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Polyhaploid Production in the Triticeae: Wheat × *Tripsacum* Crosses

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ABSTRACT

Wheat, *Triticum aestivum* L., haploid production relies heavily on its crosses with bulbous barley, *Hordeum bulbosum* L., and on anther culture, procedures influenced by genotypic specificity. Wheat × maize, *Zea mays* L., crosses are devoid of this constraint. In this study eastern gamagrass [*Tripsacum dactyloides* (L.)L.] is utilized. Cross success is anticipated to extend (i) the range of species available for Triticeae haploid production, and (ii) the crossing cycle duration. Intergeneric crosses of *T. aestivum* (2*n* = 6*x* = 42; AABBDD), *T. turgidum* L. (2*n* = 4*x* = 28; AABB), and *T. turgidum* × *Aegilops squarrosa* L. (*T. tauschii*) synthetic hexaploids (2*n* = 6*x* = 42; AABBDD) with *Tr. dactyloides* (2*n* = 2*x* = 36) as the pollen donor resulted in progenies that were polyhaploids of the Triticeae parents, presumably due to elimination of the *Tr. dactyloides* chromosomes during early embryo development. Embryo recovery frequencies were 20.6% for *T. aestivum* cultivars, 26.8% for *T. turgidum* cultivars and 23.5% for the synthetic hexaploids. Plant regeneration ranged between 66.7 to 78.5% over the three maternal crossing groups. As with maize, polyhaploid production in the Triticeae with *Tripsacum* is dependent upon a post-pollination treatment with 2,4-D (2,4-dichlorophenoxyacetic acid) to promote embryo development and shows no strong genotypic specificity. Limited meiotic analyses for the *T. aestivum* cultivars and synthetic hexaploids gave metaphase I associations characteristic of nonallosyndetic chromosomal pairing. Pollinations with *Tripsacum*, together with maize pollinations offer an extended crossing cycle and in addition extend the range of alien species for producing polyhaploids in the Triticeae.

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SUCCESSFUL FERTILIZATION involving distant taxonomic members of the Pooideae and Panicoideae subfamilies of the Gramineae family has been cytologically documented in crosses of wheat with maize (Zenkteler and Nitzsche, 1984; Laurie and Bennett, 1986), sorghum [*Sorghum bicolor* (L.) Moench] (Laurie and Bennett, 1988a), pearl millet [*Pennisetum glaucum* (L.) R. Br.] (Laurie, 1989), and *Teosinte (Z. mays* spp. *mexicana;* Ushiyama et al., 1991). Successful fertilization was also observed in crosses involving maize with barley (*Hordeum vulgare* L.; Laurie and Bennett, 1988b), *T. turgidum* L., and several wild wheat relatives of *Triticum* and *Aegilops* spp. (O'Donoughue and Bennett, 1988).

These wide crosses, in addition to providing a mechanism for the possible exploitation of genetic variability between diverse gene pools through sexual hybridization, are also a means of producing haploid plants by preferential chromosome elimination of the pollen parent in early stages of embryo development (Laurie and Bennett, 1986). After zygote formation, chromosomal elimination (Panicoideae spp.) occurs very early during embryo development thus producing a haploid female parent em-

Abbreviations: GA_3, gibberellic acid; MS, Murashige and Skoog medium; IAA, indole-3-acetic acid; BAP, 6-benzylaminopurine.

Table 1. Embryo recovery and plant regeneration from hybridization of some *Triticum aestivum, T. turgidum,* and synthetic hexaploid (*T. turdigum* × *Aegilops squarrosa*) cultivars with *Tripsacum dactyloides.*

Cultivar or line	Florets pollinated	Embryos recovered	Plants regenerated
	no.		
T. aestivum cultivars			
Glennson 81	40	12	10
Seri 82	40	11	9
Opata	40	9	7
Bacanora	40	13	9
Alondra/Pavon	40	12	10
Spinebill	156	20	16
Bau	150	27	21
Bobwhite/Pavon	148	31	24
Total	654	135	106
Percentage		20.6	78.5
T. turgidum cultivars			
Altar 84	88	19	13
Memo/Mexicali	40	12	9
Chen "S"	40	14	8
Total	168	45	30
Percentage		26.8	66.7
Synthetic hexaploids (*T. turgidum* × *Ae. squarrosa*)			
Ruff "S" × *Ae. squarrosa*†	204	28	21
Altar 84 × *Ae. squarrosa*‡	86	18	13
Altar 84 × *Ae. squarrosa*‡	40	16	12
Chen "S" × *Ae. squarrosa*‡	40	11	8
Doy "S" × *Ae. squarrosa*‡	40	18	14
Laru "S" × *Ae. squarrosa*‡	40	15	12
Total	450	106	80
Percentage		23.5	75.5

† Ruff "S"/*Ae. squarrosa* synthetic was obtained from Dr. H. Dhaliwal, Ludhiana, India.
‡ *Ae. squarrosa* accessions involved in synthetics are INTER-VER 178, 218, 224, 488, and 309 respectively.

bryo (Pooideae spp.). Normally, the embryos abort very early. Exogenous treatment with the synthetic auxin 2,4-D, however, enhances seed and embryo development until the excised embryo is plated on a synthetic medium for continued growth and plant regeneration. Using this method, haploid cereal plants have been recovered from wheat × maize (Comeau et al., 1988; Laurie and Bennett, 1988b; Suenaga and Nakajima, 1989), durum wheat × maize (Riera-Lizarazu et al., 1992), wheat × pearl millet (Ahmad and Comeau, 1990), wheat × *Teosinte* (Ushiyama et al., 1991), wheat × sorghum (Ohkawa et al., 1992) and barley × maize (Furusho et al., 1991) crosses.

Haploid production of small grain Triticeae cereals has mostly relied on anther culture and sexual crossings with *H. bulbosum*. Limitations to these haploid production strategies include genotypic specificity, aneuploidy, and somaclonal variation in the anther culture approach (for review see Picard, 1989). Homoeologous group 5 genetic crossability loci (*Kr1, Kr2, Kr3*) are the essential limiting factors in the *H. bulbosum* method (Snape et al., 1979; Falk and Kasha, 1983). In order to avoid tissue culture associated somaclonal variation, a sexual route to haploid production is seemingly more desirable. Since maize appears to be insensitive to *Kr* crossability alleles of wheat (Laurie and Bennett, 1987), polyhaploids can be recovered across different genotypes (Inagaki and Tahir, 1990; Laurie and Reymondie, 1991; Riera-Lizarazu et al., 1992), thus making it superior to the *H. bulbosum* system. In addition, gametoclonal variation induced in doubled haploid lines using the maize system was similar to that in doubled haploids obtained from wheat × *H. bulbosum* (Laurie and Snape, 1990).

These reports and the taxonomic proximity of eastern gamagrass to maize have encouraged us to initiate this study, an evaluation at cross combinations involving wheat (*T. aestivum* and *T. turgidum*) and *T. turgidum* × *Ae. squarrosa* amphiploids with *Tr. dactyloides* as a novel and alternate sexual route for the production of cereal polyhaploids. It may also facilitate extending the crossing cycle using field grown pollen donor plants by at least 8 wk.

MATERIALS AND METHODS

Plant Materials

Cultivars of bread wheat, durum wheat and amphiploids (synthetic hexaploids) of durum wheat × *Aegilops squarrosa* L. ($2n=6x=42$, AABBDD) grown in pots outdoors at El Batan, CIMMYT, Mexico, were used as pistillate parents in crosses with a single *Tr. dactyloides* accession (CIG-T-ATR-1) also growing outdoors (Table 1).

Crossing Procedure and Embryo Rescue

Spikes were hand-emasculated before anthesis and covered with glassine bags. When the stigmatic surface was receptive (3–4 d after emasculation), the spikes were pollinated with fresh *Tripsacum* pollen. One day after pollination, the emasculated floral cups were flooded with an aqueous solution of 50 mg L^{-1} 2,4-D and 150 mg L^{-1} GA_3. To evaluate the effect of 2,4-D on embryo recovery, crosses involving the hexaploid wheat cultivar Ciano 79 and the tetraploid wheat cultivar Altar 84 were given one of three treatments: (i) Some crossed spikes did not receive 2,4-D, (ii) Others received 2,4-D but were not pollinated, and (iii) Others were pollinated and received a 2,4-D treatment. Between 18 and 20 d after pollination spikes were collected. Caryopses extracted from the spikes were surface-sterilized in a chlorine bleach solution (200 mL L^{-1}) for 15 min and rinsed thrice in sterile deionized distilled water. Embryos were aseptically excised under a stereomicroscope (2×) in a laminar flow hood decontaminated with 750 mL L^{-1} ethanol. Excised embryos were transferred to vials containing a half strength MS (Murashige and Skoog, 1962) basal medium supplemented with 20 g L^{-1} sucrose, 0.4 mg L^{-1} IAA, 0.1 mg L^{-1} BAP and 2 g L^{-1} Gelrite (Scott Laboratories, West Warwick, RI). Vials with embryos were kept refrigerated in the dark at 4 °C for 2 wk and then at room temperature (18–20 °C) for 1 to 2 wk. After germination followed with 2 wk growth, the plants were transferred to peatpots and eventually to pots filled with a steam-sterilized 2:1:1 (soil/sand/peat moss) soil mix for subsequent growth in a greenhouse. Greenhouse temperature regimes were 25/12 °C (day/night), a 16-h photoperiod and 45 to 60% relative humidity.

Cytology

Somatic cytology of the regenerated plants was conducted according to the method of Mujeeb-Kazi and Miranda (1985). For meiotic analysis young spikes were fixed in 6:3:1 (990 mL L^{-1} ethanol/chloroform/glacial acetic acid) for 48 h and stored in 700 mL L^{-1} ethanol in the freezer (−10 °C) until use. Anthers at metaphase I were stained in alcoholic carmine and processed according to the modified procedure of Mujeeb-Kazi et al. (1993). Mean metaphase I pairing associations were calculated for some polyhaploids from at least 25 meiocytes each.

RESULTS AND DISCUSSION

Caryopses taken 18 to 20 d post-pollination from crosses of bread wheat, durum wheat and the synthetic hexap-

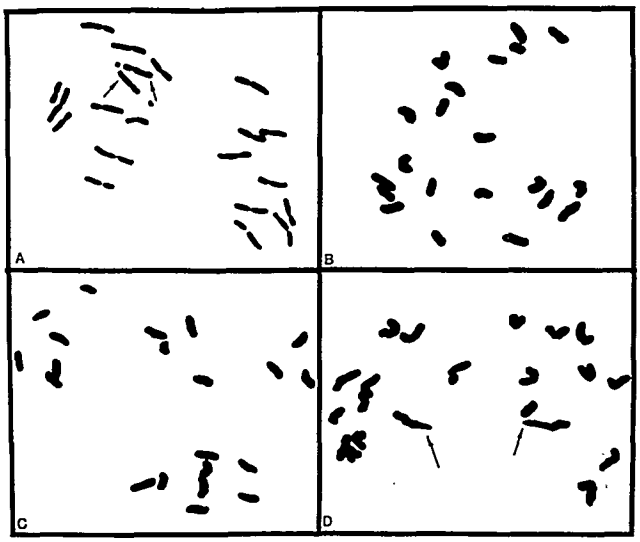

Fig. 1. Somatic and meiotic cytology of a $n = 3x = 21$, ABD polyhaploid derived from a hexaploid wheat × *Tripsacum dactyloides* cross (a) 21 somatic chromosomes with 1B and 6B satellited chromosomes (arrowed); (b) A meiocyte at metaphase I with 21 univalents; (c) Metaphase I cell with 21 univalents; and (d) A metaphase I cell with 21 chromosomes associated as 19 univalents + 1 rod bivalent (arrowed).

loids with *Tr. dactyloides* as the pollen source lacked a normal endosperm. Embryos were lodged at the seed micropylar end in shrivelled caryopses or were floating in a watery solution (probably translocated solutes) in well developed caryopses. A failure of normal endosperm development also occurs in caryopses from wheat × maize crosses. With the post-pollination application of 2,4-D however, ovary tissues enlarge as happens in normal caryopsis development, appear turgid, but filled with liquid (Suenaga and Nakajima, 1989). Inside these caryopses, embryos may or may not be found.

If 2,4-D is not applied, seeds and embryos are not recovered (Suenaga and Nakajima, 1989). From our preliminary trials, it appears that 2,4-D is also important for embryo recovery following crosses with *Tripsacum*. In crosses involving bread wheat cv. Ciano 79 and durum wheat cv. Altar 84, embryos were recovered only from pollinated florets receiving the 2,4-D treatment. Embryos were not recovered from unfertilized eggs after 2,4-D treatment, or from pollinated florets without a 2,4-D treatment. Exogenous 2,4-D treatments may be important in early stages of embryo development in wheat × *Tripsacum* crosses, although increased fertilization frequencies cannot be ruled out.

In crosses receiving 2,4-D and GA_3 treatment 24 h after pollination, the mean embryo recovery frequencies observed were 20.6% for bread wheats, 26.8% for durum wheats and 23.5% for the durum wheats/*Ae. squarrosa* synthetic hexaploids, respectively (Table 1). There was no genotype specificity apparent, implying that *Tripsacum*, like maize and other Panicoideae, is insensitive to the *Kr* crossability alleles of wheat. A more detailed study is needed, however, to reveal the extent of this insensitivity in different *Tripsacum* accessions since variation among maize cultivars has been observed (Suenaga and Nakajima, 1989).

Embryo recovery frequencies were slightly low in this experiment compared with those reported earlier (Riera-Lizarazu and Mujeeb-Kazi, 1990), an aspect where variations in technique may augment results. This lower frequency was coupled with the observation that embryos were smaller (averaging 0.5 mm) than those resulting from wheat × maize crosses (averaging 1 mm). In the post-pollination treatments, GA_3, which is routinely used in intergeneric hybrid production (Mujeeb-Kazi et al., 1987), was added at a concentration of 150 mg L^{-1} in addition to 2,4-D (Suenaga and Nakajima, 1989; Furusho et al., 1991). Our doubling of the commonly used GA_3 concentration might have been detrimental to normal embryo development. This variable needs further evaluation to determine whether embryo size could be improved by omitting GA_3 or by using a lower concentration. With normal embryo development better germination frequencies are anticipated.

Table 2—Mean chromosome pairing with ranges in parenthesis at metaphase I in some polyhaploids of *Triticum aestivum* L. and *T. turgidum* cv. Ruff"S" × *Aegilops squarrosa* synthetic hexaploids.

Polyhaploid ($n = 3x = 21$) entries	Metaphase I chromosomal associations				
		Bivalents		Total	
	I	Rings	Rods	II	Trivalents
Bobwhite/Pavon	17.4 (15–19)†	0	1.8 (1–3)	1.8	0
Opata	17.6 (15–19)	0	1.7 (1–3)	1.7	0
Bacanora	18.2 (17–19)	0	1.4 (1–2)	1.4	0
Ruff/*Ae. squarrosa*	20.8 (19–21)	0	0.1 (0–1)	0.1	0
Ruff/*Ae. squarrosa*‡	21.0	0	0	0	0

† Numbers in parenthesis indicate ranges.
‡ Includes four polyhaploid plants.

All plants were cytologically analyzed and possessed 21 chromosomes for bread wheats polyhaploids (Fig. 1a), 14 chromosomes for durum wheats and 21 chromosomes for polyhaploids from synthetic hexaploids. The satellite chromosomes 1B and 6B were visible in all samples (Fig. 1a).

Meiotic analyses of some $n = 3x = 21$, ABD polyhaploids demonstrated negligible allosyndetic chromosome pairing at metaphase I (Table 2; Fig. 1b-d). Similar low chromosome pairing relationships have been reported in polyhaploids of bread wheats by Riley and Chapman (1958). No meiotic abnormalities were detected.

Embryo germination frequencies were 78.5% for bread wheats, 66.7% for durum wheats, and 75.5% for synthetic hexaploids; these rates are similar to the earlier regeneration frequencies of 68.5, 73.9, and 74.5% of polyhaploids from maize combinations (Riera-Lizarazu et al. 1992) in which colchicine doubling of polyhaploids ranged between 63.6 and 69.5%.

In the present study, spontaneous seed set was observed on seven durum wheats cv. Ruff"S" × *Ae. squarrosa* polyhaploids; B91-7086 to 7089, B-91-10327 to 10329; and somatic cell chromosome counts on three progeny plants from each polyhaploid were in agreement with an expected genome composition of $2n = 6x = 42$, AABBDD. As mentioned earlier, each polyhaploid possessed $n = 3x = 21$ chromosomes; hence, a meiotic restitution related process may have produced the dou-

bled seed progeny, an event of frequent occurrence in intergeneric and interspecific hybridization (Islam and Shepherd, 1980).

Crosses between wheat and *Tripsacum* resulted in the production of wheat polyhaploids of various genotypes. Unlike wheat anther culture or sexual hybridization of wheat with *H. bulbosum*, genotypic specificity and aneuploidy were not detected in this study. Thus, the *Tripsacum*-mediated system, like the maize-mediated one, is potentially superior to anther culture or the *H. bulbosum*-mediated system for wheat polyhaploid production. The merits of using *Tripsacum* instead of maize, or a combination of both, are worthy of consideration and further evaluation. In the field at El Batan, Mexico, *Tr. dactyloides* flowers 6 to 8 wk earlier than maize, allowing for a prolonged crossing cycle to wheat if both maize and *Tripsacum* are used as pollen donors. Regardless of the male parent used, polyhaploid production in the Triticeae by way of wide sexual hybridizations is interesting for the acceleration of cereal breeding programs and in its application to other wide-cross cytogenetic areas. The ease with which doubled haploid populations from different Triticeae genotypes (Riera-Lizarazu et al., 1992) are produced will also facilitate genetic segregation and mapping studies in cereals. Finally, a long term projection of the utility of wheat × *Tripsacum* hybridization is the possibility of transferring some desirable traits found in *Tripsacum*, such as drought tolerance and insect resistance, to cultivated wheats. Such a concept was earlier suggested by Laurie and Bennett (1986) for the transfer of the C-4 photosynthetic pathway to wheat from maize. Retention of alien chromosomes will be the crucial step if such introgressions are to materialize.

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