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Dormancy Spreads Seed Germination over a Long Period with a Discontinuous Procession in *Aegilops tauschii*, the D-genome Donor Species of Bread Wheat

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Abstract: *Aegilops tauschii* Coss. is the donor species of D-genome of bread wheat. This species has been widely utilized in wheat improvement. However, *Ae. tauschii* has been becoming the high-risk weed in the bread wheat fields of China. Dormancy is the vital factor for the weed reproduction during its life cycle. In the present study, we firstly observed the dormancy for a long time by monitoring the germination procession of three *Ae. tauschii* accessions under laboratory conditions for 120 days. The results revealed that all *Ae. tauschii* accessions had long and discontinuous dormancy. There were differences between intact spikelets and threshed seeds. Intact spikelets of all the three *Ae. tauschii* accessions displayed two obvious peaks of germination at about 50 and 90th day. However, time of peak appearance of threshed seeds was different among accessions. The dormancy characteristic of *Ae. tauschii* provides the possibility for this species as weed under a wide range of environments.

Key words: *Aegilops tauschii* (syn: *Triticum tauschii*), dormancy, germination, sprouting, *Triticum aestivum*, weed

INTRODUCTION

Common wheat or bread wheat (*Triticum aestivum* L., 2n = 6x = 42, genome AABBDD) is the very important food source for humankind, with some 600 million tons of grain production annually. Bread wheat is the product of hybridization between tetraploid wheat (*T. turgidum* L., 2n = 4x = 28, genome AABB) as the female parent and diploid *Aegilops tauschii* Coss. [Synonyms: *Triticum tauschii* (Coss.) Schmal. and *Aegilops squarrosa* L., genome DD, 2n = 14] as the male parent (Kihara, 1944; McFadden and Sears, 1944). *Ae. tauschii* is the donor species of the D-genome of bread wheat. The chromosomes of D-genome in *Ae. tauschii* show complete homology with that of common wheat. Thus, it is easy to transfer *Ae. tauschii* genes into common wheat by recombination between homologous chromosomes.

Only a few genotypes of *Ae. tauschii* were involved in the evolutionary origin of hexaploid wheat. Due to the evolution bottleneck, much of the genetic variation in the ancestral species *Ae. tauschii*, is not represented at common wheat. *Ae. tauschii* possess substantial levels of desirable genetic

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variability for characters of commercial significance (Ogbonnaya *et al*., 2005). Close evolutionary relationship and extensive genetic diversity for desirable traits make *Ae. tauschii* especially interesting for improving the genetic variability of common wheat.

Ae. tauschii has a center of natural distribution in the south Caspian area, spreading westwards to Turkey and eastwards to Afghanistan, Pakistan and China (Yen and Yang, 1999). The wide geographic distribution embraces a wide range of climate conditions with the likelihood of adaptations to extremes of heat, cold and moisture deficit. Besides it can grow under a broad range of environmental conditions, *Ae. tauschii* was considered to possess other characteristics commonly associated with successful weeds (Basu *et al*., 2004), such as strong seed dormancy (Lan *et al*., 1997; Liu *et al*., 1998; Gatford *et al*., 2002a, b), rapid vegetative growth (Villar *et al*., 1998) and high seed dispersal achieved by a brittle stem, which releases the seeds at maturity. This suggests that *Ae. tauschii* has a strong competitive ability and has the potential to develop into an invasive weed in bread wheat fields, which has been already proved by the quick spread of *Ae. tauschii* as a weed in China during the past 20 years. Before 1984, there were only two different distribution areas of *Ae. tauschii* in China (Yen *et al*., 1983, 1984). Along the Yili River valley of Xinjiang province, the species was distributed as a native species, which grows in natural vegetation. In Henan, Shannxi and Shanxi, three provinces at some places along the middle reaches of the Yellow River, the species was distributed as a weed race in bread wheat fields. There had been no reports of *Ae. tauschii* becoming a weed in other provinces of China that time. However, it was found that *Ae. tauschii* as an invasive weed has been quickly stretched into Heilongjiang, Shandong and Hebei provinces during the past 20 years. Recently, *Ae. tauschii* weed has distributed in wheat fields of many places in Jiangsu and Guangdong provinces besides above areas (Li *et al*., 2004; Peng and Zhuang, 2005). Not only *Ae. tauschii* has been recognized as a big problem of bread wheat production in above places in China, but also the troublesome numbers of *Ae. tauschii* plants in these wheat fields is quickly increasing.

Data on weed biology of *Ae. tauschii* are still scare. Dormancy is the vital factor for the weed reproduction during its life cycle. Only a few studies were related to the dormancy of *Ae. tauschii* (Lan *et al*., 1997; Liu *et al*., 1998; Gatford *et al*., 2002a, b). Previous these reports were aimed to improve wheat resistance to pre-harvest sprouting by exploiting dormancy of *Ae. tauschii.* All these studies germination pattern were studied only for a short period of no more than 21 days after planting (Lan *et al*., 1997; Liu *et al*., 1998; Gatford *et al*., 2002a, 2b). In a previous study, we found that many *Ae. tauschii* accessions showed low germination percentages at 21 days (Liu *et al*., 1998). On the contrary to *Ae. tauschii*, most of bread wheat cultivars could reach 100% germination after only a few days. To understand the dormancy behavior of *Ae. tauschii* seeds, it seems to be necessary to observe their germination during a much longer period of time. In this report, therefore, we firstly studied the germination traits of threshed seeds and intact spikelets from three *Ae. tauschii* accessions for a long time, 120 days.

MATERIALS AND METHODS

Bread wheat landrace Chinese Spring (CS) and three *Ae. tauschii* accessions were used in this study. *Ae. tauschii* AS60 is native to Middle East and AS65 is native to USSR, which belongs to subspecies *tauschii*. *Ae. tauschii* AS2404 (TQ-29) belongs to subspecies *strangulata*, provided by Prof. Moshe Feldman in Department of Plant Genetics, Weizmann Institute of Science, Israel. During 2004--2005 crop seasons, all plant materials were planted in the field of Triticeae Research Institute of Sichuan Agricultural University, located in Dujiangyan City of Sichuan province, China. These plants were grown as individual plants spaced 10 cm apart within rows and 30 cm between rows with 2 m length.

Random spikes from *Ae. tauschii* were harvested according to Gatford *et al*. (2002b). CS, AS60, AS65 and AS2404 were begun to be harvested on May 18, June 6, May 24 and June 16, respectively.

Within a spike, there are different spikelets located in different rachis joints. *Ae. tauschii* AS60, AS65 and AS2404 had 10, 10 and 12 spikelets within a spike, respectively. For each accession, spikelets at the same position within the spikes were clustered. Then, some of these spikelets were hand-threshed to obtain undamaged grains. About 10 hand-threshed seeds from spikelets at the same position were placed into the same petri dish. Ten, 10 and 12 petri dishes were used for these threshed seeds located in different positions from *Ae. tauschii* AS60, AS65 and AS2404, respectively. Similarly, 10, 10 and 12 petri dishes were used for intact spikelets of *Ae. tauschii* accessions AS60, AS65 and AS2404, respectively. Each of petri dishes contained about 10 intact spikelets.

These threshed seeds and intact spikelets were sterilized by immersion in 0.1% mercuric chloride solution for two minutes and rinsed throughoutly with distilled water. They were then placed in petri dishes for germination based on previous methods by Liu *et al*. (1998). During the period of 120 days, all the samples were germinated at room temperature with a vary from 20 to 35°C and a 12 h photoperiod.

Germination of threshed seeds or intact spikelets was monitored daily within a period of 120 days from 14 July to 11 November, 2005, when bread wheat in farm fields had been planted and grown as seedling in Dujiangyan city of Sichuan province. The period of 120 days represented a span from harvesting to sprouting season of *Ae. tauschii* at normal crop growing season. A threshed seed was considered germinated if the pericarp over the embryo ruptured by the emerging coleoptile. Grain from an intact spikelet was considered germinated if coleoptile and/or root protruded from the spikelet. The germination percentage for every day was calculated, which was derived from number of germinated seeds at that day divided by total number of germinated seeds. The cumulative germination figures were automatically produced by the program provided by Microsoft Excel 2003 according to germination percentage for every day. The frequency distribution figures were also automatically produced with an interval of 10 days by Microsoft Excel 2003.

RESULTS AND DISCUSSION

Variation on Cumulative Germination Percentages

Within the *Ae. tauschii* material used there was no observable effect on germination due to the position of the spikelets within the spikes (data not shown). Thus, 10, 10 and 12 petri dishes, which contain threshed seeds or intact spikelets from different positions within the spikes of AS60, AS65 and AS2404, were treated as replication in the further data analysis.

After five days, seeds of bread wheat CS achieved 100% germination. However, threshed seeds of *Ae. tauschii* accessions AS60, AS65 and AS2404 germinated at only 1.8, 0 and 0%, respectively. Threshed seeds of *Ae. tauschii* accessions AS60, AS65 and AS2404 began germination after four, eight and eight days, respectively. On 21 days, germination percentage for AS60, AS65 and AS2404 were 49, 7 and 8%, respectively. The present study and the results of our previous one (Liu *et al*., 1998) indicated that a final count after 21 days is insufficient to demonstrate the complete dormancy behaviours of *Ae. tauschii*. In this study, 86, 116, 120 days were needed for AS60, AS65 and AS2404, respectively, to finish germination and reach a germination percentage of 100%. These results suggest that some seeds of all the three *Ae. tauschii* accessions showed a strong dormancy.

Intact spikelets of all *Ae. tauschii* accessions did not germinate within 5 days after planting. Intact spikelets of AS60, AS65 and AS2404 began germination after 10, 25, 41 days, respectively. This indicates that longer times were needed for visible germination of seeds from intact spikelets than for germination of threshed seeds. The germination differences between threshed seeds and intact spikelets could be caused by the glumes. All the *Ae. tauschii* accessions were non-free-threshing and exhibited extremely hard, stiff, tough and tenacious glumes, which may prolong the dormancy (Liu *et al*., 1998; Gatford *et al*., 2002a).

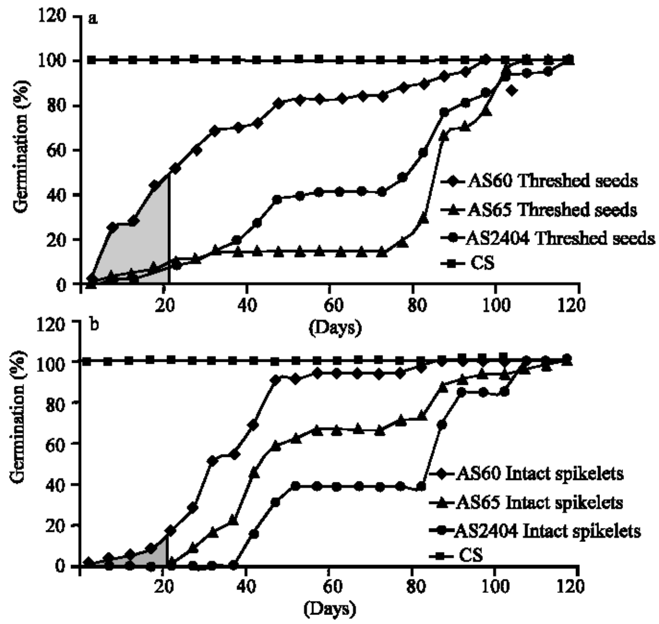

Fig. 1: Cumulative germination of three *Ae. tauschii* accessions and bread wheat CS during 120 day period for (a) threshed seeds and (b) intact spikelets. The sprayed areas indicate the germination for 21 day

During the total germination progress, there were also variations among *Ae. tauschii* accessions AS60, AS65 and AS2404. Germination speed of threshed seeds and intact spikelets of AS60 was fastest. In comparison with that of AS2404 for germination of threshed seeds, AS65, respectively showed a quicker speed at the beginning and slower afterward (Fig. 1a). For germination of intact spikelets, AS65 showed quicker speed than that of AS2404 (Fig. 1b).

Double Peaks of Germination and Variation during 120-Days

The germination progress for both threshed seeds and intact spikelets was discontinuous. According to the frequency distribution of germination over time, at least two independent germination peaks were evident in both the intact spikelets and threshed seeds of all the three accessions during 120 days (Fig. 2a-b). The germination peaks of threshed seeds for AS65 were respectively appeared about 90 and 110th days (Fig. 2a). The first peak was higher than the second. The germination peaks of threshed seeds for AS2404 were, respectively appeared at the 50 and 90th day. However, the first peak was lower than the second. There were three germination peaks for AS60 at about the 10, 50 and 100th day, respectively. The peak was highest on the 10th day and lowest on the 100th day (Fig. 2a). These results suggest that the germination peaks of threshed seeds showed more variation among the accessions than those of intact spikelets. All the three *Ae. tauschii* accessions displayed for intact spikelets two obvious peaks of germination at about the 50 and 90th day, respectively (Fig. 2b). The difference between threshed seeds and intact spikelets may reflect the complex interaction of dormancy mechanisms between glumes and seeds.

Ae. tauschii is the progenitor of the D genome of bread wheat. Among the progenitors of bread wheat, *Ae. tauschii* has the widest geographic distribution, westwards to Turkey and eastwards to Afghanistan, Pakistan and China (Yen and Yang, 1999). Due to the wide geographic distribution, *Ae. tauschii* species are subject to a very variable environment. It seems that *Ae. tauschii* has developed

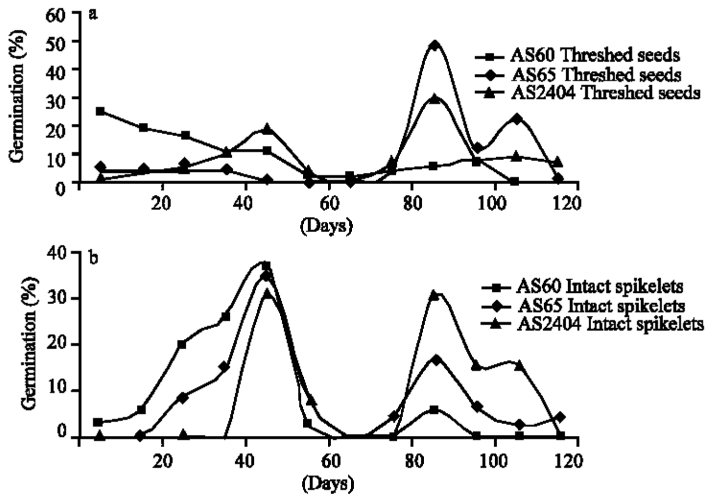

Fig. 2: Frequency distributions of germination percentages of three *Ae. tauschii* accessions for (a) threshed seeds and (b) intact spikelets

a dormancy mechanism to deal with the erratic timing or season of germination. The gradual and discontinuous germination allows *Ae. tauschii* to survive temporary, unfavorable conditions and exhibit strong plasticity to season of germination, which is very useful for the distribution of this species under a wide range of environments. Meanwhile, our research indicated germination variability among the three *Ae. tauschii* accessions. Germination variability might be part of a general-purpose genotype strategy to promote germination and colonization in a wide range of environments (Silvertown and Charlesworth, 2001).

Temperature can be a factor regulating seed dormancy. Fandrich and Mallory-Smith (2005) indicated that germination of *Ae. cylindrica* (2n = 4x = 28, genome CCDD) seed was promoted by low temperatures. A high temperature was not favor to the germination. Additionally, *Ae. cylindrica* seed germinated better with alternating temperature regimes compared to constant regimes. Fandrich and Mallory-Smith (2005) suggested that thermal dormancy prevents germination during the summer, even if rain wets the soil, because soil temperatures are above those required for germination. Both *Ae. cylindrica* and *Ae. tauschii* belong to genus *Aegilops*. Both of two species share the common D-genome. In the present study, all the seeds of *Ae. tauschii* were germinated under a moist condition and high temperature vary from 20 to 35°C. However, it is unclear that whether or not the gradual and discontinuous germination of *Ae. tauschii* in this study reflects the high temperature regulation on seed germination.

The gradual and discontinuous germination is favor to a species as weeds (Basu *et al*., 2004). In China, *Ae. tauschii* has been becoming the high-risk weed in many bread wheat fields. Before 20 years, *Ae. tauschii* weed was only distribution in northwards of China (Yen *et al*., 1983, 1984). Today, however, *Ae. tauschii* has spread to southwards of China (Li *et al*., 2004; Peng and Zhuang, 2005). There have quite different environment and climate conditions, especially in temperature and rainfall, between southwards and northwards of China. The dormancy mechanism developed by *Ae. tauschii* may be important for the species as weeds in the very variable environment.

Meanwhile, there is much concern today with the biological risk of genes moving from cultivated species to weedy relatives. Our previous study from field trials has indicated the possibility of natural wide-hybridization between *Ae. tauschii* and either hexaploid or tetraploid wheat in an agronomic situation (Liu *et al*., 2002). Considering the movement of herbicide tolerance, therefore, cautions should be highly paid on gene flow and introgression from transgenic wheat to *Ae. tauschii*.

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