

Invited Review Article

**Ecogeography, genetic diversity, and breeding value of wild emmer wheat
(*Triticum dicoccoides* Körn ex Asch. & Graebn.) Thell.**

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*Corresponding author: abdullah.jaradat@ars.usda.gov**Abstract**

Wild emmer wheat (*Triticum dicoccoides* Körn ex Asch. & Graebn.) Thell. is the allotetraploid ($2n=4x=28$; genome BBAA) progenitor of cultivated wheat. It is fully compatible with the tetraploid (BBAA) durum wheat (*Triticum durum*), and can be crossed with the hexaploid ($2n=6x=42$; BBAAADD) wheat (*Triticum aestivum*). In the Fertile Crescent, the centre of origin and centre of diversity of wild emmer wheat, the wild progenitor exhibits a wide phenotypic and genotypic variation and displays a rich adaptive genetic diversity which is ecologically and genetically structured as an “archipelago.” The fertile hybrids between wild emmer wheat and domesticated durum wheat point to the early, and probably current, extensive gene flow that must have enriched the genetic structure of both subspecies in the Fertile Crescent. Specific alleles and allele combinations predominate, at the macro- and microgeographic scales, as co-adaptive blocks of genes adapted to diverse biotic and abiotic stresses. Wild emmer wheat is recognized as a source of genes for agronomically important traits. These include genes for large spike and grain size, high grain and protein yield, desirable composition of storage proteins, photosynthetic yield, herbicide response, salt tolerance, drought tolerance, disease (leaf rust, stripe rust, powdery mildew, and soil-born mosaic virus) resistance, profuse tillering, and genes for other quantitative traits. For millennia, the vast genetic diversity in wild emmer wheat must have contributed to the spatially and temporally sustainable wheat production as a major component of dynamic cropping systems in the Fertile Crescent. With the advent of, and easy access to, molecular genetics and breeding tools, wild emmer wheat is expected to contribute the full range of its diversity in quantitative and qualitative traits for a more globally sustainable wheat production. It is expected that the current and future detailed records of phenotypes and genotypes and their spatio-temporal variation patterns in the Fertile Crescent will form an integral part of a relational database that can serve future strategies for *in situ* conservation, collection, evaluation, and utilization by wheat geneticists and breeders.

Keywords: Breeding; Ecogeography; Fertile Crescent; Genetic diversity; Population structure; *Triticum dicoccoides*; Wild emmer.

Abbreviations: AFLP, Amplified Fragment Length Polymorphism; ARS, Agricultural Research Service; BAC, Bacterial Artificial Chromosome; BP, Before Present; Cu, Copper; DNA, Deoxyribonucleic Acid; FAOSTAT, Food and Agriculture Organization Statistics; Fe, Iron; GA, Gibberellic Acid; *Gpc*, Grain protein content; HMW, High Molecular Weight; LMW, Low Molecular Weight; Mg, Magnesium; Mn, Manganese; QTL, Quantitative Trait Loci; RAPD, Random Amplified Polymorphic DNA; S, Sulphur; UJV, Upper Jordan Valley; USDA, United States Department of Agriculture; Zn, Zinc.

Introduction

Wheat is a major staple crop in many parts of the world, contributing ~30% of the world's edible dry matter and ~60% of the daily calorie intake in several developing countries (FAOSTAT, 2008). Demand for wheat for human consumption is expected to grow at about 2% per year during the next 10 years; therefore, its yield and nutritional quality have significant impact on human health and wellbeing in large parts of the world. With the current and expected increase in world population, it is important to improve the yield and quality of the crop and to enhance its tolerance to biotic and abiotic stresses, and adaptation to climate change (Katz, 2001; Lemaux and Qualset, 2001). Wild emmer wheat (*Triticum dicoccoides* Körn ex Asch. & Graebn.) Thell. is the wild progenitor of domesticated wheat; natural populations of the species are confined to the Fertile Crescent (Zohary and Hopf, 1993) and are fully compatible with cultivated durum wheat and can be crossed with bread wheat (Feldman and Sears, 1981). Wheat domestication was responsible for the

increase in human population by enabling humans to produce food in large quantities, thereby contributing to the emergence of human civilization (Harlan and Zohary, 1966; Harlan, 1995). The domestication of wild emmer was one of the key events during the emergence of agriculture in Southwest Asia, and was the prerequisite for the evolution of tetraploid durum and hexaploid bread wheat (Zohary and Hopf, 1993; Willcox, 1998). The domestication of wild emmer in the Fertile Crescent and the subsequent breeding of domesticated durum and bread wheat drastically narrowed their genetic diversity (Nevo, 2001; Lou et al., 2007). Upon domestication, Haudry et al. (2007) estimated that initial diversity was reduced by 84% in durum wheat and by 69% in bread wheat. This genetic bottleneck severely eroded allelic variation in cultivated wheats compared with the wild progenitor, making them increasingly susceptible to biotic and abiotic stresses (Frankel and Soulé, 1981). The amount, composition, and distribution of genetic diversity at the

morphological, agronomic, biochemical and molecular levels in wild emmer, similar to other natural plant populations (Nevo, 1986; Nevo et al., 1998), is the basis for its evolutionary change that led to its domestication and constitutes a potential value for wheat improvement. Tetraploid wheat species of domesticated wheat were derived from wild emmer, the donor of the A and B genomes (Feldman and Sears, 1981; Feldman and Kislev, 2007); free-threshing forms evolved soon after domestication. Hexaploid wheat (*Triticum aestivum*) evolved after a subsequent “accidental” cross between tetraploid wheat and the goat grass *Aegilops tauschii*, the donor of the D genome. However, most of the evidence accumulated thus far (Dvorak et al., 1998) suggests that the *Triticum aestivum* D genome is (geographically) more related to the *strangulata* gene pool from the southwestern Caspian region than to the *tauschii* gene pool of *Aegilops* spp. Nevertheless, domestication and modern plant breeding have presumably narrowed the genetic base of bread wheat, which could jeopardize future crop improvement (Nevo, 2001; Rajaram et al., 2001). The number of independent crosses between the progenitors of hexaploid wheat is considered limited (Dvorak et al., 1998), resulting presumably in loss of diversity. Dvorak et al. (2006) stated that reproductive isolation between the tetraploid and hexaploid levels is weak in wheat and pentaploid hybrids from backcrosses to either ploidy level, forming a bridge via which genes could potentially flow between the ploidy levels.

These researchers presented molecular evidence revealing the existence of past gene flow from wild tetraploid wheat to cultivated hexaploid wheat based on genetic variation at the single-copy *Xpsr920* locus in the A genome. Undoubtedly, wild emmer has a reservoir of useful genes for wheat breeding and improvement (Avivi, 1978; 1979; Anikster and Noy-Meir, 1991; Nevo, 2001); the evidence relevant to its potential value in wheat improvement derives from a wide range of studies, including population genetics and ecology, climatology, phytopathology and immunology, biochemistry, physiology, agronomy, and breeding practices. The discovery and re-discovery of wild emmer (Aarohson, 1909; Katz, 2001) opened new possibilities for cytogenetic and evolutionary studies in wheat and its relatives, and facilitated the study of the origin, domestication, and evolution of wheats under cultivation. It also rendered possible the exploitation of this wild genetic resource for wheat improvement.

Historical background

A wild emmer specimen was first collected by the Austrian botanist Theodor Köttschy in 1855 from the north-western foothills of Mount Hermon in the west arc of the Fertile Crescent (approximately 33° 26' N; 35° 47' E); however, it was not properly identified as *Triticum dicoccoides* until 1873 by the cereal investigator Friedrich Körnicke (Katz, 2001). Botanical studies during the last few years of the 19th century renewed the interest in wild emmer and considered it as the progenitor of cultivated wheat, and in 1906, it was found by Aaronshon (1909) in and around the original site of its initial discovery in 1855 by Köttschy. Neolithic agriculture in the Fertile Crescent and the larger Near East, which was founded some 10,000 years ago on wild emmer and other founder crops (i.e., barley, einkorn and emmer wheat, pea, lentil, chickpea, bitter vetch, and flax) (Zohary and Hopf, 1993), spread over the next ~2,000-3,000 years northwest across Anatolia and southeast to the southern Zagros

mountains. Further expansions to the northwest into Europe, southwest to the Nile Valley, southeast towards the Indus Valley, and northeast to Central Asia came at later dates (Bar-Yosef and Meadow, 1995). By the end of Pre-Pottery Neolithic B (~7,500 Before Present, BP), Neolithic agriculture based on crop cultivation and animal grazing was supporting the livelihoods of most people in the Fertile Crescent through a village-based economy (Blumler, 1991; 1992; 1998; Nesbitt, 1995), and was considered as a uniquely self-sustaining subsistence system, unlike the hunter-gatherer system it progressively replaced (Harris, 1998b). Archaeological evidence (Willcox, 1998; 2005) indicated that wild emmer, along with the progenitors of the other founder crops, were exploited as food crops by hunter-gatherers of the pre-Neolithic in the Fertile Crescent and the larger Near East long before their domestication. Environmental change could have resulted from climatic change or human activities in the upper Jordan valley (UJV) area and triggered a transition from subsistence system to a production economy in the Fertile Crescent and the larger Near East region (Willcox, 1998; 2005); grain yields of wild emmer and wild barley 1-1.5 Mg ha⁻¹ were feasible some 10,000 years ago (Araus et al., 2007). Wild emmer was domesticated, most probably, by the second half of the 10th millennium BP; however, seed of the wild emmer type were found in mixtures with cultivated emmer almost a thousand years after domestication suggesting that it persisted as a part of the crop complex (Zohary and Hopf, 1993; Blumler, 1998). Whether the initial cultivation of wild emmer led to its rapid domestication and the simultaneous beginnings of agriculture in a nuclear part of the Fertile Crescent or in different sites in the larger Near East region is still debatable (Blumler, 1991; 1992; Harlan, 1992).

Nevertheless, simultaneous cultural and environmental changes, presumably caused by climate change (Harris, 1998a; 1998b; Willcox, 1998), may have triggered or contributed to a gradual transitioning to sedentary life and the establishment of full-scale farming economy with guaranteed food supply that led to a steep rise in population. It is speculated that these changes were gradual and might have happened simultaneously along the western and eastern arcs of the Fertile Crescent (Harlan, 1992; Zohary and Hopf, 1993). Wild emmer, a founder of the Neolithic agriculture, is the progenitor through domestication of a complex of tetraploid wheats in which cultivated emmer and durum wheats are the main representatives (Feldman and Sears, 1981; Feldman and Kislev, 2007); whereas, bread wheat originated through natural hybridization between the cultivated durum wheat and the wild goat grass known as *Aegilops tauschii* (Feldman and Millet, 2001). Many of the crops that founded Neolithic agriculture, including cultivated emmer and durum wheats, retained their importance in food production throughout the last 10,000 years, and are now being cultivated throughout the Old and the New World (Zohary and Hopf, 1993). Due to their high nutritive value, modern wheat cultivars are superior to other cereals in providing energy and high quality protein for billions of people around the world (Law and Payne, 1983; FAOSTAT, 2008). However, the need is urgent to increase the yield potential and improve nutritive quality and tolerance to biotic and abiotic stresses of cultivated wheat in view of climate change, rising demand for healthy wheat products, and the increasingly alarming loss of its wild gene pool (Katz, 2001; Kosina et al., 2007). It is expected that wild emmer, with its remarkable valuable genetic diversity, will contribute to wheat improvement (Nevo, 2001, and references therein; Xie and Nevo, 2008).

Origin and distribution of wild emmer wheat

Wild emmer, the ancestor of most cultivated wheats, is an annual, predominantly self-pollinated, tetraploid wheat. It is the only wild progenitor that is cross-compatible and fully inter-fertile with cultivated *T. turgidum* wheats (Feldman and Sears, 1981; Zohary and Hopf, 1993). Although it is distributed throughout the Fertile Crescent (Fig. 1), it is more common in its western arc (Nevo, 1986; Jaradat, 1987; van Slageren, 1994; Valkoun et al., 1998). In most regions where agriculture began, wild emmer and other primary crops were domesticated once or a very few times (Harlan, 1992; 1995; Blumler, 1998). The species was pre-adapted for domestication due to its annual growth habit during the mild Mediterranean winters and its ability to endure the dry, hot summer as seed in the soil (Anikster and Noy-Meir, 1991; Noy-Meir et al., 1991); it has large, well-protected grains that assist the safe and rapid re-establishment of the stand; its spike and seed characteristics rendered it very attractive to ancient gatherers (Ladizinsky, 1998; Feldman and Kislev, 2007); and it was amenable for dry-land farming due to its annual growth habit, self-pollination system and its favourable response to improved growing conditions and inputs (Blumler, 1992; Araus et al., 2007) (Fig. 2). Earlier botanical evidence (Harlan and Zohary, 1966) led to the conclusion that it was domesticated in or near the UJV. However, its discovery in the northern and eastern portions of the arc led to a revision of that opinion (Zohary, 1969) and indicated that the wild species may have been domesticated almost anywhere in the Fertile Crescent. Plants collected from the UJV (Poyarkova, 1988; Poyarkova et al., 1991) and central mountains east of the river Jordan (Jaradat, 1987; 1997a) resemble domesticated durum wheat in being robust, large-seeded, early (in UJV) or late (in Jordan) maturing, and in other phenotypic traits.

The Fertile Crescent

The “historical” Fertile Crescent is a crescent-shaped territory that covered roughly the area from the Nile to Mesopotamia, including the eastern Mediterranean coastal strip (Zohary and Hopf, 1993; Blumler, 1991). The Fertile Crescent is one of four major centres of domestication; a region of southwest Asia comprising the valleys of the Twin Rivers (the Tigris and the Euphrates in Mesopotamia), the River Jordan, and their adjacent hilly areas. The region had favourable climate and biotic conditions to become not only the site of the origins of agriculture, but also of human civilization. After the most recent glacial period, the climate of this region has undergone several changes affecting the natural settings and biodiversity (Harlan, 1992); ecologically, however, the environment of the Fertile Crescent and the east Mediterranean region is fragile. Large areas of the once Fertile Crescent are now desert, semi-desert, steppe, or heavily eroded or salinized terrain unsuited for agriculture due to overexploitation of ecological resources that led to the destruction of the resource base (Nesbitt, 1995; Jaradat, 1998). Despite the scarcity of water and cultivable land, the Fertile Crescent was one of the major food-producing regions of the Old World for many centuries (Harlan, 1992). Today, it can barely support a rapidly growing population. It has become the largest food-importing region in the developing world due to its rapidly growing population at a time of sluggish growth in its agricultural production. The centre of wild emmer diversity (UJV) is a region of rocky Eocene limestone, receiving 400-600 mm of annual rainfall, and covered mostly by Mediterranean grassland vegetation (Noy-

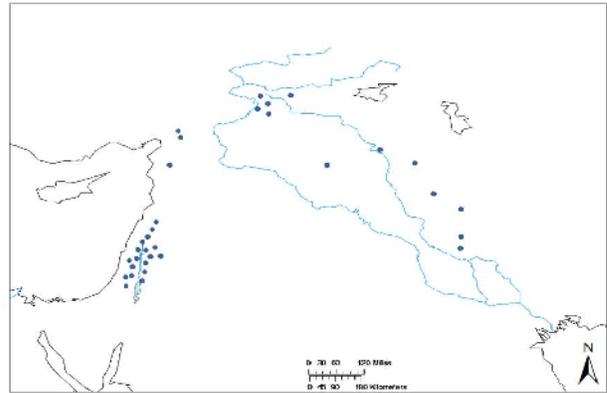


Fig 1. Map showing the approximate distribution of natural populations of wild emmer wheat in the Fertile Crescent (adapted from Zohary and Hopf, 1993).

Meir et al., 1991). The evidence of the sensitivity of wild emmer to intensive livestock grazing has interesting implications for the paleoecology and domestication history of the species. Most important factor was the existence, in the Mediterranean upland landscape, of small natural grazing refuges, where wild emmer plants and other species were relatively protected from grazing (Noy-Meir, 2001). Bonfil and Kafkafi (2000) investigated wild wheat adaptation in different soil ecosystems as expressed in the mineral concentration of the seeds. These researchers found that a genotype-habitat adaptation exhibited by yield components was related to yield quality rather than to yield quantity, and when a mineral nutrient is deficient in a natural soil, natural selection led to establishment of plants that store a higher concentration of that nutrient in the seed, for the benefit of the succeeding generation.

The plant community

Long before the beginning of agriculture, the Fertile Crescent was rich in what are still the most essential natural resources for mankind, i.e., a natural abundance of wild animals and plants that provided a protein-rich diet (Nesbitt, 1995; Harris, 1998a; 1998b). Phyto-geographically, the Fertile Crescent is strategically located in an area where the Mediterranean, Irano-Turanian, Saharo-Arabian, and Sudanian regions converge (Harlan and Zohary, 1966). Elements of all four phyto-geographical regions are found in parts of the Fertile Crescent, including wild relatives of a large variety of economically important plants such as cereals, legumes, fruit trees, vegetables, forage and pasture plants, aromatic plants, and medicinal plants (Harlan, 1992). Grasslands with scattered trees became the native habitat of early wild forms of wheat and barley, which still grow in many locations throughout the Fertile Crescent today. For many centuries, these wild cereals were harvested by hunter-gatherers but were gradually domesticated and cultivated along with other major crop plants, including vegetables, oil crops, fibre crops, spices, fruit and nut trees (Ladizinsky, 1998). Thus, a particular environment, a special plant community, and an adaptive population combined to initiate the Neolithic – the New Stone Age – in the Fertile Crescent about 10,000 years ago in which the systematic development of organized settlements occurred (Zohary and Hopf, 1993; Willcox,



Fig 2. Wild emmer wheat in its natural habitats (left, photo of wild emmer in Karadag-Gaziantep region of Turkey by H. Ozkan) and under high input agriculture (right, photo by AA Jaradat).

1995). Eight species, traditionally considered as the founder crops (Harlan, 1992) domesticated in the Fertile Crescent, are comprised of three cereals (diploid einkorn wheat, *Triticum monococcum*, tetraploid emmer wheat, *T. dicoccum*, and barley, *Hordeum vulgare*), three food legumes (chickpea, *Cicer arietinum*, lentil, *Lens culinaris*, and pea, *Pisum sativum*), flax as an oil/fibre crop (*Linum usitatissimum*), and a forage/feed legume, bitter vetch (*Vicia ervilia*).

Ecogeography

Wild emmer is uniquely adapted at the morphological, developmental, isozyme and seed storage protein levels to habitat variation in order to meet local micro- and macroenvironmental conditions (Xie and Nevo, 2008, and references therein). This adaptation potential explains the species' distribution over large ecological amplitude in the Fertile Crescent. The wide range of adaptation of wild emmer is impressive (Aaronsohn, 1909; 1910; Jaradat and Humeid, 1990; Valkoun et al., 1998); however, the local distribution and the dynamics of its populations are determined by local ecological factors (Noy-Meir, 2001), among which the nature of the substrate (i.e., rock and soil) and the regime of disturbance (cultivation, grazing, fire, perennials, etc.) are most important. Although the species is an east Mediterranean element, its distribution extends into marginal and semi-steppe regions; it grows in a variety of ecological conditions from hot and dry valleys to cool and humid mountains. The gradient in annual rainfall in its distributional range is wide (250-900 mm). It grows on different soil types such as terra rossa, basalt, and erosion products of Nubian sandstone. It is a constituent of the herbaceous cover of the deciduous oak-park forest (Aaronsohn, 1909; 1910; Nevo, 1986), in evergreen dwarf shrub formations, in pastures (where it is threatened by grazing), in abandoned fields, and on edges of, and occasionally within cultivated fields (Jaradat, 2001a; Valkoun et al., 1998), abundant in some places and very thin and scattered in others. The discovery of wild emmer (Aaronsohn, 1909; 1910; Katz, 2001) and the study of its geographical distribution and ecological requirements (Noy-Meir et al., 1991) greatly contributed to the delimitation of the geographical region where this wild wheat was taken into cultivation and to understanding the course of domestication of tetraploid and hexaploid wheats. Domestication of these wheats took place within the geographical distribution area of wild emmer suggesting that the wild species was harvested from wild stands throughout

the Levant in the western arc of the Fertile Crescent long before actual farming began (Bar-Yosef and Meadow 1995). An in-depth understanding of the ecology and dynamics of wild emmer in its native environment is essential for the conservation and management of its populations (Noy-Meir, 2001). Wild emmer is ecologically more demanding than most other wild grasses (Zohary and Hopf, 1993); it is not a weedy plant, was never a dominant species, and its present-day distribution is discontinuous. This discontinuity suggests that the species now occurs less widely than in earlier times. Harlan (1992) suggested that it may have been displaced during the last ice age down slope in the Zagros Mountains towards the Fertile Crescent; its discovery at Çayönü (40° 12' N and 37° 23' E) ~ 900 km north of the UJV in the Fertile Crescent suggested a rather wider distribution at the time of its domestication. Therefore, it is necessary to study the ecological affinities of given phenotypes in order to establish a quantitative relationship between heterogeneous habitats and phenotypic diversity of the species (Anikster et al., 1991).

Genetic diversity of wild emmer wheat

Wild emmer is a genetically and morphologically highly polymorphic species for a wide range of qualitative and quantitative traits of value for wheat breeding. The genetic diversity of wild emmer populations, throughout its distributional range in the Fertile Crescent, is ecogeographically structured and largely adaptive at the local and regional levels. The macrogeographical contexts of wild emmer genetic diversity involved studies across a relatively short (~200 km) gradient of increasing aridity from the mesic to xeric habitats and across the western and eastern arcs of the Fertile Crescent, whereas; the microgeographical contexts involved topographical, climatic, edaphic, and geological contrasts.

Macrogeographical diversity

The geographical distribution of wild emmer in the Fertile Crescent encompasses central, peripheral, and marginal populations (Poyarkova et al., 1988; Valkoun et al., 1998; Jaradat, 2001a). Central populations thrive in favourable but heterogeneous environments and found to be more diverse, especially in readily observable morphological and qualitative traits, than peripheral or marginal populations. Peripheral populations are usually scattered over relatively

large area, while marginal populations, in which specialized traits narrowly adapted to particular niches may have undergone fixation (Horovitz and Feldman, 1991), are confined to small patches or are sparsely scattered. Wherever it is quite common and locally abundant, wild emmer occupies a variety of primary and secondary habitats and grows in batches in mixed stands with grasses (e.g., wild barley and wild oat) and several legumes (Anikster and Noy-Meir, 2001; Noy-Meir, 2001). At the macrogeographical scale, Nevo and Payne (1987) found that gene diversity increases towards the more arid regions; however, at a microgeographical scale, the relationship between gene diversity and habitat heterogeneity was not clear (Felsenberg et al., 1991). On the other hand, regional studies on allozyme diversity indicated the presence of distinct local differences over short geographical distances. Populations from mesic environments were genetically more variable than those from the xeric environments; this variation is predictable by climatic regimes and soil type (Nevo, 1998; Jaradat, 1997c). Most studies (Nevo, 2001 and references therein; Jaradat, 2001b), however, concluded that genetic differentiation, at the macrogeographical level, displayed the typical “archipelago” population genetics and ecology structure of the species.

Microgeographical genetic diversity

Micro-geographical studies of storage proteins, phenotypic, allozymes and DNA differentiation in wild emmer could contribute to a better understanding of the nature and dynamics of genetic polymorphisms and the evolutionary forces shaping their genomic structure (Nevo et al., 1991; Felsenberg et al., 1991). The levels of genetic diversity vary non-randomly among populations, and the genetic diversity, based on biochemical and molecular markers, is partly correlated with, and predictable by ecological factors (Nevo et al., 1998; Li et al., 2000; Fahima et al., 2002). Significant differences were found among wild emmer populations at the micro-geographical level for morphological, germination, and phenological traits when grown under standardized controlled conditions. Obviously, sporadic selection pressures, high selfing rates, and limited gene flow are shaping the genetic structure (see below) and the evolution of multi-locus structures in wild emmer at the micro-scale level (Nevo et al., 1998; 1991). DNA polymorphisms were found to be significantly associated with unique microclimatic stresses (Peleg et al., 2008a; 2008b). Linkage disequilibrium found in wild emmer populations under contrasting microclimate conditions, suggests that natural selection impacts both two-locus and multi-locus DNA associations, and that microclimate selection plays an important role in the maintenance of DNA and protein polymorphisms in the wild species. Soil divergence at a microscale was reported to be as selective as microclimatic selection (Nevo et al., 1991; Nevo, 1998); this divergence created substantial allozyme differentiation in wild emmer between soil types, and several allozymes displayed consistent specific associations with soil type. On average, multilocus organization intensity is higher in wild emmer growing on terra rossa than on basaltic-derived soils. If allozymes diversity indeed varies dynamically with the environment, then not only its macro- but also its microgeographic structure is tractable by ecological factors. Such clues may help in optimizing the exploitation, conservation and utilization of wild emmer genetic resources in wheat breeding (Feldman and Kislev, 2007; Chatzav et al., 2010). Due to allozyme diversity at the spatio-temporal level and at both the macro- and

microgeographic scales, sampling strategies of wild emmer germplasm should be designed to accommodate these factors and capture the maximum genetic diversity available in natural populations. Therefore, sampling strategies, exploitation, conservation, and utilization of wild emmer genetic resources for breeding could be substantially optimized if macro- and microecological differentiations are closely followed (Levy and Feldman, 1988; Anikster and Noy-Meir, 1991; Felsenberg et al., 1991).

Population genetic structure and dynamics

The genetic structure and the underlying genetic diversity of natural populations of wild emmer and the manner this diversity is partitioned within and among populations, as well as the factors maintaining the variation in these populations, have been studied extensively (e.g., Nevo et al., 1991; Li et al., 2000; Nevo, 1998; Jaradat, 2001a; 2001b; Ozbek et al., 2007). These studies used germplasm collected from central, peripheral, and marginal populations, and from the southwestern and northeastern groups of populations in the Fertile Crescent and employed different analytical methods, including morphological, biochemical, molecular and disease-reaction methods. Although the southwestern and northeastern groups of populations of wild emmer are geographically semi-isolated, there are sporadic connections in northern Syria between the two groups (Valkoun et al., 1998). Both groups may contain desirable, and complementary, genetic diversity to be used in future breeding programs.

Population genetic structure

Wild emmer, with its central, peripheral, and marginal populations, has a unique ecological-genetic structure. Central populations are massive and lush and represent their centre of origin and diversity. Peripheral, and to some extent marginal, populations become fragmented into sporadic semi-isolated and isolated populations that are characterized by an archipelago genetic structure in which alleles are built up locally in high frequency but are often missing in neighbouring localities (Poyarkova, 1988; Jaradat, 1997a). The influence of unique ecogeographic conditions in the Fertile Crescent have been demonstrated on the genetic structure of many wild emmer populations based on the biochemical and molecular markers (Li et al., 2000; Nevo, 2001; Jaradat, 2001a; 2001b). Extensive data at different levels of genome organization (Li et al., 2000; Ozbek et al., 2007) indicated that the population genetic structure of wild emmer is mosaic. This structure appears to reflect the underlying ecological heterogeneity which derives from local and regional geological, edaphic, climatic, and biotic differentiations in the Fertile Crescent (Nevo, 2001). The mosaic genetic structure of wild emmer is manifested in the large inter-population and inter-regional polymorphisms obtained with DNA and microsatellite analyses and were consistent with those obtained with isozymes and different DNA markers for different collections of wild emmer covering a wide geographical range (Li et al., 2000; Ozbek et al., 2007; Peleg et al., 2008a; 2008b). These polymorphisms demonstrate geographical and genomic congruence and continuity from macro- to microscale and from coding to noncoding DNA (Li et al., 2000, and references therein), and could represent a regulatory adaptation to the climatically fluctuating environment in the Fertile Crescent. Moreover, these polymorphisms may be considered as adaptation to shorten the life cycle and avoid the early summer drought,

especially in the xeric parts of the species' distribution (Nevo and Chen, 2010). For example, a large portion of the HMW-glutenin and allozymes variant alleles were localized, especially in xeric habitats (Nevo, 1988). Gene differentiation estimates based on HMW-glutenins and allozymes among and within populations were found to be smaller in xeric as compared to mesic habitats in the Fertile Crescent. Population differentiation estimates indicated that population divergence in wild emmer does not always conform to the isolation by distance model. This "island" population model holds for populations from the more arid part of the western arc of the Fertile Crescent as well (Jaradat, 2001b). In addition, Pagnotta et al. (1995) uncovered a patchy distribution of alleles and genotypes at the micro- and macrogeographic levels. These researchers attributed it to environmental heterogeneity which has a potential for generating significant spatial structuring in populations that occupy patchy habitats. Therefore, environmental heterogeneity may have been involved in generating significant spatial structuring in the species as evidenced by a gradual increase in allozymes monomorphism with aridity suggests that polymorphism is more likely to be found in heterogeneous environments (Jaradat, 2001b; Nevo and Chen, 2010), and that variable traits in this selfing species with restricted gene flow are expected to have a patchy rather than diffused distribution (Hamrick and Godt, 1990; Nevo, 1998). The characteristic population structure of wild emmer is reinforced by the findings that spatial factors accounted for large portions (>60%) of total variation in phenotypic diversity indices, suggesting strong provenance specificity (Anikster et al., 1991). Whereas, temporal variation was less pronounced than spatial variation, and there were no drastic changes between years in frequency of genotypes, and both spatial and temporal variation varied among populations (Nevo, 1986; 1998; Jaradat, 2001a; 2001b).

Population dynamics

Population dynamics of wild emmer was the subject of long-term studies in the western arc of the Fertile Crescent (Noy-Meir et al., 1991; Horovitz and Feldman, 2001; Jaradat, 2001a, 2001b). These studies were based on spatio-temporal variation in phenotypic, allozymes, and seed storage proteins, and identified rainfall, rockiness, and grazing as the primary factors that interact to affect demographic processes in wild emmer populations; hence they are probably the major selection forces also affecting its genetic structure and genetic diversity. Moreover, population dynamics for morphological, phenological and yield traits varied non-randomly among plant progenies from different habitats (Anikster et al., 1991; Nevo et al., 1991; Nevo, 2001), and the variation in quantitative productivity traits had a very large environmental component and the environment modified the 2-trait and multi-trait associations (Nevo et al., 1991; Jaradat, 2001a). Similarly, the spatial distribution of HMW-glutenin genotypes was non-random; however, temporal changes in genotypes had little effect on the frequency of different HMW-glutenin genotypes, and a high affinity was found between specific HMW-glutenin genotypes and certain habitats (Felsenburg et al., 2001; Jaradat, 2001b). Also, population dynamics were identified at the allozymes' diversity level in response to spatio-temporal ecological factors, especially aridity stress, and were considered partially adaptive (Nevo et al., 1991; Jaradat, 2001b). A general conclusion derived from these studies suggested that in central populations, the within-populations diversity was

larger than among-populations diversity; whereas, it was the opposite in marginal and peripheral populations. Also, these studies showed that genetic differentiation was primarily regional and local, not clinal, with approximately 70% of the variant alleles were common and not widespread, but rather localized and sporadic, displaying the typical "archipelago" population genetics and ecology structure of the wild species. This conclusion was reinforced by results of microgeographic allozymes analyses based on edaphic, topographic, and temporal differentiation, and on microclimatic local differentiation (Nevo et al., 1998 and references therein; Xie and Nevo, 2008). Similar genetic patterns to those of the allozymes analyses were obtained with DNA analyses at macro- and microgeographic scales (Li et al., 2000), and supported by the analyses of allele distribution where sharp local differentiations were found over short geographical distances (Nevo, 2001). Nevertheless, temporal changes in population density (Noy-Meir et al., 2001), size, and the occasional loss of small (marginal) populations are warning signs indicating that these populations may be vulnerable. Also, Jaradat (2001b, 1997c) remarked that marginal and peripheral wild emmer populations are becoming semi-isolated and smaller in population size over time; such populations may experience extreme ecological conditions, representing the boundaries of the climatic range of the species, and may become extinct.

Genetic resources of wild emmer wheat

Potential and actual genetic resources of wild emmer for wheat breeding have been the subject of numerous studies covering large parts of the species' distribution in the Fertile Crescent (e.g., Horovitz and Feldman, 1991; Jaradat, 1987; 1993; Feldman and Millet, 2001). These studies revealed the availability of rich and diverse *in situ* and *ex situ* genetic resources applicable in wheat improvement. However, most of the discovered resources are not tapped, yet (Feldman and Millet, 2001), and it may take many years to explore, evaluate, and utilize these genetic resources in wheat improvement. Genetic mapping techniques have been extensively used in mapping the wheat genomes (e.g., Krugman et al., 1997; Li et al., 2000; Lou et al., 2007) and revealed linkages between genetic markers and agronomically important traits (QTLs); these genetic maps are expected to enhance the conservation and utilization of wild emmer genetic resources (Li et al., 2000). The wild emmer genetic resources available either *in situ* or stored and partially characterized and evaluated in genebanks (*ex situ*) have been described by many authors (e.g., Felsenburg et al., 1991; Ciaffi et al., 1993; Nevo, 1998; Cakmak et al., 2004). These genetic resources harbour genotypic variation for morphological, phenological, agronomic, biochemical, and molecular traits. Valuable genetic variation was also discerned for tolerance or resistance to biotic (e.g., foliage diseases), and abiotic (e.g., drought, salinity, heat) stresses (e.g., Dinooor et al., 1991; Kumar et al., 2007; Farooq, 2009). In addition to wild emmer, domesticated emmer (*Triticum dicoccum*), after being cultivated for ~7,000 years in a large range of ecogeographic conditions in the Fertile Crescent and the larger Near East region (Giuliani et al., 2009; Zaharieva et al., 2010) became a potential genetic resource for wheat improvement. Cultivated emmer mirrors the geographic subdivision of wild emmer into the northern and southern populations in the Fertile Crescent (Lou et al., 2007); gene flow between wild and domesticated emmer occurred across the entire area of wild emmer distribution (Dvorak et al., 2006; Lou et al., 2007), and was found to harbour

tremendous genetic diversity for nutritional quality, resistance to pests and diseases, and tolerance to abiotic (heat and drought) stress (Al Hakimi et al., 1998; Dinoor et al., 1991). Cultivated emmer harbours more diverse alleles for synthesis of gluten-type, a very important quality trait which determines the commercial value of the wheat crop, than modern cultivated wheats, and could be considered as a potential source for gluten strength improvement in durum and bread wheats. A potentially valuable genetic resource derived from wild emmer and other wild wheat relatives is “synthetic” wheat, i.e., a product of conventional cross between the highly diverse wild parents of wheat (Berzonsky et al., 2004; Ogbonnaya et al., 2007). Synthetic wheats may have many novel genes and can be crossed to bread wheat and would result in promising synthetic derivatives. Among the derivatives, several showed high yield, large grains, deep roots, tolerance to biotic and abiotic stresses and increased or novel quality traits (Rajaram et al., 2001; Warburton et al., 2006; Vasil, 2007); other derivatives, adapted to changing production conditions, out yielded commercial cultivars by 18-30% and have genetic diversity similar to wheat landraces (Ginkel and Ogbonnaya, 2007). Ogbonnaya et al. (2007) reported significant yield advantages of synthetic backcross-derived lines across diverse rain-fed and irrigated environments in Australia, with yield advantage of 8-30% over the best local check, and concluded that useful genetic variation for yield potential exists in synthetic wheat.

Phenotypic and morphological traits

Morphology and phenology vary geographically in the wide altitudinal distributional range of wild emmer. Robust, early-maturing types grow on the warm winter slopes at low altitude; whereas, slender and late-flowering types are more abundant at higher elevations (>900 masl). Two races were identified and described by Poyarkova et al. (1991); whereas, three ecotypes have been described by Jaradat (1997a). N.I. Vavilov (c.f. Poyarkova et al., 1988) concluded that *T. dicoccoides* is a complex species, divided into two groups: the narrow-spiked forms (*T. dicoccoides* subsp. *horanum*) located in Hauran plateau (east of UJV) and the wide-spiked forms (*T. dicoccoides* subsp. *judaicum*), located in Palestine. Poyarkova et al. (1988) confirmed the existence of two distinct morphological types within *T. dicoccoides*. One is barely distinguishable from the wild einkorn, whereas the other is similar to cultivated durum wheat. The morphological and phenological traits of these “sub-species” are associated with some of their yield-related and phenotypic traits. First- and second-order associations identified among phenotypic traits reflect functional adaptation of the species to arid and semi-arid Mediterranean environments (Nevo, 1998; Jaradat, 2001a). Recently, however, two different genetic taxa have been identified (Ozkan et al., 2002; 2005) within wild emmer – a western race and a central-eastern race along the Fertile Crescent. The latter is more closely related to cultivated wheat, suggesting that this group only contributed to the germplasm of domesticated wheat. Phenotypic distances among populations were highly influenced by latitude and rainfall quotient of collection sites. Nevertheless, most, if not all phenotypic and morphological traits may be valuable and merit testing because they are potentially useful in a wheat breeding programs. The potential value of the wild species, either for *in situ* conservation, or more importantly for breeding purposes, can be initially gauged by its phenotypic traits. Large variation was found among and within populations at local and regional levels for functional adaptation of growth

type, leaf architecture, tillering capacity, spike quantitative traits, and phenology (Nevo, 1986; Jaradat, 1993; 1997a; Nevo, 2001). Temporal variation in phenotypic and morphological traits, although not as large as spatial variation, may reflect the species’ reaction to climatic and biotic differences and constitutes a measure of the species’ phenotypic plasticity in response to different stresses (Nevo et al., 1988; Peleg et al., 2008a; 2008b). Genes regulating ecological adaptation for biotic and abiotic stresses are found on genome B of wild emmer which was derived from *Aegilops* spp. (Feuillet et al., 2007).

Agronomic traits

Spatio-temporal variation in yield-related traits of wild emmer in the Fertile Crescent reflects genotypic interaction with, and adaptation to, habitat-specific variation patterns (Anikster and Noy-Meir, 2001; Feldman and Kislev, 2007). Functional adaptation (Jaradat, 2001a) is displayed by wild emmer germplasm as strong phenotypic trait associations, coupled with large level of diversity (>60%) which was accounted for by differences among collecting sites for a number of agronomic (stem, leaf, spike and seed) traits. Some wild emmer genotypes currently growing in the Fertile Crescent can display grain weight values ranging from 20-35 mg suggesting that the domestication process did not necessarily result in a considerable increase in grain weight (Ferrio et al., 2007). Genes controlling some of the most important agronomic traits are found preferentially on the A genome of wild emmer which was derived from *Triticum urartu*; (Feuillet et al., 2007). Wild emmer populations, especially those adapted to xeric habitats evolved an escape mechanism manifested by their early heading in hot dry environments. These populations are characterized by shorter vegetative period which was necessarily associated with lower vegetative dry matter and stem length; however, these adaptations may result in more favourable conditions during grain development leading to greater spike dry matter and harvest index (Araus et al., 2007). In addition to the agronomic traits available in wild emmer for cultivated wheat improvement, a relatively high level of genetic diversity was found in cultivated emmer for agronomic traits of value for the health food industry (Giuliani et al., 2009). The potential breeding value of cultivated emmer accessions collected from its primary and secondary centres of diversity was found to be equally valuable for wheat improvement (Teklu et al., 2007; Zaharieva et al., 2010).

Biochemical markers

Wild emmer is a rich genetic resource for seed storage proteins (Avivi, 1987; Desefeld et al., 2007), a very important quality trait which determines the commercial value of wheat crops. Seed storage proteins (mainly HMW-glutenins) have been studied intensively in wild emmer, not only because of their nutritional value (Uauy et al., 2006), but because they provide a biological model system for the spatio-temporal regulation of gene expression (Levy and Feldman, 1988; Felsenberg et al., 2001). As genetic markers, HMW-glutenin subunits are easily resolved by electrophoresis, highly polymorphic, their pattern of polymorphism is species- and genome-specific, and their various alleles are co-dominant; therefore, the genotype can be determined directly from gel patterns. However, because they are located on the long arm of three homoeologous chromosomes (i.e., 1AL, 1BL, and 1DL), they cover only a small part of the wheat genome (Nevo; 1998; Felsenberg et

al., 2001). Due to their high polymorphism, these genes have been used extensively in wheat population genetics studies to complement studies based on allozyme markers (see below). Their pattern of spatial distribution in natural wild emmer populations is not random; therefore, it affects population structure (i.e., variation within and among populations) and helps associate certain genotypes with specific environments due to affinity between certain genotypes and specific habitats (Felsenburg et al., 1991; Jaradat, 2001b). Their temporal variation is generally stabilized by the buffering capacity of the seed bank in the soil as it responds to fluctuations in population size or extreme environmental conditions (Anikster and Noy-Meir, 2001). Cultivated emmer harbours more diverse alleles than modern cultivated wheats for the synthesis of gluten-type proteins (Giuliani et al., 2009; Zaharieva et al., 2010) and is considered as a potential genetic resource for gluten strength improvement in tetraploid and hexaploid cultivated wheats (Al Hakimi and Monneveux, 1998; Gomez-Becerra et al., 2010). Genetic differentiation of wild emmer based on isozyme markers was demonstrated at the macro- and micro-geographical levels (Nevo et al., 1991; Li et al., 2000; Jaradat, 2001b). Allozyme diversity was found to vary with the environmental conditions; this may help maximize the exploration, conservation and utilization of wild emmer genetic resources in wheat breeding. Isozyme markers in wild emmer are controlled by a larger number of loci as compared to HMW-glutenins (Nevo, 1991); however, each locus exhibits a much narrower polymorphism and has a smaller value of genetic diversity. Almost all population studies (e.g., Nevo et al., 1991; Li et al., 2000; Jaradat, 2001b) concluded that spatial factors were more important than temporal factors in maintaining allozyme polymorphism in wild emmer, and aridity of population habitat is a major differentiating factor (Nevo et al., 1991). Population studies (Hamrick and Godt, 1990) also suggested that allozymes polymorphism in wild emmer are partly adaptive and are differentiated primarily at the multilocus level by climatic factors (e.g., temperature, water availability, and light intensity stresses). Population differentiation based on allozyme variation (approximately 40% partitioned within and 60% between populations) support the archipelago population structure of wild emmer (Hamrick and Godt, 1990; Nevo et al., 1991). Allozyme variation was significantly correlated with, and partly predictable by climatic and edaphic factors, and no similar geographic patterns were found across loci, thus eliminating migration as a major factor of population genetic differentiation (Nevo, 1998). The numerous genes and rich polymorphisms found in wild emmer - and -amylases may provide unique genetic resources of agricultural importance for improving wheat germination and growth under less favourable conditions (e.g., drought) (Nevo and Chen, 2010). In addition, the wide range of diversity in dimeric -amylase inhibitors of wild emmer is candidate for control of seed weevils (Wang et al., 2008).

Molecular markers

Several molecular markers have been employed to characterize genetic resources, quantify genetic diversity, identify trait associations and decipher population structures of wild emmer (Li et al., 2000; Dvorak et al., 2006; Ozbek et al., 2007). Significant correlates of RAPD (i.e., noncoding) loci have been found with various climatic and soil factors and suggested that natural selection causes adaptive RAPD ecogeographical differentiation. The RAPD markers, besides being useful for the estimation of genetic diversity in wild

emmer, they have been used for the identification of suitable parents for the development of mapping populations and tagging agronomically- important traits derived from wild emmer. Results of RAPD polymorphism analyses, in agreement with allozyme patterns in the predominantly selfing species, indicated that migration is not an important factor in shaping population structure of wild emmer. However, genetic diversity estimates based on RAPD analyses are much higher than those based on allozymes (Li et al., 2000). Although Southeastern Turkey is considered an important area in the context of wheat domestication (Salamini et al., 2002; Ozkan et al., 2002; 2005), Tanyolac et al. (2003) found low genetic diversity in wild emmer from Southeastern Turkey as revealed by RFLP markers. This could be attributed to differences in effective population size, or mutation rate. On the other hand, Ozbek et al. (2007) used AFLP diversity to assess the contribution of spatial versus temporal factors to the maintenance of genetic variation in wild emmer and found that genetic diversity was much larger within populations than between populations and that the temporal genetic diversity was considerably smaller than the spatial one. In-depth molecular analyses based on nucleotide diversity (Haudry et al., 2007) indicated that wild emmer is not a highly polymorphic species. Supposedly, wild emmer evolved through a relatively recent allopolyploidy event that may have resulted in a large decrease in diversity in the new wild species as compared to its diploid ancestors (i.e., donors of the A and B genomes). Also, upon crop domestication and the spread of agriculture, the natural range of wild emmer might have been restricted, potentially accounting for a low effective population size (Dvorak et al., 1998; 2006).

Breeding value of wild emmer wheat

The primary genetic basis of hexaploid wheat was very narrow compared to the wider genetic base of tetraploid wheat (Reif et al., 2005; Haudry et al., 2007). The tetraploid evolved through populations; whereas hexaploid wheat evolved through single genotypes. Upon domestication of wild emmer, it was estimated that initial diversity was reduced by 84% in durum wheat and by 69% in bread wheat as a result of massive loss of nucleotide diversity in the evolution of durum wheat, which was one of the largest reported so far for a crop species (Haudry et al., 2007). Although the genetic base available in cultivated wheat is expanding, molecular evidence has affirmed that it remains very narrow (Reif et al., 2005; Warburton et al., 2006). Whereas, it is unclear whether continued reshuffling of alleles by breeders in the existing elite gene pool can achieve the same level of genetic gain achieved during the past ~60 years, wheat breeders and geneticists agree that enrichment of the cultivated gene pool will be necessary to meet the challenges that lie ahead (Lemaux and Qualset, 2001; Feldman and Kislev, 2007). The evidence relevant to wheat improvement using wild emmer genetic resources derives from numerous studies on the species' population genetics and ecology, climatology, phytopathology and immunology, biochemistry, physiology, agronomic traits, and breeding practices (Nevo, 1998). The tremendous enhancements of yield by modern wheat breeding may have inadvertently reduced its diversity (Harlan, 1995) and would threaten future selection progress (Rajaram et al., 2001; Warburton et al., 2006). If modern wheats become genetically more uniform, the vulnerability of global wheat production to a devastating new disease or insect pest outbreak would be high (Rajaram et al., 2001). Therefore, increased genetic diversity derived from wild emmer and other wild relatives of

wheat can provide a buffer against such risks. Aaronsohn (1909) recognized the agronomic importance of certain traits he observed on the wild emmer specimens he collected; these included large grain size, drought tolerance, and resistance to rust. He recommended using the wild species in wheat improvement, especially for drought tolerance and rust resistance. The early attempts during the 1900s to use wild emmer in breeding programs (reviewed in Katz, 2001) demonstrated the possibility of gene transfer to cultivated wheat; however, these attempts failed to achieve their objective in improving bread wheat due to lack of genetic and cytogenetic knowledge of wheat species, and a poor understanding of the relationship between wild emmer and domesticated bread wheat. Later in the 20th century however, a renewed interest in wild emmer as a genetic resource resulted in successful transfer of a number of desirable traits to bread wheat (Avivi, 1978; 1979; Feldman and Millet, 2001). Traits that were identified in wild emmer and those transferred to cultivated wheat include agronomic traits (e.g., biomass, earliness, grain N content, micronutrients, and yield), protein quality and quantity traits (e.g., high grain protein, novel gliadins, and HMW- and LMW-glutenins), abiotic stress tolerances (e.g., salt, drought, and heat), and biotic stress tolerance (e.g., powdery mildew, Fusarium head blight, leaf rust, stem rust, stripe rust, wheat soil-born mosaic virus, tan spot, leaf blotch, and resistance to insect pests) (Bennet, 1984; Berzonsky et al., 2004). However, despite the extensive knowledge of its potential as a donor for a large number of agronomic, biochemical and molecular traits, both direct and indirect evidences (Horovitz and Feldman, 1991; DePauw et al., 2005; Xie and Nevo, 2008) indicate that wild emmer has not been very widely and fully exploited in wheat breeding.

Abiotic stresses

Heat and drought have been identified as the most important factors associated with the largest economic losses of wheat yield in ~90% of the wheat-producing countries (Chatrath et al., 2007; Kosina et al., 2007). The genepool of wild emmer is a rich resource for allelic variants of agronomically important traits required for wheat improvement such as drought (Peleg et al., 2005; 2008b) and salinity tolerance (Nevo et al., 1993; Nevo and Chen, 2010). In the hot, dry environment of the Fertile Crescent, wild emmer populations evolved an escape mechanism as manifested by shorter vegetative growth period and early heading. This adaptation may lead to greater spike dry matter and larger harvest index (Araus et al., 2007). Genetic dissection of drought related traits, through QTL analyses, provided valuable insights into drought adaptive mechanisms. Results of a study of the allelic diversity associated with aridity gradient (Peleg et al., 2008a) exemplify the unique opportunities to exploit favourable alleles that were excluded from the domesticated genepool and may serve as a starting point for introgression of promising QTLs into cultivated wheat via marker-assisted selection and breeding. The greatest allelic diversity (Peleg et al., 2008b) and drought tolerance (Peleg et al. (2005) found in wild emmer populations collected from intermediate, mesic aridity levels and exposed to large climatic fluctuations, may be valuable for increasing fitness of cultivated wheat in the more fluctuating environments (Nevo and Chen, 2010). The strong unimodal relationship identified (Peleg et al., 2008a) between allelic diversity in wild emmer and annual rainfall ($r=0.74$) suggests that populations originated from habitats with intermediate environmental stress have higher allelic diversity for drought tolerance. This

finding demonstrated that the “intermediate-disturbance hypothesis,” explaining biological diversity at the ecosystem level, also applies at the genetic diversity level within wild emmer. Some of the ancient and obsolete tetraploid wheats are rich sources for drought tolerance-related traits. Past (Al Hakimi and Monneveux, 1998) and recent (Zaharieva et al., 2010) reports indicated that many accessions are potentially useful for the improvement of drought tolerance in durum wheat. The use of old tetraploid wheats combined with a bulk modified breeding method is promising not only for increasing yields in durum wheat in drought-prone environments but also to improve durum wheat yield stability across a wide range of climatic conditions (Al Hakimi and Monneveux, 1998). Global climate change, including global warming, drought, and salinity, threaten the world’s food supply (Semenov et al., 2009). Although substantial advances have been made in breeding wheat for saline environments that will also improve its performance in dry environments, real salt-tolerant wheat genotypes derived from wild relatives that can be used in farmers’ fields have not yet been produced (Farooq, 2009). With global change, characterized by shifts in weather patterns and increases in frequency and magnitude of extreme weather events, new wheat ideotypes will be required with a different set of physiological traits (Semenov et al., 2009). Therefore, breeding strategies for the future climate, especially at higher latitudes where most global wheat is currently produced, might need to focus on wheat varieties tolerant to high temperature; whereas, drought and salinity tolerance might become the focus of breeding programs at lower latitudes.

Biotic stresses

Sources of host plant resistance have been identified in wild relatives of cultivated wheat, including wild emmer; they were widely and efficiently used in national (Gerchter-Amitai and Grama, 1974; Duveiller et al., 2007) and international (Rajaram et al., 2001) wheat breeding programs. The utilization of wild emmer in breeding programs for disease resistance began with the discovery of its resistance to stripe rust (Gerchter-Amitai and Stubbs, 1970), then the discovery of its high protein content (20-24%) (Avivi, 1978), and large seed weight (~35 mg seed⁻¹), the three of which were combined in hexaploid wild emmer-derivatives and tested for a number of milling and baking quality traits (Rao et al., 2010). Seedling and adult plant resistances to leaf and stem rusts were identified in recently collected wild emmer germplasm, especially from the centre of its diversity (UJV) where wild emmer populations are most extensive and genetically diverse (Anikster et al., 2005). Resistance genes derived from wild emmer were used in conferring resistance in breeding populations (Gerchter-Amitai and Stubbs, 1970; Gerchter-Amitai et al., 1989). New partial resistance genes for durable protection against leaf rust in cultivated wheat are expected to come from this collection; whereas, novel genes for Fusarium head blight QTL have been recently identified on chromosome 7A in wild emmer (Kumar et al., 2007). In addition to resistance genes derived from wild emmer, those from cultivated emmer proved of significant value in wheat breeding. Cultivated emmer cv. “Yaroslav” was used in crosses with hexaploid wheat to develop cv. “Hope” (and other resistant varieties) which had a high degree of adult plant resistance to stem rust (conferred by the *Sr2* gene) in many field trials (McFadden, 1930). The *Sr2*-complex has been incorporated, and remained effective, into numerous wheat varieties grown globally in stem rust-prone areas of the world. The *Sr2* gene derived from “Yaroslav” was

responsible for control of stem rust epidemics at a global scale (Rajaram et al., 2001). Wild emmer germplasm was used in the development of transgenic lines expressing genes that confer resistance to non-selective herbicides, and to pests and pathogens (Krugman et al., 1997). Also, sources of host plant resistance to Hessian fly (*Mayetiola destructor*), a major pest in the Near East, especially North Africa, have been identified in cultivated emmer and wild wheats and widely used in breeding programs (Miller and Pike, 2002). Amylase genes and alleles, and their regulator GA_3 genes, may be unique in some wild emmer populations, particularly those collected from xeric habitats of the Fertile Crescent. Rapid germination and quick growth of these populations are adaptations to escape the early hot dry summer climate (Nevo et al., 1991; Jaradat, 2001b; Wang et al., 2008). Also, - and -amylases can be used as useful markers for chromosomal locations of QTLs. As biochemical markers, the -amylase loci, in particular, can be resolved simultaneously and they are better than morphological loci because they are easily identifiable; they have been used as probes to map herbicide resistance genes in wild emmer (Krugman et al., 1997).

Nutritional quality

Temporal stability of grain protein and nutrient concentrations, as indicators of nutritional quality, is of interest for plant breeders and for both commercial and subsistence producers in the developed as well as the developing world (Cakmak et al., 2010). Also, micronutrient malnutrition, especially deficiency in Fe and Zn, afflicts more than three billion people, mostly in the developing world (Distefeld et al., 2007). The high genotype x environment interactions for grain protein and nutrient concentrations have been reported in cultivated wheat as well as for wild emmer under contrasting conditions of water availability (Peleg et al., 2008a; Gómez-Becerra et al., 2010); therefore, temporal stability should be considered when selecting donor wild emmer germplasm for breeding purposes. On the other hand, Oury and Godin (2007) confirmed the negative relationship between grain yield and grain protein, whether in extensive or intensive cropping systems, and concluded that this relationship is highly variable due to high genotype x environment interactions for both quality traits. However, DePauw et al. (2007) concluded that the undesirable correlations between grain yield, grain protein concentration and time to maturity can be shifted by developing wheat genotypes that can produce and partition more dry matter to the grain, while having better water- and nitrogen-use efficiencies than current genotypes.

Seed storage proteins

Genetic diversity for grain protein, including HMW-glutenin subunits, and its temporal stability was reported for wild emmer from large parts of the Fertile Crescent and led to its use for the improvement of high protein content and bread-making quality in bread wheat (Felsenburg et al., 1991; Ciaffi et al., 1991; 1993; Jaradat, 2001b). The utilization of wild emmer in breeding programs followed the discovery of its high protein content (20-24%), and large seed weight (~35 mg seed⁻¹), both of which, along with rust resistance, were combined in hexaploid wild emmer-derivatives and tested for a number of milling and baking quality traits. Another set of wild emmer-derivatives was recently identified and proved superior to standard bread wheat in total content of grain nitrogen and flour protein (Rao et al., 2010). The high protein concentration gene (*Gpc-B1*), derived from wild

emmer, was used to increase grain yield while holding protein concentration at a market acceptable level (Joppa and Cantrell, 1990; DePauw et al., 2007). Whereas, Kushner and Halloran (1984) combined high grain weight and high protein content from wild emmer in hexaploid wheat lines. The wild emmer accession "FA-15-3" showed very high grain protein content and was the source of the locus *Gpc-B1* (Joppa et al., 1997). This trait was transferred to hexaploid wheat and resulted in the release of cv. "Glupro," a bread wheat variety with high grain protein content (DePauw et al., 2007; Brevis et al., 2010).

Macro- and micronutrients

Increasing nutrient concentration of cereal seeds through breeding requires the existence of substantial and useful genetic variation, especially for micronutrients in seed of donor parents (Cakmak et al., 2010). Wild emmer has a wide and promising genetic variation for grain concentration of both micro- and macronutrients, and is a potential resource for the genetic improvement of nutrient content in the grain of modern wheat (Cakmak et al., 2004; Gómez-Becerra et al., 2010). However, other species of the Triticeae (Garg et al., 2009; Farooq, 2004), besides wild emmer, harbour genes that control mineral uptake, as was shown for example in the case of K/Na discrimination under saline conditions (Farooq, 2009). Strong associations were found between eco-geographical origin and grain nutrients in germplasm of wild emmer collected from different habitats across the Fertile Crescent (Peleg et al., 2008b; Chatzav et al., 2010; Gómez-Becerra et al., 2010); these association may indicate the existence of one or more common genetic-physiological mechanisms involved in mineral uptake, translocation, and remobilization to the grain and accumulation in the developing grain. The genotype-habitat adaptation exhibited by yield components of wild emmer in different soil ecosystems, as expressed by the mineral concentration of its seeds, is related to yield quality rather than to yield quantity (Bonfil and Kafkafi, 2000). This adaptation is demonstrated by the ability of wild emmer plants to concentrate in the grains the highest amount of a particular soil-deficient nutrient. Natural selection leads to the establishment of plants that can store in the seed higher concentration of a particular soil-deficient nutrient (Bonfil and Kafkafi, 2000). Numerous studies explored the genetic variation and environmental stability of grain mineral nutrient concentration in wild emmer (e.g., Cakmak et al., 2004; Chatzav et al., 2010; Gómez-Becerra et al., 2010) and concluded that the genetic variation for some nutrients, especially Fe and Zn, in seed of cultivated wheat is relatively narrow and limits the options to breed wheat genotypes with better profiles of these two essential nutrients. Normal distribution, wide level of variation, strong genetic control, and positive correlation with grain protein and productivity traits were found in wild emmer seed for Zn (14-190 mg kg⁻¹ dry seed weight) and Fe (15-109 mg kg⁻¹), but not for P, Mg or S (Cakmak et al., 2004). Furthermore, grain Zn and Fe are significantly higher in wild emmer from the southern part of the Fertile Crescent; whereas, grain protein content was higher in wild emmer from the northern part. Therefore, the species is considered an important genetic resource for increasing Zn and Fe concentration in modern cultivated wheat (Cakmak et al., 2004; Gómez-Becerra et al., 2010). Calcium and sulphur showed the largest variation among macronutrients; whereas, Mn, and to some extent Fe and Zn, had the largest variation among micronutrients in emmer wheat germplasm (Cakmak et al., 2004; Gómez-Becerra et al., 2010). The strong and

positive associations found between grain protein and each of two groups of micro- (Zn, Fe, Cu and Mn) and macronutrients (Ca, Mg, K, P and S) (Gómez-Becerra et al., 2010) suggest that higher grain Zn and Fe, in particular, are not necessarily associated with small grain size or lighter seed weight. Heritability of these nutrients range from high (Cu, Mg, Mn, Zn and S) to low (Fe) (Cakmak et al., 2010). The *Gpc-B1a* allele, derived from wild emmer and already known to increase grain protein content (Avivi, 1978; Joppa et al., 1997), also plays an important and heritable role in grain mineral accumulation (Distelfeld et al., 2007). The incorporation of this allele into commercial wheat cultivars has the potential to improve both protein and micronutrient concentrations in the grain. However, of the two most important wheat species, durum wheat has been quite responsive to breeding for nutritional quality by making full use of the genetic diversity of Zn and Fe concentrations available in wild emmer, domesticated emmer and synthetic wheat germplasm (Cakmak et al., 2010).

Baking and pasta quality

The wild and domesticated emmer wheat gene pool is a rich resource for allelic variants of agronomically important traits required for improvement of bread-making and pasta quality in bread and durum wheat, respectively (Ciaffi et al., 1992; Distelfeld et al., 2008). The introgression of the high grain protein content locus *Gpc-B1* (Joppa et al., 1997) in durum wheat resulted in significant increases in grain protein content, mixing time, and spaghetti firmness; and in bread wheat was associated with higher grain protein content, water absorption, mixing time and loaf volume (Brevis et al., 2010). Rao et al. (2010) reported on the baking quality of emmer-derived durum wheat breeding lines and attributed their higher loaf volume to elevated and heritable gluten strength and increased dough extensibility derived from emmer wheat. Similarly, transgenic bread wheat lines with improved bread-making and nutritional qualities have been produced using wild emmer germplasm; some of these breeding lines are ready for commercial production (Lemaux and Qualset, 2001).

Future perspectives

Despite the extensive knowledge about the ecogeography, genetic diversity, and breeding value of wild emmer, its use in wheat breeding is not fully exploited. On the other hand, the genetic base of cultivated wheat, although expanding, remains limited despite the use of wild germplasm for wheat improvement. The tremendous enhancements of yield by modern wheat breeding may have contributed to significant decrease in its diversity and would threaten future selection progress. This situation calls for a thorough understanding of the fundamental biology of the wheat plant, and to assign functions to the tens of thousands of genes which are already or will be identified using functional genomics as prerequisites for continued progress in wheat breeding. The goal of functional genomics is to discover genes controlling important functions for the study of their basic biological effects and for eventual use in breeding. This strategy will provide new approaches for basic biochemical, physiological, and genetic studies, as well as for the possible use of the information for wheat improvement. As a potential strategy for using wild genetic resources in molecular breeding of wheat, it is proposed to integrate association analysis into conventional breeding programs. This strategy should entail a population-based survey of genotypes that can be used to

identify trait-marker relationships based on linkage disequilibrium. The marker-assisted selection for improving complex traits was identified as one of the most important challenges facing wheat breeders. Therefore, marker-assisted gene introgression will be crucial to avoid undesirable traits of wild emmer and to facilitate the utilization of desirable genes, particularly for disease resistance and high protein content. Genetic transformation facilitated the incorporation of a wide variety of genes from wild genetic resources into the wheat genome that could not have been accessed through conventional breeding and mark only the beginning of wheat improvement. However, it is cautioned that transgenic wheat should be produced and used only when it provides substantial improvements and advantages over wheat produced by conventional, mutation, or marker-assisted breeding and selection methods. The largely unknown ecological risks of introducing transgenic wheat into the Fertile Crescent, a centre of origin and diversity of wheat, have to be taken into consideration. Genome analysis of wild emmer will be tremendously facilitated due to the development of Bacterial Artificial Chromosome library (BAC); this will provide the basis for future map-based cloning of agronomically important genes derived from wild emmer that are already or will be identified in the future. Also, the construction of a wild emmer BAC library will facilitate the development of molecular markers in targeted regions, will facilitate the cloning of the genes discovered and mapped, and will be a long-term research tool for evolutionary studies in wheat. Future wheat genetics and breeding research will contribute tremendously to yield enhancement if molecular techniques and genetic determination procedures are capable of de-convoluting complex traits in wild and domesticated wheat such as phenology, water use efficiency, water stress avoidance and tolerance, duration of grain filling period, high protein, kernel weight, and optimum micronutrient (e.g., Fe, Zn) densities. The effect of variation in these traits on grain yield can be simulated, and the parameters estimated by simulation models can be linked with specific QTLs or specific genes in the wheat genome. In addition, a predictive methodology, based on ecology and genetic markers, is suggested to optimize sampling strategies and maximize the screening and evaluation of elite populations and genotypes of wild emmer appropriate for breeding cultivated wheat. Climate-change scenarios predict an increased aridity, especially in mid-latitudes of the world. Genetic dissection of drought related traits in wild emmer, through QTL analyses, will help elucidate drought adaptive mechanisms. These results exemplify the unique opportunities to exploit favourable alleles that were excluded from the domesticated gene pool and may serve as a starting point for introgression of promising QTLs into elite cultivated wheat via marker-assisted selection and breeding. The development of novel wheat cultivars with more water-use efficiency and greater drought tolerance capacity is a sustainable and economically viable solution to this problem. It is speculated that climate change is likely to modify the wheat disease spectrum in some wheat-growing regions of the world, and pathogens or pests considered unimportant may pose potential new threats in the future. Therefore, future studies, in support of current and projected wheat breeding objectives for biotic stresses, need to further analyse the genetic determination of vertical and horizontal resistance and increase the efficiency of screening for resistance to foliar diseases. Practically, wheat breeders do not have access to the climatic conditions of even the near future in which to carry out field experiments, and they do not know which constitutive plant traits might be

important in the future, especially in the face of a rapidly changing climate. Nevertheless, breeding strategies for the future climate, especially at higher latitudes where most global wheat is currently produced, might need to focus on wheat varieties tolerant to high temperature; whereas, drought and salinity tolerance might become the focus of breeding programs at lower latitudes.

Conclusions

The origin of domesticated wheats and their evolution under domestication have been central questions for botanists, archaeo-botanists, geneticists, agronomists, and students of human civilization. Wild emmer played a central role in the domestication of wheat which symbolizes human intervention that led to its domestication as a major food crop. Farmer-breeders modified the crop by selection for a non-shattering rachis and free threshing grain, and adapted its growth cycle to meet local soil and climate conditions of the Fertile Crescent. The genetic bottleneck imposed on wheat throughout early domestication, and modern wheat breeding severely eroded allelic variations of the crop compared with its wild progenitors, making the crop increasingly susceptible to biotic and abiotic stresses. During much of the 20th century, wheat breeders raced against time to produce disease-resistant, drought-tolerant, and high-yielding varieties of wheat to minimize losses and increase yield. However, in the post green revolution era of the 1960s, a reduced wheat genetic base resulted in increased vulnerability of wheat to biotic and abiotic stresses, and limited the yielding capacity and yield quality of this major food crop. Wild emmer, the progenitor of cultivated wheats, witnessed a renewed interest as a subject of evolutionary and genetic studies, and as a source of agronomically important traits for wheat improvement. The species grows in diversity of primary and secondary habitats and floristic associations and on a variety of soil types and elevations in the Fertile Crescent; therefore, it developed, during its long evolutionary history, tremendous amount of variation at the molecular, biochemical, phenological, morphological and agronomic levels. Wild emmer, along with other wild relatives of cultivated wheat, contributed greatly towards the economic improvement of cultivated wheat. Genes for disease resistance, protein content and micronutrient concentration have been identified and successfully transferred to cultivated wheat. Nevertheless, many theoretical and practical agronomic problems remain to be solved before the wide genetic diversity in wild emmer can be readily available for utilization in wheat breeding and improvement. However, with the advent of, and easy access to, molecular genetics and breeding tools, wild emmer wheat is expected to contribute the full range of its diversity for higher yields under favourable environments, and is likely to provide breeders with the opportunity to significantly improve wheat yield beyond what was previously possible under stress environments.

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References

- Aaronsohn A (1909) Contribution à l'histoire des céréales. Le Blé, l'Orge et le Seigle à l'état sauvage. Bull. Soc. Bot. Fr. 56:196-203; 237-245; and 251-258
- Aaronsohn A (1910) Agricultural and botanical explorations in Palestine. U.S. Department of Agriculture, Bureau of Plant Industry, Bull. No. 180, Washington, D.C. 63 pages
- Al Hakimi A, Monneveux P (1998) Utilization of ancient tetraploid wheat species for drought tolerance in durum wheat wheat (*Triticum durum* Desf.). In: Damania AB, Valkoun J, Wellcox G, Qualset CO (eds.) The origins of agriculture and crop domestication. Proc. Harlan Symp. 10-14 May, 1997. Aleppo, Syria. Published jointly by ICARDA, IPGRI, FAO, and UC/GRCP, pp 273-278
- Anikster Y, Eshel S, Ezrati S, Horovitz A (1991) Patterns of phenotypic variation in wild tetraploid wheat at Ammiad. Isr J Bot 40:397-418
- Anikster Y, Manisterski J, Long DL, Leonard KJ (2005) Leaf rust and stem rust resistance in *Triticum dicoccoides* population in Israel. Plant Disease 89:55-62
- Anikster Y, Noy-Meir I (1991) The wild-wheat field laboratory at Ammiad. Isr J Bot 40:351-362
- Araus JL, Ferrio JP, Buxó R, Voltas J (2007) The historical perspective of dryland agriculture: lessons learned from 10,000 years of wheat cultivation. J Exp Bot 58:131-145
- Avivi L (1978) High protein concentration in wild tetraploid *Triticum dicoccoides* Korn. In: Ramanujam S (ed) International wheat genetics symposium. New Delhi, India, pp 372-380
- Avivi L (1979) Utilization of *Triticum dicoccoides* for the improvement of grain protein quantity and quality in cultivated wheat. Monogr Genet Agrar 4:27-38
- Bar-Yosef O, Meadow RH (1995) The origins of agriculture in the Middle East. pp 39-49. In: T.D. Price and A.B. Gebauer (eds) Last Hunters-First farmers: New perspectives on the Prehistoric Transition to Agriculture. School of American Research Press, Santa Fe, New Mexico, USA
- Bennet FAG (1984) Resistance to powdery mildew in wheat: a review of its use in agriculture and breeding programs. Plant Pathol 33:279-300
- Berzonsky WA, Hartel KD, Kianian SF, Leach GD (2004) Registration of four synthetic hexaploid wheat germplasm lines with resistance to Fusarium head blight. Crop Sci 44:1500-1501
- Blumler MA (1992) Independent inventionism and recent genetic evidence on plant domestication. Econ Bot 46:98-111
- Blumler MA (1998) Introgression of durum into wild emmer and the agricultural origin question. In: Damania AB, Valkoun J, Wellcox G, Qualset CO (eds.). pp 252-268. The origins of agriculture and crop domestication. Proc. Harlan Symp. 10-14 May, 1997. Aleppo, Syria. Published jointly by ICARDA, IPGRI, FAO, and UC/GRCP
- Blumler MA, Byrne R (1991) The ecological genetics of domestication and the origins of agriculture. Curr Anthropol 32:23-54
- Bonfil DJ, Kafkafi U (2000) Wild wheat adaptation in different soil ecosystems as expressed in the mineral concentration of the seed. Euphytica 114:123-134
- Brevis JC, Morris CF, Manthey F, Dobcovsky J (2010) Effect of the grain protein content locus *Gpc-B1* on bread and pasta quality. J Cereal Sci
- Cakmak I, Torun A, Millet E, Feldman M, Fahima T, Korol A, Nevo E, Braun HJ, Ozkan H (2004) *Triticum*

- dicoccoides*: an important genetic resource for increasing zinc and iron concentration in modern cultivated wheat. *Soil Sci Plant Nutr* 50:1047-1054
- Cakmak I, Pfeiffer WH, McClafferty B (2010) Biofortification of durum wheat with zinc and iron. *Cereal Chem* 87:10-20
- Chatrath R, Mishra B, Ferrara GO, Singh SK, Joshi AK (2007) Challenges to wheat production in South Asia. *Euphytica* 157:447-456
- Chatzav M, Peleg Z, Ozturk L, Yazici A, Fahima T, Cakmak I, Sarangal Y (2010) Genetic diversity for grain nutrients in wild emmer: potential for wheat improvement. *Annals of Botany*. 10 p. doi:10.1093/aob/mcq024
- Ciaffi M, Benedettelli S, Giorgi B, Porceddu E, Lafiandra D (1991) Seed storage proteins of *Triticum turgidum* ssp. *dicoccoides* and their effect on the technological quality in durum wheat. *Plant Breeding* 107:309-319
- Ciaffi M, Dominici L, Lafiandra D, Porceddu E (1992) Seed storage proteins of wild wheat progenitors and their relationships with technological properties. *Hereditas* 116:315-322
- Ciaffi M, Lafiandra D, Porceddu E, Bendettelli S (1993) Storage-protein variation in wild emmer (*Triticum dicoccoides* ssp. *dicoccoides*) from Jordan and Turkey II. Patterns of allele distribution. *Theor Appl Genet* 86:518-525
- DePauw RM, Knox RE, Clarke FR, Wang H, Fernandez MR, Clarke JM, McCaig TN (2007) Shifting undesirable correlations. *Euphytica* 157: 409-415
- DePauw RM, Townley-Smith TF, Humphreys G, Knox RE, Clark FR, Clarke JM (2005) Lilian hard red spring wheat. *Can J Plant Sci* 85:397-401
- Dinoor A, Eshed N, Anikster Y (1991) Fungal diseases of wild tetraploid wheat in a natural stand in northern Israel. *Isr J Bot* 40:481-500
- Distefeld A, Cakmak I, Peleg Z, Ozturk L, Yazici AM, Budak H, Saranga Y, Fahima T (2007) Multiple QTL-effects of wheat *Gpc-B1* locus on grain protein and micronutrient concentrations. *Phyiol Plant* 129:635-64
- Duveiller E, Singh RP, Nicol JM (2007) The challenges of maintaining wheat productivity: pests, diseases, and potential epidemics. *Euphytica* 157:417-430
- Dvorak J, Akhunov ED, Akhunov AR, Deal KR, Lou M-C (2006) Molecular characterization of a diagnostic DNA marker for domesticated tetraploid wheat provides evidence for gene flow from wild tetraploid wheat to hexaploid wheat. *Mol Biol Evol* 23:1386-1396
- Dvorak J, Lou M-C, Yang Z-L (1998) Genetic evidence of the origin of *Triticum aestivum* L. In: Damania AB, Valkoun J, Wlcox G, Qualset CO (eds.) The origins of agriculture and crop domestication. Proc. Harlan Symp. 10-14 May, 1997. Aleppo, Syria. Published jointly by ICARDA, IPGRI, FAO, and UC/GRCP, pp 253-251
- Fahima T, Röder MS, Wendenhake K, Kirzhner VM, Nevo E (2002) Microsatellite polymorphism in natural populations of wild emmer wheat, *Triticum dicoccoides*, in Israel. *Theor Appl Genet* 104:17-29
- FAOSTA (2008) <http://faostat.fao.org> Verified 8 Nov. 2010
- Farooq S (2004) Salt tolerance in *Aegilops* species: a success story from research and production to large-scale utilization of salt-tolerant wheats. In: Taha FS, Ismail S, and Jaradat AA (eds) Prospects of saline Agriculture in the Arabian Peninsula, pp 121-134. Amherst Scientific Publishers, Amherst, MA
- Farooq S (2009) Triticeae: the ultimate source of abiotic stress tolerance improvement in wheat. In Ashraf M et al. (eds) Salinity and Water Stress, pp. 65-71. Springer-Verlag, Berlin.
- Feldman M, Kislev M (2007) Domestication of emmer wheat and evolution of free-threshing tetraploid wheat. *Isr J Plant Sci* 55:207-221
- Feldman M, Millet E (2001) The contribution of the discovery of wild emmer to an understanding of wheat evolution and domestication and to wheat improvement. *Isr J Plant Sci* 49:25-35
- Feldman M, Sears ER (1981) The wild gene resources of wheat. *Sci Am* 244:102-112
- Felsenburg T, Levy AA, Galili G, Feldman M (1991) Polymorphism of high-molecular-weight glutenins in wild tetraploid wheat: spatial and temporal variation in a native site. *Isr J Bot* 40:451-480
- Ferrio JP, Alonso N, Voltas J, Araus JL (2006) Grain weight changes over time in ancient cereal crops: potential roles of climate and genetic improvement. *J Cereal Sci* 44:323-332
- Feuillet C, Langridge P, Waugh R (2007) Cereal breeding takes a walk on the wild side. *Trends in genetics* 24:24-32
- Frankel OH, Soule M (1981) Conservation and Evolution. Cambridge University Press, Cambridge, UK
- Garg M, Tanaka H, Tsujimoto H (2009) Exploration of Triticeae seed storage proteins for improvement of wheat end-product quality. *Breed Sci* 59:519-528
- Gerchter-Amitai ZK, Grama A (1974) Use of alien genes in wheat breeding. *Ann Wheat Newsletter* 23:57-58
- Gerchter-Amitai ZK, Stubbs RW (1970) A valuable source of yellow rust resistance in Israeli populations of wild emmer, *Triticum dicoccoides*. *Euphytica* 19:12-21
- Gerchter-Amitai ZK, van Silfhout CH, Grama A (1989). *Yr15*- a new gene for resistance to *Puccinia striiformis* in *Triticum dicoccoides* sel. G-25. *Euphytica* 43:187-190
- Ginkel van M, Ogbonnya F (2007) Novel genetic diversity from synthetic wheat in breeding cultivars for changing production conditions. *Field Crop Res* 104:86-94
- Giuliani A, Karagöz A, Zencirci N (2009) Emmer (*Triticum dicoccon*) production and market potential in marginal mountainous areas of Turkey. *Mountain Res Dev* 29:220-229
- Gómez-Becerra HF, Yazici A, Ozturk L, Budak H, Peleg Z, Morgounov A, Fahima T, Saranga Y, Cakmak I (2010) Genetic variation and environmental stability of grain mineral nutrient concentrations in *Triticum dicoccoides* under five environments. *Euphytica* 171:39-52
- Hamrick JL, Godt MJW (1990) Allozyme diversity in plant species. In: Brown AHD, Cleg MT, Kahler AL, Weir BS (eds) pp. 43-64 Plant population genetics, breeding and genetic resources. Sunderland, MA, USA
- Harlan JR (1992) Crops and man. 2nd edition. American Society of Agronomy, Madison, WI, USA
- Harlan JR (1995) Agricultural origins and crop domestication in the Mediterranean region. *Diversity* 11:14-16
- Harlan JR, Zohary D (1966) Distribution of wild wheats and barley. *Science* 153:1074-1080
- Harris DR (1998a) The origins of agriculture in Southwest Asia. *Rev Archaeol* 19:5-11
- Harris DR (1998b) The spread of Neolithic agriculture from the Levant to Western Central Asia. In: Damania AB, Valkoun J, Wlcox G, Qualset CO (eds.) The origins of agriculture and crop domestication. Proc. Harlan Symp. 10-14 May, 1997. Aleppo, Syria. Published jointly by ICARDA, IPGRI, FAO, and UC/GRCP, pp 65-82

- Haudry A, Cenci A, Ravel C, Bataillon T, Brunel D, Poncet C, Hochu I, Poirier S, Santoni S, Glémin S, David J (2007) Grinding up wheat: a massive loss of nucleotide diversity since domestication. *Mol Biol Evol* 24:1506-1517
- Horovitz A, Feldman M (1991) Evaluation of the wild-wheat study at Ammiad. *Isr J Bot* 501-508
- Jaradat AA (1987) Collecting wild emmer wheat in Jordan. *FAO/IBPGR Plant Genetic Resources Newsletter* 69:19-22
- Jaradat AA (1993) Eco-geographical races in natural populations of *Triticum dicoccoides*. In: A.B. Damania (ed.) *Biodiversity and Wheat Improvement*. pp. 397-408 John Wiley & Sons
- Jaradat AA (1997a) Wild emmer wheat in Jordan I. Ecotypes and morphological variation. *Isr J Plant Sci* 45:31-37
- Jaradat, A.A. (1997b). Wild emmer wheat in Jordan II. A core collection. *Isr J Plant Sci*. 45:39-44
- Jaradat AA (1997c) Wild emmer wheat in Jordan III. Genetic distances among and within populations. *Isr J Plant Sci* 45:45-51
- Jaradat AA (1998) Biodiversity and sustainable agriculture in the Fertile Crescent. In Albert, J., Bernhardtsson, M. and Kenna, R. (eds.) *Transformations of Middle Eastern natural environments: Legacies and lessons*. pp. 31-57 Bull. Series, Yale School of Forestry and Environmental Studies. Number 103. Yale Univ., New Haven, CT
- Jaradat AA (2001a) Spatial and temporal genetic structure of wild emmer wheat in Jordan I. Phenotypic traits. *Isr J Plant Sci* 49:S-53—S-64
- Jaradat AA (2001b) Spatial and temporal genetic structure of wild emmer wheat in Jordan II. High-molecular weight glutenins and isozymes. *Isr J Plant Sci* 49:S-65—S-76
- Jaradat AA, Humeid BO (1990) Morphological variation in wild *Triticum dicoccoides* from Jordan. In: J.P. Srivastava and B.A. Damania (eds). pp 215-222. *Wheat genetic resources: meeting diverse needs*. John Wiley & Sons
- Joppa LR, Cantrell RG (1990) Chromosomal location of genes for grain protein content of wild tetraploid wheat. *Crop Sci* 30:1059-1064
- Joppa LR, Du C, Hart GE, Hareland GA (1997) Mapping gene(s) for grain protein in tetraploid wheat (*Triticum turgidum* L.) using a population of recombinant inbred chromosome lines. *Crop Sci* 37:1586-1589
- Katz S (2001). On the wings of the brittle rachis: Aaron Aaronsohn from the rediscovery of wild wheat (“*Urweizen*”) to his vision “for the progress of mankind.” *Isr J Plant Sci* 49:S-5—S-18
- Kosina P, Reynolds M, Dixon J, Joshi A (2007) Stakeholder perception of wheat production constraints, capacity building needs, and research partnerships in developing countries. *Euphytica* 157:475-483
- Krugman T, Levy O, Snape JW, Rubin B, Korol AB, Nevo E (1997). Comparative RFLP mapping of the chlorotoluron resistance gene (*Su1*) in cultivated wheat (*Triticum aestivum*) and wild wheat (*Triticum dicoccoides*). *Theor Appl Genet* 94:46-51
- Kumar S, Stack RW, Friesen TL, Faris JD (2007) Identification of a novel fusarium head blight resistance quantitative trait locus on chromosome 7A in tetraploid wheat. *Phytopathology* 97: 592-597
- Kushner U, Halloran GM (1984) Transfer of high kernel weight from wild tetraploid wheat (*Triticum turgidum dicoccoides*) to bread wheat (*T. aestivum*) using homologous and homoelogenous recombination. *Euphytica* 33:249-255
- Ladizinsky G (1998) Plant evolution under domestication. Kluwer, Dordrecht, pp 123-175
- Law CN, Payne PI (1983) Genetical aspects of breeding for improved grain protein content and type in wheat. *J Cereal Sci* 1:79-93
- Lemaux PG, Qualset CO (2001) Advances in technology for wheat breeding. *Isr J Plant Sci* 49:S-105—S-115
- Levy AA, Feldman M (1988) Eco-geographical distribution of HMW glutenin alleles in populations of the wild tetraploid wheat, *Triticum turgidum* var. *dicoccoides*. *Theor Appl Genet* 75:651-658
- Li YC, Krugman T, Fahima T, Beiles A, Korol AB, Nevo E (2000) Parallel microgeographic patterns of genetic diversity and divergence revealed by allozymes, RAPD, and microsatellites in *Triticum dicoccoides* at Ammiad, Israel. *Conserv Genet* 1:191-207
- Lou M-C, Yang Z-L, You FM, Kawahara T, Waines JG, Dvorak J (2007) The structure of wild and domesticated emmer wheat populations, gene flow between them, and the site of emmer domestication. *Theor Appl Genet* 114:947-959
- McFadden ES (1930) A successful transfer of emmer characters to *vulgare* wheat. *J Am Soc Agron* 22:1020-1034
- Miller RH, Pike KS (2002) insects in wheat-based systems. In: Curtis BC, Rajaram S, Gomez Macpherson H (eds) *Bread wheat: improvement and production, plant production and protection series no 30*, pp 367-393. FAO, Rome
- Nesbitt M (1995) Clues to agricultural origins in the Northern Fertile Crescent. *Diversity* 11:142-143
- Nevo E (1986) Genetic resources of wild cereals and crop improvement: Israel, a natural laboratory. *Isr J Bot* 35:255-278
- Nevo E (1998) Genetic diversity in wild cereals: regional and local studies and their bearing on conservation *ex situ* and *in situ*. *Genet Resour Crop Evol* 45:355-370
- Nevo E (2001) Genetic resources of wild emmer, *Triticum dicoccoides*, for wheat improvement in the third millennium. *Isr J Plant Sci* 49:S-77—S-92
- Nevo E, Beiles A, Kaplan D (1988) Genetic diversity and environmental associations of wild emmer wheat in Turkey. *Heredity* 61:31-45
- Nevo E, Chen G (2010) Drought and salt tolerance in wild relatives for wheat and barley improvement. *Plant Cell Environ* 33:670-685
- Nevo E, Krugman T, Beiles A (1993) Genetic resources for salt tolerance in the wild progenitor of wheat (*Triticum dicoccoides*) and barley (*Hordeum spontaneum*) in Israel. *Plant Breed* 11:338-341
- Nevo E, Noy-Meir I, Beiles A, Krugman T, Feldman M (1991) Natural selection of allozymes polymorphism: micro-geographical spatial and temporal ecological differentiation in wild emmer wheat. *Isr J Bot* 40:419-450
- Nevo E, Payne PI (1987) Wheat storage proteins: diversity of HMW glutenin subunits in wild emmer wheat from Israel I. Geographical patterns and ecological predictability. *Theor Appl Genet* 62:241-254
- Noy-Meir I (2001) Ecology of wild emmer wheat in Mediterranean grassland in Galilee. *Isr J Plant Sci* 49:S-43-S-52
- Noy-Meir I, Agami M, Cohen E, Anikster Y (1991) Floristic and ecological differentiation of habitats within a wild wheat population at Ammiad. *Isr J Bot* 40:363-384

- Ogbonnaya FC, Ye G, Trethowan R, Dreccer F, Lush D, Sheppard J, van Ginkel M (2007) Yield of synthetic backcross-derived lines in rain-fed environments of Australia. *Euphytica* 157:321-336
- Oury F-X, Godin C (2007) Yield and grain protein concentration in bread wheat: how to use the negative relationship between the two characters to identify favourable genotypes? *Euphytica* 157:45-57
- Ozbek O, Millet E, Anikster Y, Arslan O, Feldman M (2007) Comparison of the genetic structure of populations of wild emmer wheat, *Triticum turgidum* ssp. *dicoccoides*, from Israel and Turkey revealed by AFLP analysis. *Genet Resour Crop Evol* 54:1587-1598
- Ozkan H, Brandolini A, Pozzi C, Effgen S, Wunder J, Salamini F (2005) A reconsideration of the domestication geography of tetraploid wheat. *Theor Appl Genet* 110:1052-1060
- Ozkan H, Brandolini A, Schafer-Pregl R, Salamini F (2002) AFLP analysis of a collection of tetraploid wheats indicates the origin of emmer and hard wheat domestication in southeast Turkey. *Mol Biol Evol* 19:1797-1801
- Ozturk L, Yazici MA, Yucel C, Torun A, Cekic C, Bagci A, Ozkan H, Braun H-J, Sayers Z, Cakmak I (2006) Concentration and localization of zinc during seed development and germination in wheat. *Physiol Plant* 128:144-152
- Pagnotta MA, Nevo E, Beiles A, Porceddu A (1995) Wheat storage proteins: glutenin diversity in wild emmer, *Triticum dicoccoides*, in Israel and Turkey. 2. DNA diversity detected by PCR. *Theor Appl Genet* 91:409-414
- Peleg Z, Fahima T, Abbo S, Krugman T, Nevo E, Yakir D, Saranga Y (2005) Genetic diversity for drought resistance in wild emmer wheat and its eco-geographical associations. *Plant Cell Environ* 28:176-191
- Peleg Z, Fahima T, Sarang Y (2008a) Drought resistance in wild emmer wheat – physiology, ecology and genetics. *Isr J Plant Sci* 55:289-296
- Peleg Z, Saranga Y, Krugman T, Abbo S, Nevo E, Fahima T (2008b) Allelic diversity associated with aridity gradient in wild emmer wheat populations. *Plant Cell Environ* 31:39-49
- Poyarkova H (1988) Morphology, geography and infraspecific taxonomics of *Triticum dicoccoides* Körn. A retrospect of 80 years of research. *Euphytica* 38:11-23
- Poyarkova H, Gerchter-Amitai ZK, Genizi A (1991) Two variants of wild emmer (*Triticum dicoccoides*) native to Israel: morphology and distribution. *Can J Bot* 69:2772-2789
- Rajaram S, Pena RJ, Vellareal RL, Mujeeb-Kazi A, Singh R, Gilchrist L (2001) Utilization of wild and cultivated emmer and diploid wheat relatives in breeding. *Isr J Plant Sci* 49:S-93—S-104
- Rao BN, Pozniak CJ, Hucl PJ, Briggs C. 2010. Baking quality of emmer-derived durum wheat breeding lines. *J Cereal Sci* doi:10.1016/j.jcs.2010.01.004
- Reif JC, Zhang P, Dreisigacker S, Warburton ML, Ginkel M van, Hoisington D, Bohn M, Melchinger Ae (2005) Wheat genetic diversity trends during domestication and breeding. *Theor Appl Genet* 110:859-864
- Reynolds MP, Braun H-J, Pietragalla J, Ortiz R (2007) Challenges to international wheat breeding. *Euphytica* 157:281-285
- Salamini F, Özkan H, Brandolini A, Schäfer-Pregl R, Martin W (2002) Genetics and geography of wild cereal domestication in the Near East. *Genetics* 3:429-441
- Semenov MA, Halford NG (2009) Identifying target traits and molecular mechanisms for wheat breeding under a changing climate. *J Exp Bot* 60:2791-2804
- Tanyolac B, Linton E, Ozkan H (2003) Low genetic diversity in wild emmer from south-eastern Turkey revealed by Restriction Fragment Length Polymorphism. *Genet Resour Crop Evol* 50:829-833
- Teklu Y, Hammer K, Röder MS (2007) Simple sequence repeats marker polymorphism in emmer wheat (*Triticum dicoccon* Schrank): analysis of genetic diversity and differentiation. *Genet Resour Crop Evol* 54:543-554
- Uauy C, Distefeld A, Fahima T, Blechl A, Dubcovsky J (2006) A NAC gene regulating senescence improves grain protein, zinc and iron content in wheat. *Science* 314:1298-1301
- Valkoun J, Waines JG, Konopka J (1998) Current geographic distribution and habitat of wild wheats and barley. In: Damania AB, Valkoun J, Wellcox G, Qualset CO (eds.) The origins of agriculture and crop domestication. pp 293-299. Proc. Harlan Symp. 10-14 May, 1997. Aleppo, Syria. Published jointly by ICARDA, IPGRI, FAO, and UC/GRCP
- van Slageren MW (1994) Wild wheats: a monograph of *Aegilops* L. and *Amblyopyrum* (Jaub. & Spach) Eig (Poaceae). Wageningen Agricultural University and International Center for Agricultural Research in the Dry Areas.
- Vasil IK (2007) Molecular genetic improvement of cereals: transgenic wheat (*Triticum aestivum* L.). *Plant Cell Rep* 26:1133-1154
- Wang JR, Wei YM, Long XY, Yan ZH, Nevo E, Baum BR, Zheng YL (2008) Molecular evolution of dimeric --amylase inhibitor genes in wild emmer wheat and its ecological association. *BMC Evol Biol* 8:91. doi:10.1186/147-2148-8-91
- Warburton ML, Crossa J, Franco J, Kazi M, Trethowan R, Rajaram S, Pfeiffer W, Zhang P, Dreisigacker S, van Ginkel M (2006) Bringing wild relatives back into the family: recovering genetic diversity in CIMMYT improved wheat germplasm. *Euphytica* 149:289-301
- Willcox G (1998) Archaeobotanical evidence for the beginning of agriculture in Southwest Asia. In: Damania AB, Valkoun J, Willcox G, Qualset CO (eds.) The origins of agriculture and crop domestication. Proc. Harlan Symp. 10-14 May, 1997. Aleppo, Syria. Published jointly by ICARDA, IPGRI, FAO, and UC/GRCP, pp 25-36
- Willcox G (2005) The distribution, natural habitats and availability of wild cereals in relation to their domestication in the Near East: multiple events, multiple centers. *Veg History Archaeobot.* doi:10.1007/s00334-005-0075-x
- Xie W, Nevo E (2008) Wild emmer: genetic resources, gene mapping and potential for wheat improvement. *Euphytica* 164:603-614
- Zaharieva M, Ayana NG, Al Hakimi A, Misra SC, Monneveux P (2010) Cultivated emmer wheat (*Triticum dicoccon* Schrank), an old crop with promising future: a review. *Genet Resour Crop Evol* 57:937-962
- Zohary D (1969) The progenitors of wheat and barley in relation to domestication and agriculture dispersion in the Old World. In: Ucko PJ, and Dimbleby GW (eds) pp 47-66. The domestication and exploitation of plants and animals. Duckworth, London
- Zohary D, Hopf M (1993) Domestication of plants in the Old World. 2nd edn. Clarendon Press, Oxford, UK