

HISTORICAL ASPECTS AND SIGNIFICANCE OF THE DISCOVERY OF WILD WHEATS

(*origin of wheat, evolution, gene pools*)

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INTRODUCTION

The origin of cultivated plants and the development of agriculture have always stimulated man's curiosity and imagination. In the ancient world, where every phenomenon and every event were explained in a mythological manner, the philosophers and historians of many nations considered cultivated plants to be a generous gift from the gods. Thus the ancient Egyptians were grateful to Isis and Ozyris for bringing wheat and barley to Egypt and teaching people how to cultivate them. Similarly, the ancient Greeks ascribed the gift of these important cereals to Demeter and the Romans to the goddess Ceres.

During the last few centuries, botanists and students of agricultural history have attempted to explain the origin of cultivated plants and their evolution under domestication on a scientific basis. Driven by the desire to find the historical and evolutionary truth, LINK (1816), DE LA MALLE (1826), and particularly DE CANDOLLE (1886) were the first to realize

that historical, linguistic and folkloristic evidence is, by itself, insufficient to trace the origin of cultivated plants. Botanical, geographical and archaeological studies are necessary for advancement in this field of science. Even so, as they stated, the only definite demonstration of the origin of a cultivated plant is the discovery and identification of its wild prototype. In those cases where the wild prototype is unknown or extinct, the origin and full history of the cultivated plant can never be ascertained.

The first attempt to identify the progenitor of cultivated wheats was in the middle of the 19th century when several botanists regarded the natural hybrids and hybrid derivatives of common wheat x *Triticum ovatum* (nomenclature after MORRIS and SEARS 1967) as the ancestral forms of the cultivated wheats. The hybrid was first discovered by Requier in 1821 in southern France, and later on it was also collected in northern Italy and North Africa. Because of its resemblance to cultivated wheats, REQUIEN (see FABRE 1852) named it *Aegilops triticoides*. From the fact that there were also many intermediate forms between *Ae. triticoides* and some forms of cultivated wheats, FABRE (1852, 1855) concluded that all wheats had originated from *T. ovatum*. Since he found, in several cases, that grains from ears of *T. ovatum* growing near wheat fields yielded *Ae. triticoides* plants, he assumed that under domestication *T. ovatum* was gradually transformed into cultivated wheat. This hypothesis, which was accepted by several botanists, was disproved by GODRON (1854, 1856, 1858a, 1858b, 1869, 1876), who demonstrated the hybrid nature of *Ae. triticoides* and all other intermediate forms between *T. ovatum* and common wheat. He produced similar forms by crossing common wheat with *T. ovatum* and backcrossing the hybrids to the two parental species.

The *Ae. triticoides* episode emphasizes the need for a better definition of key features characterizing the wild prototype of the cultivated wheats. The wild prototype must be a valid species and, therefore, a self-propagating plant. Thus it should contain a spike which is similar to that of cultivated wheats but with a brittle rachis that disarticulates into single spikelets when mature. The single spikelet seed-dispersal units facilitate self-dispersal and self-burial in the soil. This brittle rachis must have proved a nuisance to the ancient farmer, who had to collect most of the spikelets from the ground or cut the culms before the grains were mature. No wonder, therefore, that one of the first steps in domestication was to select types with a non-brittle rachis. In addition, the wild prototype, like all other wild grasses, should have tightly closed glumes resulting in a 'hulled' grain for protection against extreme climatic conditions and animals. Only a few of the cultivated wheats of today retain this feature. Mutations which spread under domestication led to loosely closed glumes which release the naked 'free-threshing' grain.

Ecogeographically, the prototype should be characterized by a specific distribution and occupy well-defined primary habitats.

CLASSIFICATION AND THEORIES ON THE ORIGIN OF CULTIVATED WHEATS AT THE END OF THE 19TH CENTURY

LINNAEUS (1753) was the first to include all cultivated wheats in one genus, *Triticum*. He recognized six different species in this genus, all of which were cultivated types. Since then, several new cultivated species have been discovered, and a better understanding of taxonomical relationships between the various taxa has been gained. As a result, the classification of wheats has been modified accordingly.

In 1885 KÖRNICKE and WERNER classified the wheats in only three species (Table 1). This classification was based mainly on the morphological characters of the spike and the grain and also took VILMORIN'S data (1880a, 1880b) on crossability and fertility rate of F₁ hybrids between the various taxa into account. Nevertheless, Körnicke's classification was highly artificial and did not reflect phylogenetic relationships. In spite of this, it was adopted with minor changes by most taxonomists of that time (ASCHERSON and GRAEBNER 1902). This classification, again, included only cultivated forms and was based on the assumption of independent domestication of each of the three species and therefore on the existence of three wild prototypes, i.e., the prototypes of *T. monococcum*, *T. polonicum* and *T. vulgare*. Of these three, only the progenitor of *T. monococcum*, namely, *T. monococcum* var. *boeoticum*, was known at the time.

Table 1. Classification of the species of *Triticum* (after Körnicke and Werner 1885).

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- | | | |
|----|---------------------------------|--------------------------|
| 1. | <i>Triticum vulgare</i> , Vill. | (common wheat) |
| 2. | <i>Triticum polonicum</i> , L. | (Polish wheat) |
| 3. | <i>Triticum monococcum</i> , L. | (Einkorn or small spelt) |

Triticum vulgare was divided further into six subspecies, viz:

- | | | |
|-----|---|--------------------------|
| I. | Rachis tough, grain easily separated on threshing: | |
| | 1. ssp. <i>vulgare</i> | (common wheat) |
| | 2. ssp. <i>compactum</i> | (dwarf wheat) |
| | 3. ssp. <i>turgidum</i> | (English wheat) |
| | 4. ssp. <i>durum</i> | (hard or macaroni wheat) |
| II. | Rachis fragile, grains firmly enclosed in the glumes: | |
| | 1. ssp. <i>spelta</i> | (common spelt) |
| | 2. ssp. <i>dicoccum</i> | (emmer) |
-

Since the wild progenitor of most cultivated wheats (i.e., emmer, durum, spelt and common wheat) was not known, many sci-

entists at the end of the 19th century assumed that the prototype was extinct and that the exact origin of these wheats would never be traced. Three main theories were brought forward at that time concerning the geographical region in which wheat was domesticated.

DE CANDOLLE (1886) based his theory on historical evidence. He was influenced by the fact that wild wheat from the Near East had been mentioned several times. The first historical evidence came from the Chaldean priest Berosus, who lived at about 700 B. C. He mentioned the occurrence of wild wheat in Mesopotamia (Syncellus, Frag. Hist. Graec., Vol. 2, p. 416). In more recent times, LINNAEUS (1753) mentioned that Heintrelmann found wild wheat in northwest Iran. Olivier (1807) found wheat, barley and spelt in uncultivated areas northwest of Anah, on the right bank of the Euphrates. He mentioned that he had already seen such wild wheat several times in northern Mesopotamia. Andre Michoux saw spelt wheat growing wild north of Hamadan, Western Iran, in 1877 (see DE CANDOLLE 1886). From all this evidence, De Candolle (1886) assumed that the cultivation of wheat originated in the Euphrates valley. This valley lies mainly in the middle of the belt of cultivation of wheat extending from China to the Canary Islands. De Candolle assumed further that the Euphrates basin, and maybe also Syria, was the distribution area of the wild progenitors of wheat in pre-historic times.

SOLMS-LAUBACH (1899) suggested that cultivation of wheat started in a geological period when the climatic conditions and the distribution of plants were quite different from those of today. He assumed that cultivation of *T. monococcum* and other wheats started in central Asia, at a time when the Gobi Desert was covered by sea. In a later period the prototype of *T. monococcum* migrated westward, while those of the other wheats disappeared and only their cultivated descendants migrated to the west, east and south.

MUCH (1908) assumed that many cereals, particularly wheat and barley, grew wild in Europe in an earlier geological period and were domesticated there.

T. monococcum var. *boeoticum* - THE WILD PROGENITOR OF EINKORN WHEAT

Wild one-grained wheat was first described under the name *Crithodium aegilopoides* by Link, who found it in Greece between Nauplia and Corinth in 1833 (LINK 1834). Later on, in 1854, a specimen of wild wheat was also discovered by Balanza on Mount Siphylus in Anatolia, Turkey (see BOISSIER 1884). This specimen was identified by Gay in 1860 as a wild einkorn, *T. monococcum aegilopoides*, and by Boissier, who collected it in Boeotica, Greece, as *T. boeoticum* (known today as *T. monococcum* var. *boeoticum*). This wild type is very similar to the cultivated form of the one-grained wheat, *T. monococcum* var. *monococcum* and differs from it mainly in its brittle rachis. Balanza believed that he had found the progenitor of all cultivated wheats. Most botanists who studied the problem, however, assumed that the cultivated wheats have a polyphyletic origin and

that at least two species of wild wheat progenitors were taken into cultivation. This idea was also supported by the crossing data of VILMORIN (1880a, 1880b, 1888), BEIJERINCK (1886) and TSCHERMAK (1913, 1914), which indicated that, while all the other species of wheat could be crossed with each other quite easily and yielded fertile or semi-fertile hybrids, *T. monococcum* could not be crossed with any other wheat or yielded only sterile hybrids.

This low crossability and sterility suggests that *T. monococcum* is relatively isolated from other wheat species. Therefore its wild prototype, namely *T. monococcum* var. *boeoticum*, cannot be considered the wild progenitor of the other cultivated wheats (KÖRNICKE and WERNER 1885; ASCHERSON and GRAEBNER 1902).

Triticum monococcum var. *boeoticum* was also found growing wild in Thessaly, Boeotia and Achaia in Greece, in southern Bulgaria and in southern Serbia. AARONSOHN (1909, 1910a, 1910b) was the first to find var. *boeoticum* in the southern part of the Fertile Crescent, i.e., on Mount Hermon in southern Syria. Later on, this wild form was also discovered in other parts of the Fertile Crescent such as eastern Turkey, northern Iraq and western Iran. ZHUKOVSKY (1923), found *T. monococcum* growing wild in Georgia, TUMANIAN (1930) in Armenia and JAKUBZINER (1932, 1959) in Nakhichevan.

In 1937 TUMANIAN discovered a new form of wild *T. monococcum* in Armenia. This form, which was named *T. urartu* Tum. (according to today's classification, it should be referred to as *T. monococcum* var. *urartu*), is distinct morphologically from var. *boeoticum* and characterized by two developed awns in each spikelet (TUMANIAN 1937; GANDILIAN 1972). JOHNSON (1975) also discovered var. *urartu* in northern Lebanon, southeastern Turkey and southwestern Iran. In most cases var. *urartu* forms mixed populations with var. *boeoticum*.

Wild einkorn wheats, var. *boeoticum* and var. *urartu*, occur naturally in open herbaceous oak park forests and steppe-like formations in southwestern Iran, northwestern Iraq, eastern Turkey and Syria (HARLAN and ZOHARY 1966; JOHNSON 1975; FELDMAN 1976). In this area and beyond it - in Transcaucasia, central and Western Turkey, southern Bulgaria, Greece and southern Serbia - wild einkorn is also very common in secondary habitats such as roadsides and field edges.

T. turgidum var. *dicoccoides* - THE WILD PROGENITOR OF EMMER WHEAT

At the end of the 19th century the theory of SOLMS-LAUBACH (1899) was generally accepted. Most botanists agreed with him that cultivated wheats originated in central Asia and that the wild progenitor of most cultivated wheats, i. e., Körnicke's *T. vulgare*, was lost as a result of drastic climatic changes. No serious attention was given to Körnicke and several other botanists who maintained, not only that such a prototype exists, but that they already had a part of a spike of wild wheat in their possession. Körnicke found this part of a spike in 1873 in the herbarium of the National Museum of Vienna among stems

of wild barley, *Hordeum spontaneum*, that the botanist Kotschy collected in 1855 in Rasheyya on the northwestern slope of Mount Hermon, southern Syria. Körnicke noticed that the spikelets in this material contained two grains each and that the spike very much resembled that of *T. vulgare* ssp. *dicoccum* (known today as *T. turgidum* var. *dicoccum*). Since the spike had a brittle rachis, Körnicke was sure of the wild nature of his material and considered it to be the progenitor of cultivated wheats. It was not until 1889, at a meeting of the Society of the Lower Rhine and Westphalia, that Körnicke reported his discovery (KÖRNICKE 1889). In this report he named Kotschy's plant *T. vulgare* ssp. *dicoccoides* (known today as *T. turgidum* var. *dicoccoides*) and declared it to be the progenitor of most cultivated wheats. Körnicke, like De Candolle before him, assumed that cultivation of wheat started in southwest Asia and urged all botanists who travelled into the region, and particularly to Mount Hermon, to look for wild wheats. He also tried, without success, to obtain support from the scientific academies of Vienna and Berlin to organize an expedition to the Hermon area.

Only a small number of botanists, including Schweinfurth, Ascherson and Graebner, supported Körnicke's theory. Most other scientists considered the discovery more sceptically, regarding the material as an escapist from cultivation. This sceptical approach was somewhat justified since many prominent botanists such as Post and Bornmüller had already studied the flora of Mount Hermon and the adjacent areas and did not report the existence of wild wheat in this region.

Körnicke's idea, which was not accepted in Europe, stimulated a young agronomist and zealous botanist named Aaron Aaronsohn from Israel (then Palestine) to look for this wild wheat in the vicinity of Mount Hermon. His first expedition, in 1904, was unsuccessful. However, a few years later, on June 18, 1906, while inspecting a vineyard at Rosh Pina, eastern Galilee, Israel, Aaronsohn found a single plant of wild grass growing between the rocks. From a distance it looked like an ordinary barley. At a second glance he recognized it for what it was: a two-grained wild wheat, the first specimen of its kind to be found by modern botanists growing in a natural habitat. This was the progenitor of cultivated wheat that generations of botanists had been searching for (AARONSOHN and SCHWEINFURTH 1906; AARONSOHN 1909, 1910a, 1910b, 1913).

Aaronsohn's specimen was very well developed, with perfect and very impressive spikes and large grains quite similar to those of cultivated wheats. Aaronsohn was surprised to find that wild wheat contains such large spikes and grains. However, he realized that without such large spikes and grains this wheat would not have been attractive to the ancient collectors and would not have been chosen for domestication.

Later on, AARONSOHN (1909, 1910a, 1910b, 1913) also found wild wheat on Mount Hermon as well as at other sites. The plants grew on uncultivated ground, along field edges and roadsides and among rocks. In some places he found this wheat in great abundance, showing a wide range of morphological forms.

Thus Körnicke's hypothesis on the existence of two-grained wild wheat in the Near East was fully confirmed by Aaronsohn. Aaronsohn's reports also showed that this wild wheat is native to Israel, Jordan, Lebanon and Syria and occupies well-defined primary ecological habitats. The true wild nature of this plant was thus verified.

The news of this important discovery spread quickly in the academic world and excited all those who were concerned with the origin and evolution of wheat (see SCHWEINFURTH 1906a, 1906b, 1908). The discovery of the wild plant, which can be considered as the prototype of most cultivated wheats, opened new possibilities for genetic and evolutionary studies in this important group.

The two-grained wheat *T. turgidum* var. *dicoccoides* occupies primary habitats similar to those of the wild einkorn wheat but is less continuous in its distribution. This wild taxon grows in open herbaceous oak park forests and steppe-like formations in southwestern Syria, southeastern Lebanon, northeastern Israel and northwestern Jordan. *T. turgidum* var. *dicoccoides* was also found in certain sites in western Iran, northwestern Iraq and southeastern Turkey (HARLAN and ZOHARY 1966; JOHNSON 1975; FELDMAN 1976; TANAKA and ISHII 1973).

T. Timopheevii var. *araraticum* - THE WILD PROGENITOR OF *timopheevii* WHEAT

AARONSOHN (1910a, 1910b) assumed that the distribution of *T. turgidum* var. *dicoccoides*, as well as that of other wild wheats, may extend beyond the southern part of the Fertile Crescent into other parts of the Near East. This idea was shared by other botanists, and J. Bornmüller, who worked at the herbarium in Weimar, Germany, encouraged Theodor Strauss, a botanist who served as the British vice-consul in Sultanabad, Iran, to look for wild wheats in that part of the Near East. Strauss, in fact, found several specimens of two-grained wild wheat in 1910 in Noa-kuh, near the city of Kerind in the mountainous region of western Iran. However, Strauss' death in 1911 put an end to this survey.

SCHULZ (1913a) studied the material collected by Strauss and identified it as *T. dicoccoides* (Kcke) form. *Straussiana* to distinguish it from the Syrio-Palestinian two-grained wild wheat which he called *T. dicoccoides* (Kcke) form. *Kotschyana*. Schulz (1915) assumed that var. *dicoccoides* has a continuous range from the Hermon region in Syria to Iran via Asia Minor.

Later on, specimens of two-grained wild wheat were also collected in northwestern Iraq by J. B. Gillett (see SACHS 1953) and in the Taurus Mountains in Kilikia, Turkey, by P. M. Zhukovsky (see SCHIEMANN 1956). N. I. VAVILOV and his co-workers contributed greatly to our understanding of the distribution of wild wheats in southwest Asia. In 1923 ZHUKOVSKY found a unique cultivated form of non-free-threshing two-grained wheat in western Georgia, Central Transcaucasia, U.S.S.R. He first classified it as *T. dicoccum* Schr. var. *timopheevii* Zhuk., but in 1928 he raised this taxon to the rank of species (ZHUKOVSKY 1928); today

it is known as *T. timopheevii* var. *timopheevii*.

At about the same time two-grained wild wheat was also found in Transcaucasia, i.e., in Armenia (TUMANIAN 1930) and in Nakichevan (JAKUBZINER 1932). Jakubziner (loc. cit.) placed the Armenian-Nakicheranian forms in a separate sub-species, namely *T. dicoccoides* ssp. *armeniacum*. Further studies by MAKUSHINA (1938) showed that this taxon is sufficiently distinct from the Syrio-Palestinian forms to warrant the rank of a separate species. Accordingly, she called it *T. armeniacum* Mak. But, since this name had been briefly used for another taxon, JAKUBZINER (1947) changed it to *T. araraticum* Jakub. (this taxon is known today as *T. timopheevii* var. *araraticum*). Further studies on the distribution of var. *araraticum* by Jakubziner and others (see JAKUBZINER 1959) showed that this wild wheat also grows in Azerbaijan and on the eastern slopes of the Akhsam Mountain in Caucasia.

More recent studies (HARLAN and ZOHARY 1966; JOHNSON 1975; FELDMAN 1976; TANAKA and ICHIKAWA 1972; TANAKA and ISHII 1973) have indicated that this two-grained wild winter wheat also exists in eastern Turkey, northern Iraq and western Iran. In the southern part of its distribution area it grows in mixed populations with types morphologically and cytologically resembling *T. turgidum* var. *dicoccoides*.

Cytogenetic studies (SACHS 1953) showed that the wild wheat collected by J. B. Gillett east of Rowanduz in northern Iraq (identified as *T. dicoccoides* var. *nudiglumis*) actually belongs to *T. timopheevii* var. *araraticum*. This might also be true for the specimens that were found by Strauss in 1910 in western Iran. If this is the case, then Strauss should be credited for being the first to find var. *araraticum* in nature.

Thus the wild *T. timopheevii* var. *araraticum* grows in the northern part of the Fertile Crescent and surrounding regions, i.e., western Iran, northwestern Iraq, eastern Turkey, Armenia and Transcaucasia. In this area it occupies primary habitats such as open oak park forests and steppe-like formations, as well as secondary habitats such as roadsides and edges of cultivation.

WILD WHEATS IN THE STUDY OF WHEAT EVOLUTION

The discovery of the wild prototypes of the one-grained and the two-grained cultivated wheats enabled SCHULZ (1913b) to assemble the first natural classification of wheats (Table 2). He divided the genus *Triticum* into three major taxonomic groups, i.e., einkorn, emmer and dinkel. Each group was subdivided further into wild and cultivated species; the cultivated species were separated further into hulled and naked types. SCHULZ (1913b) assumed that the cultivated (free-threshing) types derived from the cultivated hulled species, which in turn derived from the wild prototypes. He postulated the existence of three different types of wild wheats, i.e., prototypes of the einkorn, the emmer and the dinkel. Two of these prototypes were known, and Schulz believed that the wild progenitor of the dinkel wheats

would also be found.

Table 2. Phylogenetic classification of species and cultivated groups of *Triticum* (after Schulz 1913a).

	Wild Progenitors	Cultivated Wheats	
		Spelt (hulled) wheats	Naked (free-threshing) wheats
Einkorn series (one-grained wheat)	<i>T. aegilopoides</i> →	<i>T. monococcum</i>	None
Emmer series (two-grained wheats)	<i>T. dicoccoides</i> →	<i>T. dicoccum</i> →	<i>T. durum</i> <i>T. turgidum</i> <i>T. polonicum</i>
Dinkel series	Not known →	<i>T. spelta</i> →	<i>T. compactum</i> <i>T. vulgare</i>

The crossing data of TSCHERMAK (1913, 1914) on the fertility of the various interspecific F₁ hybrids supported Schulz's classification of three major groups of wheats. Schulz's grouping is also in accordance with serological relationships as determined by ZADE (1914). This classification was also supported by the pioneering cytogenetic work of SAKAMURA (1918) and SAX (1918, 1922), who showed that Schulz's three groups of wheats also differ in their chromosome number; the einkorns are characterized by 2n=14, the emmers by 2n=28 and the dinkels by 2n=42.

KIHARA (1919, 1924), SAX (1921, 1922, 1927), SAX and SAX (1924) and many others (see RILEY 1965; MORRIS and SEARS 1967) have shown that the various wheat species form a polyploid series based on X=7 and consisting of three different ploidy levels: diploid (only one species, *T. monococcum*), tetraploid (two species, *T. turgidum* and *T. timopheevii*) and hexaploid (only one species, *T. aestivum*). (For modern classification of wheats, see Table 3). In this polyploid series 7 chromosome pairs of the einkorns (genome A) plus 7 additional pairs (genome B) constitute the 14 pairs of *T. turgidum*. These 14 pairs (genome AB), plus an additional 7 (genome D), make up the 21 pairs of *T. aestivum*. *T. timopheevii*, on the other hand, differs cytogenetically from all other tetraploid and hexaploid wheats by possessing a different genomic combination, i.e., AAGG instead of AABB (LLIENFELD and KIHARA 1934). These findings indicated that polyploid wheats are allopolyploids which evolved as a result of hybridization followed by chromosome doubling. Thus the tetraploid wheats must have derived from crosses between diploid wheat and two other diploid species containing the B or the G genome. Similarly, hexaploid wheat was derived from a cross of an emmer wheat and another diploid species having the D genome (Table 3).

TSCHERMAK and BLEIR (1927) were the first to obtain a spontaneous amphiploid from the cross *T. turgidum* var. *dicoccoides* x *T. ovatum*, thus demonstrating the possibility of species formation via allopolyploidy in the wheat group. The discovery that chromosome doubling can be induced by colchicine (BLAKESLEE and

AVERY 1937) opened new possibilities for the study of wheat evolution. Attempts have been made, by intensive studies during the last 50 years, to identify the diploid donors of the B, G and D genomes and to resynthesize the various polyploid wheats.

Table 3. Present classification of cultivated wheats and closely related wild species.

Species	Genomes	Wild		
		hulled	hulled	free-threshing
<u>Diploid (2n=14)</u>				
<i>T. speltoides</i>	S(=G?)	all	-	-
<i>T. bicorne</i>	S ^b	all	-	-
<i>T. sharonensis</i>	S ¹ (=B?)	all	-	-
<i>T. longissimum</i>	S ¹ (=B?)	all	-	-
<i>T. searsii</i>	S ^S (=B?)	all	-	-
<i>T. tauschii</i>	D	all	-	-
<i>T. monococcum</i>	A	var. <i>boeoticum</i> (wild einkorn)	var. <i>monococcum</i> (cultivated einkorn)	
<u>Tetraploid (2n=28)</u>				
<i>T. timopheevii</i>	AG	var. <i>araraticum</i>	var. <i>timopheevii</i>	-
<i>T. turgidum</i>	AB	var. <i>dicoccoides</i> (wild emmer)	var. <i>dicoccum</i> (cultivated emmer)	var. <i>durum</i> var. <i>turgidum</i> var. <i>polonicum</i> var. <i>carthlicum</i>
<u>Hexaploid (2n=42)</u>				
<i>T. aestivum</i>	ABD	-	var. <i>spelta</i> var. <i>macha</i> var. <i>vavilovii</i>	var. <i>aestivum</i> var. <i>compactum</i> var. <i>sphaerococcum</i>

The donor of the D genome of hexaploid wheat has been identified as *T. tauschii* (McFADDEN and SEARS 1944, 1956; KIHARA 1944). Synthetic hexaploids have been produced from crosses of different varieties of *T. turgidum* with *T. tauschii* which resemble certain established hexaploids (McFADDEN and SEARS 1946; KIHARA and LILIENFELD 1949). Hybrids between synthetic and natural hexaploids are usually fully fertile (McFADDEN and SEARS 1946).

Presumably, hexaploid wheat originated in a cultivated field. There is some evidence suggesting that hexaploid wheat was derived from a cross between cultivated tetraploid wheat,

most probably *T. turgidum* var. *dicoccum*, and *T. tauschii* (KIHARA 1965; MORRIS and SEARS 1967; SEARS 1975, 1976a; FELDMAN 1976). It is thus most likely that the hexaploid originated in the wheat field after the spread of cultivated var. *dicoccum* into the distribution area of *T. tauschii*, i.e., Iran, eastern Turkey, Armenia and Transcaucasia. Such an origin could explain why hexaploid wheat, in contrast to all other cereal crops, has no wild progenitor.

Tetraploid wheats are a much older species than hexaploid wheat, and their genomes must have undergone considerable differentiation. It is therefore more difficult to identify the diploid donors of the B and the G genomes of polyploid wheat than the more recent donor of the D genome. Morphological, geographical and cytological evidence has been used to implicate *T. speltoides* (genome S) (SARKAR and STEBBINS 1956; RILEY et al. 1958) or *T. bicorne* (SEARS 1956) as the donor of genome B. Recent cytogenetic data (KIMBER 1973; SHANDS and KIMBER 1973), however, indicate that *T. speltoides* may have donated the G genome of *T. timopheevii* rather than the B of *T. turgidum*.

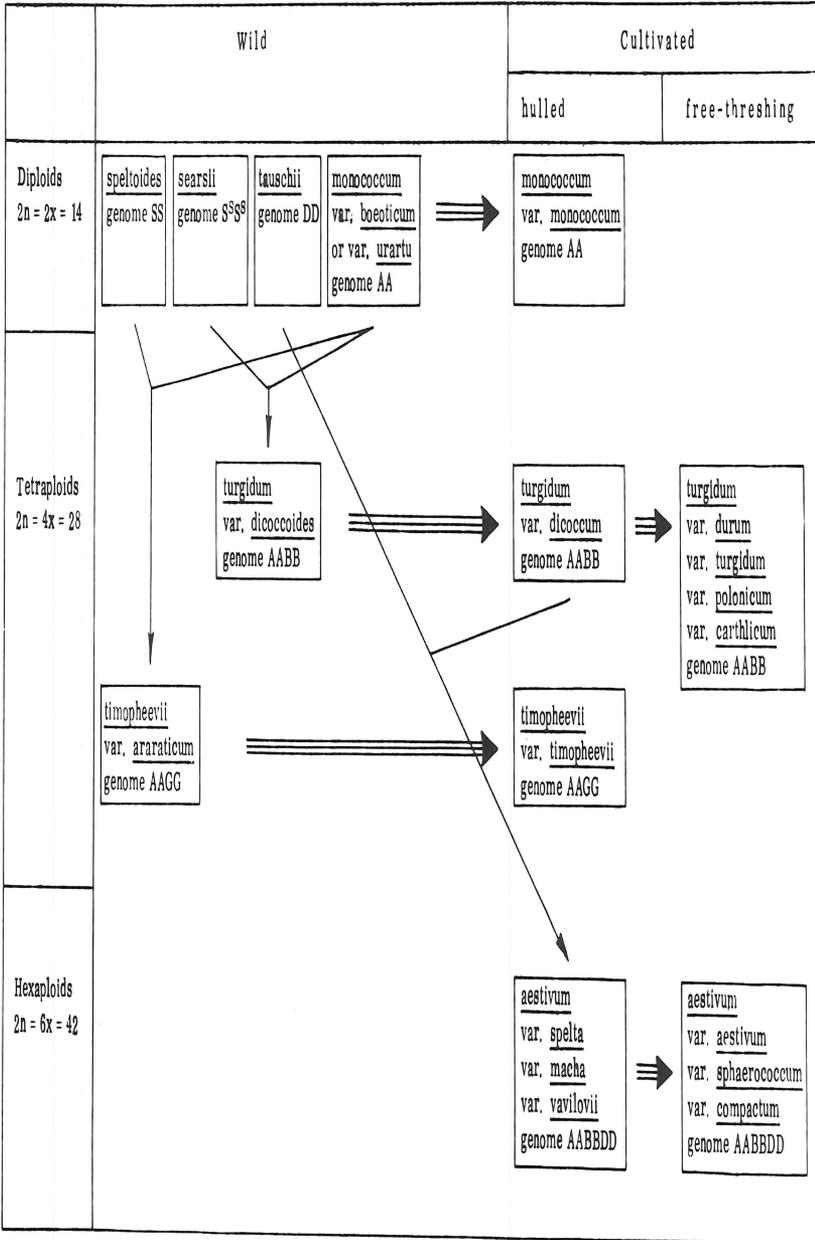
Based on chemical comparisons, JOHNSON (1975) concluded that *T. turgidum* derives from hybridization of the two diploid wheat taxa *T. monococcum* var. *urartu* and *T. monococcum* var. *boeoticum*. However, this possibility is ruled out by the cytogenetic studies of CHAPMAN et al. (1976) and DVORAK (1976). The discovery of a new diploid species, *T. searsii* (FELDMAN and KISLEV 1977a, 1977b), sheds light on the origin of the B genome. Cytogenetic and eco-geographical evidence (FELDMAN 1977 and in preparation) indicates that *T. searsii* (and/or *T. longissimum*) is the most likely putative donor of the B genome of polyploid wheats.

The evolution of the polyploid wheats is summarized in Fig. 1. Two of the genomes of polyploid wheats, A and D, have changed relatively very little on the polyploid level. On the other hand, the other two genomes, B and G, have undergone considerable differentiation and are now only partially homologous with the genomes of their diploid donors.

T. speltoides, the putative donor of genome G of *T. timopheevii*, is in massive geographical contact with wild *T. monococcum*, i.e., var. *boeoticum* or var. *urartu*, in Armenia, eastern Turkey, northwestern Iraq and western Iran. In this area there are numerous mixed populations of the two diploid species, many of which also include the wild tetraploid *T. timopheevii* var. *araraticum*. This area is, therefore, the most probable place of origin of wild *T. timopheevii*.

The main distribution of wild *T. turgidum*, i.e., var. *dicoccoides*, lies southwest of the *speltoides*/wild *monococcum* area; it ranges from southwestern Syria and southeastern Lebanon to northeastern Israel and northwestern Jordan. In this entire area, var. *dicoccoides* does not form mixed populations with *T. speltoides*; on the other hand, it grows together with wild *T. monococcum* and *T. searsii* in southeastern Lebanon and southwestern Syria, and with *T. searsii* alone in northeastern Israel and northwestern Jordan. The geographical distribution of wild

Fig. 1: Evolutionary relationships of the wheats



diploid wheat and that of *T. searsii* overlap in southwestern Syria and southeastern Lebanon. In this latter region there are mixed populations of the two diploids and the tetraploid wheat. Thus it is very likely that this is the site of origin of *T. turgidum* var. *dicoccoides*.

The sporadic populations of var. *dicoccoides* in southeastern Turkey, northwestern Iraq and southwestern Iran may be considered products of hybridization between *T. timopheevii* var. *araraticum*, which grows massively in this region, and cultivated tetraploid wheat, most probably var. *dicoccum*. Such hybridization became possible after the spread of var. *dicoccum* to the northern part of the Fertile Crescent, soon after the agricultural revolution.

WILD WHEATS IN THE STUDY OF WHEAT DOMESTICATION

Diploid Wheat

Wild diploid wheat *T. monococcum* var. *boeoticum* is morphologically very similar to the cultivated form of diploid wheat, *T. monococcum* var. *monococcum*, the main difference being the brittle rachis of the former. After the rediscovery of var. *boeoticum* in Anatolia in 1854 (by Balanza), it was assumed by most botanists that var. *boeoticum* is the progenitor of cultivated *T. monococcum* (ASCHERSON and GRAEBNER 1902; SCHULZ 1913b). The latter was derived from the wild form simply as a result of selection for a non-brittle spike. The close cytogenetic relationships between the two forms is borne out by hybrids between them which are fully fertile (VILMORIN 1880a, 1880b). These hybrids exhibit regular chromosome pairing at meiosis.

It is only natural that the domestication of diploid wheat should have taken place in the northern part of the Fertile Crescent, which is the distribution center of the wild progenitor *T. monococcum* var. *boeoticum*. Archaeological data indeed confirm that *T. monococcum* was taken into cultivation in this region. Wild einkorn was collected by ancient man throughout its distribution area, long before it was cultivated. The earliest known carbonized grains of brittle einkorn wheat were found in the prehistoric settlement of Tell Mureybit, northern Syria (eighth millennium B. C.), where the cereal was apparently collected rather than farmed (for palaeoethnobotanical data see RENFREW 1973; HELBAEK 1966). At somewhat later sites of this area, i.e., early agricultural villages from 7500 to 6750 B.C., brittle *monococcum* wheat occurs side by side with a non-brittle type and is gradually replaced by it. From this region of the Fertile Crescent cultivation of *T. monococcum* spread to several other parts of the Near East and to Central and Western Europe (about the fifth millennium B.C.) through the Danube and Rhine valleys. In subsequent eras (bronze and early iron ages), *monococcum* wheat attained a wide distribution in Europe and the Near East. In modern times, it occurs only as a relic crop in mountainous parts of Yugoslavia and Turkey, where it is used mainly for fodder.

Tetraploid Wheat

The discovery of wild tetraploid wheat *T. turgidum* var. *dicoccoides* by Aaronsohn in 1906 and the study of its geographical distribution and ecological requirements (AARONSOHN and SCHWEINFURTH 1906; AARONSOHN 1909, 1910a, 1910b, 1913; OPPENHEIMER 1957, 1963), contributed greatly to an understanding of the course of domestication of tetraploid and hexaploid wheats. Already KÖRNICKE (1889), who saw only a part of a spike of this wheat in Kotschy's herbarium collections, could conclude from its morphology that this wild wheat is the progenitor of cultivated wheats. The discovery of var. *dicoccoides* in nature enabled wider comparative morphological studies of this wild wheat, all of which supported Körnicke's assumption (AARONSOHN and SCHWEINFURTH 1906; AARONSOHN 1909, 1910a, 1910b, 1913; SCHWEINFURTH 1906a, 1906b, 1908; SCHULZ 1913b). TSCHERMAK (1914) made the first crosses between var. *dicoccoides* and cultivated forms of tetraploid wheat, such as var. *dicoccum* and var. *durum*, and concluded from the high fertility of the F₁ hybrids that the wild and cultivated forms have very close genetic affinities. He demonstrated that the main morphological difference between the wild var. *dicoccoides* and the cultivated var. *dicoccum*, i.e., the fragility of the spike, is determined by a small number of genetic factors. From his genetic studies Tschermak supported the hypothesis of Körnicke, Aaronsohn and Schweinfurth that var. *dicoccum*, the only spelt (hulled) type of *T. turgidum* and therefore the primitive cultivated tetraploid, derived from var. *dicoccoides* by a series of mutations. PERCIVAL (1921) also mentioned that var. *dicoccoides* crosses readily with cultivated forms of *T. turgidum* and *T. aestivum*. He reported the occurrence of hybrids between these taxa in Israel (then Palestine) and Syria, as well as spontaneous hybridization wherever the taxa are brought into contact with each other in experimental fields. In accordance with this, cytological analysis of hybrids between var. *dicoccoides* and cultivated wheats (see PERCIVAL 1921) showed that the chromosomes of the wild form are fully homologous with those of all cultivated varieties of *T. turgidum* and with those of the A and B genomes of hexaploid wheat.

A completely different theory was presented by VAVILOV (1926, 1927), who rejected the view that the cultivated forms of *T. turgidum*, i.e., vars. *dicoccum*, *durum*, etc., derive from wild emmer. Vavilov (loc. cit.) did not accept the direct descent of barley and wheat from the wild grasses *Hordeum spontaneum* and *Triticum dicoccoides*, although he accepted the descent of rye and oats from *Secale afghanicum* and *Avena fatua*, respectively. Vavilov regarded var. *dicoccoides* as a parallel form which developed in a similar manner to the cultivated form, var. *dicoccum*, but from a different progenitor. From the wealth of varieties and forms of the primitive cultivated var. *dicoccum* in Ethiopia and the relatively little variation in such forms in Israel and Syria, VAVILOV (1926, 1927) concluded that cultivated tetraploid wheats may have originated in Ethiopia. Vavilov's conclusion may have been biased by the fact that his hybrids between var. *dicoccoides* and var. *dicoccum* or var. *durum* were only partially fertile. This partial sterility could have

been caused by Vavilov's use of wild material from Armenia and Transcaucasia in these crosses, namely *T. timopheevii* var. *araraticum*, and not *T. turgidum* var. *dicoccoides*. Sterility barriers between var. *araraticum* and vars. *dicoccum* and *durum* are now known to exist (SVETOZEROVA 1939).

Vavilov did not ascribe any importance to the fact that the wild wheat var. *dicoccoides*, which so much resembles var. *dicoccum*, is native to the southern part of the Fertile Crescent and does not grow in Ethiopia. He considered Aaronsohn's eco-geographical data insufficient for regarding var. *dicoccoides* as the progenitor of cultivated tetraploid wheat and southwest Asia as the place of its origin. Instead, Vavilov accepted the eco-geographical theory of SOLMS-LAUBACH (1899). Vavilov regarded the centers of variation of the cultivated tetraploid as the centers of origin. The centers of variation in which domesticated tetraploid arose are, according to him, Ethiopia, the Mediterranean basin and Transcaucasia. This concept is not borne out by morphological, eco-geographical, cytogenetic and archaeological data (SCHIEHMANN 1948, 1951, 1956); all cultivated forms of *T. turgidum* derived from var. *dicoccoides* and the domestication of these wheats took place in the geographical distribution area of var. *dicoccoides*, i.e., in the southern part of the Fertile Crescent and not in Ethiopia, the Mediterranean basin and Transcaucasia. Data from excavations in prehistoric villages in the Near East show that the distribution of tetraploid non-brittle, hulled var. *dicoccum* at the dawn of agriculture overlapped with the distribution of wild var. *dicoccoides*. Brittle forms of wild tetraploid wheats, i.e., *T. turgidum* var. *dicoccoides* and *T. timopheevii* var. *araraticum*, were possibly harvested, together with brittle forms of wild *T. monococcum*, in the wild state throughout the Fertile Crescent long before actual farming began. Parallel to the situation in *T. monococcum*, *T. turgidum* var. *dicoccum*, which presumably derived from var. *dicoccoides* as a result of selection for non-brittle rachis, began to appear in prehistoric sites of the Near East as early as 7500 B.C. In these sites it occurs together with brittle forms and, later on, replaces them completely. The domestication of var. *dicoccoides* and the selection of var. *dicoccum* took place in the main distribution area of this wild species, i.e., in northern Israel, northern Jordan, southern Syria and southern Lebanon. In this area, mutants having semi-brittle and non-brittle rachis can be found in wild populations (KAMM 1974). From here, non-brittle emmer spread rapidly to all seventh millenium farming sites of the Near East.

Var. *dicoccum* was the most prominent cereal in the early farming villages of the Near East. From the hilly and mountainous areas of the Fertile Crescent it was taken to the lowlands of Mesopotamia in the sixth millenium B.C. and to Egypt, the Mediterranean basin, Europe, Central Asia and India during the fifth and fourth millenia. It was taken to Ethiopia some 5000 years ago by the Hamites. In all these regions it remained the principal cereal until the first millenium B.C., when it was replaced by the more advanced free-threshing tetraploid form, *T. turgidum* var. *durum*. Today, var. *dicoccum* is grown on a limited scale in Ethiopia, Iran, Transcaucasia, eastern Turkey

and the Balkans.

The *durum* wheats presumably originated from cultivated emmer, i.e., var. *dicoccum*, by an accumulation of mutations that reduced the toughness of the glumes to the point at which free-threshing was attained (McFADDEN and SEARS 1946; MORRIS and SEARS 1967; SEARS 1969a). Most other naked grain tetraploid wheats (Table 3) are probably of relatively recent origin, deviating from var. *durum* in only single characters (MacKEY 1966; MORRIS and SEARS 1967) and sharing the genetic system which determines the free-threshing habit.

The *T. timopheevii* group is distinguished from *T. turgidum* cytogenetically (LILLENFELD and KIHARA 1934; KOSTOFF 1937; SVETOZAROVA 1939; SACHS 1953; WAGENAAR 1961, 1966; FELDMAN 1966), by the electrophoretic pattern of its seed proteins (JOHNSON 1967), by its DNA content (REES and WALTERS 1965) and by its different cytoplasm (WILSON and ROSS 1962; KIHARA 1968; MAAN 1973). This group includes a cultivated form, var. *timopheevii*, and a wild form, var. *araraticum*. Cytogenetic studies have shown that var. *timopheevii* is closely related to var. *araraticum* and contains the same genomic constitution, AAGG (SVETOZAROVA 1939; WAGENAAR 1961; TANAKA and ICHAKAWA 1972). Thus cultivated var. *timopheevii* may have derived from wild var. *araraticum* in the distribution area of the latter, i.e., in Transcaucasia, Armenia, eastern Turkey, northwestern Iraq and western Iran. The cultivation of var. *timopheevii* today is limited to several localities in Transcaucasia.

Hexaploid Wheat

There is no wild progenitor of cultivated hexaploid wheat, *T. aestivum*. It is assumed (MORRIS and SEARS 1967; SEARS 1976a; FELDMAN 1976) that hexaploid wheat originated recurrently from crosses between cultivated tetraploid wheat, most probably var. *dicoccum*, and the wild diploid *T. tauschii*. Hexaploid wheat can have arisen and entered cultivation only after the more or less simultaneous domestication of diploid and tetraploid forms. It appears in archaeological data from prehistoric villages of the Near East in the seventh and sixth millennia B.C. Between 6000 and 5000 B.C., *T. aestivum* penetrated, together with cultivated emmer, into the irrigated agriculture of the plains of Mesopotamia and, in the fifth millennium, into the Nile basin. In the same millennium *T. aestivum* also appears in archaeological finds from the central and western Mediterranean basin. Forms of hexaploid wheat appear in central and western Europe at the end of the fourth millennium, where they are found associated (together with einkorn and emmer) with the first traces of agricultural activities. *T. aestivum* spread into central Asia and, by way of the highlands of Iran, to the Indus valley, where it appears at the beginning of the third millennium B.C.

The hexaploid varieties (Table 3) *spelta*, *vavilovii* and *macha* are hulled, while vars. *aestivum*, *compactum* and *sphaerococcum* are free-threshing and thus more advanced. The free-threshing character is determined by a compound genetic locus, the Q factor, and therefore the evolution from hulled to free-threshing type required the mutation of q to Q (McFADDEN and

SEARS 1946; MORRIS and SEARS 1967; SEARS 1948, 1959b, 1975). The advanced varieties, i.e., vars. *aestivum*, *compactum* and *sphaerococcum*, differ from each other only in single genes (Mac KEY 1954).

The hulled varieties of *T. aestivum* are cultivated today only in several areas of central Europe, Transcaucasia and western Iran. Of the free-threshing varieties, var. *aestivum*, i.e., common wheat, is economically by far the most important wheat and is now grown on a world-wide scale. The cultivation of var. *compactum* is restricted to certain areas of Europe, the Near East and western United States, and that of var. *sphaerococcum* to Central Asia and India.

THE POTENTIAL OF WILD WHEATS IN WHEAT IMPROVEMENT

Although Aaronsohn started his search for wild wheat merely from theoretical and purely scientific motivation, he soon realized the great practical value that his studies might have. He was impressed (AARONSOHN 1909, 1910a, 1910b, 1913) by the wide range of adaptations of wild emmer. The altitude of its habitats ranges from 1600-1800 m above sea level on Mount Hermon to 100-150 m below sea level near the Jabok river in Jordan. It occupies a range of very different climatic regions from cool and humid mountains to hot and dry valleys. In Israel alone the gradient in annual rainfall in the var. *dicoccoides* area ranges from 900 to 350 mm. Wild emmer grows on different types of soils such as terra-rossa, basalt and erosion products of Nubian sandstone.

Among the agronomically important characters first noticed by Aaronsohn in certain specimens of var. *dicoccoides* are large grain size, ability to grow in relatively dry habitats and resistance to rust (AARONSOHN 1910a, 1910b, 1913). He recommended utilizing wild emmer in breeding programs, especially for improving the resistance of cultivated wheats to drought, extreme climatic and soil conditions, and rusts, as well as for increasing grain size and yield. Aaronsohn believed that "the cultivation of wheat might be revolutionized by the utilization of wild wheat. Such utilization might facilitate the formation of many new varieties, some of which will be hardy and able to grow in dry and warm habitats or in areas with poor soil and can thus expand the wheat growing area" (AARONSOHN 1910a, p.52).

Aaronsohn's belief that var. *dicoccoides*, as well as other wild wheats, can serve as an excellent source for many agronomically important characters and can be utilized in the improvement of cultivated wheats was shared by other scientists such as SCHWEINFURTH (1906a, 1906b, 1908), COOK (1913), TSCHERMAK (1914) and others. They hoped to make use of the exceptional hardiness and adaptability of wild emmer to produce cultivated varieties that would be adapted to arid regions. Selected specimens of var. *dicoccoides* were introduced to various research stations in Europe and the United States for observation and crosses with cultivated wheats. The fertile or partially fertile F_1 hybrids produced by TSCHERMAK (1914) first indicated

the possibility of gene transfer from wild into cultivated types.

In 1909 Aaronsohn was invited to the United States. He visited many universities and agricultural research stations, where he lectured on the properties and importance of the wild wheat and distributed samples of grains. The severe conditions under which the plant grew in Israel (then Palestine) were similar to those found in many parts of the United States, and Aaronsohn hoped that wild wheat would soon be used by American agricultural breeding experts.

Aaronsohn himself grew lines of var. *dicoccoides* at Atlit, which was the first experimental farm in Palestine, established and headed by Aaronsohn himself. On this farm he carried out various observations on selected types of wild wheat and started to cross them with cultivated material. His tragic death in a plane crash in 1919 put an end to all this original and pioneering work.

Attempts elsewhere to utilize var. *dicoccoides* or other wild wheats in breeding programs met with very little success, and Aaronsohn's vision of using the wild gene resources for the improvement of cultivated wheats was soon forgotten. The reasons for this failure were lack of genetical and cytological knowledge of wheats as well as a poor understanding of relationships between wild emmer var. *dicoccoides* and cultivated wheats. Since most cultivated wheats belong to common wheat *T. aestivum*, the crosses of tetraploid var. *dicoccoides* with hexaploid common wheat yielded pentaploid hybrids with reduced fertility. Moreover, the hybrids exhibited many wild characters, such as a brittle rachis and adherent glumes, which were undesirable to breeders. Because of lack of knowledge, it was difficult to select against them. Wheat breeders were thus discouraged from utilizing wild wheat in breeding programs and instead used genetic material already available in other common wheat varieties of hexaploid wheat.

In recent years this situation has changed completely, and there is a renewed interest in var. *dicoccoides* as a source for agronomically important genes. A great deal of information on the genetic relationships between wild emmer as well as other wild wheats and cultivated wheats has been accumulated during the last 50 years. Cytogenetic methods for proper genetic analysis and interspecific transfer of desirable characters have been developed (SEARS 1954, 1959a, 1965, 1966, 1969a, 1969b, 1972, 1976b). The availability of aneuploid lines of *T. aestivum* makes the genetic analysis of individual var. *dicoccoides* chromosomes on the genetic background of cultivated wheat possible and facilitates transfer of selected chromosomal segments.

Although wheat yields have increased dramatically in the past three decades, they are obviously insufficient for the needs of the growing world population. In the general drive to fulfill this need, the genetic material present in the cultivated wheats has been utilized almost to its fullest capacity. Moreover, continuous selection for high-yielding varieties under modern farming conditions and for varieties that answer the demands of the market has considerably reduced the genetic

variability. In many regions of the world new varieties produced during the last thirty years have largely replaced the old traditional ones. In this process of replacement the old varieties were not conserved, and thus the gene pool of cultivated wheats, which was already narrow, has become greatly reduced. Since most of the new varieties were derived from a small number of genetic stocks, they contain similar genetic material. This genetic uniformity and narrow basis not only limits the ability to further improve wheat, but also makes wheat very vulnerable to diseases and climatic hazards.

Consequently, there is an urgent need to increase the genetic variation of cultivated wheats. Attempts to enrich this variation by induced mutations either by irradiation or chemical treatment have not been very successful.

The new developments not only make the utilization of wild wheat feasible but also an urgent necessity. Recent surveys of samples of var. *dicoccoides* collected throughout its distribution area have confirmed Aaronsohn's findings that this wild wheat indeed contains many agronomically important genes, such as genes for disease resistance (GERECHTER-AMITAI and STUBBS 1970), drought resistance, large grains and others (AVIVI et al. 1977). Also, COOK'S (1913) observation that var. *dicoccoides* is much more outcrossing than its domesticated derivatives was confirmed.

In a recent study (AVIVI et al. 1977; AVIVI 1977) it was found that this wild tetraploid wheat contains much more protein in its grains than all other cultivated wheats. Several genotypes contain as much as 26-31% grain protein, approximately twice the amount of grain protein in cultivated material. Some of the var. *dicoccoides* collections which contain high quantities of grain protein also have a high amount of lysine per unit dry weight, i.e., the highest nutritional value (AVIVI et al. 1977). Some of these types are also characterized by very large grains (1000 grain weight is around 50 g).

The screening of populations of var. *dicoccoides* for economically important characters is only in its initial stages, and the full extent of this genetic treasurehouse is not yet completely known. This wild taxon should be rich in genes conferring resistance to pests and diseases, greater resistance to drought and heat, higher grain protein quantity and quality, larger grain size, spike size and number of tillers, and more. Var. *dicoccoides* can be crossed easily with cultivated wheats, giving fully fertile F₁ hybrids when crossed with tetraploid wheats and partially fertile hybrids in crosses with hexaploid wheats. The chromosomes of var. *dicoccoides* pair regularly with those of the A and B genomes of tetraploid and hexaploid cultivated wheats, and every gene can be transferred from the wild chromosomes to the cultivated ones by means of crossing over. Thus the transfer of selected genes from var. *dicoccoides* to cultivated wheats can be induced, in most cases, by simple, conventional plant breeding procedures. Because of this, var. *dicoccoides* is an excellent source for desirable genetic material and should be used extensively in the improvement of cultivated wheats.

Aaronsohn believed that "the cultivation of wheat may be revolutionized by the utilization of the various wild forms of var. *dicoccoides*". At the beginning of the century this phrase was only a dream and ahead of its time. But now, due to the cytogenetic knowledge obtained during the last 50 years, the day is not far when genes from var. *dicoccoides* will indeed contribute to the improvement of cultivated wheat.

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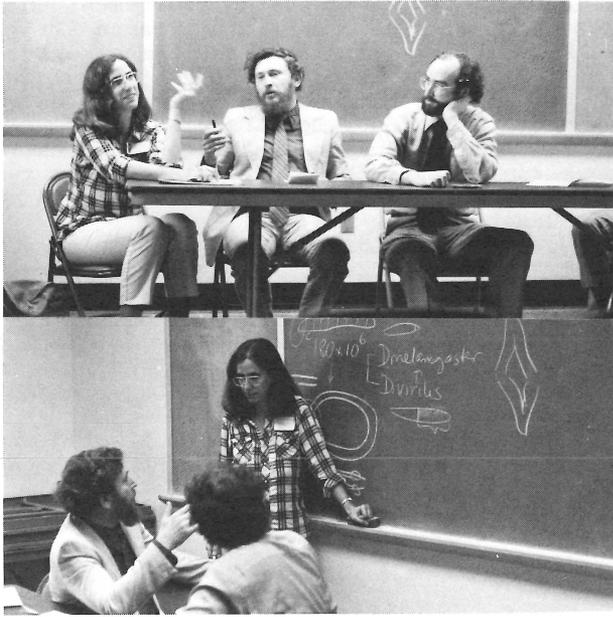
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Dr. Moshe Feldman at the 9th Stadler Symposium



Drs. Ruth Kavenoff, M. Feldman and J. Allen



Drs. Allen and Kimber