this issue are accepted any time, not later than July 1, 1970.

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

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Subscription

Three hundred and sixty yens (¥360) or the equivalent should be paid yearly into an account of WIS at the Dai-Ichi Bank Ltd. or at the Sumitomo Bank Ltd., Kyoto, Japan, or by the Foreign Postal Money Order, otherwise considerable loss is caused due to the bank charges. Back numbers are available.

Acknowledgement

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The Managing Editor

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Remarks: Figures in boldface indicate numbers, and figures in parentheses indicate pages.

Explanation of the Figure on the Cover

Relations between seed germination and X-ray dosage in 2n, 4n and 6n species of wheat (cf. GOTTSCHALK and M. IMAN, PP. 15~20 in the present issue).