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The utilisation of *Triticum* and *Aegilops* species for the improvement of durum wheat

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**SUMMARY** – An evaluation of the potential interest, for durum wheat improvement, of different species belonging to the *Triticum* and *Aegilops* genera is attempted. Main results concerning the evaluation of the different species for biotic stress resistance are presented and examples of successful introgression of diseases or pests resistance genes from alien species into durum (and bread) wheat are given. Some perspectives of utilising related species for improving abiotic stress tolerance and increasing yield potential are presented.

**Key words:** Durum wheat, *Triticum*, *Aegilops*, biotic and abiotic stresses, yield potential.

**Introduction**

By 2020, the world demand for wheat will be 40% greater than it is today. In response to this challenge, breeders must enhance the yield and simultaneously reduce the impact of agriculture on the environment. Durum wheat only represents 8% of total wheat production but 80% is growing under Mediterranean climates. In these regions drought considerably limits yield, together with heat, salinity, pests and diseases. Special efforts must consequently be made to increase the tolerance/resistance to biotic and abiotic stresses in this species. Since an important part of durum wheat is cultivated under irrigation, yield potential also needs to be increased.

A more efficient use of biodiversity in breeding programs is a key of this progress. Genes of resistance to various pests and diseases are present in durum wheat related species. 12 of the 40 known genes for leaf rust resistance and 20 of the 41 known genes for stem rust resistance originated in *Triticum* species other than the cultivated ones (McIntosh et al., 1998). A general survey of species belonging to the *Triticum* and *Aegilops* genera for their resistance to biotic stresses is attempted. Special attention is given to pests and diseases concerned by durum wheat cultivation in the Mediterranean area. Some perspectives of utilising related species for improving abiotic stress tolerance and increasing yield potential are presented. The nomenclature used for *Triticum* and *Aegilops* is according to Croston and Williams (1981) and Van Slageren (1994), respectively.

**Triticum and Aegilops: Phylogenetic relationships**

Wheat belongs to the genus *Triticum*, which originated almost 10,000 years ago in the Fertile Crescent. The center of origin of *Triticum* is Southwest Asia, near the Fertile Crescent (Tigris-Euphrates region). In this region, diploid and polyploid *Triticum* species exhibit tremendous morphological and ecological diversity.

The *Aegilops* genus comprises 22 diploid, tetraploid and hexaploid species (Van Slageren, 1994). The genus would probably originate from Transcaucasia (Hammer, 1980). The most primitive species (as *Ae.*...
The origin of the B genome is still under discussion: Ae. tauschii and Ae. longissima have been successively proposed as donors of this genome (see Kerby and Kuspira, 1988 and Fernandez-Calvin and Orellana, 1994). The genome constitution of durum wheat, and its crossability with other species leads to focus the search of useful genes in the A, AB and AG Triticum, and in Aegilops species.

The interest of Triticum and aegilops genepool for the improvement of biotic stress resistance

Diploid Triticum species

Diploid wheat pool comprises three species, T. urartu, T. boeoticum and T. monococcum (“cultivated einkorn”). T. monococcum which is widely distributed throughout the Near East, Transcaucasia, the Mediterranean region and the Balkans, was one of the first cereals cultivated for food. Today, einkorn cultivation is limited to small regions of South Europe and India.

Diploid wheats have a very high level of resistance to leaf rust (Puccinia recondita f. sp. tritici) (Jacobs et al., 1996). Genes of leaf rust resistance have been transferred into wheat from T. monococcum and T. boeoticum by Hussien et al. (1997). Resistance to stem rust (Puccinia graminis f. sp. tritici) was also found in these two species by Soshnikova (1990) and a resistance gene (SrTm) transferred from T. monococcum to wheat by Volkoun et al. (1989). AAB amphiploids derived from crosses of diploid Triticum with T. durum and resistant to stripe rust can be used to transfer resistance to durum wheat (Ma et al., 1997). T. monococcum is considered by Mihova (1988) as the most useful diploid Triticum to improve stripe rust (Puccinia striiformis West.) resistance. Major gene for powdery mildew resistance was transferred from T. boeoticum to bread wheat by Shi et al. (1998). Sources of resistance to the M-PAV strain of BYDV was identified in the three diploid wheat species (Goletti et al., 1999). Resistance to root rot (Fusarium roseum + Cochliobolus sativus) was found to be closely associated with A genome (Yamaleev et al., 1989). In T. monococcum were also found some sources of resistance to scab (Saur, 1991), Septoria tritici, avenae (Yu and Sun, 1995) and nodorum (Ma and Hughes, 1993).

Bouhssini et al. (1997) identified resistance to Hessian fly (Mayetiola destructor Say) in T. monococcum. According to Pietro et al. (1998), diploid Triticum present considerable interest for breeding for resistance to aphids. Two T. monococcum lines, Tm44 and Tm46 were identified by Caillaud and Niemeyer (1996) as being rejected as hosts by Sitobion avenae. Some T. monococcum and T. boeoticum lines were also found to be resistant to the Russian wheat aphid, Diuraphis noxia (Deol et al., 1995).

Tetraploid Triticum species

AB genome

The tetraploid wheat group is composed by ten species, carrying either AB or AG genome and growing in a wider range of environments than diploids. Cultivated emmer (T. dicoccum) was the predominant cultivated wheat during Neolithic Age. During Bronze Age the naked tetraploid wheats slowly displaced emmer wheat which however remains an important crop in Ethiopia and Yemen.

T. dicoccoides has been recognised as a valuable source of powdery mildew resistance and leaf rust resistance by El-Morshidy et al. (1983). Leaf rust resistance has been transferred into wheat by Dyck (1994). Yr15, a gene for resistance to stripe rust, was described in T. dicoccoides by Gerechter-Amitai et al. (1989). Molecular markers linked to the Yr15 gene were further identified by Sun et al. (1997). T. dicoccum is considered as resistant to powdery mildew (Simeone et al., 1998) and also constitutes a

speltoides) are found near of this centre of origin. All the diploid species have rather limited areas of distribution, while the tetraploid and hexaploid have a wider ecological adaptation (Hammer, 1980). The Aegilops genus has played a major role in the constitution of durum and bread wheat genomes. Allotetraploid Triticum (2n=4x=28), which include durum wheat, arose from the cross of two diploid wild grasses. Tetraploid wheat later crossed to diploid goat grass (Ae. tauschii) and gave rise to hexaploid wheats, among them bread wheat (T. aestivum L., 2n=6x=42). According to Dvorak (1988), the A genome from the AB and ABD wheats would originate from T. urartu. The D and G genomes would come from Ae. tauschii (=Ae. squarrosa) (Rayburn and Gill, 1987) and Ae. speltoides (Tsunewaki, 1980), respectively. The origin of the B genome is still under discussion: Ae. speltoides, Ae. bicornis, Ae. sharoneensis, Ae. longissima and Ae. searsii have been successively proposed as donors of this genome (see Kerby and Kuspira, 1988 and Fernandez-Calvin and Orellana, 1994). The genome constitution of durum wheat, and its crossability with other species leads to focus the search of useful genes in the A, AB and AG Triticum, and in Aegilops species.
valuable source of resistance to leaf and stem rusts (Knott and Zang, 1990). Among AB species, *T. dicoccum* was found to have the lowest natural susceptibility to the Russian Wheat Aphid (*Diuraphis noxia*) (Robinson and Skovmand, 1992; Liu et al., 1996).

Some lines with resistance to *Septoria* were also identified within AB *Triticum* (Yu and Sun, 1995). *T. dicoccum* was found to have the lowest natural susceptibility to the Russian Wheat Aphid (*Diuraphis noxia*) (Robinson and Skovmand, 1992; Liu et al., 1996). Some lines with resistance to *Septoria* were also identified within AB *Triticum* (Yu and Sun, 1995).

*AG genome*

*T. timopheevi* and *T. araraticum* species are known as valuable sources of resistance to the main fungal diseases (Tomerlin et al., 1984 and Brown-Guedira et al., 1996, respectively). *T. araraticum* was found to be resistant to root-rot (Yamaleev et al., 1988). Transfer of rusts and mildew resistance from *timopheevi* into wheat was performed by Sawhney and Goel (1979) and Malinski et al. (1984). Successful transfers from *araraticum* have concerned leaf rust (Brown-Guedira et al., 1999a) and powdery mildew (Xiang et al., 1996; Zhang et al., 1997; Brown-Guedira et al., 1999b).

*Aegilops* species

All the diploid *Aegilops* species as well as tetraploid species carrying the U genome appear to be very resistant to all foliar diseases (Dimov et al., 1993; Mamluk and Van Slageren, 1994). *Ae. ventricosa* (DN) shows resistance to *Septoria nodorum* (Jahier and Trottet, 1980). *Ae. speltoides* (S genome) present some sources of scab resistance (Saur, 1991). Resistant accessions to BYDV were found in *Ae. biuncialis* (UM), *Ae. neglecta* (UM), *Ae. triuncialis* (UC) and *Ae. caudata* (C) (Makkouk et al., 1994). Some resistant accessions have also been identified in *Ae. geniculata* (M. Henry, pers. comm.). Resistance to *Heterodera avenae* is present in *Ae. comosa* (M), *Ae. uniaristata* (N) and *Ae. umbellulata* (U) (Rivoal et al., 1986). The screening of a collection of *Ae. geniculata* (MU) populations originating from different regions of the Mediterranean area allowed to identify populations with resistance to different cereal cyst pathotypes (Rivoal et al., in this Workshop). *Ae. tauschii* (D), *Ae. cylindrica* (CD), *Ae. ventricosa* (DN) and *Ae. geniculata* (MU) show resistance to Hessian fly, *Mayetiola destructor* (Amri et al., 1992) and to green bug, *Schizaphis graminum* (Raupp et al., 1988).

Lists of the main diseases and pests resistance genes already transferred from *Aegilops* species into cultivated wheats are given on Tables 1 and 2, respectively.

<table>
<thead>
<tr>
<th>Diseases</th>
<th>Species</th>
<th>Genes</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf rust</td>
<td><em>Ae. umbellulata</em></td>
<td>Lr9</td>
<td>Sears (1956)</td>
</tr>
<tr>
<td>Stem rust</td>
<td><em>Ae. speltoides</em></td>
<td>Sr32</td>
<td>McIntosh (1988) McIntosh et al. (1982)</td>
</tr>
<tr>
<td><em>(Puccinia graminis)</em></td>
<td><em>Ae. comosa</em></td>
<td>Sr34</td>
<td>McIntosh (1988) McIntosh et al. (1982)</td>
</tr>
<tr>
<td>Stripe rust</td>
<td><em>Ae. comosa</em></td>
<td>Yr8</td>
<td>Riley et al. (1968) McIntosh et al. (1988)</td>
</tr>
<tr>
<td><em>(Puccinia striiformis)</em></td>
<td><em>Ae. tauschii</em></td>
<td>Yr28</td>
<td>McIntosh et al. (1988)</td>
</tr>
<tr>
<td>Powdery mildew</td>
<td><em>Ae. speltoides</em></td>
<td>Pm12</td>
<td>Miller et al. (1988)</td>
</tr>
<tr>
<td><em>(Erysiphe graminis)</em></td>
<td><em>Ae. longissima</em></td>
<td>Pm13</td>
<td>Ceoloni et al. (1988)</td>
</tr>
</tbody>
</table>
Table 2. Genes of resistance to the main pests already transferred in cultivated wheats

<table>
<thead>
<tr>
<th>Pests</th>
<th>Species</th>
<th>Genes</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cyst Nematodes (Heterodera avenae)</td>
<td>Ae. ventricosa</td>
<td>Dosba and Rivoal (1981)</td>
<td></td>
</tr>
<tr>
<td>Root knot nematodes (Meloidogyne naasi)</td>
<td>Ae. peregrina</td>
<td>Mn1</td>
<td>Yu et al. (1990)</td>
</tr>
<tr>
<td>Hessian Fly (Mayetiola destructor)</td>
<td>Ae. tauschii</td>
<td>H13, H22, H23, H24</td>
<td>Raupp et al. (1993)</td>
</tr>
<tr>
<td>Greenbug (Schizaphis graminum)</td>
<td>Ae. speltoides</td>
<td>Gb5</td>
<td>Tyler et al. (1987)</td>
</tr>
</tbody>
</table>

**Improvement of abiotic stress tolerance**

**Drought tolerance**

A wide evaluation of wild relatives for their survival in dry conditions has been realised by Damania et al. (1992), who found Ae. tauschii, Ae. umbellulata, Ae. columnaris, Ae. peregrina and Ae. triuncialis to be the most resistant. A better knowledge of the physiological mechanisms involved in the tolerance was however needed to precise the effects on the final productivity. Under drought, T. dicoccum was found to maintain high water potential (Sinha and Bansal, 1991), high relative water content (Al Hakimi and Monneveux, 1993) and to strongly reduce its transpiration rate (Morant-Avice et al., 1994). A high capacity of osmotic adjustment has been noted in some populations of T. dicoccoides and Ae. geniculata (Rekika et al., 1998a,b). Selection for several morphophysiological traits related to drought tolerance has been performed in populations issued from crosses between durum and other AB wheats species and the most promising lines are being used in durum wheat breeding programs in Syria and Yemen (Al Hakimi, 1998).

Carbon isotope discrimination (\(\Delta\)) appears to be a valuable tool to evaluate water-use-efficiency (WUE) in C3 plants (Farquhar and Richards, 1984). Evaluation of \(\Delta\) performed by Waines et al. (1993) in Aegilops revealed a high intraspecific variation in most species. \(\Delta\) was higher in Ae. speltoides than in Ae. sharonensis. Zaharieva (unpublished) also found higher \(\Delta\) values in Ae. speltoides than in other tetraploid species. A wide variation was noted for \(\Delta\) in Ae. geniculata. High \(\Delta\) values were noted under water stress in grain and flag leaf of T. durum/T. carthlicum and T. durum/Ae. columnaris interspecific lines (O. Merah, pers. comm.). Close correlations were noted between WUE, grain or biomass yield and \(\Delta\), which appears as a valuable criteria to screen genetic resources and recombinant lines for those characters.

**Cold tolerance**

Frost resistance has been studied in Triticum and Aegilops by Barashkova (1981) and Limin and Fowler (1981), who evaluated a great number of species and populations. They concluded that species carrying the D genome (especially Ae. tauschii) are the most resistant, while those carrying the S genome are the most susceptible. Barashkova (1981) also noted a high frost resistance in T. timopheevi (AG genome). Within the species of the Sitopsis section, Ae. speltoides (the supposed donor of the G genome) was found to be the most resistant (Barashkova and Vavilov, 1991) and among the AB wheats, the highest level of resistance was registered in T. turgidum (Barashkova et al., 1990). By comparing tetraploid species Stankova et al. (1995) concluded that Ae. cylindrica (D) was the most resistant and Ae. geniculata (MU) and Ae. biuncialis (UM) the most susceptible. Ae. trilicaulis (CU) and Ae. neglecta (UM) were intermediate. The most susceptible species were however as resistant as the frost resistant bread wheats “Mironovska 808” and “Ulianovka” and much more resistant than the best durum wheat checks.

Little is known about chilling tolerance in wheat and related species. Recently, Rekika et al. (1997) used chlorophyll fluorescence to evaluate the sensitivity of photosynthetic membranes to low temperatures. All the Aegilops genotypes examined by these authors were more sensitive to chilling stress than the durum wheat checks whereas the score of T. dicoccoides was intermediate.
Heat tolerance

In field conditions, heat tolerance during the vegetative stage was noted by Waines (1994) to be higher in *Ae. speltoides* and *Ae. tauschii* than in *T. urartu* and *T. boeoticum*. Reproductive heat tolerance was found to be higher in the cultivated wheat than in the wild relatives. Tolerant accessions were however identified in *Ae. speltoides*, *Ae. longissima*, and *Ae. searsii*. Tolerance of photosynthetic membranes to high temperatures (evaluated by chlorophyll fluorescence measurements) was noted to be lower in *Aegilops* (*longissima*, *geniculata*, *speltoides*, *umbellulata*, *triuncialis* and *neglecta*) than in the most tolerant durum wheat varieties (e.g., Cham1) (Rekika et al., 1997). A high level of tolerance was registered by the same authors in the line *T. dicoccoides* 600808 from Jordan, and further confirmed in *T. durum* cv. Korilfa/*T. dicoccoides* 600808 lines (Y. Kara, pers. comm.)

Salt tolerance

In field conditions, *T. dicoccum* was found by Hunshal et al. (1990) as salt tolerant as barley. High level of salt tolerance was also noted in *T. dicoccoides* in controlled conditions by Sayed (1985), and Nevo et al. (1993). *Aegilops* species possessing the D genome could represent another source of salt tolerance (Farooq et al., 1989; Xu et al., 1993). A high level of tolerance was registered by the same authors in the line *T. dicoccoides* 600808 from Jordan, and further confirmed in *T. durum* cv. Korilfa/*T. dicoccoides* 600808 lines (Y. Kara, pers. comm.)

Ion toxicity and deficiency

Ion toxicity and deficiency have been poorly investigated in wheat related species. The diploid *Triticum* and *Ae. speltoides* were found by Dinev and Netcheva (1995) to be tolerant to manganese toxicity, and *Ae. tauschii* to be a high accumulator of aluminium. Accessions of *T. carthlicum* have been identified by Gamzikova and Barsukova (1996) as sources of nickel and cadmium resistance. For zinc deficiency, *T. dicoccoides* was found as susceptible, *Aegilops* species carrying the U genome as resistant and *Ae. tauschii* and *Ae. speltoides* as intermediate (Cakmak et al., 1999). A list of *Aegilops* species considered as potential sources of salt, cold, and drought tolerance is given on Table 3.

Improvement of yield potential

Wild related species have been considered until now much more as genitors of resistance to pests and diseases than as sources of diversity permitting deep modifications of architecture and physiology of the cultivated species. According to Evans (1993), wild related species could be used to increase the maximum photosynthetic rates (Pmax) in cultivated wheats. Flag leaf of several diploid ancestors species have a Pmax up to 40% greater, both *per* leaf area and *per* chlorophyll, than those of modern wheat varieties (Kaminski *et al.*, 1990) and could then better adapt could adapt to higher light intensities (Dunstone *et al.*, 1973). The smaller size of the leaves and mesophyll cells of diploids, leading to a shorter diffusion distance for CO	extsubscript{2} from the chloroplasts within the mesophyll is not the only one explanation for their higher Pmax values, since differences persist even with saturated CO	extsubscript{2} concentrations (Austin *et al.*, 1987). Differences in Rubisco activity have also been invoked (Austin *et al.*, 1987). There is also some evidence that the light reactions of photosynthesis are faster and rates of electron flow higher in wild diploid *Triticum* than in cultivated wheats (Miginiac-Maslow *et al.*, 1979). Grown at high light intensities, these species also have a higher Chla:Chlb ratio than wheat, indicating a higher concentration of photosystems *per* chlorophyll (Austin *et al.*, 1987). Transfer of high Pmax values to hexaploid wheats have been attempted by Austin (1990) and Rees *et al.* (1994). Austin (1990) attempted to increase Pmax in wheat by crossing durum wheats with the A genome *T. urartu*. The resulting amphiploids had higher Pmax than *T. aestivum* and some of them had higher biomass. *T. urartu* was also crossed and back-crossed with bread wheat. Some lines exhibited higher Pmax values, but did not have significantly higher biomass (Rees *et al.*, 1993). In CIMMYT, hexaploid lines were produced by crossing durum wheats with *Ae. tauschii*. The obtained synthetics had higher biomass production, larger flag leaves (with similar specific leaf dry weigh, SLDW), higher Chla/Chlb ratio.
indicating a higher photosystem concentration per unit chlorophyll). Photosynthetic rate and Chla/Chlb were found to be slightly higher in the synthetics than in bread and durum wheats. Their grain yield was however lower, due to their low HI.

Table 3. Aegilops species considered as potential sources of abiotic stress tolerance

<table>
<thead>
<tr>
<th>Abiotic stress</th>
<th>Species</th>
<th>Genome</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salt</td>
<td>Ae. tauschii</td>
<td>D</td>
<td>Farooq et al. (1989), Gorham (1990),</td>
</tr>
<tr>
<td></td>
<td>Ae. comosa</td>
<td>M</td>
<td>Xu et al. (1993), Farooq (1994)</td>
</tr>
<tr>
<td></td>
<td>Ae. umbellulata</td>
<td>U</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ae. cylindrica</td>
<td>CD</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ae. neglecta</td>
<td>UM</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ae. triuncialis</td>
<td>UC</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ae. kotschyi</td>
<td>SU</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ae. crassa</td>
<td>DDM</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ae. juvenalis</td>
<td>DMU</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ae. vavilovii</td>
<td>DMS</td>
<td></td>
</tr>
<tr>
<td>Cold</td>
<td>Ae. tauschii</td>
<td>D</td>
<td>Barashkova (1981),</td>
</tr>
<tr>
<td></td>
<td>Ae. umbellulata</td>
<td>U</td>
<td>Limin and Fowler (1981),</td>
</tr>
<tr>
<td></td>
<td>Ae. cylindrica</td>
<td>CD</td>
<td>Barashkova and Vavilov (1991)</td>
</tr>
<tr>
<td></td>
<td>Ae. neglecta</td>
<td>UM</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ae. triuncialis</td>
<td>UC</td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>Ae. tauschii</td>
<td>D</td>
<td>Damania et al. (1992),</td>
</tr>
<tr>
<td></td>
<td>Ae. sharonensis</td>
<td>S¹</td>
<td>Waines et al. (1993),</td>
</tr>
<tr>
<td></td>
<td>Ae. longissima</td>
<td>S¹</td>
<td>Rekika et al. (1998b)</td>
</tr>
<tr>
<td></td>
<td>Ae. kotschyi</td>
<td>SU</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ae. geniculata</td>
<td>MU</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ae. triuncialis</td>
<td>UC</td>
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</tbody>
</table>

**Conclusion**

Thousands of *Triticum* and Aegilops accessions have been collected and are stored in various genetic resources centers. These resources evolved an assortment of alleles needed for resistance/tolerance to diseases, pests and abiotic stresses. However, this germplasm is still insufficiently used in breeding programs. Chapman (1989) estimated that these materials may have been used in approximately 10 percent of all crosses based on the pedigrees of recently released cultivars. As emphasised above, several specific genes have however get major impact on wheat breeding. As far as the role of different morphophysiological traits in yield potential is now better known, wide crosses could be in the next future one of the more efficient ways to develop alternate plant types and physiological processes and could then result to be fundamental to our efforts to improve agricultural productivity. But many researchers are until now reluctant to include genetic resources in their programs. A major reason is the difficulty in evaluating materials, particularly in the case of physiological traits. When useful characteristics have been identified, the difficulty of transferring them to the cultivated species can represent a second obstacle. In addition, complete transfer can take several years. Hopefully, some promising new approaches are becoming available. New apparatus allows rapid measures of various plant parameters on large populations. Embryo rescue methods will facilitate the crosses between wide species and haplodiplodisation will accelerate the fixation of promising lines. Molecular genetics would allow to precise gene identification and provide highly heritable markers for the useful trait, avoiding the “linkage drag” (introgression of undesirable linked traits) frequently encountered in conventional backcross approaches.

**References**


