A CYTOGENETIC STUDY OF NATURAL AND CONTROLLED HYBRIDS BETWEEN AGROPYRON TRACHYCAULUM AND HORDEUM JUBATUM

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VIGOROUS but sterile plants identifiable as *Elymus macounii* Vasey or in some cases *Agropyron saundersii* (Vasey) Hitchc. were frequently observed in northern Utah. The morphology of these plants and the species associated with them together with their sterility indicated that they might be F_1 hybrids between *Agropyron trachycaulum* (Link) Malte and *Hordeum jubatum* L. Such a possibility was suggested by STEBBINS *et al.* (1946b). The present paper reports the results of our investigations on the cytology, comparative morphology, origin and taxonomic status of these plants.

MATERIALS AND METHODS

Anthers of the suspected hybrids and putative parents were fixed in 3:1 acetic-alcohol. Those of the controlled hybrids were fixed in NEWCOMER's (1953) solution which proved superior to the acetic-alcohol. Observations and photographs were taken from acetocarmine smears in temporary mounts.

Three crossing techniques were utilized: hand emasculation, hot water emasculation and mass pollination without emasculation or bagging; the first two methods were ineffectual. Approximately 2000 florets were emasculated and bagged with pollinator culms in vials of water during three successive field seasons without success. Hand pollination following emasculation was likewise ineffectual. Hot water emasculation at 47°C as described by KELLER (1944) was not successful. Higher temperatures were not attempted.

The successful crosses were made by surrounding a single culm of the plant to be used as the female parent with hundreds of pollinator culms placed in jars of water and changed three times at two-day intervals. All of the seed produced was planted and the plants grown to anthesis when the hybrids could be easily detected from the non-hybrids. Three hybrids were obtained using *A. trachycaulum* as the female parent and two using *H. jubatum* as the female parent. The reciprocal crosses were essentially indistinguishable.

Herbarium specimens were prepared of representative field and experimental plants and are deposited in the Intermountain Herbarium at Utah State Agricultural College.

CYTOLOGY OF THE PARENTS AND HYBRIDS

A. trachycaulum and *H. jubatum* are both tetraploids and in all probability, allotetraploids. Fourteen bivalents were consistently observed at diakinesis and metaphase I. The meiotic divisions were without abnormalities. Both species are highly

self-fertile. Twenty-eight chromosomes have been repeatedly reported for these species (MYERS 1947; COVAS 1948; others). NIELSEN (1939) reported 28 chromosomes in a root tip count of *Elymus macounii*.

The meiotic chromosome behavior of the natural and controlled hybrids between *A. trachycaulum* and *H. jubatum* is summarized in table 1. That the sterility of the hybrids is due primarily to the failure of the two complements to undergo normal

TABLE 1

Comparative meiotic chromosome behavior of natural and controlled hybrids between Agropyron trachycaulum *and* Hordeum jubatum

Chromosome association diakinesis and meta. I				No. cells	Laggards per cell ana. I	No. cells	Laggards per dyad ana. II	No. cells	No. micronuclei per pollen gr.	No. cells	No. micronuclei per tetrad	No. tetrads
I	II	III	IV									
A. Natural hybrids												
14	7			16	0	6	0	2	0	1	12	2
12	8			4	1	7	2	2	1	3	14	3
16	6			4	2	5	3	12	2	14	15	4
10	9			1	3	6	4	14	3	27	16	3
10	8			1	4	7	5	12	4	23	17	4
13	7			1	5	4	6	10	5	18	18	1
20	4			1	6	4	7	12	6	25	19	4
14	5		1	1	7	2	8	11	7	14	20	2
11	7	1		1	8	2	9	2	8	4	21	1
					10	1	10	2	9	1	22	2
					11	1	11	2	10	3	23	1
											25	2
											27	2
											30	1
B. Synthesized hybrids (combined data reciprocal crosses)												
18	5			19	3	1	4	1	0	4	3	1
14	7			13	6	1	7	1	1	37	5	1
16	6			11	10	1			2	27	6	3
20	4			7	12	1			3	21	7	9
12	8			7	13	1			4	8	9	4
16	4		1	6					5	5	10	1
14	5		1	4					6	2	11	3
16	5			2							12	3
18	3		1	2							13	1
15	5	1		2								
10	9			2								
20	5			2								
17	4	1		1								
8	7	2		1								
10	6	2		1								
8	8		1	1								
14	6		1	1								
26	1			1								
24	2			1								
22			1	1								

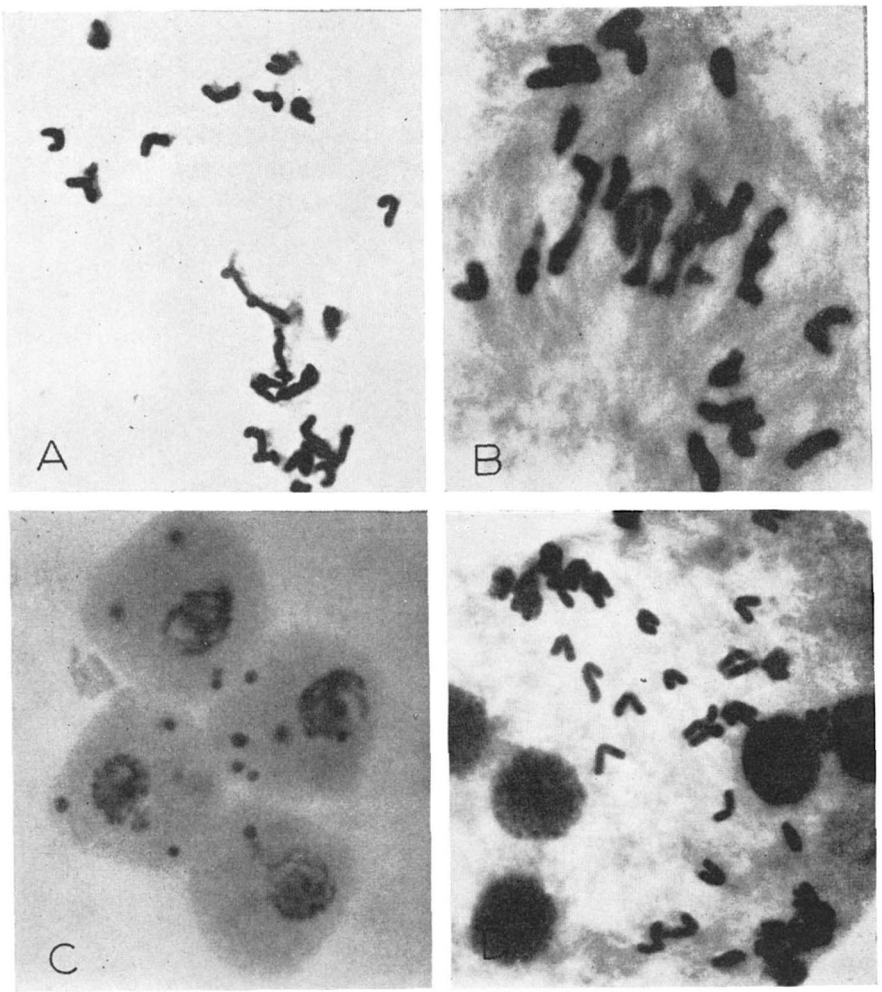

FIGURE 1.—Meiosis in the natural hybrid. A: metaphase I; 7 II, 14 I; 618×. B: metaphase I; 8 II, 12 I; 1180×. C: tetrad with micronuclei; 900×. D: anaphase I with laggards; 1030×.

pairing is apparent (fig. 1, 2). All pollen mother cells examined showed numerous unpaired univalents at diakinesis and metaphase I. These ranged from 10 to 20 with a mean of 13.8 in the natural hybrids. Univalents in the controlled hybrids ranged from 8 to 22 with a mean of 17.1. Multivalents were more frequently found in the controlled hybrids. One trivalent and one quadrivalent were observed in the natural hybrids compared with six trivalents and six quadrivalents in the controlled hybrids. In the hybrids 89 percent of the cells observed contained at least 10 chromosomes associated in pairs or occasionally with one or two multivalents. They averaged 6.3 bivalents per cell. Chromatid bridges were very rarely observed. Eighty-nine percent of the bivalents in the controlled hybrids were rods compared with 83 percent in the natural hybrids.

Practically every pollen grain of both natural and controlled hybrids contained

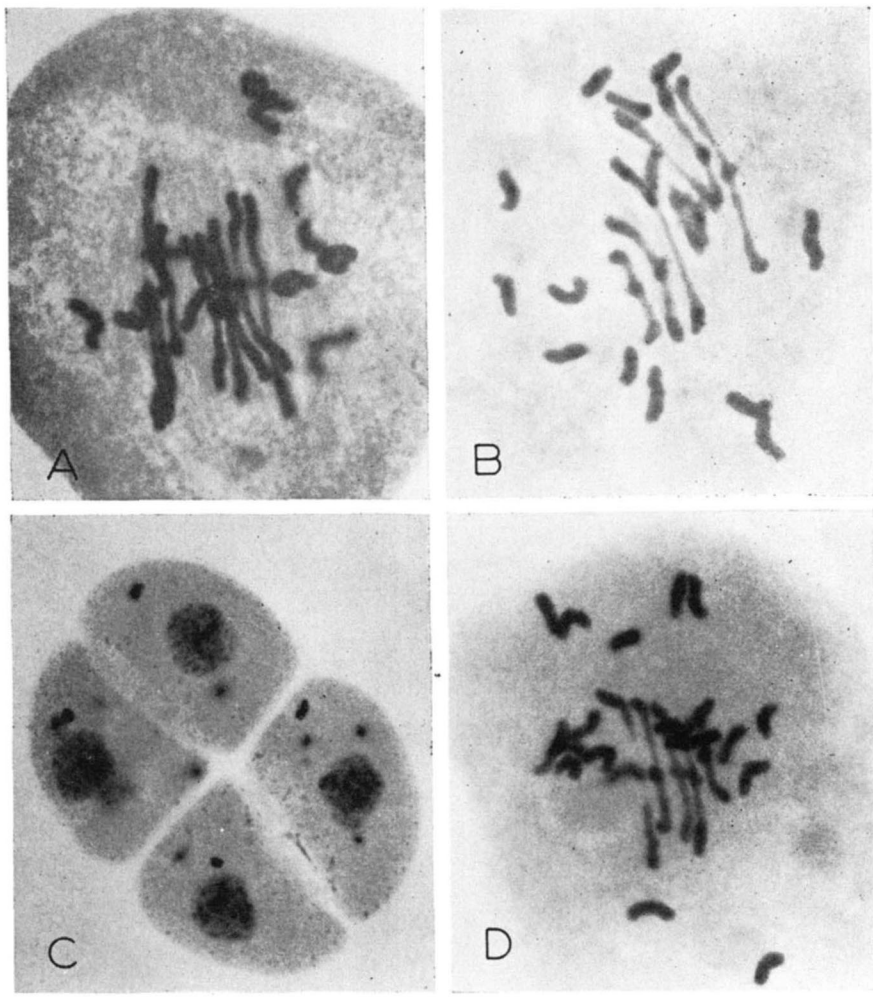

FIGURE 2.—Meiosis in the controlled hybrid. A: metaphase I; 8 II, 12 I; 827×. B: metaphase I; 1 IV, 5 II, 14 I; 1054×. C: tetrad with micronuclei; 1114×. D: metaphase I; 5 II, 18 I; 1090×.

micronuclei (fig. 1 C, 2 C). The large micronuclei probably represent anaphase I laggards which failed to be included in the new nuclei and the small micronuclei having their origin in anaphase II laggards. Practically 100 percent of the pollen appeared abortive in both natural and controlled hybrids.

The minor differences in chromosome associations between natural and controlled hybrids can probably be explained on the basis of different size samples studied. The meiotic divisions in general are definitely comparable.

MORPHOLOGY OF THE PARENTS AND HYBRIDS

The *Hordeum jubatum* found in northern Utah shows very little variation and is morphologically similar to plants found throughout the Intermountain region.

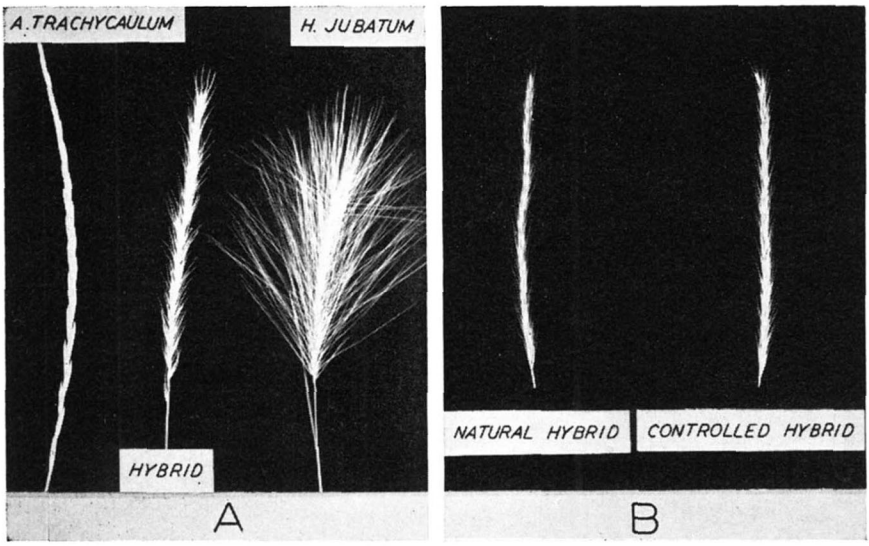

FIGURE 3.—A: spikes of *Agropyron trachycaulum*, F_1 hybrid, and *Hordeum jubatum*. B: spikes of natural and controlled hybrid.

Plants which were associated with the hybrids (herb. no. 8139) and which served as the parent plants were collected northwest of Logan in Cache County.

Agropyron trachycaulum is a highly variable species as the long synonomy list suggests (*Hitchcock* 1950). Several strains are to be found in northern Utah but plants associated with the hybrids and *H. jubatum* were rather consistent in their morphological characteristics (herb. no. 8142). These plants were generally shorter than cultivated strains, being 50–65 cm tall with spikes from 12–15 cm long and closely imbricated spikelets. Plants of this strain were successfully used as parents in reciprocal crosses.

The hybrids are more or less intermediate between the two parents (fig. 3 A). The rachis in *H. jubatum* disarticulates readily while the rachis in *A. trachycaulum* is continuous; the rachis in the hybrid disarticulates rather tardily. The lemmas in *H. jubatum* have awns 4-5 cm long while the lemmas in *A. trachycaulum* are awnless. Awns of the lemmas in the hybrid are 6–9 mm long. The hybrid differs from either of its parents in that the plants are taller (60–80 cm) and often stand 10–15 cm above the taller parent, *A. trachycaulum*.

The characteristic morphology found in natural hybrids was duplicated in the controlled hybrids and they are essentially indistinguishable (fig. 3 B). Natural hybrids with one spikelet per node are more common than those with two spikelets per node. Plants with one spikelet at a node usually have two glumes but three-glumed spikelets are common. The third glume is placed laterally on the spikelet on the side away from the rachis and is scabrous and narrow. The lemmas are usually glabrous or slightly scabrous towards the apex. The rachilla is often somewhat distorted at the base as in Elymus but otherwise the plants could be placed in either Elymus or Agropyron. Our hybrids, natural and controlled, would be referred to *E. macounii* in the Manual of Grasses (HITCHCOCK 1950).

DISCUSSION

STEBBINS, *et al.* (1946) stated that the type of *A. saundersii* "is probably an F_1 hybrid between *A. pauciflorum* (*A. trachycaulum*) and *Sitanion hystrix.*" They also concluded that naturally occurring hybrids between *A. pauciflorum* and *Sitanion jubatum* correspond to *A. saundersii.* The same authors (1946b) stated that the presumed natural hybrid between *A. pauciflorum* × *H. nodosum* fits the description of *E. macounii.* They conclude finally that "the most likely hypothesis is that most specimens classified as *E. macounii*. . .are a collection of F_1 sterile hybrids between species of Agropyron and either *H. jubatum* or *H. nodosum*". KELLER (1948) stated that *A. saundersii* is the natural hybrid between *A. trachycaulum* and *Sitanion jubatum* and *Elymus macounii* is the natural hybrid between *A. trachycaulum* and *H. jubatum.*

However, so far as the present authors are aware the actual synthesis of plants which can be identified as *A. saundersii* and *E. macounii* has not previously been made nor has the meiotic chromosome behavior of either of these entities been reported. Our investigations on the meiotic chromosome behavior, comparative morphology and field observations of the parents and both natural and controlled hybrids demonstrate that at least some entities identifiable as *E. macounii* are simply F_1 sterile hybrids between *A. trachycaulum* and *H. jubatum.* These plants are therefore treated as X *Agrohordeum macounii* (Vasey) Lepage (LEPAGE 1952). Sufficient evidence to clarify the status of *A. saundersii* is not yet available.

The relative ease with which species in the genera Agropyron, Hordeum, Elymus Sitanion, Secale and Hystrix can form "intergeneric" hybrids makes possible the production of F_1 plants which may be morphologically similar yet have different origins (STEBBINS *et al.* 1946, 1946b; BRINK, COOPER and AUSHERMAN 1944).

The nature of pairing in the hybrids is difficult to completely establish. The possibility of autosyndesis cannot be completely dismissed as has been recently emphasized by STEBBINS and PUN (1953). However, the complete absence of quadrivalents in either *H. jubatum* or *A. trachycaulum* in our observations and those of other investigators argues against this interpretation here. Allosyndesis between chromosomes of *A. trachycaulum* and *H. jubatum* appears a much more logical interpretation. The formation of trivalents and quadrivalents possibly results from allosyndesis within one of the parents as suggested by STEBBINS *et al.* (1946) as one explanation for trivalents found in a hybrid between *A. trachycaulum* and *H. nodosum.* Their alternative interpretation, that of structural hybridity seems less likely in the present hybrids in view of the rarity of bridge fragments observed.

If the pairing is allosyndetic between chromosomes of *H. jubatum* and *A. trachycaulum* as seems very probable, then we can reasonably suggest that these two species have one set of chromosomes which are largely homologous. The genomic formulae AABB and AACC are therefore suggested for *A. trachycaulum* and *H. jubatum*, respectively.

SUMMARY

Both natural and controlled hybrids between *Agropyron trachycaulum* and *Hordeum jubatum* were studied. They are morphologically intermediate between the two parents, indistinguishable, sterile and very similar in the high incidence of unpaired

univalents and lagging chromosomes with resultant micronuclei. Eighty-nine percent of the cells observed contained at least 10 chromosomes associated in pairs or occasionally with one or two multivalents. They averaged 6.3 bivalents per cell. The evidence suggests that Hordeum and Agropyron have one genome in common.

These hybrids are comparable in every way to *Elymus macounii*. Our evidence from investigations on the meiotic chromosome behavior, comparative morphology and field observations of the parents and both natural and controlled hybrids demonstrates that at least some entities identifiable as *E. macounii* are simply F_1 sterile hybrids between *A. trachycaulum* and *H. jubatum*.

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