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NOTE

INFLUENCES OF DURUM WHEAT AND *AEGILOPS* GENOTYPES ON PRODUCTION OF AMPHIHAPLOID PLANTS

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ABSTRACT

Wild relatives of common wheat (*Triticum aestivum* L.) and durum wheat (*T. turgidum* L. var *durum*) are valuable sources of desirable characters for improving wheat cultivars. Since the genus *Aegilops* L. bears a close and important relationship with durum and bread wheat, more detailed study of them should also be beneficial in understanding these polyploid wheats. In this study, seven durum wheat landraces were crossed as the female parent with 32 accessions of *Aegilops* belonging to five species (*Ae. squarrosa*, *Ae. crassa*, *Ae. triuncialis*, *Ae. caudata* and *Ae. cylindrica*). Spikes were harvested 12-15 d after pollination for embryo rescue and some spikes were left to evaluate the formation of direct amphihaploid seeds. *Aegilops* species had a major influence on crossability (seed set), embryo culturability and plant recovery. The highest efficiency of amphihaploid plant recovery from rescuing embryos (42.1%) was obtained from *Triticum turgidum* (4*x*)×*Ae. crassa* (4*x*). This was followed by *Triticum turgidum* (4*x*)×*Ae. crassa* (6*x*) cross (37.8%). An efficient direct

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synthesis of viable amphihaploid seeds from crosses between durum wheat landraces and *Ae. crassa* (4*x*) originating from western Iran is also reported. The high crossability together with the direct germination of F_1 hybrid seeds of *Ae. crassa* (4*x*), provides new evidences concerning close phylogeny of this species and the polyploid species of wheat.

Key words: Amphihaploid, Crossability, *Triticum turgidum*, *Aegilops*, Interspecific cross.

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تاثیر ژنوتیپ هـــای گنـــدم دوروم و ایژیلوپـــس بـــر تولیـــد گیاهـــان آمفی هاپلوئید

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چکیده

خویشاوندان وحشی گندم معمولی (*Triticum aestivum* L.) و گنـدم دوروم (*T. turgidum* L. var. durum) منا بـع ارزشـمندی از خصوصیـات مطلـوب بـرای اصـلاح ارقـام گنـدم می باشند. از آن جا که جنس *Aegilops* رابطه نزدیک و مهمـی بـا گنـدم هـای دوروم و نـان دارد، مطالعـه

بیشتر آن ها در آشنایی با این گندم های پلی پلوئید سودمند است. در این مطالعه، ۷ نژاد بومی گندم دوروم به عنوان والد ماده با ۳۲ نمونه *Aegilops* متعلق به پنج گونه *Ae. crassa, Ae. squarrosa, Ae. cylindrica, Ae. triuncialis, Ae. caudata* تلاقی داده شد. ۱۵-۱۲ روز پس از گرده افشانی، سنبله ها برای نجات رویان برداشت شده و برخی از سنبله ها برای ارزیابی تشکیل بذر آمفی هاپلوئید مستقیم دست نخورده باقی گذاشته شدند. نژادهای بومی گندم دوروم فقط از لحاظ تلاقی پذیری (تشکیل بذر) تفاوت معنی داری داشتند، در حالی که گونه های *Aegilops* تاثیر زیادی بر تلاقی پذیری، کشت پذیری رویان و حصول گیاه داشتند. حد اکثر کارائی حصول گیاه آمفی هاپلوئید از نجات رویان (۴۲/۱٪ گیاه در هر ۱۰۰ گلچه گرده افشانی شده) از دو رگه گیری *T. turgidum* × *Ae. crassa* (4 x) به دست آمد. دورگه گیری *T. turgidum*× *Ae. crassa* (6x) با ۳۷/۸٪ گیاه در هر ۱۰۰ گلچه گرده افشانی شده از این نظر مرتبه دوم را کسب نمود. در این مطالعه یک روش کارای مستقیم برای تهیه بذر های زنده آمفی هاپلوئید از تلاقی بین نژادهای بومی گندم دوروم و *Ae. crassa* (4 x) که از غرب ایران منشاء یافته اند، نیز گزارش می شود. تلاقی پذیری زیاد به همراه تولید مستقیم مقدار نسبتا" چشمگیر بذر دو رگه بین گونه ای *Ae. crassa* (4 x) نشان دهنده شواهد جدیدی در رابطه با فیلوژنی این گونه و گونه پلی پلوئید گندم است.

INTRODUCTION

Common wheat (*Triticum aestivum* L.) is an allohexaploid (AABBDD) that was first domesticated about 8000 years ago in Iran (4). Amphiploids have been widely used for wheat improvement, as well as evolutionary and cytogenetical studies in the *Triticeae* (23). Amphiploids from interspecific crosses between tetraploid wheats and *Aegilops* species, as their close relatives, are useful bridging germplasm for the introduction of desirable alien characters to common wheat (4, 5). Hence, there have been several collecting trips to I.R. Iran for this resources, e.g. Kihara *et al.* (10), Halloran (8) and Zohary *et al.*

(23). *Ae. squarrosa* is the most intensively used alien germplasm for improvement of common wheat. Friebe *et al.* (5) considered *Ae. squarrosa* as the primary gene pool for common wheat, since gene transfer from this species can be achieved by direct hybridiztion, homologous recombination, backcrossing, and selection. Accessions of *Ae. squarrosa*, particularly those from Iran, are a diverse genetic storehouse of potentially useful characteristics for incorporation into modern wheat cultivars (13, 18). Two successful approaches have been used to efficiently introgress desireable genes from *Ae. squarrosa* to the bread wheat. These were direct crossing (6, 13) and via producing synthetic hexaploid wheat from *T. turgidum* × *Ae. squarrosa* (13, 9).

Aegilops crassa is characterized by a large degree of morphological variation and a wide area of distribution, including Palestine, Lebanon, Syria, Iraq, Iran, Turkey, Afghanistan, and Turkmenistan and has a tetraploid ($2n = 4x = 28$) and a hexaploid ($2n = 6x = 42$) cytotype (2, 11). Kihara (9) suggested the genomic formula DMCr for 4*x* *Ae. crassa* and $DD^2 MC_r$ for 6*x* *Ae. crassa*. It has been shown that the two D genomes of 6*x* *Ae. crassa* differ from each other and may also differ from the D genome of common bread wheat and that of *Ae. squarrosa* (2, 3). Kimber and Zhao (12) suggested that the two D genomes of 6*x* *Ae. crassa* are very similar to each other, but became differentiated during evolution from the D genome present in *Ae. squarrosa, Ae. ventricosa, Ae. cylindrica,* and in *T. aestivum*. Badaeva *et al.* (1) demonstrated that *Ae. crassa, Ae. vavilovii*, and *Ae. juvenalis* were derived from the common ancestor species 4*x* *Ae. crassa*. Badaeva *et al.* (2) recently conducted C-banding and *in situ* hybridization analysis of tetraploid and hexaploid *Ae. crassa*, and found a similar chromosome pattern of the D^2 genome of hexaploid *Ae. crassa* to those of D-genome chromosomes of *Ae. squarrosa*. However, 6*x* *Ae. crassa* was used in interspecific and intergeneric hybridizations (3, 7, 20, 21), and the studies of interspecific and intergenic hybrids involving 4*x* *Ae. crassa* are necessary.

Interspecific hybridization to incorporate alien genetic variation primarily, requires production and establishment of viable hybrids. The main crossability barriers to interspecific hybridization are hybrid breakdown, hybrid weakness, and hybrid sterility (15). These may be caused by arrested embryo developmemt, endosperm disintegration, abnormal development of ovular tissue, or chromosomal or genetic instability (17). Although numerous synthetic amphiploids have been produced, from the evolutionary point of view they are of limited value, since most of them could never have arisen spontaneously in nature. The present study was primarily designed to produce synthetic amphiploid wheat by crossing durum wheat landraces with *Aegilops* species, both collected from Ilam Province, western Iran. The idea for this work came from the authors' observation that native upland tetraploid wheat landraces grew next to the wild *Aegilops* at different areas within Ilam province. Since previous research on the phylogenies of durum and bread wheats was based on geographically diverse tetraploid wheats and *Aegilops*, results of our study may also be useful for the analysis of the evolutionary relationships in the polyploid *Triticum* species.

MATERIALS AND METHODS

Plant Materials

Thirty-two accessions of *Aegilops* (*Ae. squarrosa*, 4x and 6x *Ae. crassa*, *Ae. triuncialis, Ae. caudata* and *Ae. cylindrica*) as shown in Table 1 were used in this study. Seven durum wheat (*Triticum turgidum* L. var *durum*) landraces namely Ghalavandi, Khodaei, Golkoh, Sofihasani, Golkar, Zardak and Shaghatagol originating from western Iran were also used. Plants were grown at four planting dates in the greenhouse from mid-October (early autumn). In order to fullfil their probable vernalization requirement, pots were moved to outside of the greenhouse (temperature range -5/15° C, night/day), during the early tillering stage.

Hybridization

In the spring of 1997, the emasculated plants of seven durum wheat landraces were pollinated by seven accessions of *Aegilops*, all of which originated from Ilam province. The uppermost internode of individual florets was filled with 0, 5 and 10 mg l^{-1} 2,4-dichlorophenoxyacetic acid (2,4-D) 24 and 48 hrs after pollination by means of a hypodermic syringe. Spikes from each treatment were harvested 12-15 d after pollination for the embryo rescue but some spikes were retained on the plants to allow normal formation of amphihaploid seeds.

In the spring of 1998, the experiment was repeated with the additional 25 *Ae. squarrosa* originating from the southern coast of the Caspian Sea, I.R. Iran (Table 1).

Table 1. The ploidy, genomes, source and number of *Aegilops* accessions used.

Species	Ploidy	Genomes†	Source	Number
Ae. crassa	4*x*	DMCr	Ilam, Iran	1
Ae. crassa	6*x*	DD2MCr	Ilam, Iran	1
Ae. triuncialis	4*x*	CuC	Ilam, Iran	1
Ae. cylindrica	4*x*	CD	Ilam, Iran	2
Ae. caudata	2*x*	C	Ilam, Iran	1
Ae. squarrosa	2*x*	D	Ilam, Iran	1
Ae. squarrosa	2*x*	D	Southern Caspian Sea coast, I.R. Iran	25

† Genomic formula based on Kihara (9).

Embryo Rescue

The immature seeds were surface-sterilized in 70% ethanol for 1 min, and the embryos were excised. Six embryos were placed in each petri-dish (69× 15 mm) and a minimum of 50 embryos were plated per treatment. MS medium (14) supplemented with 1 mg l^{-1} indole-3 acetic acid (IAA), 1 mg l^{-1} 6-benzylaminopurine (BA) and 30 g l^{-1} sucrose was used. The pH of the medium was adjusted to 5.8 and solidified by 2.8 g l^{-1} agarose (type 1A, Sigma). The cultures were incubated in the dark at 25 °C for one wk or until the embryos germinated, and then moved to an illuminated incubator at 22±2° C, 12 hr day length and 65 µmol m^{-2} s^{-1} fluorescent light intensity. Plantlets with good root formation were transferred to pots and kept in a growth chamber for two wk before being transplanted to larger pots and grown in the greenhouse.

Cytological Observations

The root-tip chromosome number of F_1 hybrid seedlings in pots were determined. The root tips were pretreated in a saturated solution of 1-bromonaphthalene for 5 hrs at 20° C and fixed in a chromic acid-formaldehyde fluid (1:1 of 1% chromic acid + 10% formaldehyde) for 24 hr at 4° C. Then, the root tips were hydrolyzed in 1 N HCl at 60° C for 10 min, stained for 24 hr in hematoxylin stain at 30° C, and squashed in 45% glacial acetic acid. Chromosome images were taken with an Olympus BH2-RFCA microscope using a C35 AD4 Olympus camera.

Statistical Analysis

The influence of durum wheat genotypes and the *Aegilops* species on crossability was assessed according to percentage of crossability (seed set per 100 pollinated florets) and embryo culturability (regenerated plants per 100 cultured embryo). All percentage data was transformed using arcsin$\sqrt{x}$. A 7×7 factorial experiment in a completely randomized design with unequal number of replications was used in this study. Seven durum wheat landraces and seven accessions of *Aegilops*, both originating from western Iran were subjected to the analysis of variance. Analysis of variance was carried out using the GLM procedure of SAS computer package (16). Mean comparisons were conducted using the LSD test.

RESULTS

Analyses of variance for crossability and embryo culturability traits of interspecific crosses in 1997 are presented in Table 2. The results of the analysis of variance showed that *Aegilops* accessions had a major effect on crossability and embryo culturability (Table 2). Durum landraces, as the female parent, differed in crosssability, but not in embryo culturability. The durum × *Aegilops* interaction was not significant for either trait. No significant effects were observed for the 2,4-D treatments (data not presented).

Table 2. Analysis of variance (ANOVA) for crossability of *T. turgidum* and *Aegilops* .

Source of variation	Degree of freedom	Mean square crossability (% seed set)	Mean square embryo culturability (% plants recovered)
Aegilops accession (A)	6	1966.4***	2182.2***
Durum landrace (D)	6	224.5**	63.7ns
A× D	36	79.3ns	45.0ns
Error	79	64.6	48.5

** and *** significant at P<0.01 and P<0.001, respectively.

Means for both the crossability and culturability traits of the *Aegilops* parents averaged over durum landraces are presented in Table 3. The *Aegilops* parent means for culturability were the highest for *Ae. cylindrica* and the lowest for *Ae. crassa* (6*x*). On the other hand, the accessions of *Ae. crassa* (4*x*) and *Ae. crassa* (6*x*) gave the highest proportion of regenerated plants from the cultured embryos, 42.1% and 37.8%, respectively. The remaining four species of *Aegilops* did not differ significantly for embryo culturability. No significant differences were detected among the four *Aegilops* species *(Ae. triuncialis*, *Ae. caudata*, *Ae. cylindrica* and *Ae. squarrosa)* for the culturability.

Table 3. Means[†] (±s.e.) of crossability (seed set) and embryo culturability (amphihaploid plant recovery) as affected by different species of *Aegilops* used as male in *T. turgidum* × *Aegilops* sp. crosses.

Species	No. of pollinated florets	Crossability (%)	Embryo culturability (%)
Ae. crassa (4*x*)	451	48.3 ± 1.5c	42.1 ± 1.6a
Ae. crassa (6*x*)	428	45.5 ± 1.0c	37.8 ± 2.1a
Ae. triuncialis	302	63.9 ± 2.0ab	19.0 ± 1.3b
Ae. cylindrica	651	71.1 ± 1.7a	18.4 ± 1.0b
Ae. caudata	320	67.6 ± 1.9ab	16.1 ± 1.8b
Ae. squarrosa	1348	60.7 ± 2.3b	14.7 ± 2.2b

† Means within columns followed by the same letter are not significantly different at P≤0.01 according to Fishers's protected least significant difference.

Morphologically, the interspecific F_1 hybrid plants resembled the *Aegilops* parent with the exception of those derived from *Ae. crassa* accession. The interspecific hybrid plants of *T. turgidum*×*Ae. crassa* resembled durum wheat more than *Ae. crassa* at the vegetative stages and were more similar to *Ae. crassa* in spike morphology (Fig. 1).

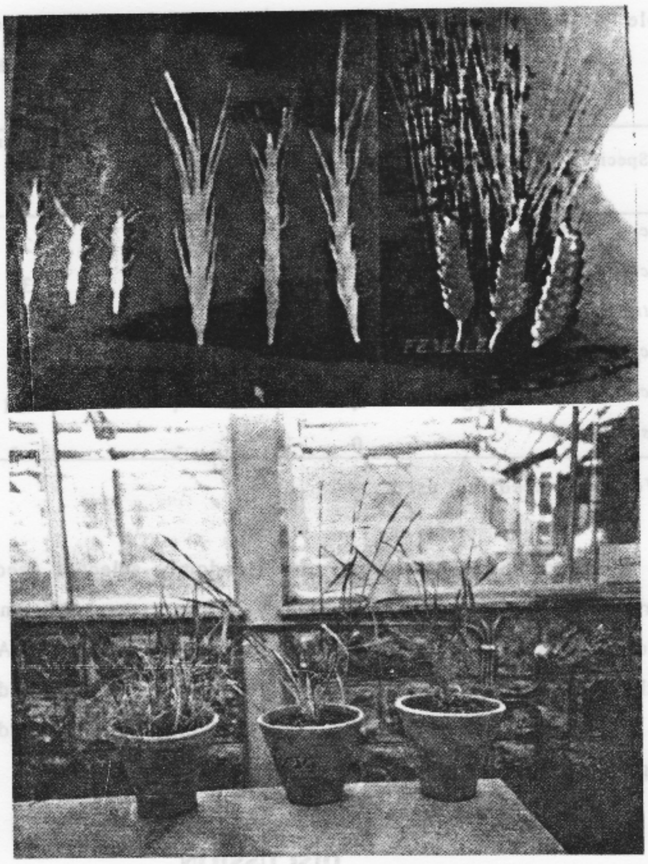

Fig. 1. *Aegilops crassa* (4*x*) plants as male parent (left), F_1 hybrid plant (middle), and *Triticum turgidum* plant as female parent (right).

The highest viable seed was obtained from the F_1 hybrids of *T. turgidum*×*Ae. crassa* (4*x*) with 97 surviving seedlings (Table 4). The interspecific F_1 hybrids derived from the accessions of other species did not produced seed, with the exception of *Ae. crassa* (4*x*) and *Ae. caudata* that produced only 16 and 2 viable seeds, respectively.

Table 4. Germination rate of F_1 seeds† sown in pots and chromosome counts of resulting seedlings in *T. turgidum*×*Aegilops* sp. crosses (direct seed set).

Species	No. of seeds	No. of seeds germinated	No. of seedlings chromosome no. determined	Chromosome no.	No of surviving seedlings
Ae. crassa (4*x*)	157	132	12	28	97
Ae. crassa (6*x*)	65	24	5	35	16
Ae. triuncialis	0	0	-	-	-
Ae. cylindrica	0	0	-	-	-
Ae. caudata	10	4	4	21	2
Ae. squarrosa	0	0	-	-	-

† Very poor seeds not used.

Chromosome counts from some randomly selected seedlings of the F_1 hybrids derived from direct seed set, in the crosses presented in Table 4, indicated that all of the tested F_1 hybrids were amphihaploid. As shown in Fig. 2, the F_1 hybrid of durum wheat with tetraploid and hexaploid *Ae. crassa* had 28, and 35 chromosomes, respectively. Growing these F_1 hybrids to maturity in the greenhouse also proved that they were completely sterile.

DISCUSSION

The effectiveness of routinely producing amphidiploids from durum wheat ×*Aegilops* depends on many factors including the efficiency of crossability (seed set), development and differentiation of hybrid embryos *in vivo*, and

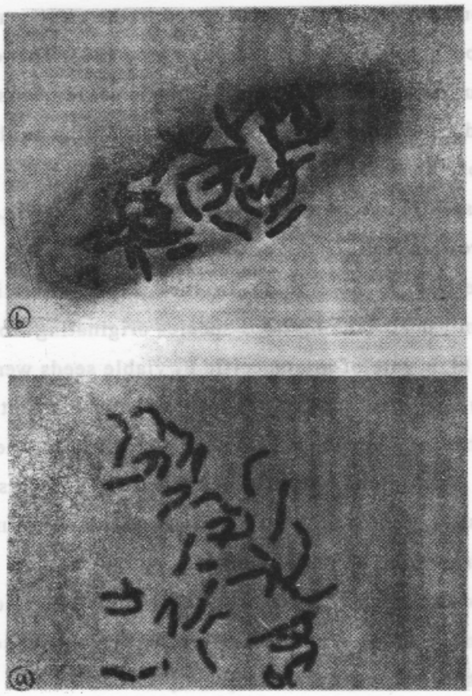

Fig. 2. Chromosome numbers of a) amphihaploid plants (n=28) derived from *T. turgidum*×*Ae. crassa* (4*x*), and b) amphihaploid plants (n=35) derived from *T. turgidum*×*Ae. crassa* (6*x*).

culturability of embryos when rescued *in vitro*. In previous reports, amphihaploid hybrid plants of durum wheat×*Aegilops* invariably resulted from rescuing the hybrid embryo. Wagenaar (20, 21) reported the cytology of the F_1 hybrid and genotypic effect leading to meiotic restitution and viable gamete formation by crossing *Ae. crassa* (6*x*)×*T. turgidum*. He observed a low chromosome pairing and bivalent formation in this amphiploid hybrid, which produced consistent seedset with an average of 2.8% per plant. Cytological studies of several successive generations of this spontaneous polyploid showed that 14 chromosomes were rapidly eliminated in the early generation, and th chromosome number became stabilized at 2n = 56 (20). This observation is in agreement with our results that the tetraploid form of *Ae. crassa* is more cross-compatible with durum wheat than its hexaploid form. In the present study, however, we report an efficient direct synthesis of viable F_1 amphihaploid seeds from crosses between durum wheat landraces and *Ae. crassa* (4*x*) originating from western Iran.

It is interesting to note that in the present investigation 1) native cultivars of durum wheats and *Aegilops* species originating from the same area were used; 2) a high rate of interspecific F_1 viable seeds were obtained from *Triticum turgidum* (4*x*)×*Ae. crassa* (4*x*) and 3) for the first time, tetraploid *Aegilops crassa* having the genome DMCr was used in the production of *Triticum-Aegilops* amphiploid. All of interspecific F_1 plants were obtained either by direct seed germination or embryo rescue were functionally male-sterile, since their pollen is largely aborted and the anthers did not dehisce. These interspecific hybrids, however, are heavily exposed to open-pollination by parental pollen in nature, and significantly they do set some (backcross) seed. Meiotic restitution may also frequently occur in the interspecific F_1 hybrid, that is caused by durum wheat parent (22), or *Aegilops* parent (20).

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