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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.

RESUME – “L’utilisation des espèces *Triticum* et *Aegilops* pour l’amélioration du blé dur”. Cet article tente d’évaluer l’intérêt potentiel de différentes espèces des genres *Triticum* et *Aegilops*. Les principaux résultats concernant l’évaluation de ces espèces pour leur résistance aux stress biotiques, ainsi que quelques exemples d’introgression chez le blé dur (ou le blé tendre) de gènes de résistance à des maladies et parasites sont donnés. Quelques perspectives d’utilisation des espèces voisines pour améliorer la résistance aux stress abiotiques et augmenter le rendement potentiel du blé sont présentées.

Mots-clés : Blé dur, *Triticum*, *Aegilops*, stress biotiques et abiotiques, rendement potentiel.

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.*

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. sharonensis*, *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.

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 Valkoun *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.*, 1990). 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

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. carthlicum* was found to have also resistance to leaf and stripe rusts (Dekapreleevitch and Naskidashvili, 1976). *T. polonicum* is considered by Mishra *et al.* (1996) as the best AB species for increasing yield as it had the highest yielding ability, number of grains per spike and tillering ability.

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 Trotter, 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 1. Genes of resistance to the main diseases already transferred in cultivated wheats

Diseases	Species	Genes	References
Leaf rust (<i>Puccinia recondita</i>)	<i>Ae. umbellulata</i>	Lr9	Sears (1956)
	<i>Ae. speltoides</i>	Lr28, Lr35, Lr36	Dvorak (1977) McIntosh (1988) McIntosh <i>et al.</i> (1991)
	<i>Ae. tauschii</i>	Lr21, Lr22, Lr32, Lr39, Lr41	Kerber and Dyck (1969) Dyck and Kerber (1970) Kerber (1987) Cox and Gill (1992)
Stem rust (<i>Puccinia graminis</i>)	<i>Ae. speltoides</i>	Sr32	McIntosh (1988)
	<i>Ae. comosa</i>	Sr34	McIntosh <i>et al.</i> (1982)
Stripe rust (<i>Puccinia striiformis</i>)	<i>Ae. comosa</i>	Yr8	Riley <i>et al.</i> (1968)
	<i>Ae. tauschii</i>	Yr28	McIntosh <i>et al.</i> (1988)
Powdery mildew (<i>Erysiphe graminis</i>)	<i>Ae. speltoides</i>	Pm12	Miller <i>et al.</i> (1988)
	<i>Ae. longissima</i>	Pm13	Ceoloni <i>et al.</i> (1988)

Table 2. Genes of resistance to the main pests already transferred in cultivated wheats

Pests	Species	Genes	References
Cyst Nematodes (<i>Heterodera avenae</i>)	<i>Ae. ventricosa</i>		Dosba and Rivoal (1981) Rivoal <i>et al.</i> (1986, 1993)
Root knot nematodes (<i>Meloidogyne naasi</i>)	<i>Ae. peregrina</i>	<i>Mn1</i>	Yu <i>et al.</i> (1990)
Hessian Fly (<i>Mayetiola destructor</i>)	<i>Ae. tauschii</i> <i>Ae. ventricosa</i>	<i>H13, H22, H23, H24</i> <i>H27</i>	Raupp <i>et al.</i> (1993)
Greenbug (<i>Schizaphis graminum</i>)	<i>Ae. speltoides</i>	<i>Gb5</i>	Tyler <i>et al.</i> (1987)

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 (Δ) appears to be a valuable tool to evaluate water-use-efficiency (WUE) in C3 plants (Farquhar and Richards, 1984). Evaluation of Δ performed by Waines *et al.* (1993) in *Aegilops* revealed a high intraspecific variation in most species. Δ was higher in *Ae. speltoides* than in *Ae. sharonensis*. Zaharieva (unpublished) also found higher Δ values in *Ae. speltoides* than in other tetraploid species. A wide variation was noted for Δ in *Ae. geniculata*. High Δ 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 Δ , 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. triuncialis* (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. Korifla/*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). Enhanced K/Na discrimination character, which has been proved to confer salinity tolerance (Storey *et al.*, 1985), is present in species possessing the D genome (Gorham, 1990).

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 Natcheva (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 (P_{max}) in cultivated wheats. Flag leaf of several diploid ancestors species have a P_{max} 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 CO₂ from the chloroplasts within the mesophyll is not the only one explanation for their higher P_{max} values, since differences persist even with saturated CO₂ 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 Chl_a:Chl_b ratio than wheat, indicating a higher concentration of photosystems *per* chlorophyll (Austin *et al.*, 1987). Transfer of high P_{max} values to hexaploid wheats have been attempted by Austin (1990) and Rees *et al.* (1994). Austin (1990) attempted to increase P_{max} in wheat by crossing durum wheats with the A genome *T. urartu*.

The resulting amphiploids had higher P_{max} 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 P_{max} 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 Chl_a:Chl_b ratio

(indicating a higher photosystem concentration *per* unit chlorophyll). Photosynthetic rate and Chl_a/Chl_b 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

Abiotic stress	Species	Genome	References
Salt	<i>Ae. tauschii</i>	D	Farooq <i>et al.</i> (1989), Gorham (1990), Xu <i>et al.</i> (1993), Farooq (1994)
	<i>Ae. comosa</i>	M	
	<i>Ae. umbellulata</i>	U	
	<i>Ae. cylindrica</i>	CD	
	<i>Ae. neglecta</i>	UM	
	<i>Ae. triuncialis</i>	UC	
	<i>Ae. kotschyi</i>	SU	
	<i>Ae. crassa</i>	DDM	
	<i>Ae. juvenalis</i>	DMU	
	<i>Ae. vavilovii</i>	DMS	
Cold	<i>Ae. tauschii</i>	D	Barashkova (1981), Limin and Fowler (1981), Barashkova and Vavilov (1991)
	<i>Ae. umbellulata</i>	U	
	<i>Ae. cylindrica</i>	CD	
	<i>Ae. neglecta</i>	UM	
	<i>Ae. triuncialis</i>	UC	
Drought	<i>Ae. tauschii</i>	D	Damania <i>et al.</i> (1992), Waines <i>et al.</i> (1993), Rekika <i>et al.</i> (1998b)
	<i>Ae. sharonensis</i>	S ¹	
	<i>Ae. longissima</i>	S ¹	
	<i>Ae. kotschyi</i>	SU	
	<i>Ae. geniculata</i>	MU	
	<i>Ae. triuncialis</i>	UC	

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 haplodiploidisation 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.

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