***Aegilops sharonensis*: Origin, genetics, diversity, and potential for wheat improvement**

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Abstract: *Aegilops sharonensis* Eig (Sharon goatgrass; section *Sitopsis*) is an annual diploid grass species growing endemically in the coastal plains of Israel and southern Lebanon. It is a wild relative of wheat, with a genome closely related to the B genome of cultivated bread wheat. With the most limited distribution of any species in the genus *Aegilops*, *Ae. sharonensis* is rapidly losing its habitats, owing to the combined effects of modern agricultural intensification and expansion of urban and industrial areas. *Aegilops sharonensis* is known to be a rich source of genes providing resistance to important wheat diseases and abiotic stresses, but it has not been widely exploited. The presence of gametocidal genes that control preferential transmission of chromosome 4S^{sh} increases the difficulty of introgressing genes from *Ae. sharonensis* into wheat. However, successful introgression of the genes for resistance to leaf rust, stripe rust, and powdery mildew has been achieved. Studies on genetic and phenotypic diversity indicated that *Ae. sharonensis* is a highly diverse species, comparable with others that have a wider geographic distribution and more variable environments. Targeting the regions and sites with the highest diversity in *Ae. sharonensis* will facilitate the capture of the greatest variability and also the identification of novel and diverse genes for wheat improvement.

Key words: wild wheat, wheat improvement, diversity.

Résumé : L'égilope de Sharon (*Aegilops sharonensis* Eig; section *Sitopsis*) est une espèce herbacée diploïde annuelle venant à l'état endémique dans les plaines côtières d'Israël et du sud du Liban. C'est une espèce sauvage apparentée au blé pourvue d'un génome étroitement apparenté au génome B du blé à pain cultivé. Ayant la distribution la plus limitée de toutes les espèces du genre *Aegilops*, l'*Ae. sharonensis* perd rapidement ses habitats sous les effets combinés de l'intensification de l'agriculture moderne et l'expansion des surfaces urbaines et industrielles. L'*Ae. sharonensis* constitue une source importante et diversifiée de gènes de résistance contre des maladies importantes du blé et ses stress abiotiques, mais n'a pas été mise en valeur. La présence de gènes gamétocides qui contrôlent la transmission préférentielle du chromosome 4S^{sh} augmente la difficulté de l'introgression des gènes de l'*Ae. sharonensis* dans le blé. Cependant, l'introgression des gènes de résistance à la rouille foliaire, à la rouille striée et au mildiou poudreux a été réalisée. Les études sur la variation génétique et phénotypique indiquent que l'*Ae. sharonensis* constitue une espèce fortement diversifiée comparable à d'autres, mais avec une distribution géographique plus étendue et des environnements plus variables. Il importe de cibler les régions et les sites montrant la plus forte diversité chez l'*Ae. sharonensis*, afin de conserver la plus grande variabilité et également d'identifier des gènes nouveaux et diversifiés pour l'amélioration du blé.

Mots-clés : blé sauvage, amélioration du blé, diversité.

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Introduction

Bread wheat (*Triticum aestivum* L.) is one of the world's most important food crops, providing nearly 20% of the calories consumed by people worldwide (Wiese 1987). It is also the most widely planted crop in the world, being cultivated on over 217 million hectares (Food and Agriculture Organization of the United Nations (FAO) 2008). The loss

of important genetic diversity, owing to intensive breeding, coupled with the expansion of cultivation into marginal areas, have made the wheat crop increasingly vulnerable to various biotic and abiotic stresses. Wild wheats and their relatives are important sources of genetic diversity for cultivated wheat improvement, contributing many genes for resistance to both biotic and abiotic stresses (Sharma 1995; Schneider et al. 2008). Thousands of accessions of wild wheats and their relatives have been collected and stored in gene banks around the world (van Slageren 1994), but only a few species have been well characterized and extensively used for wheat improvement (Hajjar and Hodgkin 2007). *Aegilops* is the genus most closely related to *Triticum*. One of the least studied species in this genus is *Aegilops sharonensis* Eig (common name: Sharon goatgrass). *Aegi-*

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lops sharonensis has a very narrow geographic range (coastal plains of Israel and southern Lebanon), and its remaining populations are being threatened by increasing urban and agricultural development. Information on the biology, genetics, and diversity of *Ae. sharonensis* is important for conserving populations of the species and utilizing them for wheat improvement. The purpose of this paper is to review the current literature on *Ae. sharonensis* and the potential of this species for facilitating wheat improvement.

Name and taxonomy

AEGILOPS SHARONENSIS EIG: Common name, Sharon goatgrass.

ETYMOLOGY: *Aegilops* is the ancient Greek name for *aigilops* (αιγιλωψ), a long awned and bearded grass. Discorides applied it to describe an ulcer or fistula in the inner angle of the eye. *Aigilos* is also an herb consumed by goats. The ancient Latin name for *aegilops* is derived from *aegilopa* and *opis*, which describe an eye disease (Quattrocchi 2000). *Sharonensis* refers to the Sharon Plain in Palestine (a coastal plain in Israel), where the species was first described (Eig 1928a).

DESCRIPTION: The taxonomic classification of *Ae. sharonensis* is as follows: Order *Poales* (Small 1903, Flora of the South-eastern United States); Family *Poaceae* Barnhart 1895, Bull. Torrey Bot. Club 22:7), nom. cons. alt.: Gramineae Juss.; Subfamily *Pooideae*; Macfarlane and Watson 1980, Taxon 29: 646 Supertribe *Triticanae* T. D. Macfarlane and Watson, 1982, Taxon 31:192 Tribe, *Triticeae* Dumortier 1824, Observ. Gramin. Belg. 84 Subtribe *Triticinae* Grisebach 1846, Spic. Fl. Rumel. 2(5/6): 422 (1846); Genus *Aegilops* L. Sp. Pl. (ed. 1) 2:1050 (1753); Section *Sitopsis* (Jaub. and Spach 1850–1853) Zhuk. Jaubert & Spach, Ill. Pl. Orient. 10–23 (1850–51).

Aegilops is the most closely related genus to *Triticum* (Kimber and Feldman 1987; Jiang et al. 1994) and comprises 22 species that include diploid, tetraploid, and hexaploid genomes (van Slageren 1994). The section *Sitopsis* (SS genome; S for *Sitopsis*) includes four other diploid species in addition to *Ae. sharonensis*: *Aegilops bicornis* (Forsskål) Jaub. & Spach, *Aegilops longissima* (Schweinf. & Muschl. in Muschl.) Eig, *Aegilops searsii* Feldman & Kislev ex K. Hammer, and *Aegilops speltoides* Tausch. (van Slageren 1994). Based on the presence or absence of awns, *Ae. sharonensis* var. *typica* and *Ae. sharonensis* var. *mutica* are distinguished, respectively. The first description of *Ae. sharonensis* was by Zhukovsky (1928) and Eig (1928a). Since that time, the scientific name and species status of *Ae. sharonensis* have changed on several occasions according to the different taxonomic revisions of the *Triticeae* (Table 1). Zhukovsky (1928) considered *Ae. sharonensis* as a subspecies of *Ae. longissima* and named it *Ae. longissima* subsp. *aristata* Zhuk. var. *polycarpa* Zhuk. However, Eig (1928a) first described *Ae. sharonensis* as a race of *Ae. bicornis*, and named it *Ae. bicornis* (Forssk.) Jaub. & Spach. var. *major* Eig. The same year, Eig (1928b) assigned the plant a species status and named it *Ae. sharonensis* Eig. Bowden (1959) merged the entire genus of *Aegilops* with *Triticum*, based on the occurrence of spontaneous hybridization and the production of allopolyploids between species of both genera. He considered *Ae.*

sharonensis as a subspecies of *T. longissimum* (*Triticum longissimum* (Schweinf. & Muschl. in Muschl.) Bowden subsp. *sharonensis* Eig). This merging of the two genera was accepted by Morris and Sears (1967), Kimber and Sears (1987), and Kimber and Feldman (1987), but all of these investigators considered *T. sharonense* as a separate species, named *Triticum sharonense* (Eig) Feldman & Sears. Chennaveeraiah (1960) transferred the section *Sitopsis* from the genus *Aegilops* to the genus *Triticum* based on karyomorphology and plant morphology. Under this new classification, *Ae. sharonensis* was considered to be a subspecies of *T. longissimum* and was named *T. longissimum* (Schweinf. & Muschl.) Bowden subsp. *sharonensis* (Eig) Cheenav. Twenty years later, Hammer (1980) published a complete taxonomic review of *Aegilops* and *Amblyopyrum*. He considered *Sitopsis* to be a subgenus of *Aegilops* L., and classified *Ae. sharonensis* as a subspecies of *Ae. longissima* (*Ae. longissima* Schweinf. & Muschl. subsp. *sharonensis* (Eig) Hammer). Following a different approach, Löve (1984) reorganized the tribe *Triticeae* into a genus based on genome composition. Under his taxonomical revision, *Sitopsis* was considered to be a genus that included five diploid species carrying the S genome. *Aegilops sharonensis* was named *Sitopsis sharonensis* (Eig) A. Löve. Finally, van Slageren (1994) introduced the latest taxonomic revision of the *Triticeae*, where *Aegilops* and *Triticum* are considered as separate genera; the genus *Aegilops* was divided into five sections and *Ae. sharonensis* was placed in the section *Sitopsis*.

History and origin of *Aegilops sharonensis*

In his first description of *Ae. sharonensis*, Eig (1928a) considered the species as a “climatic race” of *Ae. bicornis*, another diploid species of the *Sitopsis* that grows along the Mediterranean coast of Libya, Egypt, and the Negev desert in Israel (Kimber and Feldman 1987). The morphological similarities between the two species led Eig (1928a) to conclude that *Ae. sharonensis* was just a race of *Ae. bicornis* with larger plants owing to the higher relative precipitation in the Sharon Plain of Israel compared with the more xeric environments where the latter species grows. However, in his second publication, Eig (1928b) recognized *Ae. sharonensis* as a separate species. This taxonomic change was based on a re-examination of morphological characters of the species, extensive knowledge about its geographic distribution and edaphic requirements, and the absence of hybrid populations or intermediate forms in the distribution borders of *Ae. sharonensis* and *Ae. bicornis*.

Sears (1948) described *Ae. sharonensis* as taxonomically very close to *Ae. longissima*, but considered them as separate species. Kihara (1954), Tanaka (1955), and Roy (1959) studied the fertility and chromosome pairing of hybrids between these species. The authors observed the regular occurrence of five bivalents and one tetravalent at meiosis in hybrids, indicating that *Ae. sharonensis* and *Ae. longissima* differ by a reciprocal translocation. They also reported the hybrid plants as vigorous, showing intermediate characters between the two parents and having high pollen- and seed-fertility. Based on these results, the three authors considered *Ae. sharonensis* as a variety of *Ae. longissima* and assigned the two taxa the same genome formula (S^1 , ($1 = longissima$)).

Table 1. Summary of the taxonomic classifications of *Aegilops sharonensis*.

Year	Author(s)	Classification
1928	Zhukovsky	<i>Aegilops longissima</i> (Schweinf. & Muschl.) ssp. <i>aristata</i> Zhuk. var. <i>polycarpa</i> Zhuk.
1928	Eig	<i>Aegilops bicornis</i> (Forssk.) Jaub. & Spach. var. <i>major</i> Eig
1928	Eig	<i>Aegilops sharonensis</i> Eig
1959	Bowden	<i>Triticum longissimum</i> (Schweinf. & Muschl. in Muschl.) Bowden subsp. <i>sharonensis</i> Eig
1960	Chennaveeraiah	<i>Triticum longissimum</i> (Schweinf. & Muschl.) Bowden subsp. <i>sharonensis</i> (Eig) Cheenav.
1980	Hammer	<i>Aegilops longissima</i> Schweinf. & Muschl. subsp. <i>sharonensis</i> (Eig) Hammer
1984	Löve	<i>Sitopsis sharonensis</i> (Eig) A. Löve
1987	Kimber and Feldman	<i>Triticum sharonense</i> (Eig) Feldman & Sears
1994	van Slageren	<i>Aegilops sharonensis</i> Eig

The occurrence of a reciprocal translocation between the distal regions of chromosome arms 4S¹ and 7S¹ in *Ae. longissima* was later confirmed by Friebe et al. (1993). This translocation is not present in *Ae. sharonensis* and the other species of the *Sitopsis*. Although other taxonomists and cytogeneticists (Bowden 1959; MacKey 1968) adopted this classification, contrary evidence was forwarded by other authors. Ankori and Zohary (1962) studied the morphology and cytology of natural and artificial hybrids between *Ae. sharonensis* and *Ae. longissima*. They described both species as morphologically well-differentiated in nature and apparently separated by seasonal and ecological factors for natural hybridization and, therefore, treated them as different species. Based on morphological and ecological differences, Kimber and Feldman (1987) also considered *Ae. sharonensis* as a species separate from *Ae. longissima*. Using the C-banding pattern of metaphase cells, Teoh and Hutchinson (1983) observed that *Ae. sharonensis* and *Ae. longissima* share some similarities, but their differences are large enough to warrant treatment as different species. They assigned *Ae. sharonensis* the S^{sh} (sh = *sharonensis*) genome formula.

Waines and Johnson (1972) found that the electrophoretic pattern of ethanol-extracted seed proteins of *Ae. sharonensis* was intermediate between *Ae. longissima* and *Ae. bicornis*. The authors concluded that *Ae. sharonensis* is genetically different from these two species and should be considered a separate species with the S^{sh} genome formula. They also suggested that *Ae. sharonensis* may have originated from a segregant of a hybrid between *Ae. longissima* and *Ae. bicornis*. In an attempt to test this hypothesis, Waines (1978) produced hybrids between *Ae. longissima* and *Ae. bicornis*. F₁ hybrids were fertile, but derived F₃ plants were morphologically more similar to the F₁ hybrid than to *Ae. sharonensis*. Considering these results, Waines et al. (1982) concluded that although the hybrid hypothesis is still a possibility, the independent evolution of *Ae. sharonensis* from *Ae. bicornis*, *Ae. longissima*, or an ancestral *Aegilops* stock also should be considered. From a study of allelic variation in 20 electrophoretically discernable enzyme loci, Brody and Mendlinger (1980) found very close relationships among the three species *Ae. sharonensis*, *Ae. longissima*, and *Ae. bicornis*. The authors also supported the idea of *Ae. sharonensis* as a valid species. Moreover, by evaluating 16 water soluble leaf proteins, Mendlinger and Zohary (1995) found *Ae. sharonensis* equally close to *Ae. longissima* and *Ae. bicornis* and defined *Ae. sharonensis* as a true species. Asins and Carbonell (1986b) studied the variation of peroxidases and phosphatases in *Aegilops* species and also found close relationships among *Ae. sharonensis*, *Ae. longissima*, and *Ae. bicornis*.

Based on their results, the previously reported similarities found between *Ae. sharonensis* and *Ae. bicornis* by Tanaka (1955), and the presence of reciprocal translocations between both species and *Ae. longissima* (Tanaka 1955; Kimber 1961), Asins and Carbonell (1986b) suggested that *Ae. sharonensis* and *Ae. bicornis* may have independently originated from *Ae. longissima*. Studies of the 5S short- and long-spacer sequences and ITS sequence of ribosomal RNA genes also indicated very close relationships among *Ae. sharonensis*, *Ae. longissima*, and *Ae. bicornis* (Kellogg and Appels 1995; Kellogg et al. 1996). This result is in agreement with Huang et al. (2002a; 2002b), who reported that these three species formed one clade in their analysis of the origin and evolution of the *Acc-1* (plastid acetyl-CoA carboxylase) and *Pgk-1* (plastid 3-phosphoglycerate kinase) genes in *Triticum* and *Aegilops* species.

Yen and Kimber (1990) studied the genomic relationship of *Ae. sharonensis* with *Ae. longissima*, *Ae. bicornis*, and *Ae. speltoides* through the analysis of meiotic pollen mother cells in F₁ hybrids between *Ae. sharonensis* and the other species of the section *Sitopsis*. Their results suggested a close and equidistant relationship between *Ae. sharonensis* and both *Ae. longissima* and *Ae. speltoides*, but a comparatively more distant one to *Ae. bicornis*. This result is in conflict with many later studies made to reconstruct the phylogenetic relationships in *Triticum* and *Aegilops* species and to uncover the origin of hexaploid wheat based on genomic (Jaaska 1978; Talbert et al. 1991; Dvorak and Zhang 1992; Sasanuma et al. 1996; Dvorak et al. 1998; Giorgi et al. 2002; Petersen et al. 2006; Salina et al. 2006; Kilian et al. 2007; Wang et al. 2007; Goryunova et al. 2008), mitochondrial (Terachi and Tsunewaki 1992; Wang et al. 1997), chloroplast (Wang et al. 1997; Provan et al. 2004; Yamane and Kawahara 2005) and ribosomal (Zhang et al. 2002; Salares and Brown 2004) DNA. All of these studies showed a very close relationship between *Ae. sharonensis* and *Ae. longissima* (the shortest distance found for any pair of species) with *Ae. speltoides* as a divergent species that does not form a monophyletic cluster with these or the other two species of the section *Sitopsis*.

Raskina et al. (2004) proposed that *Ae. sharonensis* is a derivative of *Ae. speltoides* adapted for new edaphic (light and sandy soils) and climatic environments and originating through quantum speciation. To test their hypothesis, the authors studied the changes in rRNA-encoding DNA (rDNA) patterns of genotypes from two isolated populations of *Ae.*

speltoides and *Ae. sharonensis*. They found that several genotypes exhibited an intermediate rDNA pattern between *Ae. speltoides* and *Ae. sharonensis*. They excluded the possibility of an origin through natural hybridization between both species (owing to seasonal and mating system isolation) and proposed a speciation process by repatterning of ribosomal RNA (movement of rDNA clusters to a new site with subsequent stabilization) and colonization of new environments by the stabilized adaptive form. A close relationship between *Ae. sharonensis* and *Ae. speltoides* also was reported by Gong et al. (2006) in their study of genomic evolution in the genus *Aegilops* based on 31 inter-simple sequence repeat (ISSR) markers. In this study, *Ae. sharonensis* and *Ae. speltoides* exhibited a high genetic similarity and clustered together in a branch separated from the other species of the *Sitopsis*. This result indicates that the genomic constitution of both species is very similar.

Morphology and life cycle

Descriptions of the morphology and life cycle of *Ae. sharonensis* are based on the publications of Eig (1929), Waines et al. (1982), Witcombe (1983), Kimber and Feldman (1987), van Slageren (1993, 1994), and Olivera (2008). *Aegilops sharonensis* is a grass that initially grows with a prostrate habit (geniculate stems), after which the stems turn upright reaching a height of 40–100 cm at maturity. Under natural conditions, plants produce just a few stems, usually ranging from three to six. However, taller plants (130–140 cm) with 15 to 30 stems have been observed at sites with heavier soil types (e.g., Rishon LeZiyyon area, southeast of Tel Aviv) (P. Olivera, unpublished data). Stems have a variable number of nodes that range from 3 to 10. Leaves are mainly basal, but some can cover up to three quarters or the entire length of a culm. Leaves are mostly hirsute, but some glabrous leaves have been reported. Leaf margins are ciliate, mainly in the basal part of the stem. Leaf blades are linear, 1–20 cm long, and 0.1–0.8 cm wide. The leaf sheath has a short membranous ligule and can be ciliate or glabrous. *Aegilops sharonensis* has a two-rowed spike 7–20 cm long (Fig. 1A). Spikes are broad-linear, flattened, and narrowed to some extent in the basal and apical extremes. The spike has a zig-zag rachis that disarticulates at maturity into 8–18 spikelets (only the basal spikelet remains attached to the rachis). The apical spikelet is horizontally rotated at a 90° angle compared with all those below it. Spikelets are elliptical to linear, slightly flattened, and 0.8–1.3 cm long (Fig. 1B). Each spikelet consists of three to five florets with the upper two florets always sterile. Spikes usually have awned terminal lemmas (*Ae. sharonensis* var. *typica*), but awnless forms (*Ae. sharonensis* var. *mutica*) also exist (Fig. 1C). Glumes are coriaceous, elliptical, 6–7 mm long and 2.5 mm wide with two teeth, one of which is sometimes elongated. Glumes have six to eight parallel veins that are narrow, rough, and yellowish (Figs. 1F and 1G). Terminal lemmas are boat-shaped or elliptical, 8–11 mm long, five-veined, and awned (Fig. 1D). Awns are narrow, triangular, three-veined with the middle vein markedly separated from the laterals by wide furrows, setulose, and with two short lateral teeth at either side of the base. Awns are most developed on terminal spikelets (3–9 cm) and least developed (0.4–0.8 cm) or absent in lower spike-

lets. Paleas are boat-shaped, 0.8–1.1 cm long, and with two keels (Fig. 1E). The caryopsis adheres to the lemma and palea when mature (Fig. 1H).

Aegilops sharonensis is morphologically similar to *Ae. bicornis* and *Ae. longissima* (Eig 1929), and the metrics of its main morphological characters (e.g., plant height, spike length, spikelet number) lie between both of the related species (Waines et al. 1982). The characters that *Ae. sharonensis* shares with *Ae. bicornis* are as follows: two-rowed spikes, awns in all the spikelets, spike disarticulation into single spikelets, and the shape of the lemmas (Eig 1929). However, the former can be distinguished from the latter species by its larger plant organs, less compact spike, and two-dentate glume with more veins. Extreme forms of *Ae. sharonensis* share similarities with *Ae. longissima*, including large and almost single-rowed spikes, and highly developed awns in terminal spikelets (Eig 1928b). These similarities occur mostly where both species share the same habitat or are found in close proximity to each other (Eig 1929).

Aegilops sharonensis is an annual grass that flowers between March and June (Feinbrun-Dothan 1986; van Slageren 1994) in its native habitat, depending on soil type and water availability. Full maturity occurs between May and June. In a field evaluation, Brody (1983) reported a heading date ranging from 93 to 111 d after planting, making *Ae. sharonensis* the second earliest heading species of the *Sitopsis*. Brody (1983) suggested that earliness traits (i.e., heading date and anthesis date) are related to the ecogeographical habitat occupied by the species. This is why *Ae. bicornis* (present in southern and xeric habitats) is the earliest heading species, followed by *Ae. sharonensis* (coastal plains of Israel). Flowering time starts 2 weeks earlier and seeds mature one month earlier in *Ae. bicornis* than *Ae. sharonensis* (Eig 1929). Species with wider geographical distributions than *Ae. sharonensis*, such as *Ae. speltoides* and *Ae. longissima*, have the latest heading time among members of the *Sitopsis*. *Aegilops longissima* starts flowering 2 weeks later than *Ae. sharonensis* and ripens about one month later (Eig 1929; Ankori and Zohary 1962).

Ecology and geographic distribution

Aegilops sharonensis grows in a very limited geographical area — the most limited distribution of any species in the genus *Aegilops* (Eig 1928b). It originated in, and appears to be endemic to, the coastal plains of Israel and southern Lebanon (south of the Letani River) (Auerbach and Schmida 1985; Feinbrun-Dothan 1986; Feinbrun-Dothan and Danin 1991; van Slageren 1994) in an area that extends about 200 km from north to south and no more than 15 km east from the Mediterranean Sea (Fig. 2). *Aegilops sharonensis* occurs in dense stands in sandy soils, well-drained sandy loams with weathered marine dilluvial rocks (kurkar rocks), and consolidate sand dunes (Eig 1928b; Post 1933; Witcombe 1983; Kimber and Feldman 1987) (Fig. 3). It is commonly found in open parks, small woodlands, roadsides, and abandoned fields (Zohary and Orshan 1959) (Fig. 3).

Early publications (Eig 1928b, 1929; Post 1933) described a few locations where *Ae. sharonensis* was found and (or) collected in Israel (e.g., Be'er Ya'akov, Tel Aviv, Herzliyya, Arsuf, Binyamina, Caesarea, Hadera, and Haifa). Millet et

Fig. 1. Spike morphology of *Aegilops sharonensis*. (A) Green (left) and mature (right) spikes (1.5×); (B) spikelet with three fertile flowers (2.5×); (C) awnless (left) and awned (right) spikelet (1.5×); (D) lemmas of floret (3×); (E) palea and immature ovary of floret (4×); (F and G) glumes (4×); (H) seeds (3×).

al. (2006) conducted a comprehensive survey across the coastal plains of Israel to determine the distribution of *Ae. sharonensis* and describe its ecological habitats. They characterized 42 major sites across 170 km from Tel-Katifa (Gaza Strip) in the south to the basin of Na'aman River in the north. Millet et al. (2006) described the populations as abundant stands distributed in the form of islands of variable

size, growing only on stabilized sand dunes and sandy loams. Kutiel and Danin (1987) and Kutiel (1998) considered stable sandy plains as typical sites for *Ae. sharonensis*. These soils have higher organic matter, fine texture particles, and water content than the shifting sands or semi-stable sand dunes. Little is known about the distribution of *Ae. sharonensis* in Lebanon, because information is only

Fig. 2. Map of Israel and southern Lebanon showing the geographic distribution of *Aegilops sharonensis*.

available from a few specimens in different herbaria collections: one from Tyre (viewed by P. Olivera and E. Millet), one from North of Tyre (van Slageren 1994), and one from Bir Hassan (van Slageren 1994).

Aegilops sharonensis grows in the most densely populated areas of Israel, where agriculture and urbanization are rapidly replacing its natural habitat. Since World War II and after the establishment of the state of Israel, the combined effects of intensification of modern agriculture, expansion of urban and industrial areas, and outdoor recreation resulted in increased disturbance of the open landscape and a rapid reduction of the natural coastal habitats (Naveh and Kutiel 1990), resulting in the disappearance of many *Ae. sharonensis* populations (Kutiel 1998; Millet et al. 2006). Indeed, at least 38 *Ae. sharonensis* specimens housed in the Hebrew University of Jerusalem herbarium are from populations that no longer exist (e.g., Schunat Borochoy, Ramat Gan, and Ramat Aviv (Tel Aviv) and Nordiya) owing to the expansion of urban areas. Millet (2006) reported that the *Ae. sharonensis* sites of Kefar-Ganim, Ein-Hakore, and Ashdod in Israel have highly endangered populations, and one has recently become extinct (Even Yehuda) (Y. Anikster, personal communication). These sites are located in the Philistine and

Sharon Coastal Plains between the cities of Ashdod and Netanya, and have experienced severe habitat disruption owing to highway and building construction.

Aegilops sharonensis is sympatric to other species belonging to the *Sitopsis*. The overlapping distribution of *Ae. sharonensis* and *Ae. longissima* and their frequently-shared habitats has been described by Eig (1929), Ankori and Zohary (1962), and Millet et al. (2006). Although *Ae. longissima* exhibits a wider geographic distribution and soil type range in its habitats than *Ae. sharonensis*, both species can be found together in locations with sandy soils and heavy sandy loams (Kimber and Feldman 1987). Millet et al. (2006) identified mixed populations at Deror Junction, Kefar Ganim, and Ein HaKore in the Sharon Plain, which comprise some of the easternmost sites of *Ae. sharonensis* distribution in Israel. These sites consist of sandy loam soils, which are suitable for both species to grow.

The occurrence of intermediate types between *Ae. sharonensis* and *Ae. longissima* in mixed populations in the Sharon Plain was first reported by Eig (1929). Later, Ankori and Zohary (1962) observed that hybrid populations occurred in mixed populations mainly in disturbed habitats, i.e., along roadsides and the edges of crop cultivation. Millet et al. (2006) also observed the occurrence of morphologically intermediate types (in Kefar Ganim), and the occurrence of hybrids at this site has been supported by molecular genotyping (Ezrati et al. 2005). The geographic distribution of *Ae. sharonensis* and *Ae. bicornis* overlaps in the southern coastal plains (Eig 1929; Millet et al. 2006), but no hybrids between these species have been reported. The range of *Ae. sharonensis* also marginally overlaps with the southern range of *Ae. speltoides*, as populations of both species were found in the Haifa Bay area and Akko Plain (Raskina et al. 2004). Even though populations of both species occur at short distances from each other, neither mixed groups nor hybrid populations were reported by the authors.

Genomic constitution

Data on the cytogenetics and genome constitution of wild wheat relatives are essential for the study of biosystematic relationships in the *Triticeae*, genomic reorganization and modifications during evolutionary processes, and also for the exploitation of wild species in wheat improvement.

Ploidy level, genome formula, and homoeologous relationship with hexaploid wheat

Aegilops sharonensis is a diploid species ($2n = 2x = 14$) with an S^l or S^{sh} genome. The homoeologous (Gupta 1972) relationship between *Ae. sharonensis* and wheat chromosomes was demonstrated by Friebe and Gill (1996) using C-banding pattern. They compared the pattern of *Ae. sharonensis* chromosomes (S^{sh}) described by Teoh and Hutchinson (1983) with those of *Ae. longissima* chromosomes, whose homoeologous relationships were previously classified by Friebe et al. (1993). Then, they assigned the seven S^{sh} chromosomes of *Ae. sharonensis* to each homoeologous group in wheat. Later, Maestra and Naranjo (1997) established the homoeologous relationship of *Ae. sharonensis* chromosomes to hexaploid wheat by C-banding analysis of specific pairing between individual chromosomes at Metaphase I. The use of inter-specific

Fig. 3. Natural habitats of *Aegilops sharonensis* in Israel. (A) Consolidated sand dunes in Shefayyim; (B) abandoned field by cemetery in Rishon LeZiyyon; (C) open park in Ashdod; (D) coast of Mediterranean Sea in Nahsholim.

hybrids between standard-type, high-pairing mutant (*ph2b* and *ph1b*) Chinese Spring wheat and *Ae. sharonensis* allowed them to identify normal homoeologous relationships for the seven chromosomes of *Ae. sharonensis* and the B genome chromosomes of hexaploid wheat. The authors also found no alteration in the arm specificity between chromosomes of *Ae. sharonensis* and *T. aestivum*, indicating that the genome of *Ae. sharonensis* maintains the chromosome structure of the B genome of hexaploid wheat without evidence of any chromosomal rearrangements. Maestra and Naranjo (1997) confirmed the same C-banding pattern described by Friebe and Gill (1996) in *Ae. sharonensis*.

Genome size

Using flow cytometry, Eilam et al. (2007) estimated the genome size (nuclear DNA content (1C value)) of *Ae. sharonensis* at 7.52 pg — the largest found for any species in the genus *Aegilops*. The authors also found that the genome size of species belonging to the *Sitopsis*, in particular those of *Ae. sharonensis* and *Ae. longissima*, was larger than that of wild and domesticated diploid wheats with the A genome. Similar results were previously observed by Furuta et al.

(1986), who described the genome size of *Ae. sharonensis* equal to that of *Ae. longissima* and larger than those of *Ae. searsii* and *Ae. speltoides*.

Gametocidal factors in *Aegilops sharonensis*

Wheat–alien chromosome addition and substitution lines have been an important tool in determining homoeologous relationships of alien chromosomes. Complete series of addition lines have been produced in species belonging to the *Sitopsis*, including *Ae. longissima* (Feldman 1975), *Ae. searsii* (Friebe et al. 1995), and *Ae. speltoides* (Friebe et al. 2000). A complete set of wheat – *Ae. sharonensis* addition and substitution lines could not be produced owing to the presence of a preferentially transmitted chromosome that conditions the production of other addition and substitution lines (Maan 1975; Endo 1982; Miller et al. 1982). Monosomic additions produced fertile male and female gametes all containing the *Ae. sharonensis* chromosome, whereas gametes lacking this alien chromosome were functionless. Miller et al. (1982) studied this chromosome by C-banding and in situ hybridization and found that it compensated well for the deficiency of chromosome 4B and 4D of ‘Chinese Spring’ wheat. This *Ae. sharonensis* chromosome was

named 4S¹. These preferentially retained chromosomes identified in *Ae. sharonensis*, as well as other *Aegilops* species, were named “gametocidal” (Endo 1982) or “cuckoo” chromosomes (Miller et al. 1982), and the genes that caused this effect were called gametocidal (*Gc*) genes or *Gc* factors (Endo 1990). These selectively retained chromosomes cause sterility in gametes that lack the alien chromosome, ensuring their own transmission to the progeny (Maan 1975; Finch et al. 1984; Endo 1990; Nasuda et al. 1998). Endo (1985) found that the three *Gc* chromosomes identified in *Ae. sharonensis* (Maan 1975; Endo 1982; Miller et al. 1982) belong to two different homoeologous groups (2 and 4), and that the chromosomes in different homoeologous groups possess different modes of action. King et al. (1991a) demonstrated that the transmission of chromosome 4S¹ occurs at a very high frequency (>98%) across a range of different wheat cultivars. The authors discussed the importance of the high frequency transmission of 4S¹ for exploiting favorable traits carried on this chromosome. King et al. (1991b) also proposed a scheme for the production of hybrid wheat based on the use of the preferentially transmitted 4S¹ chromosome from *Ae. sharonensis* to produce male sterile plants.

***Aegilops sharonensis*, a putative donor of the B genome in wheat?**

Although there is strong and conclusive evidence that *Triticum urartu* and *Ae. tauschii* are the source of the A and D genomes of hexaploid wheat (*T. aestivum*), respectively, there is still no complete agreement about the donor of the B genome (Kerby and Kuspura 1987). After Sarkar and Stebbins (1956) proposed that the B genome of wheat was derived from an *Aegilops* species in the section *Sitopsis*, numerous studies were advanced to understand the genome relationships in polyploids and to determine the putative B genome donor.

Based on meiotic pairing and morphological analyses of hybrids between *Ae. sharonensis* and diploid (*T. monococcum*), tetraploid (*T. turgidum*), and hexaploid (*T. aestivum* – *ph_{1b}* cultivar ‘Chinese Spring’) wheat, Kushnir and Halloran (1982a) concluded that *Ae. sharonensis* could be considered as the putative donor of the B genome. This conclusion was based on the following observations: (i) cytoplasm compatibility between *Ae. sharonensis* and *T. turgidum*; (ii) similarity between chromosomes with satellites in *Ae. sharonensis* and *T. turgidum*; (iii) *Ae. sharonensis* – *T. monococcum* hybrids that morphologically resemble *T. turgidum*; (iv) a high level of chromosome pairing and fertility of amphiploid *Ae. sharonensis* – *T. turgidum* plants; and (v) a high level of chromosome pairing in *Ae. sharonensis* – ‘Chinese Spring’ (*ph_{1b}* mutant) wheat hybrids. Kushnir and Halloran (1982b, 1982c) also observed that the expression of developmental and morphological characters of an F₂ plant derived from a hybrid between *T. turgidum diccoides* and an F₁ amphiploid (*Ae. sharonensis* – *T. monococcum*) lie within the ranges found in the cereal and “grassy” forms of *T. turgidum diccoides*. Moreover, the chromosome stability and high fertility found for the F₂ plants suggested the possibility of gene flow between both parents. The authors considered these results as additional evidence for *Ae. sharonensis* being the B genome donor of wheat. Kushnir et al. (1984) provided additional support for this idea through their study

of grain gliadin proteins in *Ae. sharonensis* and wild tetraploid wheat. The presence of gliadin band 45 (coded by a gene on chromosome 1B of wheat) in *Ae. sharonensis* served as further support for this species as the B genome donor. Teoh and Hutchinson (1983) observed a high similarity in the C-banding pattern between two chromosomes of *Ae. sharonensis* and chromosomes 3B and 6B of wheat, and between three chromosomes of *Ae. speltoides* and chromosomes 1B, 5B, and 7B of wheat. Based on these observations, the authors suggested *Ae. sharonensis* and *Ae. speltoides* as putative donors of the wheat B genome.

However, evidence rejecting *Ae. sharonensis* as the donor of the wheat B genome has been forwarded by several authors. Tanaka (1955) and Riley et al. (1958) discounted *Ae. sharonensis* as the B genome donor based on incomplete chromosome pairing in hybrids between *Ae. sharonensis* and both *T. monococcum* and *T. turgidum*, and the differences in morphology between the satellite chromosomes found in *Ae. sharonensis* and *T. turgidum*. Hirai and Tsunewaki (1981) also discounted *Ae. sharonensis* as the cytoplasm donor of polyploid wheats based on differences found in the migration pattern of Fraction I protein in alloplasmic lines containing *Ae. sharonensis* cytoplasm and those of polyploid wheats. The same conclusion was reached by Tsunewaki and Ogihara (1983) and Ogihara and Tsunewaki (1988) after observing a different restriction fragment pattern of chloroplast DNA of *T. aestivum*, *T. turgidum*, *T. monococcum*, and *Ae. sharonensis*. Fernandez-Calvin and Orellana (1993, 1994) studied homoeologous pairing in C-banded metaphase I cells of ‘Chinese Spring’ wheat – *Ae. sharonensis* hybrids (ABDS^{sh}) and found preferential pairing associations between wheat B genome chromosomes and those from *Ae. sharonensis*. They also found that pairing frequency between the S^{sh} and B genomes was lower than the pairing between the A and D genomes. This result was considered as sufficient evidence to exclude *Ae. sharonensis* as a possible donor of the B genome of wheat. Maestra and Naranjo (1997) also reported a higher frequency of A–D genome pairing compared with B–S^{sh} pairing in hybrids between *Ae. sharonensis* and ‘Chinese Spring’ wheat *ph_{2b}* and *ph_{1b}* mutants. The authors concluded that even though the genome of *Ae. sharonensis* maintains the chromosome structure of the B genome of hexaploid wheat, it is not sufficient evidence to consider *Ae. sharonensis* as the B genome donor.

Even though definitive evidence for the progenitor of polyploid wheats is still lacking, recent studies (Zhang et al. 2002; Provan et al. 2004; Sallares and Brown 2004; Petersen et al. 2006; Kilian et al. 2007; Zhang et al. 2007) indicate that the S genome of *Ae. speltoides* has the greatest homology to the wheat B genome. These results strongly reject *Ae. sharonensis* as the B genome donor and point to *Ae. speltoides* or a closely related but now extinct species as the strongest candidate.

Phenotypic and genotypic diversity in *Aegilops sharonensis*

A comprehensive understanding of the extent and distribution of phenotypic and genotypic diversity in *Ae. sharonensis* can provide the basis for developing conservation and germplasm collection strategies and critical information for evolutionary studies.

Phenotypic diversity

Eig (1929) established that *Ae. sharonensis* does not vary in its basic characteristics such as the form of spikes and spikelets. However, he did describe common variation in traits such as the pronounced two-rowed nature of the spike and spike density, spike size, spikelet number and size, awn size, and development and size of stems and leaves. Eighteen morphologic and agronomic traits were evaluated under field conditions by Brody (1983) in 10 diploid species of the *Triticum* – *Aegilops* complex, including five Israeli accessions of *Ae. sharonensis*. Compared with other diploid species of the *Triticum* – *Aegilops* complex, *Ae. sharonensis* exhibited limited variation in traits such as spike length and spikelet number and weight. Brody (1983) found fewer traits with significant variation in *Ae. sharonensis* and *Ae. speltoides* compared with other *Aegilops* species included in the study. Earliness traits such as heading and anthesis date exhibited the most variation in *Ae. sharonensis*. A low level of variation for morphologic traits in *Ae. sharonensis* also was reported by Kimber and Feldman (1987). Waines et al. (1993) studied the variability of yield components and transpiration efficiency (straw, spike and grain yield, above-ground biomass, weight of 100 kernels, and carbon isotope discrimination) in diploid *Aegilops* (S genome) and *Triticum* (A and D genomes) species, including six *Ae. sharonensis* accessions. The authors reported the largest variation for grain yield in *Ae. sharonensis* compared with all the *Sitopsis* species. Accessions of *Ae. sharonensis* also exhibited large variation for spike yield, straw yield, and above-ground biomass, which was comparable with the level observed in *Ae. speltoides* and *Ae. longissima*. Based on their results, the authors concluded that *Ae. sharonensis*, as well as *Ae. longissima*, *Ae. speltoides*, and *Ae. bicornis*, can be used as sources of favorable genes and genetic diversity in wheat breeding programs.

Olivera et al. (2010) evaluated the level of diversity for 12 morphologic traits in 106 *Ae. sharonensis* accessions from 15 sites covering the geographic distribution of the species in Israel. A high level of variation was found for all traits, as the coefficient of variation for all of them exceeded 10% (range 10.2%–46.5%). The traits with the highest variability were the second, flag, and flag-1 leaf area and number of stems, whereas the lowest level of variability found was for the number of spikelets, days to spike emergence, and plant height. Olivera et al. (2010) concluded that *Ae. sharonensis* exhibited a level of phenotypic variability that was comparable with wild wheat species with broader geographic distributions. Estimation of the variance components of each morphologic trait revealed that the effect of geographic region on total phenotypic variability was higher than that observed for genotypic diversity (see below). Moreover, phenotypic variability among regions, locations, and accessions was more homogeneous than that observed for genotypic diversity.

Based on Shannon's index of diversity (h_s), Olivera et al. (2007) assessed the phenotypic diversity for disease reaction in a collection of 107 *Ae. sharonensis* accessions from Israel ($n = 103$) and Lebanon ($n = 4$). The diversity statistic h_s was calculated for the reaction to seven wheat fungal pathogens, including leaf rust (*Puccinia triticina*), stem rust (*Puccinia graminis* f. sp. *tritici*), stripe rust

(*Puccinia striiformis* f. sp. *tritici*), powdery mildew (*Blumeria graminis* f. sp. *tritici*), tan spot (*Pyrenophora tritici-repentis*), spot blotch (*Cochliobolus sativus*), and Fusarium head blight (*Gibberella zeae*). The authors reported substantial variation in the level of diversity to individual diseases as h_s ranged from 0.128 (to Fusarium head blight) to 1.092 (to tan spot). High and intermediate levels of diversity were observed for resistance to all the evaluated pathogens and races, except for *G. zeae* and race 0 of *C. sativus*, where most of the accessions exhibited a susceptible reaction. Moreover, marked geographic differences in the frequency of resistance were observed in *Ae. sharonensis* despite the narrow range of the species. Accessions from northern Israel (Haifa Bay region) were less diverse than ones from the central and southern coastal plain. Similar results for *P. triticina* were reported by Anikster et al. (2005), who suggested that stand density of *Aegilops* populations, rather than differences in environmental parameters between regions, might be a critical determinant in the evolution of resistance and level of diversity. The fact that fewer and smaller *Ae. sharonensis* populations are present in northern Israel around Haifa compared to the central and southern coastal plains (Millet et al. 2006) may be a reason for the low adaptation and diversity in the species.

Genotypic diversity

Brody and Mendlinger (1980) studied the extent and distribution of genetic variation of 20 enzyme loci in *Aegilops* species belonging to the *Sitopsis*. Six populations of *Ae. sharonensis* (1–15 accessions each) were included in this study. The results of this research indicated that the amount of genetic variation (alleles/locus and percent of polymorphic loci) in *Ae. sharonensis* was higher than that of *Ae. speltoides* and *Ae. bicornis*, but lower than that in *Ae. longissima*. Sixteen water soluble leaf proteins were used by Mendlinger and Zohary (1995) to study genetic diversity in wild wheats, including five *Ae. sharonensis* populations (30–100 accessions each). The authors reported high genotypic diversity in all but one (Ashdod) of the *Ae. sharonensis* populations. The level of genetic diversity in *Ae. sharonensis* populations was similar to those of *Ae. speltoides*, *Ae. longissima*, and *Ae. bicornis* included in the study. No significant correlations between environmental parameters (altitude and mean annual rainfall) and genetic diversity were observed by these authors. However, Asins and Carbonell (1986a) found that *Ae. sharonensis* had lower intraspecific variability for three isoenzymatic characters of dry mature seeds than *Ae. speltoides* and *Ae. longissima*. Surprisingly, they observed that *Ae. sharonensis*, which has the most limited geographic distribution of the *Sitopsis* members, was the only species where the level of interpopulational variability was higher than the intrapopulational component. Asins and Carbonell (1986a) concluded that *Ae. sharonensis* is a self-pollinated species with local adaptations over short distances.

Nine *Ae. sharonensis* accessions representing the geographic distribution of the species were used by Dvorak and Zhang (1992) in their assessment of the extent of variation in 46 repeated nucleotide sequence families of 10 diploid *Triticum* and *Aegilops* species. For members of the *Sitopsis*, *Ae. speltoides* and *Ae. searsii* registered the highest level of

variation, followed by *Ae. sharonensis* and *Ae. longissima*. No variation in *Ae. bicornis* was reported by the authors. In a later study, Dvorak et al. (1998) investigated 52 RFLP loci in six diploid *Aegilops* species: five belonging to section *Sitopsis* and *Ae. tauschii*. The highest average gene diversity (H) was reported for *Ae. speltoides* ($H = 0.72$) followed by *Ae. sharonensis* ($H = 0.49$), which had a significantly higher diversity than the rest of the studied species. Interestingly, these researchers also found a high proportion of heterozygous loci in *Ae. sharonensis* and *Ae. longissima* and concluded that both species (which are considered self-pollinators (Kimber and Feldman 1987)), may have a mixed mating system. Similar results were reported by Goryunova et al. (2008) using RAPD markers, where the intraspecific genotypic diversity observed in *Ae. sharonensis* and *Ae. longissima* was intermediate between the values observed for *Ae. speltoides* and those of *Ae. bicornis* and *Ae. searsii*. A low level of intraspecific variability for dimeric α -amylase inhibitor genes of *Ae. sharonensis* was reported by Wang et al. (2007). The level of diversity found was comparable to that of *Ae. longissima* and *Ae. searsii*, but lower than that found for *Ae. bicornis* and *Ae. speltoides*.

Ezrati et al. (2005) used AFLP markers to evaluate the level of diversity in 236 *Ae. sharonensis* accessions from 12 collection sites located in the northern-, central-, and southern-coastal plains of Israel. Using principal component analysis, the authors reported that individual plants from the same site clustered together. They also found that some collection sites were clearly differentiated, whereas others clustered together. Partial differentiation among populations from the northern-, central-, and southern-coastal plains also was reported. Based on their results, Ezrati et al. (2005) suggested sampling additional sites rather than more accessions within sites as a future collection strategy. Kilian et al. (2007) studied genotypic diversity in all the *Aegilops* species belonging to the *Sitopsis*. For all intraspecific pairwise comparisons, the level of genetic similarity (Jaccard's similarity) was lowest in *Ae. speltoides* (0.656), followed by *Ae. tauschii* (0.751). *Aegilops sharonensis* exhibited the highest level of genetic similarity (0.842), a level comparable with that of *Ae. searsii* (0.825) and *Ae. longissima* (0.812).

Olivera et al. (2010) studied the genetic diversity and population structure of 106 *Ae. sharonensis* accessions from 15 sites located in four coastal regions of Israel (Akko Plain, Coast of Carmel, Sharon Plain, and Philistean Plain). The 21 microsatellites used in this study identified a total of 339 alleles, with an average of 16.1 alleles per locus and average gene diversity of 0.820. The genotypic diversity found in *Ae. sharonensis* was comparable with species that have a wider geographic distribution and more variable environments. The authors identified the Sharon Plain as the region exhibiting the highest level of allele richness and average gene diversity. Because it is located in the center of the geographic distribution of the species and includes sites with the highest level of diversity (i.e., Netanya and Sheffayim), the authors suggested that the Sharon Plain may be the center of origin and diversity of *Ae. sharonensis*. The genetic structure of *Ae. sharonensis* observed by Olivera et al. (2010) is characterized by high diversity within sites (75% of total variation) and low diversity within regions (4%). The authors found that this pattern of genetic diversity fits with

the "intermediate disturbance" hypothesis (Connell 1978), which establishes that ecosystems under intermediate stress levels are the ones exhibiting the highest level of diversity by allowing the coexistence of highly competitive species, poor competitors, and species with intermediate competitive abilities for specific stresses. The monthly and seasonal fluctuations in macroclimate parameters that occur in the Mediterranean climate of Israel (Ben-Gai et al. 1998, 1999) may create a moderate selection pressure, resulting in the coexistence of *Ae. sharonensis* individuals with different relative fitness and competitive abilities (Hedrick 2006). The "intermediate disturbance" hypothesis was previously demonstrated in wild barley in Israel (Peleg et al. 2008). Genetic structure also exhibited a short distance similarity (<15 km) between collection sites (Olivera et al. 2010). The observed pattern of diversity in natural populations of *Ae. sharonensis* indicate that, to capture the highest genetic diversity possible, collection and utilization programs should include multiple individuals from as many sites as possible located in the center of distribution of the species. Using the Bayesian model-clustering algorithm (Pritchard et al. 2000), Olivera et al. (2010) identified six clusters (subpopulations) of genetically similar individuals. Accessions from the Akko Plain and Coast of Carmel clustered in two subpopulations, revealing a clear differentiation among sites in the northern regions. However, lower differentiation and higher diversity was observed in the four clusters grouping individuals from the south (Philistean and Sharon Plains).

Studies on genetic diversity have also been performed at the organelle level. The pattern of heterogeneity in *Triticum* and *Aegilops* mitochondrial DNA (mtDNA) was studied by Breiman (1987) using restriction endonuclease digestion and Southern blot hybridization. The author found that, from all the species belonging to the *Sitopsis*, *Ae. sharonensis* and *Ae. searsii* were the two exhibiting the lowest level of intraspecific variation. Moreover, both species showed no differences in their hybridization profiles. Using restriction map analysis (13 restriction enzymes), Miyashita et al. (1994) studied intraspecific variation in chloroplast DNA regions in *Triticum* and *Aegilops* species, including three *Ae. sharonensis* accessions. Of the species in the *Sitopsis*, *Ae. speltoides* (28 accessions) showed the highest number of plastotypes (nine) and was the only one that exhibited restriction site polymorphisms. The three *Ae. sharonensis* accessions included in this study were differentiated into two plastotypes, whereas only one plastotype was observed for *Ae. longissima*, *Ae. searsii*, and *Ae. bicornis*.

***Aegilops sharonensis* as a source of disease resistance and abiotic stress tolerance**

Genetic resistance is the best strategy for controlling many fungal diseases of wheat. The use of resistant cultivars to control diseases requires the availability of many sources of resistance to counter the frequent appearance of new virulence types in pathogen populations (Gill et al. 1985). From the time of first domestication, the genetic diversity of wheat has been seriously eroded. Thus, it is imperative that the wheat gene pool be expanded by incorporating new genes into breeding programs. In this regard, wild relatives of wheat, including *Ae. sharonensis*, are an important gene reservoir for resistance to wheat diseases and offer one of

the most diverse sources of unique alleles for wheat improvement.

Resistance to biotic stress

Aegilops sharonensis, like other wild grasses, has co-evolved in association with many cereal pathogens (e.g., leaf rust, stem rust, stripe rust, and powdery mildew), being exposed to reciprocal selection pressure (Wahl et al. 1978, 1984). This long-term process occurring in the center of diversity (i.e., the coastal plains of Israel) has resulted in the selection of host genotypes with different levels of resistance and pathogen isolates with a broad spectrum of virulence (Segal et al. 1980).

The highest frequency and level of resistance reported in *Ae. sharonensis* was to wheat powdery mildew. The frequency of resistance to this important disease was never lower than 80% in all the reviewed investigations (Pasquini 1980; Valkoun et al. 1985; Gill et al. 1985; Dhaliwal et al. 1993; Olivera et al. 2007). Several investigators also identified in *Ae. sharonensis* a high frequency of seedling and adult plant resistance to leaf rust (Pasquini 1980; Valkoun et al. 1985; Gill et al. 1985; Manisterski et al. 1988; Anikster et al. 1992, 2005; Snyman et al. 2004; Olivera et al. 2007), stem rust (Gerechter-Amitai and Loegering 1977; Valkoun et al. 1985; Olivera et al. 2007), and stripe rust (Valkoun et al. 1985; Anikster et al. 2005; Olivera et al. 2007). An especially noteworthy case is with stem rust race TTKSK (i.e., isolate synonym Ug99) and its variants, which are a serious threat to wheat production worldwide (Pretorius et al. 2000; Jin et al. 2008). As extensive screening of wheat varieties has yielded only a few adapted sources of resistance to race TTKSK (Jin and Singh 2006; Jin et al. 2007), the identification and introgression of effective resistance genes from all gene pools of wheat is urgently needed. Olivera et al. (2007) observed a high frequency (69.2% of 107 accessions) of resistance to race TTKS in *Ae. sharonensis*. Several accessions with potentially different resistance alleles could be used to enhance the diversity for race TTKSK resistance in wheat.

In an inheritance study of several *Ae. sharonensis* accessions to leaf rust, stem rust, and powdery mildew, Olivera et al. (2008) detected dominant resistance alleles at genes with major effects. In individual accessions from different geographic regions, the authors found different genes that were effective against all of the *P. triticina* races evaluated. Genes for powdery mildew resistance were also found in accessions native to the southern and northern coastal plains of Israel. They also identified multiple stem rust resistance genes in individual *Ae. sharonensis* accessions using two races of *P. graminis* f. sp. *tritici* (TTTT and TPMK) with different virulence spectra. The presence of a variety of stem rust resistance genes appears to be a common feature in *Ae. sharonensis* as Gerechter-Amitai and Loegering (1977) postulated 12 to 13 different stem rust (*Sr*) resistance genes in 44 selected accessions of *Ae. sharonensis* and *Ae. longissima* using 20 cultures of *P. graminis* f. sp. *tritici*. These results demonstrate the existence of diversity for leaf rust, stem rust, and powdery mildew resistance genes in *Ae. sharonensis*.

Resistance to spot blotch (Dhaliwal et al. 1993; Olivera et al. 2007; Smurova and Mikhailova 2007), tan spot (Olivera et al. 2007), and Karnal bunt (Warham et al. 1986) also has

been reported in *Ae. sharonensis*. Olivera et al. (2007) observed a lower frequency and level of resistance to spot blotch and tan spot in comparison to the rusts and powdery mildew. Moreover, the marked differences observed in the frequency of resistance to the different pathogen races used suggested that *Ae. sharonensis* may carry different resistance genes to spot blotch and tan spot. Olivera et al. (2007) screened 107 *Ae. sharonensis* accessions for resistance to Fusarium head blight, but no resistant accessions were identified. The authors identified two accessions that exhibited slow and restricted disease development (intermediate reaction), but these may not be of high value for introgression into cultivated wheat.

Resistance to abiotic stress

Discrepancies exist about the level of salt tolerance present in *Ae. sharonensis*. Based on the ability to discriminate efficiently between potassium (K) and sodium (Na) during transport (Shah et al. 1987), Farooq et al. (1989) classified *Ae. sharonensis* as sensitive to salinity, being a species that accumulated Na in plant shoots and therefore had a low K/Na ratio. Similar results were obtained by Gorham (1990), who found that *Ae. sharonensis* lacked enhanced K/Na discrimination, resulting in low salt tolerance. A different conclusion was obtained by Xu et al. (1993) when the salt tolerance of several *Triticum* and *Aegilops* species was assayed. Based on the effect of salt on root and aerial vegetative growth, proline accumulation, and inhibition of chlorophyll fluorescence, the authors identified *Ae. sharonensis* as salt tolerant. The species also was considered as a potential gene donor in breeding programs for this phenotypic trait. Waines et al. (1993) evaluated the transpiration efficiency in *Ae. sharonensis* and other wild wheats by measuring carbon isotope discrimination under well-watered field conditions. The authors found that S (including *Ae. sharonensis*) and D genome species are more transpiration efficient than the A genome species and are therefore potential sources of drought tolerance.

Manyowa (1989) identified tolerance to aluminum (Al) and boron (B) in *Ae. sharonensis*. In an attempt to study the genetics of B tolerance, Manyowa (1989) studied 'Chinese Spring' wheat – *Ae. sharonensis* addition lines. The author found that chromosomes 3S¹, 5S¹, and 7S¹ expressed a level of tolerance higher than that of 'Chinese Spring' with the 5S¹ addition line being the most tolerant. Nutrition and variation in nitrogen and phosphorus efficiency was evaluated among cultivated and wild wheats by Gorny and Garczynski (2008). The authors identified *Ae. sharonensis* and *Ae. speltoides* as the species with the highest tolerance to nutrient shortage and attributed this characteristic to the thin roots these species have at the juvenile stage.

Genes transferred from *Aegilops sharonensis* into hexaploid wheat

Harlan and de Wet (1971) introduced the gene pool concept in an attempt to provide a framework in which cultivated plants can be treated in a comparative way with their wild relatives. Based on the genome constitution, fertility of hybrids and chromosome pairing, and ease of gene transfer, wild relatives and cultivated species were classified into primary, secondary, and tertiary gene pools. *Aegilops sharo-*

nensis belongs to the secondary gene pool of wheat, as the S^{sh} genome shares homoeology with the B genome of wheat (Jiang et al. 1994; Friebe et al. 1996). The transfer of genes from species in the secondary gene pool is not routine, but is possible. Cytogenetic methods such as wheat–alien amphiploid production and development of wheat–alien addition, substitution and translocation lines may result in the successful introgression of resistance genes (Sharma and Gill 1983; Sharma 1995; Jiang et al. 1994; Friebe et al. 1996). Gene introgression from *Ae. sharonensis* is difficult, owing to the presence of gametocidal genes that control the preferential transmission of chromosome 4S¹ (Endo 1982; Miller et al. 1982). However, Friebe et al. (2003) produced a mutation of the *Ae. sharonensis* Gc2 gametocidal gene (*Gc2^{mut}*) which opened the way for *Ae. sharonensis* introgression into wheat. This knockout mutation is at the gene that encodes the chromosome breaking agent, allowing the production of functional gametes and fully fertile spikes (Friebe et al. 2003). Heterozygous (*Gc2/Gc2^{mut}*) plants exhibit normal transmission rather than a preferential one, facilitating the introgression of genetic material from all the *Ae. sharonensis* chromosomes.

Zhirov and Ternovskaya (1993) published the first report on the introgression of a disease resistance gene (to powdery mildew) from *Ae. sharonensis* into wheat. Gene introgression was achieved through the generation of a genome-substitution form of wheat cultivar ‘Aurora’ (Aurosis, AABBS^{sh}S^{sh}), where the D genome of ‘Aurora’ wheat was substituted for the genome of *Ae. sharonensis*. After crossing the powdery mildew resistant lines with ‘Aurora’, the authors observed that all the substitution lines carried the same *Ae. sharonensis* chromosome, but some lines differed in the wheat chromosome replaced by the one from *Ae. sharonensis*. Chromosome 6D was replaced in one substitution line, whereas the other substituted chromosome did not belong to the D genome. The powdery mildew resistance gene has not been assigned to a specific chromosome arm and has yet to be included in the catalog of resistance genes in wheat (Hsam and Zeller 2002). Antonov and Marais (1996) reported the production of an interspecific cross between ‘Chinese Spring’ wheat and *Ae. sharonensis* accession 174 from Israel, which was shown to be resistant to five *P. tritici* races from South Africa. The direct hybridization was followed by colchicine treatment (anti-mitotic agent) to produce amphiploids and ensure the fertility of the F₁. After producing the F₁ hybrids (resistant to leaf rust), the authors backcrossed the viable ones six times to the wheat parent, and the homozygous resistant plants were evaluated for resistance to a wide range of South African *P. tritici*, *P. graminis* f. sp. *tritici*, and *P. striiformis* f. sp. *tritici* races (Marais et al. 2003). Marais et al. (2003) reported the full expression of resistance genes to leaf rust and stripe rust in the hexaploid wheat background, but susceptibility to stem rust races. Using monosomic and telosomic analysis and mapped microsatellite markers, Marais et al. (2006) found these linked resistance genes to be located on chromosome 6A of ‘Chinese Spring’ wheat and named them *Lr56* and *Yr38*. Both genes exhibited strong preferential transmission in the ‘Chinese Spring’ background, perhaps owing to the presence of the gametocidal gene (Marais et al. 2006). Millet et al. (2007) also are

conducting studies to introgress stripe rust and stem rust resistance from *Ae. sharonensis* into hexaploid wheat. This group is using an introgression approach that allows homoeologous pairing and eliminates the gametocidal gene present in chromosome 4S¹ through the use of a highly pairing wheat (*ph1b* mutant) (Sears 1977) and the gametocidal mutant (*Gc2^{mut}*) developed by Friebe et al. (2003). This approach involves both the production of synthetic wheat (AABBS¹S¹) through a cross between *Ae. sharonensis* and tetraploid wheat, and the production of direct crosses between *Ae. sharonensis* and hexaploid wheat.

To facilitate gene introgression from *Ae. sharonensis* into cultivated wheat, Olivera (2008) constructed the first genetic linkage map of the species from a cross between accessions resistant (1644) and susceptible (1193) to wheat leaf rust and stem rust. The linkage map was based on 389 markers (377 diversity arrays technology (DArT) and 12 simple sequence repeat (SSR) loci) and comprised 10 linkage groups. The total genetic length of the map was 818 cM, with an average interval distance of 3.63 cM. A single gene (provisionally designated *LrAeSh1644*) where a dominant allele conferred resistance to leaf rust race THBJ in accession 1644 was positioned to chromosome 6S^{sh} and was flanked by DArT markers wpt-9881 (at 1.9 cM from the gene) and wpt-6925 (4.5 cM). A single gene (provisionally designated *SrAeSh1644*) where a dominant allele conferred resistance to stem rust race TTTT in accession 1644 mapped to chromosome 1S^{sh} and was flanked by DArT markers wpt-9845 (1.7 cM) and wpt-0.158 (6.3 cM). The identification of markers closely linked to the resistance genes will facilitate their introgression into cultivated wheat and their further use in breeding programs employing marker assisted selection.

With the objectives of increasing the genetic diversity and incorporating useful traits into hexaploid triticale (*Triticale hexaploide* Lart.), Orlovskaya et al. (2007) introgressed *Ae. sharonensis* chromatin into triticale through hybridization between winter hexaploid triticale and the genome-substitution from ‘Aurosis’ wheat (AABBS^{sh}S^{sh}). Morphologic (spike morphology and coloration, awns, glume hairiness) and biochemical (gliadin profile) analysis allowed the authors to identify hybrids carrying *Ae. sharonensis* chromatin. The maintenance of genetic material from *Ae. sharonensis* in the F₄ generation was also confirmed. The authors selected forms of triticale exhibiting properties of *Ae. sharonensis* for further genetic and breeding studies.

Cloning resistance genes from Aegilops sharonensis

Linkage drag is one of the most important problems associated with introgressing genes from unadapted species into cultivated crops. If a target gene could be cloned from the wild species donor and introduced into wheat by transformation, the deleterious chromatin associated with the gene could be eliminated. Two leaf rust resistance genes, *Lr10* and *Lr21*, were cloned from the wild diploid wheat species *T. monococcum* (Feuillet et al. 2003) and *Ae. tauschii* (Huang et al. 2003), respectively. With the development of various genomic tools, advances in bioinformatics, and availability of low-cost sequencing, it is now possible to clone resistance genes from wild wheats like *Ae. sharonensis* in a more efficient manner. In this regard, we have initiated a project to clone genes for resistance to stem rust race

TTKSK in *Ae. sharonensis*. The availability of cloned resistance genes from various wild species will significantly increase the diversity of resistance in wheat to important diseases.

Conclusions

Aegilops sharonensis (Sharon goatgrass) is a diploid relative of wheat with an annual growth habit and a genome (S^{sh}) closely related to the B genome of cultivated bread wheat. It has the most limited distribution of any species in the genus *Aegilops* and is rapidly losing populations owing to the expansion of urban areas and modern agriculture in the coastal plains of Israel. Studies on genetic and phenotypic diversity indicated that *Ae. sharonensis* is highly diverse and a rich source of novel resistance genes for cultivated wheat. Although the species has not been exploited to any great extent for wheat improvement, recent progress in overcoming the genetic constraints for gene transfer from *Ae. sharonensis* (*Gc2* mutant) and the potential for efficient gene cloning opens new possibilities for fully exploiting the genetic diversity of the wild species and incorporating new traits into wheat.

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