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Interspecific hybridization with *Hordeum bulbosum* and development of hybrids and haploids

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A total of 64 interspecific crossing combinations with *H. bulbosum* (2x and 4x) were attempted. The maximum seed set was generally very high. Progeny was obtained in 19 combinations with diploid and 13 combinations with tetraploid *H. bulbosum*. As a result of selective chromosome elimination, haploids were recorded in 7 interspecific combinations with diploid and 7 with tetraploid *H. bulbosum*. There are 7 new haploid-producing combinations, viz. *H. cordobense* monohaploids, *H. marinum* mono- and dihaploids, and *H. brevisubulatum* di- and trihaploids in crosses with *H. bulbosum* (4x), *H. capense* dihaploids and *H. murinum* dihaploids with *H. bulbosum* (2x). The theory of a hierarchical chromosome elimination system is strengthened by the present results.

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Interspecific hybridization with *Hordeum bulbosum* L. remained sporadic after the initial attempts with cultivated barley (KUCKUCK 1934). The discovery of haploid formation (KAO and KASHA 1969; KASHA and KAO 1970; LANGE 1971a,b; SYMKO 1969) following hybridization of *H. vulgare* with *H. bulbosum* via the selective elimination of *bulbosum* chromosomes led to a period of intense work with this combination (SUBRAHMANYAM and KASHA 1973; BENNETT et al. 1976.) This method of haploid production is currently used in barley breeding programmes in more than 20 different countries (KASHA and REINBERGS 1981).

The rate and degree of chromosome elimination in *vulgare-bulbosum* hybrid embryos is dependent on a well-defined ratio of parental genomes under the influence of genetic factors on *vulgare* chromosomes 2 and 3 whose dose ratio to *bulbosum* chromosomes is critical to the elimination (HO and KASHA 1975; SUBRAHMANYAM and KASHA 1973). The phenomenon of selective chromosome elimination is widespread among *Hordeum* interspecific crosses (RAJHATHY and SYMKO 1974; SUBRAHMANYAM 1976, 1977, 1978, 1979, 1980, 1981, 1982; JACOBSEN and BOTHMER 1981; BOTHMER et al. 1983; GAJ and GAJ 1985; BOTHMER and JACOBSEN (1985) and intergeneric crosses involving *Hordeum* species (BARCLAY 1975; MILLER and CHAPMAN 1976; FALK and KASHA 1981; SHIGENBU and SAKAMOTO 1977; FEDAK 1977; BOTHMER et al. 1984). To determine the levels of crossability and the distribution of selective chromosome elimination in the barley genus, interspecific *Hordeum* crosses were made with di- and tetraploid *H. bulbosum* as one of the parents. We report eight new combinations from which haploids are obtained via chromosome elimination.

Material and methods

The material was obtained from various sources but especially from the botanical expeditions of BOTHMER and JACOBSEN (1980; cf. BOTHMER 1983). A list of species used in this investigation is given in Table 1.

Crosses were made at the Department of Crop Genetics and Breeding, Svalöv, Sweden, at Risø National Laboratory, Roskilde, Denmark, and at the Research School of Biological Sciences, Canberra, Australia. Emasculation, pollination, gibberellic acid treatment, embryo culture and chromosome number determination were carried out accor-

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Table 1. The *Hordeum* species and number of populations used in the present investigation

Section	Distribution	Species	Ploidy	Abbreviation	No. of populations
Hordeum	The Mediterranean-the Middle East	*H. murinum* L.	2x, 4x, 6x	MURI	2, 6, 2
Anisolepis	America	*H. stenostachys* GODR.	2x	STEN	1
		H. cordobense BOTHM. & al.	2x	CORD	1
		H. muticum PRESL	2x	MUTI	3
		H. chilense ROEM. & SCHULT.	2x	CHIL	1
		H. flexuosum NEES	2x	FLEX	2
		H. euclaston STEUD.	2x	EUCL	3
		H. pusillum NUTT.	2x	PUSI	3
		H. intercedens NEVSKI	2x	INTE	2
Critesion	America	*H. jubatum* L.	4x	JUBA	1
	(-NE Asia)	*H. comosum* PRESL	2x	COMO	1
		H. pubiflorum HOOK. f.	2x	PUBI	3
		H. lechleri (STEUD.) SCHENCK	6x	LECH	2
		H. procerum NEVSKI	6x	PROC	2
		H. arizonicum COVAS	6x	ARIZ	1
Stenostachys	Eurasia	*H. marinum* HUDS.	2x, 4x	MARI	4, 3
		H. secalinum SCHREB	4x	SECA	2
		H. bogdani WIL.	2x	BOGD	2
		H. roshevitzii BOWDEN	2x, 4x	ROSH	1, 1
		H. brevisubulatum (TRIN.) LINK	2x, 4x, 6x	BREV	3, 2, 2
	South Africa	*H. capense* THUNB.	4x	CAPE	1
	North America	*H. brachyantherum* NEVSKI	2x, 4x, 6x	BRAC	4, 4, 1
		H. depressum (SCRIBN. & SM.) RYDB.	4x	DEPR	2
	South America	*H. patagonicum* (HAUM.) COVAS	2x	PATA	7
		H. tetraploidum COVAS	4x	TETR	2
		H. parodii COVAS	6x	PARO	1

ding to KASHA et al. (1978) and BOTHMER et al. (1983). The progeny plants were classified as either hybrids or haploids depending on their morphology and chromosome number.

Results

Hordeum bulbosum functioned poorly as the female parent. A few crosses with both cytotypes were attempted (Table 2). The tetraploid combination averaged 9 % seed set with the highest (32 %) observed in a cross with *H. secalinum*. Four out of the five attempts with diploid *H. bulbosum* failed; a single cross with *H. secalinum* had 21 % seed set. In none of the attempted crosses were any hybrids raised.

The success with *H. bulbosum* as the male parent was much higher. The percentage of seed set in each cross was variable, depending on the vigour of the parents and the environmental conditions at the time of pollination and during development. Thus, comparison of seed setting ability among the different crosses may not be valid. The highest percentage of seed set in each cross can be said to represent the potential level of success.

Only a few combinations failed to set any seeds (Tables 4 and 5), but only in the cross *H. stenostachys* × *H. bulbosum* (4x) were a fair number of

Table 2. Results of interspecific crosses with *H. bulbosum* as the female parent

	No. of crosses	No. of florets	Seed set		No. of plants
			No.	%	
H. bulbosum, 2x	5	71	3	4.2	0
H. bulbosum, 4x	8	117	11	9.4	0

Table 3. Development of embryos and endosperms, germination and development of adult plants in interspecific crosses with ***Hordeum bulbosum***. ***Embryos:*** 1: lacking; 2: very small; 3: good. ***Endosperms:*** 5: watery; 6: deformed; 7: good. ***Germination*** +: germinated, (+): callus; 0: not germinated. ***Plants:*** +: adult plants; 0: no adult plants obtained; –: no information

	Embryo bulbosum		Endosperm bulbosum		Germination bulbosum		Plants bulbosum	
Species	2x	4x	2x	4x	2x	4x	2x	4x
MURI 2x	2	2	5	-	0	0		
4x	2,3	2,3	5,6	5,6	+	(+)	+	0
6x	-		5		+		+	
STEN	2,3	-	-	-	+	0	+	
CORD		2		5		+		+
MUTI	-	1,2	-	5	+	+	+	+
CHIL	3	2,3	-	5	+	+	+	+
FLEX	2,3	3	5,6	5	+	0	+	
EUCL	1,3	2	6	5	+	0	+	
PUSI	-	2	-	5	+	+	+	0
INTE	2	1	5	5	+	0	0	
JUBA	2,3	3	5	5,6	+	+	+	+
COMO	3	1,2	6	5	+	0	0	
PUBI	1,2	1,2,3	5	5	0	+		0
LECH	-	-	-	-	+	+	+	+
PROC	-	-	-	-	+	+	+	+
ARIZ		2		5		(+)		0
MARI 2x	2	1,2,3	5	5,6	+	+	0	+
4x	-	2	-	5,6	+	+	+	+
SECA	2	2,3	-	5,6,7	+	+	+	+
BOGD	2	2	6	-	+	+	+	0
ROSH 2x	-		-		0			
4x	-	3	-	5	+	+	0	+
BREV 2x		3		5		+		0
4x	3	1,3	7	5	+	+	+	+
6x		-		-		+		+
CAPE	2	2	5	5	+	0	+	
BRAC 2x	1,3	1,2	5,6	5	+	+	+	0
4x	3	3	5	7	+	+	0	0
6x	3	2	5	5	(+)	+	0	0
DEPR	2	2	6	5	+	+	+	+
PATA	2	2	5	5	+	+	+	0
TETR	3	2	5	5	+	+	+	+
PARO	1		5		0		0	

attempts made. The crossing failure in the other cases may well be due to unfavourable environmental conditions. In all other combinations the maximum, and in many cases also the average, seed set was high. For the whole material, the combinations with hexaploid species had the highest seed set, viz. 68 % with diploid *H. bulbosum* and 38 % with tetraploid *H. bulbosum* (Table 6). The development of embryos and endosperms varied within wide limits (Table 3) and is most likely a result of particular genotypic combinations. Germination of the cultured embryos occurred in many cases (Table 3), but the seedling lethality was very high.

Out of 31 combinations with diploid *H. bulbosum,* 23 gave progeny plants (Table 4) of which haploids of 7 different species were obtained

Table 4. **Results of interspecific crosses with diploid *Hordeum bulbosum* as the male parent. * Only the results obtained at Canberra are included and the number of differentiated embryos are given in parenthesis**

Species		No. of crosses	No. of florets	Seed set No.	Seed set Average %	Seed set Max %	Embryos* cultivated	No. of plants
MURI	2x	16	236	47	19.9	90	25	0
	4x	43	777	156	20.1	100	57 (18)	7
	6x	2	30	20	66.7	73		6
MARI	2x	18	282	24	8.5	60	8 (3)	1
	4x	2	26	21	81.7	85		11
SECA	4x	43	1119	16	1.4	54		2
BREV	2x	1	11	0	0			
	4x	60	2019	97	4.8	45	67 (18)	2
BOGD	2x	18	537	149	27.7	83	46 (39)	3
ROSH	2x	2	33	0	0			
	4x	2	42	33	78.6	100		12
CAPE	4x	1	13	11	84.6	85		3
DEPR	4x	2	21	12	57.1	92		2
BRAC	2x	17	335	47	14.0	100	7 (2)	2
	4x	2	23	22	95.7	100		0
	6x	1	14	12	85.7	86		0
TETR	4x	1	17	16	94.1	94		6
PARO	6x	1	13	9	69.2	69		0
JUBA	4x	6	190	8	4.2	33		5
LECH	6x	1	24	13	54.2	54		7
PROC	6x	1	12	9	75.0	75		3
PUBI	2x	1	12	7	58.3	58		0
COMO	2x	15	330	66	20.0	84	29 (11)	2
PATA	2x	3	41	27	65.9	77		8
PUSI	2x	3	32	15	46.9	70		2
EUCL	2x	1	17	15	88.2	88		4
FLEX	2x	37	1046	93	8.9	61	48 (23)	4
MUTI	2x	1	14	14	100	100		1
CHIL	2x	17	531	63	11.9	78	38 (25)	6
STEN	2x	38	1677	45	2.7	32	24 (8)	1
CORD	2x	18	754	54	5.0	38	31 (23)	0

(Table 7). In the literature 4 additional combinations yielding haploids have been reported. With tetraploid *H. bulbosum*, 13 out of the 32 interspecific combinations resulted in progeny plants (Table 5) of which 7 consisted of haploids of other species (Table 7). In the literature three additional haploids have been reported. Of the haploid-producing crosses, haploids of *H. arizonicum, H. procerum, H. secalinum* and *H. brevisubulatum* (4x) were obtained irrespective of the ploidy level of the *H. bulbosum* parent. Both hybrids and haploids were obtained or have been reported in combinations with *H. bulbosum* (4x) and *H. vulgare, H. lechleri, H. procerum* and *H. arizonicum,* and with *H. bulbosum* (2x) and *H. vulgare, H. murinum* (4x) *H. brevisubulatum* (4x), *H. brachyantherum* (4x), and *H. depressum.* There are 7 new haploid producing combinations, viz. *H. cordobense* monohaploids, *H. marinum* mono- and dihaploids, *H. brevisubulatum* di- and tri-haploids in crosses with *H. bulbosum* (4x) *H. capense* and *H. marinum* dihaploids with *H. bulbosum* (2x). The morphology of a selected number of hybrids and haploids are shown in Fig. 1.

Discussion

The interspecific crosses with *H. bulbosum* coincide with the results obtained with *H. vulgare* (Bothmer et al. 1983). Both species, for example, functioned poorly as the female parent. Despite a much lower seed set in combinations with diploid species, *H. bulbosum* as the male parent had a higher germination rate than that in cultivated barley.

There does not in general seem to be any significant difference in crossability between the di- and

Table 5. Results of interspecific crosses with tetraploid *Hordeum bulbosum* as the male parent. * Only the results obtained at Canberra are included and the number of differentiated embryos are given in parenthesis

Species		No. of crosses	No. of florets	Seed set No.	Seed set Average %	Seed set Max %	Embryos* cultivated	No. of plants
MURI	2x	15	218	21	9.6	30	5	0
	4x	42	709	153	21.6	86	50 (6)	0
	6x	2	18	0	0			
MARI	2x	8	140	65	46.4	100		1
	4x	2	29	24	82.8	100		3
SECA	4x	37	715	93	13.0	100	22	4
BREV	2x	3	51	3	5.9	30		0
	4x	12	329	83	25.2	100	1	2
	6x	5	64	29	45.3	94		4
BOGD	2x	6	155	18	11.6	48	4 (1)	0
ROSH	4x	3	34	20	58.8	83		0
CAPE	4x	1	10	7	70.0	70		0
DEPR	4x	3	40	33	82.5	92		1
BRAC	2x	10	247	27	10.9	100		0
	4x	5	60	20	33.3	79		0
	6x	2	33	16	48.5	86		0
TETR	4x	1	12	9	75.0	75		1
JUBA	4x	4	106	14	13.2	42	2 (2)	6
ARIZ	6x	1	8	7	87.5	88		0
LECH	6x	1	13	10	76.9	77		4
PROC	6x	5	91	24	26.4	42		9
PUBI	2x	5	81	11	13.6	64		0
COMO	2x	14	271	10	3.7	35		0
PATA	2x	9	119	67	56.3	100		0
PUSI	2x	3	28	14	50.0	67		0
INTE	2x	1	13	8	61.5	62		0
EUCL	2x	2	19	7	36.8	58		0
FLEX	2x	23	463	34	7.5	56	18 (4)	0
CORD	2x	2	22	7	31.8	42		1
STEN	2x	23	977	0	0			
MUTI	2x	2	22	12	54.5	75		1
CHIL	2x	11	441	19	4.3	67	8 (4)	2

Table 6. Summary of crosses with diploid and tetraploid *Hordeum bulbosum* used as the male parent

	No. of taxa and cytotypes	No. of crosses	No. of florets	Seed set No.	Seed set %	No. of plants	% germination
bulbosum, 2x	16	206	5888	666	11.3	34	5.1
in crosses with tetraploids	10	162	4247	392	9.2	50	12.8
in crosses with hexaploids	5	6	93	63	67.7	16	25.4
Total	31	374	10228	1121	11.0	100	8.9
bulbosum, 4x							
in crosses with diploids	16	137	3267	323	9.9	5	1.5
in crosses with tetraploids	10	110	2044	456	22.3	17	3.7
in crosses with hexaploids	6	16	227	86	37.9	17	19.8
Total	32	263	5535	865	15.6	39	4.5

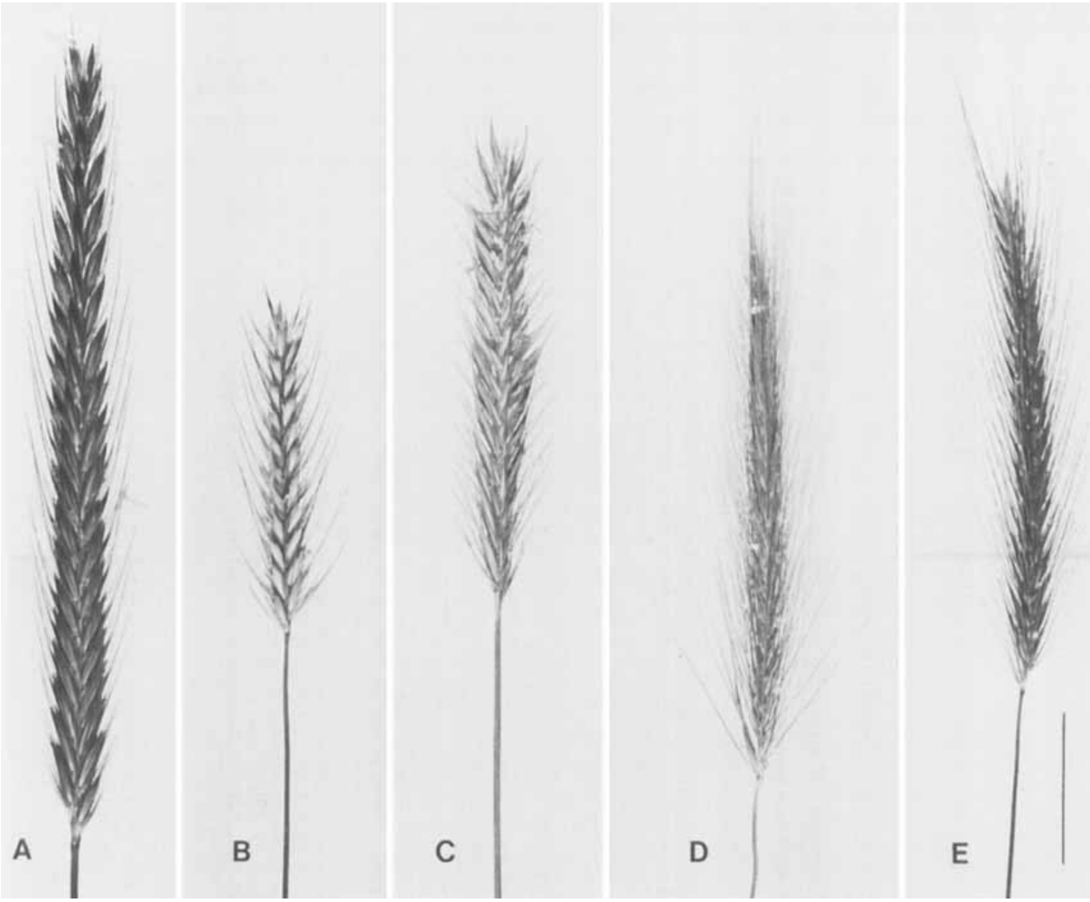

Fig. 1 A-K. Morphology of hybrids and haploids in interspecific crosses with *Hordeum bulbosum* together with their parental species. **Fig. A-E. Fig. A.** *H. bulbosum* (135Ho). **Fig. B.** *H. patagonicum* × *H. bulbosum*, hybrid (HH 1473). **Fig. C.** *H. patagonicum* (H 1240). **Fig. D.** *H. jubatum* (H 2013). **Fig. E.** *H. jubatum*, dihaploid 2n = 14 (HH 741).

tetraploid cytotypes of *H. bulbosum* in combinations with di- and hexaploid species (Table 6). The combinations with diploid species had low seed set and low germination while the combinations with hexaploid species had high seed set and also comparatively high germination. In combinations with tetraploid species *H. bulbosum* (4x) had a higher seed set but a much reduced germination compared to the diploid *H. bulbosum.*

The present results and the observations on chromosomal variability in the embryonic cells (SUBRAHMANYAM 1976, 1977, 1978, 1979, 1980) for most of the corresponding crosses are consistent with the progeny produced. The chromosome numbers of the progeny plants, and the morphological similarities of the progeny to the non-*bulbosum* parent are indicative of selective elimination of *H. bulbosum* chromosomes leading to haploid formation as occurred in three out of the four different *vulgare-bulbosum* cross combinations (SUBRAHMANYAM and KASHA 1973). Thus in 24 out of the 44 interspecific crosses with *H. bulbosum,* elimination of *H. bulbosum* chromosomes leads to the formation of haploids of the other parental species. Interspecific crosses of *H. vulgare* with hexaploids of *H. brachyantherum, H. lechleri, H. procerum* and *H. arizonicum,* and di- and tetraploid *H. marinum* result in haploids of the respective parent via selective elimination of *H. vulgare* chromosomes (BOTHMER et al. 1983; SUBRAHMANYAM 1982). Thus a total of 29 *Hordeum* interspecific cross combinations exhibit chromosome elimination.

Fig. F-K. Fig. F. *H. tetraploidum* × *H. bulbosum*, hybrid (HH 2154). **Fig. G.** *H. tetraploidum* (HH 1203). **Fig. H.** *H. secalinum* (H 296). **Fig. I.** *H. secalinum*, dihaploid 2n = 14 (HH 1103). **Fig. J.** *H. cordobense* (H 1702). **Fig. K.** *H. cordobense*, monoploid 2n = 7 (HH 1531). – Bar is equal to 2 cm.

H. cordobense (2x), *H. lechleri* (6x), *H. procerum* (6x), *H. arizonicum* (6x), *H. marinum* (2x and 4x) *H. secalinum* (4x), *H. brevisubulatum* (4x and 6x) and *H. vulgare* (4x) are capable of eliminating up to two *bulbosum* genomes. However, CAUDERON and CAUDERON (1956) reported development of *H. bulbosum* sectors in the cross *H. secalinum* × *H. bulbosum* (4x) which is contradictory to our results and to those of GAJ and GAJ (1985).

Among the successful cross combinations, the species capable of elimination of one *vulgare* genome also exhibited capacity to eliminate up to two *bulbosum* genomes. In crosses of diploid *H. bulbosum* with the tetraploids *H. jubatum*, *H. brachyantherum* and *H. depressum* and the hexaploid *H. parodii*, elimination of *H. bulbosum* chromosomes leading to haploid formation is evident. However, on increasing the number of *bulbosum* genomes, stable hybrids are obtained. This is consistent with the suggestion that the ratio of the parental genomes is important to obtain stable hybrids (SUBRAHMANYAM 1977, 1979, 1980). The present results do not alter the hierarchy of chromosome elimination proposed earlier (SUBRAHMANYAM 1982) except that *H. secalinum* eliminates *H. bulbosum* chromosomes, thus in the order *H. secalinum* (4x) >*H. bulbosum* (2x and 4x).

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Table 7. Summary of the results of interspecific hybridization with diploid (2x) and tetraploid (4x) *Hordeum bulbosum*. a) Present investigation, b) Literature; n=haploids, 2n=hybrids; . = seed set only, – = no seed set. * Based on embryonic squashes and no adult plants. ** hybrids with *H. bulbosum* sectors (CAUDERON and CAUDERON 1956)

			2x		4x	
Section	Species	Ploidy	a	b	a	b
Hordeum	*vulgare*	2x		n/2n		n/2n
	murinum	2x	.		–	
		4x	2n		.	
		6x	2n		.	
Anisolepis	*stenostachys*	2x	2n		–	
	cordobense	2x	–		n	
	muticum	2x	2n		2n	
	chilense	2x	.	2n	.	2n
	flexuosum	2x	2n	2n	.	2n*
	euclaston	2x	2n		.	
	pusillum	2x	2n		.	
	intercedens	2x			.	
Critesion	*jubatum*	4x	n	n	2n	2n
	comosum	2x	.		.	
	pubiflorum	2x	.		.	
	lechleri	6x	n	n	n/2n	2n*
	procerum	6x	n	n	2n	n/2n
	arizonicum	6x	–	n	.	n/2n
Stenostachys	*marinum*	2x	.		n	
		4x	n		n	
	secalinum	4x	n		n	**
	bogdani	2x	2n		.	
	roshevitzii	2x	–			
		4x	.		2n	
	brevisubulatum	2x	–		.	
		4x	n	n/2n	n	
		6x			n	
	capense	4x	n		.	
	brachyantherum	2x	2n		.	
		4x	.	n/2n	.	2n
		6x	.			
	depressum	4x	2n	n/2n	2n	2n
	patagonicum	2x	2n		.	
	tetraploidum	4x	2n		2n	
	parodii	6x	.	n		2n

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