

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 "Uljanovka" 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.

References

- Al Hakimi, A. (1998). Primitive tetraploid wheat species to improve drought tolerance in durum wheat. In: *Triticeae III, Proc. of the Third International Triticeae Symposium*. Science Publishers, Inc., Enfield, USA, pp. 305-312.

- Al Hakimi, A. and Monneveux, P. (1993). Morphophysiological traits related to drought tolerance in primitive wheat species. In: *Biodiversity and Wheat Improvement*, Damania, A.B. (ed.). John Wiley and Sons, Chichester, UK, pp. 199-216.
- Amri, A., El Bouhssini, M., Jlibene, M., Cox, T.S. and Hachett, J.H. (1992). Evaluation of *Aegilops* and *Triticum* species for resistance to the Moroccan Hessian Fly (*Diptera* : *Cecidomyiidae*). *Al Awamia*, 77: 109-118.
- Austin, R.B. (1990). Prospects for genetically increasing the photosynthetic capacity of crops. In: *Perspectives in Biochemical and Genetic Regulation of Photosynthesis*. Alan R. Liss Inc., New York, pp. 395-409.
- Austin, R.B., Ford, M.A., Miller, T.E., Morgan, C.L. and Parry, M.A.J. (1987). *Progress in Photosynthesis Research*, Vol. IV. Marinus Nijhoff Publishers, Dordrecht, Netherlands, pp. 361-368.
- Barashkova, E.A. (1981). Role of the D genome in increasing the frost resistance of winter wheat. *Referativnyi Zhurnal*, 2: 65-124.
- Barashkova, E.A., Filatenko, A.A. and Buren, I.V. (1990). Frost resistance of new forms of wheat species differing in genome composition [Russian]. *Nauchno-tekhnicheskii Byulleten' Vsesoyuznogo Ordena Lenina i Ordena Druzhby Narodov Nauchno-issledovatel'skogo Instituta Rastenievodstva Imeni N.I. Vavilova*, 200: 3-6.
- Barashkova, E.A. and Vavilov, N. (1991). Physiological-genetic aspects of frost resistance in winter wheat. Relationship of frost hardiness with genome composition in wheat. In: *Proc. International Symposium : Wheat Breeding - Prospects and Future Approaches*. Institute for Wheat and Sunflower, Albena, Bulgaria, pp. 379-384.
- Bouhssini, M.E., Benlhabib, O., Bentika, A., Sharma, H.C. and Lahlou, S. (1997). Sources of resistance in *Triticum* and *Aegilops* species to Hessian fly (*Diptera: Cecidomyiidae*) in Morocco. *Arab Journal of Plant Protection*, 15: 126-128.
- Brown-Guedira, G.L., Cox, T.S., Gill, B.S. and Sears, R.G. (1999a). Registration of KS96WGRC35 and KS96WGRC36 leaf rust-resistant hard red winter wheat germplasm. *Crop Science*, 39: 595.
- Brown-Guedira, G.L., Cox, T.S., Gill, B.S., Sears, R.G. and Leath, S. (1999b). Registration of KS96WGRC37 powdery mildew-resistant hard white winter wheat germplasm. *Crop Science*, 39: 596.
- Brown-Guedira, G.L., Gill, B.S., Bockus, W.W., Cox, T.S., Hatchett, J.H., Leath, S., Peterson, C.J., Thomas, J.B. and Zwer, P.K. (1996). Evaluation of a collection of wild *timopheevi* wheat for resistance to disease and arthropod pests. *Plant disease*, 80: 928-933.
- Caillaud, C.M. and Niemeyer, H.M. (1996). Possible involvement of the phloem sealing system in the acceptance of a plant host by an aphid. *Experientia*, 52: 927-931.
- Cakmak, I., Tolay, I., Ozkan, H., Ozdemir, A. and Braun, H.J. (1999). Variation in zinc efficiency among and within *Aegilops* species. *Zeitschrift für Pflanzenernährung und Bodenkunde*, 162: 257-262.
- Ceoloni, C., Del Signore, G., Pasquini, M. and Testa, A. (1988). Transfer of mildew resistance from *Triticum longissimum* into wheat by *ph1* induced homoeologous recombination. In: *Proc. 7th International Wheat Genetics Symposium*, Miller T.E. and Koebner, R.M.D. (eds). Cambridge University Press, Cambridge, UK, pp. 221-226.
- Chapman, C.G.D. (1989). Collection strategies for the wild relatives of field crops. In: *The Use of Plant Genetic Resources*, Brown, A.H.D., Frankel, O.H., Marshall, D.R. and Williams, J.T. (eds). Cambridge University Press, Cambridge, UK, pp.136-156.
- Cox, T.S. and Gill, B.S. (1992). Use of diploid progenitors to improve leaf rust resistance in hexaploid wheat. *Vortr. Pflanzenzücht*, 24: 185-187.
- Croston, R.P. and Williams, J.T. (1981). *A World Survey of Wheat Genetic Resources*. IBPGR, Rome.
- Damania, A.B., Altunji, H. and Dhaliwal, H.S. (1992). Evaluation of *Aegilops* spp. for drought and frost tolerance. *Genetic Resources Unit Annual Report 1992, ICARDA*, pp. 45-46.
- Dekapreleevitch, L.L. and Naskidashvili, P.P. (1976). *Triticum persicum* v. *stramineum*, genetic source of resistance to yellow and brown rust [Georgian]. *Soobsccheniya Akademii Nauk Gruzinskoi Ssr*. 82: 689-691.
- Deol, G.S., Wilde, G.E. and Gill, B.S. (1995). Host plant resistance in some wild wheats to the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (*Homoptera:Aphididae*). *Plant Breeding*, 114: 545-546.
- Dimov, A., Zaharieva, M. and Mihova, S. (1993). Rusts and powdery mildew resistance in *Aegilops* accessions from Bulgaria. In: *Biodiversity and Wheat Improvement*, Damania, A.B. (ed.). John Wiley and Sons, Chichester, UK, pp. 165-169.
- Dinev, N.S. and Netcheva, V. (1995). Plant mineral composition and tolerance to low pH in species of Tribe *Triticeae*. *Soil Science and Plant Analysis*, 26: 223-235.
- Dosba, F. and Rivoal, R. (1981). Les lignées d'addition blé-*Aegilops ventricosa* Tausch. II. Etude de leur comportement et de celui de leurs progéniteurs vis à vis d'*Heterodera avenae* Woll. [French]. *Agronomie*, 1: 559-564.

- Dunstone, R.L., Gifford, R.M. and Evans, L.T. (1973). Photosynthetic characteristics of modern and primitive wheat species in relation to ontogeny and adaptation to light. *Australian Journal of Biological Sciences*, 26: 295-307.
- Dvorak, J. (1977). Transfer of leaf rust resistance from *Aegilops speltoides* to *Triticum aestivum*. *Can. J. Genet. Cytol.*, 19: 133-141.
- Dvorak, J. (1988). Cytogenetical and molecular inferences about the evolution of wheat. In: *Proc. 7th International Wheat Genetics Symposium*, Miller, T.E. and Koebner, R.M.D. (eds). Institute of Plant Science Research, Cambridge, UK, pp. 187-192.
- Dyck, P.L. (1994). The transfer of leaf rust resistance from *Triticum turgidum* ssp. *dicoccoides* to hexaploid wheat. *Canadian Journal of Plant Science*, 74: 671-673.
- Dyck, P.L. and Kerber, E.R. (1970). Inheritance in hexaploid wheat of adult plant leaf rust resistance derived from *Aegilops squarrosa*. *Can. J. Genet. Cytol.*, 12: 175-180.
- El-Morshidy, M.A., Moseman, J.G., Nevo, E., Gerechter-Amitai, Z.K. and Zohary, D. (1983). *Triticum dicoccoides* as a source of resistance to powdery mildew and leaf rust diseases. *Agronomy Abstracts*: 62.
- Evans, L.T. (1993). *Crop Evolution, Adaptation and Yield*. Cambridge University Press, Cambridge, UK.
- Farooq, S. (1994). Wild species germplasm: A vital source for creation of genetic variability. *IPGRI WANA Newsletter*, 4: 1-2.
- Farooq, S., Niazi, M.L.K., Iqbal, N. and Shah, T.M. (1989). Salt tolerance potential of wild resources of the tribe *Triticeae*. II. Screening of species of genus *Aegilops*. *Plant and Soil*, 119: 255-260.
- Farquhar, G.D. and Richards, R.A. (1984). Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Aust. J. Plant Physiol.*, 11: 539-552.
- Fernandez-Calvin, B. and Orellana, J. (1994). Metaphase I-bound arms frequency and genome analysis in wheat-*Aegilops* hybrids. 3. Similar relationships between the B genome of wheat and S and S' genomes of *Ae. speltoides*, *Ae. longissima* and *Ae. sharonensis*. *Theor. Appl. Genet.*, 88: 1043-1049.
- Gamzikova, O.I. and Barsukova, V.S. (1996). Change in wheat resistance to heavy metals. *Russian Agricultural Sciences*, 3: 22-25.
- Gerechter-Amitai, Z.K., Silfhout, C.H. van, Grama, A. and Kleitman, E. (1989). Y15 – A new gene for resistance to *Puccinia striiformis* in *Triticum dicoccoides* sel. G-25. *Euphytica*, 43: 187-190.
- Goletti, T., Lio, N., Pace, C. di, Osler, R., Porceddu, E. and Scarascia Mugnozza, G.T. (1990). Comparison of techniques for diagnosing barley yellow dwarf virus (BYDV) in *Triticeae* for identification of sources of genetic resistance [Italian]. *Revista di Agricoltura Subtropicale e Tropicale*, 84: 367-375.
- Gorham, J. (1990). Salt tolerance in the *Triticeae*: K/Na discrimination in *Aegilops* species. *J. Exp. Bot.*, 41: 615-621.
- Hammer, K. (1980). Zur Taxonomie und Nomenklatur der Gattung *Aegilops* [German]. *Feddes Repert.*, 91: 225-258.
- Hunsal, C.S., Balikai, R.B. and Viswanath, D.P. (1990). *Triticum dicoccum*. Its performance in comparison with barley under salinity. *Journal of Maharashtra Agricultural University*, 125: 376-377.
- Hussien, T., Bowden, R.L., Gill, B.S., Cox, T.S. and Marshall, D.S. (1997). Performance of four new rust resistance genes transferred to common wheat from *Aegilops tauschii* and *Triticum monococcum*. *Plant disease*, 81: 582-586.
- Jacobs, A.S., Pretorius, Z.A., Kloppers, F.J. and Cox, T.S. (1996). Mechanisms associated with wheat leaf rust resistance derived from *Triticum monococcum*. *Phytopathology*, 86: 588-595.
- Jahier, J. and Trotter, M. (1980). Consequences of an attack of *Septoria nodorum* on the accumulation of dry matter in the grain of an accession of *Aegilops squarrosa*. *Cereal Res. Com.*, 8: 325-330.
- Kaminski, A., Austin, R.B., Ford, M.A. and Morgan, C.L. (1990). Flag leaf anatomy of *Triticum* and *Aegilops* species in relation to photosynthetic rate. *Ann. Bot.*, 66: 359-365.
- Kerber, E.R. (1987). Resistance to leaf rust in hexaploid wheat: *Lr32* a third gene derived from *Triticum tauschii*. *Crop Sci.*, 27: 204-206.
- Kerber, E.R. and Dyck, P.L. (1969). Inheritance in hexaploid wheat of leaf rust resistance and other characters derived from *Aegilops squarrosa*. *Can. J. Genet. Cytol.*, 11: 639-647.
- Kerby, K. and Kuspira, J. (1988). Cytological evidence bearing on the origin of the B genome in polyploid wheats. *Genome*, 30: 36-43.
- Knott, D.R. and Zang, H.T. (1990). Leaf rust resistance in durum wheat and its relatives. In: *Wheat Genetic Resources: Meeting Diverse Needs*, Srivastava, J.P. and Damania, A.B. (eds). John Wiley and Sons, Chichester, UK, pp. 311-316.
- Limin, A.E. and Fowler, D.B. (1981). Cold hardiness of some wild relatives of hexaploid wheat. *Can. J. Bot.*, 59: 572-573.
- Liu, Y.L., Zhang, R.Z. and Mannuti, M. (1996). Evaluation of natural tolerance and resistance of wheat varieties to *Diuraphis noxia* [Chinese]. *Plant Protection*, 22: 23-24.

- Ma, H. and Hughes, G.R. (1993). Resistance to *Septoria nodorum* blotch in several *Triticum*. *Euphytica*, 70: 151-157.
- Ma, H., Singh, R.P. and Mujeeb-Kazi, A. (1997). Resistance to stripe rust in durum wheats, A-genome diploids, and their amphiploids. *Euphytica*, 94: 279-286.
- Makkouk, K.M., Comeau, A. and Ghulam, W. (1994). Resistance to barley yellow dwarf luteovirus in *Aegilops* species. *Can. J. Plant. Sci.*, 74: 631-634.
- Malinski, K., Donchev, N., Iliev, I., Stoyanov, I. and Mihova, S. (1984). Study of resistance of wheat lines obtained by remote hybridization to rusts and powdery mildew [Bulgarian]. *Rasteniev' Dni Nauki*, 21: 148-155.
- Mamluk, O.F. and Van Slageren, M.W. (1994). Sources of resistance to wheat diseases in *Aegilops* and *Amblyopyrum* spp. In: *Proc. 9th Congress of the Mediterranean Phytopathological Union*. Kusadasi, Turkey, pp. 269-270.
- McIntosh, R.A. (1988). Catalogue of gene symbols for wheat. In: *Proc. 7th International Wheat Genetics Symposium*, Miller, T.E. and Koebner, R.M.D. (eds). Cambridge University Press, Cambridge, UK, pp. 1225-1324.
- McIntosh, R.A., Hart, G.E., Devos, K.M., Rogers, J. and Gale, M.D. (1998). Catalogue of gene symbols for wheat: 1998 supplement. *Wheat Information Service*, 86: 54-91.
- McIntosh, R.A., Hart, G.E. and Gale, M.D. (1991). Catalogue of gene symbols for wheat: 1991 supplement. *Wheat Inf. Serv.*, 73: 40-57.
- McIntosh, R.A., Miller, T.E. and Chapman, V. (1982). Cytogenetical studies in wheat. XII. *Lr28* for resistance to *Puccinia recondita* and *Sr34* for resistance to *Puccinia graminis tritici*. *Z. Pflanzenzüchtg*, 89: 295-306.
- Miginiac-Maslow, M., Hoarua, A. and Moyses, A. (1979). Hill reaction studies with protoplasts from cultivated wheat and their wild relatives. *Z. Pflanzenphysiol. Bd.*, 95: 95-104.
- Mihova, S. (1988). Sources of resistance to yellow rust (*Puccinia striiformis* West.) in the genus *Triticum* [Bulgarian]. *Rasteniev' Dni Nauki*, 25: 3-8.
- Miller, T.E., Reader, S.M., Ainsworth, C.C. and Summers, R.W. (1988). The introduction of a major gene for resistance to powdery mildew of wheat, *Erysiphe graminis* f. sp. *tritici*, from *Ae. speltoides* into wheat to integrated cereal production. In: *Proc. EUCARPIA Cereal Section Meeting*. Pudoc, Wageningen, The Netherlands, pp. 179-183.
- Mishra, P.C., Kurmwanshi, S.M. and Soni, S.N. (1996). Evaluation of *Triticum* species under wheat improvement programme. *Journal of Soils and Crops*, 6: 200-201.
- Morant-Avice, A., Jurvilliers, P. and Coudret, A. (1994). Stomatal movements and gas exchanges of a triticale and its parental species in water-stress conditions. *Agronomie*, 14: 113-120.
- Nevo, E., Krugman, T. and Beiles, A. (1993). Genetic resources for salt tolerance in the wild progenitor of wheat (*Triticum dicoccoides*) and barley (*Hordeum spontaneum*) in Israel. *Plant Breeding*, 110: 338-341.
- Pietro, J.P. di, Caillaud, C.M., Chaubet, B., Pierre, J.S. and Trottet, M. (1998). Variation in resistance to the grain aphid, *Sitobion avenae* (*Sternorhynca: Aphididae*) among diploid wheat genotypes: multivariate analysis of agronomic data. *Plant Breeding*, 117: 407-412.
- Raupp, W.J., Amri, A., Hatchett, J.H., Gill, B.S., Wilson, D.L. and Cox, T.S. (1993). Chromosomal location of Hessian fly resistance genes *H22*, *H23* and *H24* derived from *Triticum tauschii* in the D genome of wheat. *Hereditas*, 84: 142-145.
- Raupp, W.J., Gill, B.S., Browder, L.E., Harvey, T.L., Hatchett, J.H. and Wilson, D.L. (1988). Genetic diversity in wheat relatives for disease and insect resistance. In: *Proc. 7th International Wheat Genetics Symposium*, Miller, T.E. and Koebner, R.M.D. (eds). Cambridge University Press, Cambridge, UK, pp. 879-884.
- Rayburn, A.L. and Gill, B.S. (1987). Molecular analysis of the D genome of the *Triticeae*. *Theor. Appl. Genet.*, 73: 358-388.
- Rees, D., Ruis Ibarra, Acevedo, E., Mujeeb-Kazi, A. and Villareal, R.L. (1994). *Photosynthetic characteristics of synthetic bread wheats*. CIMMYT Wheat Special Report No. 28, Mexico D.F.
- Rees, D., Sayre, K., Acevedo, E., Nava Sanchez, T., Lu, Z., Zeiger, E. and Limon, A. (1993). *Canopy temperatures of wheat: Relationship with yield and potential as a technique for early generation selection*. CIMMYT Wheat Special Report No. 10, Mexico D.F.
- Rekika, D., Monneveux, P. and Havaux, M. (1997). The *in vivo* tolerance of photosynthetic membranes to high and low temperatures in cultivated and wild wheats of the *Triticum* and *Aegilops* genera. *Journal of Plant Physiology*, 6: 734-738.
- Rekika, D., Nachit, M.M., Araus, J.L. and Monneveux, P. (1998a). Effects of water deficit on photosynthetic rate and osmotic adjustment in tetraploid wheats. *Photosynthetica*, 35: 129-138.
- Rekika, D., Zaharieva, M., Stankova, P., Xu, X., Souyris, I. and Monneveux, P. (1998b). Abiotic stress tolerance in *Aegilops* species. In: *Durum Wheat SEWANA Workshop*, Nachit, M.M., Baum, M., Porceddu, E., Monneveux, P. and Picard, E. (eds). ICARDA, Aleppo, Syria, pp. 113-128.

- Riley, R., Chapman, V. and Johnson, R. (1968). Introduction of yellow rust resistance of *Aegilops comosa* into wheat by genetically induced homeologous recombination. *Nature*, 217: 378-384.
- Rivoal, R., Doussinault, G. and Jahier, J. (1986). Résistance au développement d'*Heterodera avenae* Woll. chez différentes espèces de *Triticum* [French]. *Agronomie*, 6: 759-765.
- Robinson, J. and Skovmand, B. (1992). Evaluation of emmer wheat and other *Triticeae* for resistance to Russian wheat aphid. *Genetic Resources and Crop Evolution*, 39: 159-163.
- Saur, L. (1991). In search of sources of resistance to head blight caused by *Fusarium culmorum* in wheat and related species. *Agronomie*, 11: 535-541.
- Sawhney, R.N. and Goel, L.B. (1979). Stem rust resistance in accessions of *Triticum timopheevi* and three *Triticum aestivum* lines with resistance from *timopheevi*. *Wheat Information Service*, 50: 56-58.
- Sayed, H.I. (1985). Diversity of salt tolerance in a germplasm collection of wheat (*Triticum* ssp.). *Theor. Appl. Genet.*, 69: 651-657.
- Sears, E.R. (1956). The transfer of leaf rust resistance from *Aegilops umbellulata* to wheat. In: *Genetics in Plant Breeding, Brookhaven Symposium in Biology*, 9: 1-22.
- Shi, A.N., Leath, S. and Murphy, J.P. (1998). A major gene for powdery mildew resistance transferred to common wheat from wild einkorn wheat. *Phytopathology*, 88: 144-147.
- Simeone, R., Sciancalepore, A. and Simonetti, M.C. (1998). Identification of powdery mildew resistance genes in tetraploid wheats. *Ewac Newsletter*, pp. 110-113.
- Sinha, S.K. and Bansal, K.C. (1991). Evaluation of drought tolerance of *Triticum aestivum* and related species under field conditions. In: *Physiology-Breeding of Winter Cereals for Stressed Mediterranean Environments*, Acevedo, E., Conesa, A.P., Monneveux, P. and Srivastava, J.P. (eds). INRA-ICARDA, pp. 255-269.
- Soshnikova, E.A. (1990). Promising species of *Triticum* for the production of donors of resistance to stem rust of wheat [Russian]. *Nauchno-tekhnicheskii Byulleten' Vsesoyuznogo Ordena Lenina i Ordena Druzhby Narodov Nauchno-issledovatel'skogo Instituta Rastenievodstva Imeni N.I. Vavilova*, 197: 4-5.
- Stankova, P., Rekika, D., Zaharieva, M. and Monneveux, P. (1995). Improvement of durum wheat for multiple stress tolerance: Potential interest of *Aegilops* sp. In: *Fibre and Cereal Crops Problems*. Cotton and Durum Wheat Research Institute, Chirpan, Bulgaria, pp. 46-56.
- Storey, R., Graham, R.D. and Shepherd, K.W. (1985). Modification of the salinity response of wheat by the genome of *Elytrigia elongata*. *Plant and Soil*, 83: 327-330.
- Sun, G.L., Fahima, T., Korol, A.B., Turpeinen, T., Grama, A., Ronin, Y.I. and Nevo, E. (1997). Identification of molecular markers linked to the Yr15 stripe rust disease resistance gene originated in wild emmer wheat, *Triticum dicoccoides*. *Theor. and Applied Genet.*, 95: 622-628.
- Tomerlin, J.R., El-Morshidy, M.A., Moseman, J.G., Baenziger, P.S. and Kimber, G. (1984). Resistance to *Erysiphe graminis* f. sp. *tritici*, *Puccinia recondita* f. sp. *tritici* and *Septoria nodorum* in wild *Triticeae* species. *Plant disease*, 68: 10-13.
- Tsunewaki, K. (1980). *Genetic Diversity of the Cytoplasm in Triticum and Aegilops*. Japan Soc. Prom. Sc., Tokyo, Japan.
- Tyler, J.M., Webster, J.A. and Merkle, O.G. (1987). Designations for genes in wheat germplasm conferring greenbug resistance. *Crop Sci.*, 27: 526-527.
- Valkoun, J., Kucerova, D. and Bartos, P. (1989). Transfer of a new gene for stem rust resistance from *T. monococcum* L. to hexaploid wheat, *T. aestivum* L. *Sbornik Uvtiz, Genetika a Sletchteni*, 25: 209-214.
- Van Slageren, M.W. (1994). *Wild Wheats: A Monograph of Aegilops L. and Amblyopyrum (Jaub and Spach) Eig (Poaceae)*. Agricultural University, Wageningen/ICARDA, Aleppo.
- Waines, J.G. (1994). High temperature in wild wheats and spring wheats. *Australian Journal of plant Physiology*, 21: 705-715.
- Waines, J.G., Rafi, M.M. and Ehdaie, B. (1993). Yield components and transpiration efficiency in wild wheats. In: *Biodiversity and Wheat Improvement*, Damania A.B. (ed.). John Wiley and Sons, Chichester, UK, pp. 173-186.
- Xiang, Q.J., Sheng, B.Q., Duan, X.Y. and Zhou, Y.L. (1996). The analysis of effective wheat powdery mildew resistance genes of some breeding lines [Chinese]. *Acta, Agronomica Sinica*, 22: 741-744.
- Xu, X., Monneveux, P., Damania, A.B. and Zaharieva, M. (1993). Evaluation for salt tolerance in genetic resources of *Triticum* and *Aegilops*. *Plant Genetic Resources Newsletter*, 96: 11-16.
- Yamaleev, A.M., Dolotovskii, I.M. and Noikonov, V.I. (1989). Relationship between resistance of wheat root rots and genome composition [Russian]. *Doklady Vsesoyuznoi Ordena Lenina i Ordena Trudovogo Krasnogo Znamenii Akademii Sel'skhozyaistvennykh Nauk Imeni V.I. Lenina*, 6: 4-6.
- Yu, M.Q., Person-Dedryver, F. and Jahier, J. (1990). Resistance to root knot nematode, *Meloidogyne naasi* (Franklin) transferred from *Aegilops variabilis* Eig. *Agronomie*, 6: 451-456.

- Yu, B.S. and Sun, G.R. (1995). Preliminary study of several spring wheat varieties for resistance to *Septoria* diseases [Chinese]. *Crop Genetic Resources*, 1: 27-29.
- Zhang, X., Zhong, S.B. and Yao, J.X. (1997). Cytological and powdery mildew resistance analyses of common wheat x *Triticum araraticum* hybrids and their progenies [Chinese]. *Jiangsu Journal of Agricultural Sciences*, 13: 185-187.