A. Horovitz
M. Feldman

The domestication and exploitation of plants and animals

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PETER J. UCKO
and
G. W. DIMBLEBY

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DANIEL ZOHARY

The progenitors of wheat and barley in relation to domestication and agricultural dispersal in the Old World

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GERALD DUCKWORTH & CO LTD
3 HENRIETTA STREET, LONDON WC2

M. Feldman

DANIEL ZOHARY

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Introduction

Students of the origin of old world cultivated plants will probably remember the present decade as the "archaeological decade". The recent archaeological activity in Western Asia clearly shows that by 7000 B.C. farming villages had been established over the wide arc spanning the western flanks of the Zagros Mountains in Iran and Iraq, Southern Anatolia, spreading southward into Palestine[1]. More important, in several excavations, such as Jarmo in Iraq, Ali Kosh and Tepe Sabz in Iran, Çatal Hüyük and Hacilar in Anatolia, and Beidha in Jordan, a considerable amount of plant remains has been unearthed. These have been critically examined and brilliantly identified by several workers and particularly by Hans Helbaek of the Danish National Museum[2]. It is now well established that the neolithic agricultural development in Western Asia depended primarily on domestication and subsequent cultivation of three species of cereals: (1) Einkorn wheat (*Triticum monococcum*), (2) Emmer wheat (*Triticum dicoccum*), and (3) Two-row barley (*Hordeum vulgare* ssp. *distichum*). Thus we have a definite answer to the cardinal question: what were the primitive crops at the initiation of agriculture. In terms of the origin of Old World cultivated plants, these archaeological finds are no doubt the critical "missing links" which enable us to reconstruct the events of domestication more definitely.

Now that the identity of the West Asiatic principal early crops is well established, the genetical and botanical information concerning relationships between tame and wild cereal species can be reassessed, and the evolution of cultivated types more soundly understood.

First, we have ample botanic and genetic evidence to determine definitely what are the wild ancestors of the neolithic primitive cultivated cereals. Following this, the distribution, ecology and various biological characteristics of the wild species can be surveyed, in order to find out whether they might have some bearing on the questions of where, when and how crop domestication began and developed in the Old World.

The present paper starts with a survey of the wild ancestors, reviewing the main genetic reasons why these wild plants should be considered as progenitors of the barley and wheats cultivated by the neolithic farmers. It continues with a review of their distinct ecology and several other biological traits, stressing features relevant to domestication and to the spread of agriculture.

Einkorn wheat

It is now clear that wild *Triticum boeoticum* (Pl. VIII) is the only candidate for the ancestry of cultivated einkorn, *T. monococcum*. The reasons for this can be summarized as follows: both wild and cultivated einkorns are morphologically similar. Both have diploid chromosome numbers ($2n = 14$), and domesticated and wild einkorns show close genetic affinities: hybrids between wild *T. boeoticum* and cultivated *T. monococcum* are completely fertile, and chromosome pairing in meiosis is normal. Genetically, the two types should be regarded as mere races and not as fully separated species.

The main distinguishing trait between wild einkorn and cultivated einkorn lies in the biology of seed dispersal. This difference is conspicuously reflected in the morphology of the rachis of the ear. In wild einkorn we have brittle ears; and the individual spikelets disarticulate at maturity to disperse the seed. In cultivated einkorn, this essential adaptation to wild conditions no longer exists. The mature ear stays intact and breaks only upon threshing. Survival depends on reaping and sowing.

Wild *T. boeoticum* shows a relatively wide distribution area. It is spread over Western Asia and penetrates also into the Southern Balkans (Greece, Turkey, Syria, North Iraq, Transcaucasia). Its distributional centre lies, however, in the Fertile Crescent Belt of Southern Turkey, Northern Iraq and adjacent territories in Northern Syria, a second, smaller centre being found in West Anatolia. In these centres, wild einkorn is massively spread as a component of open herbaceous oak park-forests and steppe-like formations. In addition to such primary habitats, wild einkorn also occurs as a weed, occupying secondary habitats such as edges of cultivation and roadsides. Sometimes it even invades fields of cultivated cereals. Edaphically, wild einkorn shows definite affinity to basaltic soils, marls and limestones. Further away from the centres, this wild wheat is less common and much more sporadic in its distribution. Significantly, in these peripheral areas, it is mainly restricted to segetal or secondary habitats, i.e. sites which were not available before the opening up of these areas by agricultural activity.

The wide geographic range of wild einkorn is also paralleled by wide morphological variation and ecotypic adaptation to a relatively wide climatic amplitude. *T. boeoticum* is distributed from the low, warm, summer-dry foothills of the Euphrates basin, to the elevated cool and continental plateaux and mountain ridges of Anatolia. In Turkey, its altitudinal amplitude is 0–1600 m.; in Iran and Iraq, 600–2000 m.

Two main eco-geographic races have been recognized by botanists in wild einkorn. A relatively small and usually one-seeded race is characteristic of the cooler Balkans and Western Anatolia, while a larger race with two-seeded spikelets is found in the warmer, summer-dry areas of Southern Turkey, Iraq and Iran. However in Anatolia, all inter-gradations and intermediates between these two extremes occur, often forming mixed, variable populations. The small one-seeded race is usually referred to as *T. boeoticum* ssp. *aegilopoides* (or *T. aegilopoides* in older floras), while the larger two-seeded race is commonly called *T. boeoticum* ssp. *thaoudar* (or *T. thaoudar* in older floras). Fig. 1 shows the known distribution of wild einkorn as assessed from field surveys and botanic collections[3]. The shaded areas in this map indicate the regions in which wild einkorn massively occupies *primary habitats*, i.e. areas in which it should be considered genuinely wild. Dots outside the shaded areas represent sites in which *T. boeoticum* occurs today exclusively as a segetal plant, i.e. places to which this grass apparently spread after the initiation of agriculture.

Emmer wheat

Genetic and morphological evidence clearly indicate that cultivated emmer (*Triticum dicoccum*) is derived from wild emmer (*T. dicoccoides*) (Pl. VIII). As in the previous case of einkorns, here too, we are confronted with a pair of closely related wild and domesticated types. *T. dicoccum* and *T. dicoccoides* both have tetraploid chromosome numbers ($2n = 28$), and hybrids between them are fully interfertile. Wild emmer also shows striking morphological similarity to cultivated emmer. Thus genetically, these two wheats (as well as the more evolved, naked *T. durum* wheats) are again not fully separated species, but rather races or sub-species of a single species complex. Also here, domesticated and wild emmers are mainly separated from one another by their distinct seed dispersal biology. Wild emmer has the typical brittle spike characteristic of all wild cereals and the individual spikelets serve as the seed dissemination units. In cultivated emmer the mature ears stay intact; they are separated only by threshing, and are thus fully dependent on man for their survival.

T. dicoccoides is more restricted in its distribution and ecology than wild einkorn. Its range covers Israel, South Syria and Transjordan (see Fig. 2), and its centre is found in the catchment area of the Upper Jordan Valley, i.e. the slopes of Eastern Galilee and Gilead facing the Sea of Galilee, the adjacent basaltic plateaux of Golan and Hauran, and further north to the eastern slopes of Mt. Hermon. In this area, *T. dicoccoides* is indeed common, particularly in places which have not been severely overgrazed.

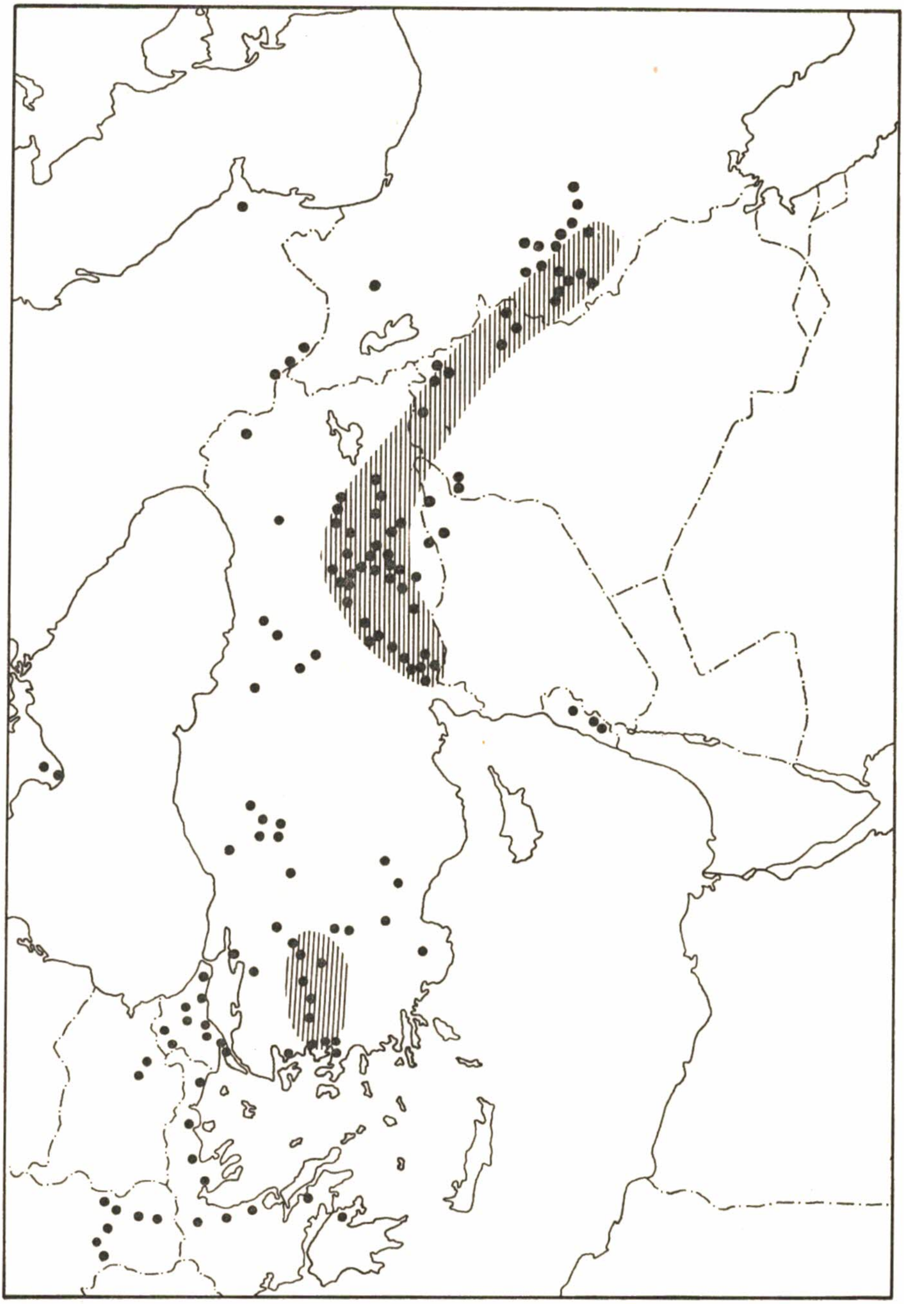

Fig 1 Distribution of wild einkorn *Triticum boeoticum.*

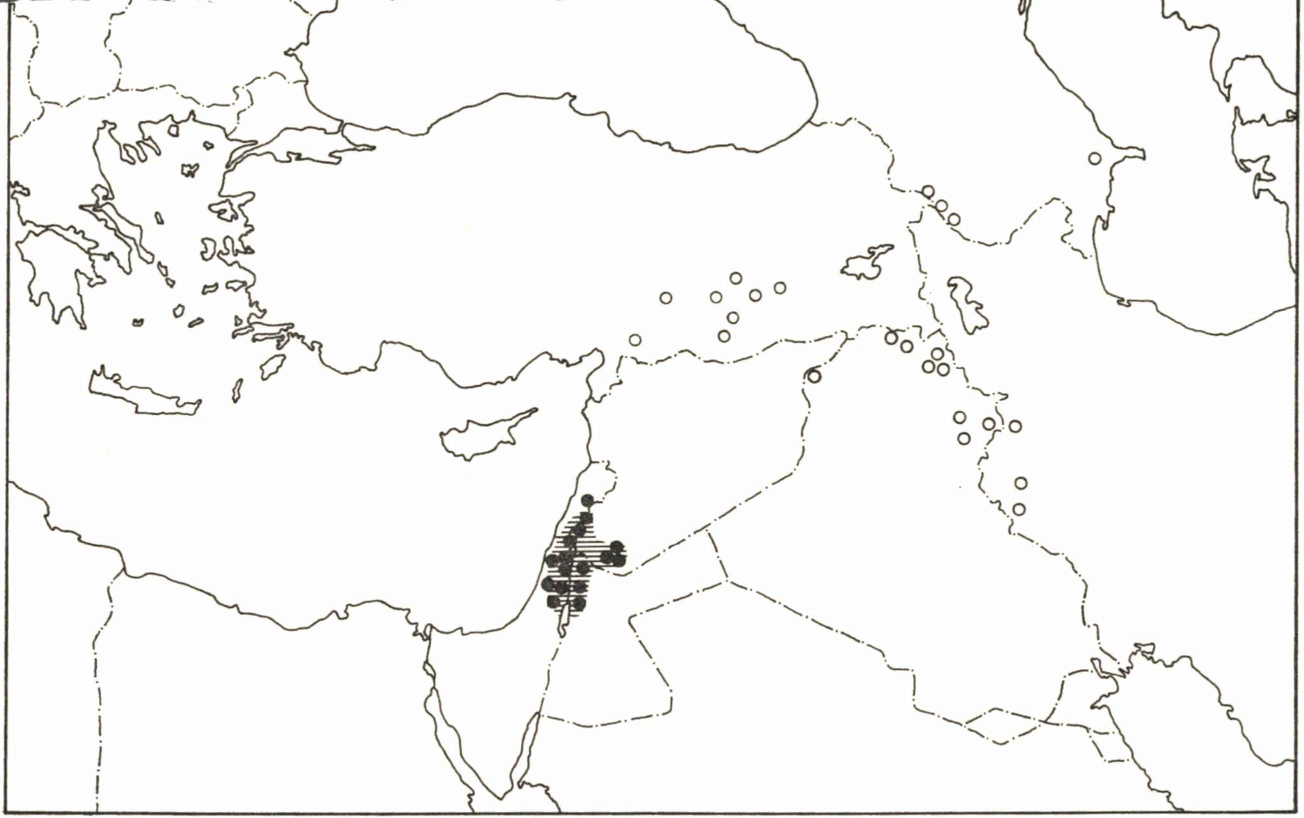

Fig 2 Distribution of wild emmer *Triticum dicoccoides*.

Dots in Palestine and South Syria represent known sites of *T. dicoccoides*, and the area in which wild emmer is common is shaded. Hollow dots represent known sites of wild tetraploid wheats in Turkey, Iraq, Iran and Transcaucasia. These were regarded as *T. araraticum* locations, but recent evidence (see text note 17) indicate that they include also *T. dicoccoides* material. (Adapted from Harlan, J. R. and Zohary, D. (1966). Distribution of wild wheats and barley, *Science*, **153**, pp. 1074–80.)

Wild emmer occurs here as a common annual component in the herbaceous cover of the *Quercus ithaburensis* park-forest belt and related semi-steppe herbaceous formations which dominate this area. *T. dicoccoides* shows close affinities to basaltic and hard limestone bedrocks. It is rare or completely absent on marls. It usually builds mixed stands with wild barley, *Hordeum spontaneum*, and wild oat, *Avena sterilis*.

In contrast to wild einkorn, *T. dicoccoides* is rarely a weed. Over all its distributional range it is restricted to what appear to be primary or more or less primary habitats.

In its geographic centre, *T. dicoccoides* shows a multitude of easily distinguishable forms, and often builds conspicuously polymorphic populations which are easily detected by the variation in hairiness and the colour of the spikes. Also, climatically wild emmer shows a considerable range and is distributed over a rather wide altitudinal amplitude. Robust early maturing types are found growing in the winter-warm basin of the Sea of Galilee (as low as 100 m. below sea level). More slender and later blooming types occur higher in the mountains and climb up to 1500–1600 m. on the east-facing slopes of Mt. Hermon.

Attention should be called to the fact that in the Middle East we have two species of wild tetraploid wheats! First, the Syro-Palestinian *T. dicoccoides* which have just been discussed, and second, *T. araraticum*, which is distributed over Soviet Transcaucasia, South-east Turkey, and Iraqi and Iranian Kurdistan (see Fig. 2). The two wild tetraploid wheats are morphologically very similar and, until recently, they have usually been lumped together and confused by botanists. But while the Syro-Palestinian wild tetraploid, *T. dicoccoides*, shows close genetic affinities and full genomic homology to our common cultivated tetraploid wheats of the emmer-durum group, *T. araraticum* does not. Crosses between *T. araraticum* and either cultivated *T. dicoccum*-*T. durum*, or wild Syro-Palestinian *T. dicoccoides*, show strong sterility barriers. Such hybrids are also characterized by very irregular meiosis. Thus, biologically we are faced with two fully divergent wild tetraploid species. The first, *T. dicoccoides*, which is genetically closely related to our cultivated tetraploid wheats. The second, *T. araraticum*, which is genetically unrelated to domesticated emmers and durums—at least to the emmer and the durum varieties as they occur today! There is, however, a single exception here: *T. araraticum* shows close genetic affinities to endemic *T. timopheevi*, a restricted, rare cultivated tetraploid wheat which was discovered by Russian botanists in a single district of Georgia, U.S.S.R.

As with the previously described wild wheats, *T. araraticum* also shows close affinities to the park-forest belt of the Fertile Crescent arc. It is a component of the herbaceous communities which characterize this belt of vegetation. As far as we know, the distribution of *T. araraticum* is rather sporadic. It has never yet been found to form the same extensive masses and "wild fields" that so characterize the other two wild wheat species, *T.*

boeoticum and *T. dicoccoides*. It is almost always found mixed with *T. boeoticum*, where the latter usually prevails. In South Turkey, North Iraq, and West Iran, it grows in what seem to be genuine primary habitats (*Quercus brantii* forest belt) as well as at the edges of cultivation. In Transcaucasia, its distribution is much more restricted, and is apparently found only in places highly disturbed by man's activity.

Barley

It is now clear that only a single genuinely wild species of barley is closely related to the various cultivated barley forms, and should be regarded as their sole ancestor[4]. This is two-row brittle *Hordeum spontaneum*. *H. spontaneum* has the same chromosome number as cultivated barley *H. vulgare*. Both are diploids ($2n = 14$); hybrids between them are fully fertile and show regular pairing in meiosis. Again, from a genetic point of view, wild *H. spontaneum* and the various forms of cultivated *H. vulgare* did not diverge to the extent of representing fully independent, separated species.

Wild barley, *H. spontaneum*, shows wider distribution than the wild wheats. It is spread over a wide area in the East Mediterranean basin and the West Asiatic countries, penetrating east as far as Turkmenia and Afghanistan[5]. Like wild einkorn, wild barley occupies, at present, both primary habitats and segetal, man-made habitats. Its distribution centre lies in the Fertile Crescent Belt, i.e. in a wide arc, starting from Israel and Transjordan in the south-west, stretching north towards South Turkey, and bending south-east towards Iraqi Kurdistan and South-west Iran (see Fig. 3). In this general area, and only here, *H. spontaneum* is massively and continuously spread over primary habitats. It constitutes an important annual component of open formations, and is particularly common in the summer-dry belt of the deciduous oak park-forest, east, north and west of the Syrian desert and the Euphrates basin, and the slopes facing the Jordan rift valley. From here, *H. spontaneum* spills over to the drier and warmer deserts. In the Fertile Crescent countries, *H. spontaneum* also occupies a whole array of secondary man-made habitats, i.e. opened-up Mediterranean maquis, abandoned cultivation, edges of fields and roadsides. Further west (Aegean region and Cyrenaica) and further east (North-east Iran, Soviet Central Asia and Afghanistan), *H. spontaneum* is rare and much more sporadic in its distribution; it rarely builds even local masses and seems to be completely restricted to segetal habitats or to sites which have been drastically churned by man's activity. Thus, in these peripheral areas, wild barley does not seem to be genuinely wild! As in the case of wild einkorn, it apparently spread to these locations as a weed, as a consequence of agricultural activity.

In general, wild barley does not tolerate extreme cold and it is only occasionally found above 1500 m. It is thus almost completely absent from the

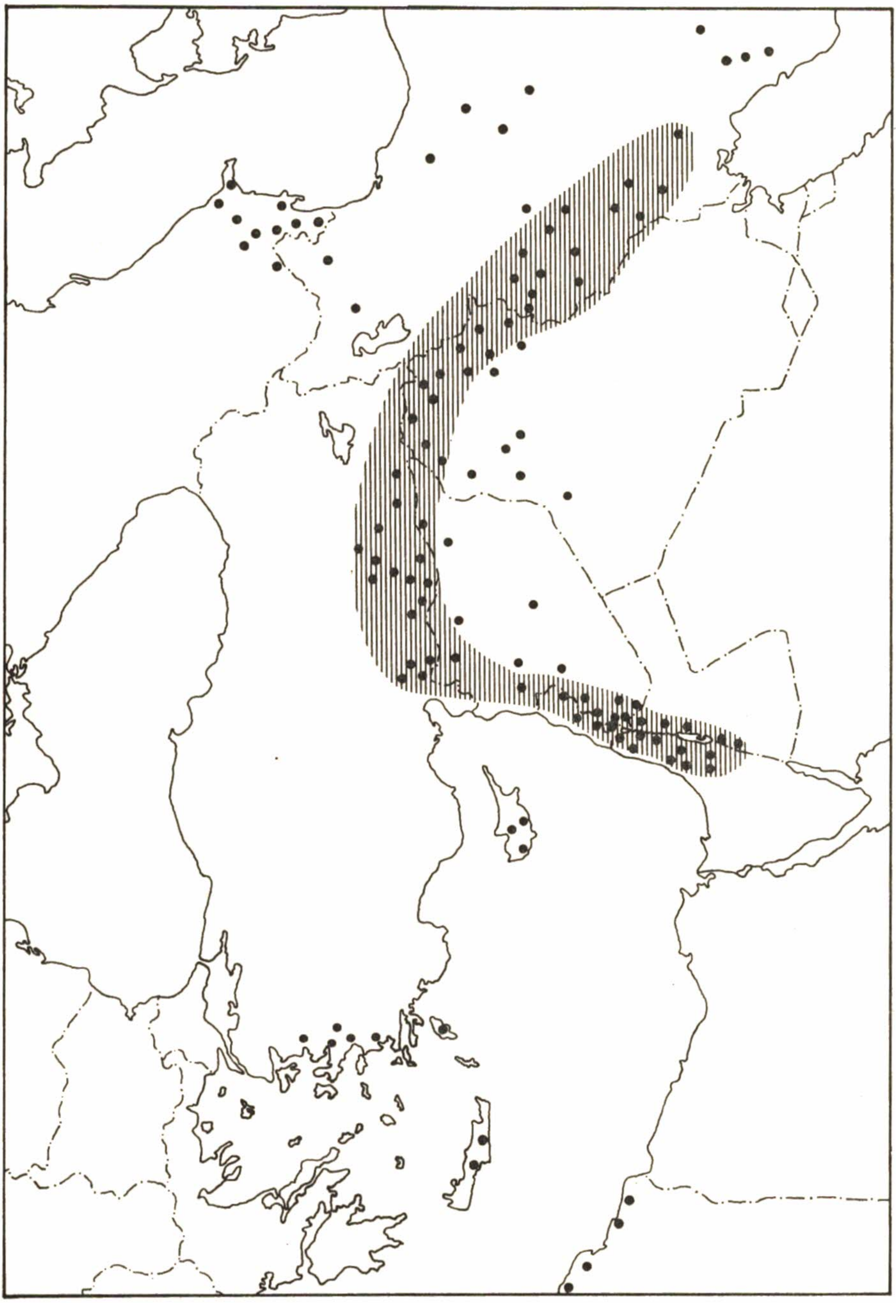

Fig 3 Distribution of wild barley *Hordeum spontaneum.*

which primary habitats occur are shaded. (Adapted from elevated continental plateaus of Turkey and Iran. On the other hand, it is somewhat more xeric as compared with the wild wheats and penetrates relatively deep into warm steppes and deserts. Morphologically too, *H. spontaneum* is quite variable and several distinct races can be distinguished. Robust types with extremely large seeds and extraordinarily long awns occur in the catchment area of the Upper Jordan Valley, often in close association with similarly robust *T. dicoccoides* forms.

A much more slender desert type is found in the drier steppes and in desert dry water courses. This race is sporadically spread from the Negev to the steppic plateaux of Transjordan, northward to the Turkish border, and eastward to Iran and Afghanistan. It is a small, grassy type with kernels only half the size of the robust races of the Eastern Galilee. All intermediate types between these extremes are widely spread in Palestine, Syria, Turkey and Iran.

Until recently, cultivated six-row barley, *H. vulgare* ssp. *hexastichum*, was considered to have arisen not from *H. spontaneum*, but from what was regarded as a second wild progenitor, brittle six-row *H. agriocrithon*. Brittle six-row barley plants have been collected in several localities in the Middle East, either as weeds in cultivation or as scattered individuals in *H. spontaneum* stands, growing at edges of barley cultivation. Recent analysis[6], however, has demonstrated that such six-row *agriocrithon* plants could not be considered as an independent, genuinely wild species. Indeed, it was found that they are not adapted to survive under true wild conditions. They were demonstrated to be secondary hybrid derivatives, resulting from occasional spontaneous hybridization between six-row cultivated *H. vulgare* and two-row wild *H. spontaneum*. These finds seem to have settled the controversy of the monophyletic vs. diphyletic origin of cultivated barleys. The botanical and genetic evidence is well corroborated by the archaeological finds. As amply stressed by Helbaek[7], the earlier archaeological deposits contain only two-row barleys. Six-row barley appears later. It seems clear now that cultivated six-row barley is derived from two-row cultivars, and that the sole wild ancestor of all cultivated barley is *H. spontaneum*.

Ecology and population structure of wild cereals

The first fact that should be emphasized is that *Hordeum spontaneum*, *Triticum boeoticum* and *T. dicoccoides* are common plants in their distribution centres. Frequently they build extensive, massive stands. In fact, all these three wild cereals are important herbaceous constituents of the "sub-Mediterranean" oak park-forest vegetation belt that arches over the Syrian desert and the Euphrates basin. This belt receives a considerable amount of rain (400–1000 mm.)—but only in winter. The summer here is very warm and dry. The vegetation is characterized by a lush growth of annuals in winter and spring.

In the few places where the oak park-forest is still preserved, thick herbaceous cover occupies the openings between the well-spaced trees (*Quercus ithaburensis* in the west, and *Q. brantii* in the east). Where the trees have been destroyed or heavily coppiced, the herbaceous cover is even more uniform, and a steppe-like landscape prevails in places unoccupied by agriculture. Particularly rich in annuals are the hard limestone and basaltic bedrocks with their relatively heavy soils. These rock formations occur over considerable parts of the "sub-Mediterranean" oak park-forest belt. *H. spontaneum, T. boeoticum, T. dicoccoides*, as well as several species of oats (*Avena*) and goat-face grasses (*Aegilops*), are frequently dominant annuals here. They are particularly conspicuous in places which have not been heavily overgrazed (such places are uncommon today in the Near East!). Under heavy grazing pressure, the wild cereals are greatly repressed, and their place is often taken by less palatable herbs. Significantly, when the grazing pressure is relaxed, the wild grasses usually re-establish their dominance within a few years.

Thus in the *Q. ithaburensis* and *Q. brantii* formations and related park-forests or "moist steppes", that stretch from Palestine to South Turkey and Iraqi and Iranian Kurdistan, one finds extensive "natural fields" of wild cereals. Conspicuous examples of such massive stands occur on the basaltic plateaus and the hard limestone slopes of Eastern Galilee and adjacent Gilead and Golan. When the State of Israel was established two decades ago, grazing had been regulated in the Upper Jordan Basin. Consequently, winter growth of the wild cereals here is now largely unimpaired. All over the slopes facing the Jordan Valley, from sea level near the Sea of Galilee to the elevated hills near the town of Safad, *H. spontaneum, T. dicoccoides* and *Avena sterilis* are spread in masses. On uncultivated slopes, natural fields of these wild cereals extend over many kilometres. In their growth and total mass, these wild fields of wheat, barley and oats are not inferior to their cultivated counterparts. These robust wild forms can be favourably compared with their cultivated relatives in grain production also. In rainy years, well developed wild Eastern Galilee stands (of *T. dicoccoides* mixed with *H. spontaneum*) are estimated to produce some 50–80 kg. of grain per dunam (1000 sq. metres). This does not fall far behind the yields which local cultivated durum and barley varieties produce in this region—under wooden plough agriculture (i.e. 50–150 kg. per dunam).

Similar extensive "fields" of wild cereals are spread over the wide arc north and east of Palestine—i.e. Syria, Southern Turkey and east into Northern Iraq and Western Iran. But in the centre and eastern flank of the arc, species composition is somewhat different. Wild barley, *H. spontaneum*, is present everywhere. But Palestinian tetraploid wild emmer, *T. dicoccoides*, is replaced in Turkey, Iraq and Iran by diploid wild einkorn *T. boeoticum*—with an occasional admixture of tetraploid *T. araraticum*. Conspicuous "fields" of wild cereals with such composition are common in Gaziantep, Malatya, Diyarbakir, Siirt provinces of Southern Turkey, and Jebel Sinjar, and the

700–1400 m. altitude zone of the Zagros ranges in Irbil-Sulaymaniya provinces of Iraqi Kurdistan. They also occur in the Shahabad-Ilam area in adjacent Western Iran. All over these hilly areas, the large robust types of two-grained wild einkorn. *T. boeoticum* ssp. *thaoudar* prevail. Turkey, in particular, is very rich in wild einkorn. The basaltic formations which characterize Diyarbakir province harbour extensive, almost pure stands of this wild diploid wheat[8].

There is, however, a very conspicuous phenological difference between fields of wild cereals and their cultivated counterparts. As already stressed, ears of the wild cereals disarticulate immediately upon maturation. Under the dry hot weather that characterizes the end of the growing season in the Near East, this process is very abrupt. In a given site and for a given wild cereal, plants mature quickly and simultaneously. Thus, wild cereal fields showing masses of maturing ears shed their fruits and turn into barren dry stalks within one or two weeks! There is only a very limited time interval in which the grain of wild cereals can be effectively collected. If an extremely dry warm spell ("hamsin") happens to occur at maturation time (and these spells are quite frequent in this season) shedding of fruit can be completed in a matter of two or three days, and the potential harvesting time shortened even more.

But differences in maturation time do exist between different cereals and in different localities or ecological niches. In Israel, in mixed stands, *H. spontaneum* matures some one to three weeks earlier than *T. dicoccoides*. Plants growing in sites with deep heavy soil mature somewhat later than those occupying shallow soils. Considerable differences in the ripening time occur, however, in different altitudes. Maturation of wild emmer at the sea level belt near the Sea of Galilee, occurs around the end of April, while higher up in the Safad area (alt. 700–800 m.) stands mature around 15th–20th May. In the adjacent east-facing slopes of Mt. Hermon (alt. 1400–1600 m.), ripening occurs still later—in early June. Similar altitudinal clines occur in Turkey, Iraq and Iran. Therefore, in regions with varied topography, altitudinal amplitude compensates for the abrupt shedding. Collectors can start their harvest in lower elevations and proceed gradually to climb the higher slope, and effective harvesting time is extended to last four to six weeks.

Seed dispersal and germination of the wild cereals

As has already been pointed out in the previous sections wild wheats and barley have fragile spikes, and their ears disarticulate immediately upon maturity. The fragility of the spike is, in fact, the main diagnostic character that serves for distinction of wild cereals from their cultivated counterparts. But what is less emphasized is that the brittleness is only the most conspicuous reflection of one of the major adaptations of these wild cereals to their wild environment: their specialization in seed dispersal. As annuals under Mediterranean summer-dry conditions, these wild cereals are heavily dependent on efficient mechanisms to disperse and plant their seed, protect them in the long dry summer, and facilitate effective germination when rains start in the subsequent season. The spikelet in wild wheats and the triplet in the wild barley are, in fact, specialized arrowshaped seed dissemination units which very effectively insert the mature fruiting units into the soil. The elongated shape of the spikelet or the triplet, the sharpness of its base (the rachis segment), the hairiness and the scabrosity of the unit, the strong awns it bears, and the sterile lateral spikelets in the barley's triplet, are all essential elements of the dissemination and planting device. Immediately after ripening, the individual spikelets (in wild wheats) and the individual triplets (in wild barley) fall to the ground and operate as effective arrow-like devices for one way "migration" of the seed into the soil. Fruit burial is a quick process; it is completed a few weeks after shedding. The summer aspect of the wild cereal "fields" is characterized by dry, barren stalks and effectively inserted fruits. Only the big awns remain protruding from the ground.

Another major adaptation of the wild cereals to their environment is regulation of germination and facilitation of rapid development of seedlings. In *T. dicoccoides* and *T. boeoticum* ssp. *thaoudar*, the dispersal unit (i.e. the spikelet) contains two kernels. The first germinates in the ensuing winter; in the second, germination is usually inhibited and only occurs a year later, safeguarding these annuals against the hazards of droughts. In barley, where only one seed occurs in each dispersal unit, differential inhibition of germination occurs between triplets of the same ear.

Wild wheats and barley are also characterized by a relatively larger seed, which are as big, or almost as big, as their cultivated counterparts. This is, apparently, also a necessary adaptation to the conditions under which these cereals germinate and start to develop in nature. In the lush, herbaceous communities of the oak park-forest belt, rapid growth commences immediately after the first effective autumn rain. A big seed, with a mass of storage material, is an obvious asset in the fierce competition for space and light which occurs here at the beginning of the growing season.

The size of the kernel in the wild wheats and barley is, so to speak, a pre-adaptation for domestication. The wild cereals produce attractive large quantities of big, easy-to-collect-and-store kernels. The main developments under domestication were not selection for bigger seed, but the breakdown of the seed dispersal mechanism and the "wild type" regulation of germination. Both are essential for survival under wild conditions; but they are useless, and even damaging, under domestication.

Places of origin of the early cultivated cereals

If we assume that the main climatic and vegetation belts which are distinguishable today in the Near East had more or less the same distribution some 10,000 years ago, the data presented in this paper on the wild cereals may provide clues to possible centres of early domestication.

One of the main aims of this paper was to emphasize that at present, we already possess ample information on the distribution, ecology and biology of the wild cereals. More important, on the basis of the field information and general geobotanical knowledge of the Near East, it is possible to assess fairly accurately where these wild progenitors occupy primary habitats in contrast to places where they occur exclusively as weeds. Of course, only in primary habitats are these grasses genuinely wild. Only here (i.e. in the "centres") could they have existed prior to the advent of agriculture.

The conclusion was reached[9] that einkorn wheat was probably domesticated in South-east Turkey, and emmer wheat in the Upper Jordan watershed. Barley could have been domesticated almost anywhere within the arc that spans the Fertile Crescent. Furthermore, since wild barley occurs also in relatively dry places, barley domestication could have started in less humid sites in this belt.

It is also clear that in the centres of their distribution, wild einkorn, wild emmer and wild barley are widely spread and their big kernels and massive stands could have been an obvious attraction to collectors. Harlan[10] amply records the remarkable yields of wild wheat he harvested in Turkey. Wild fields of all the three cereals may have been harvested long before the start of agricultural practices.

Collection stage versus cultivation

If wild wheats and barley were indeed collected in their respective centres long before they were domesticated, the question naturally arises as to whether we can distinguish between the collection stage and the advent of domestication. In other words, can we recognize domestication soon after it began? Biologically speaking, perhaps the best way to define domestication and to contrast it with the stage of collection is as follows:

When a cereal is harvested and *all* the grain yield obtained is used as food we are dealing with a *collection stage*; when a cereal is harvested and later one *part* of the yield is used as food, while a second *part* of the grain is *intentionally planted* by man, we are dealing with *domestication.*

From the point of view of population genetics and considerations of selection pressures, these two situations are diametrically opposed. Under the system of collection the wild stands maintain themselves spontaneously, i.e.

their existence depends entirely upon the wild mode of seed dispersal. When wild stands are being harvested grains from the less brittle plants which constitute these populations have of course a better chance to be gathered by man while the more brittle plants donate relatively more seed for the start of the successive generation. Mere collection of wild stands would therefore actively select for quick-shattering forms. By contrast, artificial planting would mean selection in exactly the opposite direction. Non-brittle mutants which were lethal in the first situation become advantageous under the second system. Compared to the brittle forms, they have a better chance of contributing their seed for subsequent generations. Genes for non-brittleness are thus strongly selected for by the system of harvesting-and-planting! Thus under domestication, one should expect establishment of non-brittle cereals whether or not the cultivator is conscious of this trait. Furthermore, theoretically, such a shift from brittle to non-brittle spikes should be fast, and if the planted populations of wheats and barley were large enough, it could have been accomplished in a matter of only a few generations.

In summary, the notion that man first discovered brittle mutants in wild cereal fields, realized their potentialities and subsequently introduced cultivation, is apparently a gross over-simplification. Non-brittle mutants were not the cause of domestication but rather an immediate result, the consequence of a change in the biological system when planting was introduced.

The fact that several times (as Helbaek found in Beidha) both brittle and non-brittle cereals have been found mixed together, is not necessarily an indication that we are dealing with the real beginnings of domestication. Early farmers were no doubt both collectors and cultivators, and the collection of wild cereals could have added to the harvest obtained from the cultivated plots for a long time after the advent of domestication. The critical indication that cultivation was practised is of course the presence of some non-brittle material.

Aegilops squarrosa *and the origin of bread wheats*

Hexaploid wheats or bread wheats (*Triticum aestivum*) are exclusively cultivated forms. They do not have wild counterparts in nature. Helbaek's[11] finds in Anatolia, Iran and Mesopotamia indicate that these wheats started to appear one to two millennia after the early start of domesticated einkorn and emmer. Cytogeneticists have fully analysed the mode of formation of *T. aestivum*[12]. Bread wheat has been demonstrated to be a hybridization-and-fusion product. It contains two sets of chromosomes (genomes A and B) present in the emmer-durum wheats and a third set (genome D) found in a wild goat-face grass *Aegilops squarrosa*. In other words, hexaploid ($2n = 42$) *T. aestivum* was formed by hybridization and subsequent chromosome doubling—which fused tetraploid ($2n = 28$) emmer-durum wheats with diploid ($2n = 14$) *Ae. squarrosa*.

Since no wild hexaploid wheat occurs in nature, it seems plausible to assume that the formation of the bread wheats occurred only *after* the advent of wheat agriculture, and that wild *Ae. squarrosa* combined with a cultivated tetraploid wheat to form a new cultivated wheat species.

The first conspicuous fact about *Ae. squarrosa* is that this goat-face grass is the easternmost diploid species in the *Triticum-Aegilops* group. Although its centre lies in the South Caspian area, it is widespread and very common in Northern Iran and adjacent Transcaucasia and Transcaspia (see Fig. 4). Further away from this centre, *Ae. squarrosa* spreads westward as far as Eastern Turkey and the Syrian Desert steppes, and eastward to Pakistan and Kashmir. In Soviet Central Asia it is recorded as far east as Kirghizia and adjacent parts of Khazakstan.

Like wild barley and wild einkorn, *Ae. squarrosa* occupies both primary and segetal habitats. But only in the centre of its distribution, i.e. North Iran, and adjacent Transcaspia and North Afghanistan, is this plant a frequent component in genuine steppes and "forest-steppe" formations. At the same time, it is a noxious follower of agriculture and a common weed in cereal fields. Towards the periphery of its distribution, it is almost exclusively a weed. Here, too, we are faced with a case of a wild progenitor which apparently largely expands its distribution with the opening-up of the land by agriculture.

Both morphologically and ecologically, *Ae. squarrosa* shows an extraordinarily wide amplitude and is represented by a multitude of forms. Its exact ecological range still requires detailed study. But it is clear that in its distribution centre, this diploid occurs over a strikingly wide range of rather continental climatic conditions, from the dry sage-brush steppes of the elevated Iranian and Afghan plateaus, to the margins of deserts, and to the temperate rain-soaked Hyrcanic forest belt at the southern coast of the Caspian Sea.

In summary, the morphological variation and ecological amplitude of *Ae. squarrosa* are exceptionally wide; they exceed those of the other diploid species in the *Triticum-Aegilops* group. Furthermore, in contrast to the more "Mediterranean" wild emmer, this diploid extends its range into the cold continental steppes of Central Asia. It is also a successful and agressive weed in cereal fields. As a weed, it greatly expanded its distribution—beyond the area of its primary habitats.

As already pointed out by Zohary *et al.*[13], these features provide clues to the place of origin of bread wheat *T. aestivum* and explain some of its ecological characteristics.

At the start of neolithic agriculture, the two contributors that fused to form the hexaploid wheats were evidently geographically isolated. Wild emmer *T. dicoccoides* was restricted to Palestine and Syria. *Ae. squarrosa* apparently did not spread westward from North Iran. Contacts between the tetraploid

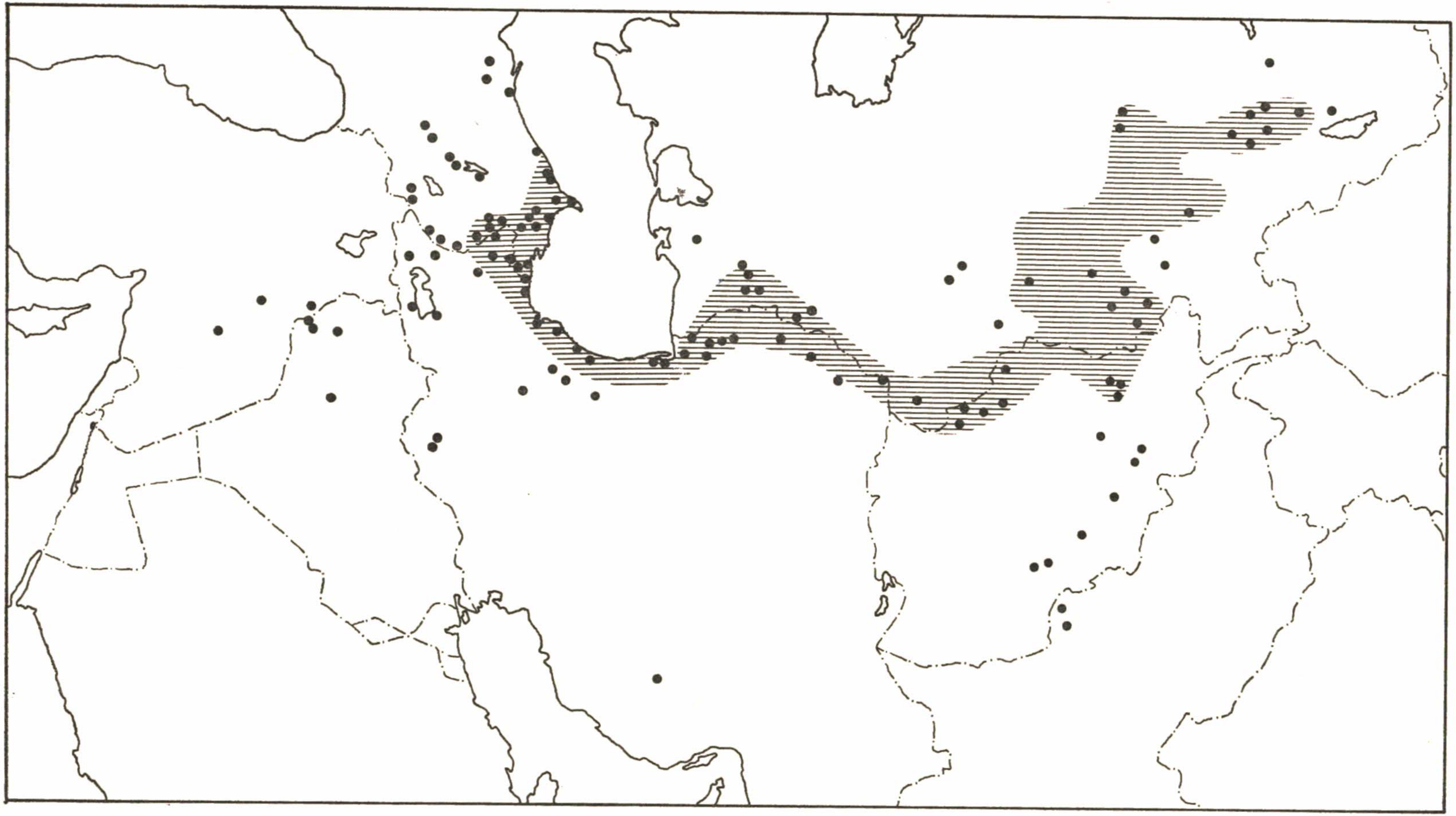

Fig 4 Distribution of wild goat-face grass *Aegilops squarrosa*.

Dots represent known sites, and the areas in which primary habitats occur are shaded. (Adapted from Zohary, D.

wheats and *Ae. squarrosa* could have been established only after the domestication of emmer and the spread of wheat agriculture to North Iran and Armenia. If this be true, the most likely place of origin of hexaploid wheat should have been somewhere near the south-west corner of the Caspian Sea. Several additional lines of evidence point to the same conclusion. As already mentioned, there is no wild hexaploid wheat in nature. Furthermore, Kihara and his group[14] have demonstrated that synthetic hexaploids between *T. dicoccoides* and *Ae. squarrosa* are weak dwarf plants, resulting from a dwarf gene which occurs in most strains of wild emmer. In contrast, this dwarf gene has not been found in cultivated emmer-durum varieties, and the synthetic hexaploids between the cultivated tetraploid and *Ae. squarrosa* develop normally.

Ecologically, the addition of the D genome greatly changed wheat adaptation. The tetraploid wheats (emmer-durum group) were derived from a "Mediterranean" progenitor, i.e. were adapted to the mild winters and warm, rainless summers which characterize the Mediterranean basin. The incorporation of the D genome rendered hexaploid wheat far more adaptive to extreme continental conditions and sub-humid temperate climates. This is most likely the main factor that facilitated the wide distribution and the apparent success of hexaploid cultivated wheats over the more continental plateaux of Asia and the colder and mesophytic areas of Europe.

The conspicuous weedy tendencies of *Ae. squarrosa* should have been another asset. When *Ae. squarrosa* was added to the cultivated wheat, it did not greatly change the already acquired adaptation of the latter to thrive under agricultural conditions. Adjustment of the new hexaploid wheats to cultivation was therefore relatively easy.

Self-pollination and its significance

Both wild and cultivated wheats and barleys are predominantly self-pollinated. Self-fertilization in these plants is ensured by the precocious dehiscence of the anthers—prior to the opening of the florets. Cross-pollination occurs occasionally, but it is a rare event amounting to only a few promils of the total pollinations. Thus in their mating system wheats and barleys differ from the majority of the plant species—which are cross-pollinated.

Was it a mere chance that the first plants which were successfully domesticated in West Asia were selfers? There is good reason to assume that this was not the case, and that at the initiation of the Middle Eastern agriculture self-pollinated plants were better suited or "preadapted" to domestication in comparison to cross-pollinated plants.

The first obvious advantage of self-pollination is the isolation established by this mating system. Self-pollination splits the population into independent pure lines. Under such a system two forms (e.g. brittle wild barley and a cultivated non-brittle barley) can co-exist in the same area. They do not face the danger that the less common type will be swamped by the more common one. If indeed domestication of cereals in the Middle East started in the same regions where the wild progenitors were common, effective isolation of the initial cultivated crop was a necessity. Self-pollinators had this advantage. Cross-pollinators did not. Under a system of cross-pollination the initial small patches of the crop would have been exposed to massive pollination by wild type pollen. Swamping would result and maintenance of the identity of the cultivated variety would be difficult. It is therefore not surprising that the first plants which were successfully domesticated in the Middle East were all selfers. Cross-pollinated crops (e.g. rye) appeared only later.

It is also important to note that wheats and barleys are not obligatory selfers but just predominantly self-pollinated. Rare cross-pollination occurs in these plants. Such a mating system is admirably suited for rapid evolution and the establishment of new forms. Inbreeding would lead to the fixation of numerous lines, and the more attractive of them could have been easily selected and maintained by man. The occasional cross-pollination would have provided the crop with genetic flexibility—the possibility of combining and reshuffling genes originating from different lines and different sources.

Introgression and its effects

In the Mediterranean basin and in the Near East, the cultivated cereals and their wild relatives are genetically not completely isolated from one another. Over wide areas they grow side by side, and occasionally hybridize. In fact, such spontaneous hybridization is followed by introgression, i.e. by gene-flow from the wild entities to the cultivated entities. For wheat and barley, the picture can be summarized as follows.

Most conspicuous are the genetic relationships between the pairs of domesticated crop and wild ancestor. In Israel, for example, wild *Hordeum spontaneum* frequently comes into contact with cultivated barley (*H. vulgare*). At edges of cultivation, roadsides and similar habitats, sporadic hybrid swarms between cultivated and wild barleys occur rather frequently, and gene-flow from wild to cultivated, and vice versa, has been demonstrated[15]. Similar relationships are found in Israel between wild *T. dicoccoides* and its genetically close related *T. durum*; while in Thrace and Western Anatolia, this type of spontaneous hybridization still occurs between wild *T. boeoticum* and cultivated *T. monococcum*.

In the wheats, introgression occurs, not only between the interfertile domesticated and wild pairs, but also with more alien wild species. In fact, polyploid *T. durum* and *T. aestivum* have been found to hybridize in nature with some dozen different species of *Aegilops* and *Triticum*, such as *Ae. cylindrica*, *Ae. triuncialis*, *Ae. variabilis* and *Ae. longissima*. Furthermore, cultivated wheats also hybridize with their diploid progenitors, i.e. *T. boeoticum*, *Ae. speltoides* and *Ae. squarrosa*. Such spontaneous interspecific hybrids are largely sterile, but significantly not completely so. They do set some seed! Subsequent backcrossing to the cultivated species results in effective introgression. Gene-flow from the wild species to the cultivated polyploid wheat is quite common and apparently contributes considerably to the genetic variation of the cultivated forms. As already stressed by Zohary[16], polyploid wheats should be considered as "genetic sponges". Polyploidy buffers the hybridization process and makes it possible for these plants to incorporate genetic material from numerous different wild species.

In the last decade, natural hybridization and introgression between cultivated cereals and their wild relatives have been intensively studied and the details of the mechanisms clarified, at least in wheats and barleys. It now seems apparent that this process played a decisive role in the rapid evolution and successful dispersal of the cultivated cereals. It effectively enriched the initial cultivated crop with a wide range of genetic variation. The build-up of variation in the cultivated crops was thus not an independent process. Initial cultivated crops were able to utilize successfully the extensive gene pools of their wild relatives.

Each initial crop should therefore be envisaged as a sponge. After the initial domestication (i.e. its becoming dependent on man) it most probably absorbed genetic variation from adjacent wild relatives. This enlarged its adaptive range and subsequently made it possible for it to spread and to adapt itself to new areas. Then a new cycle of hybridization was possible with additional locally adapted wild species—until the full range was achieved[17].

Notes

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17 New finds, pertaining to the distribution of *Triticum dicoccoides* have been recently reported on by Rao, P. S. and Smith, E. L. (1968). Studies with Israeli and Turkish accessions of *Triticum turgidum* L. emend. Var. *dicoccoides* (Koern). Bowden, *Wheat Inform. Service*, **26**, pp. 6–7. These workers performed a cytogenetic analysis in several Turkish wild wheats, recently collected by J. R. Harlan. Their results indicate clearly that the wild tetraploid wheats in Southern Anatolia are not cytogenetically uniform, and they do not belong exclusively to the *araraticum* type as was previously assumed by Harlan and Zohary. Instead these Turkish collections contained both *araraticum* and *dicoccoides* types! Thus wild tetraploid wheats which have close cytogenetic affinities to cultivated *T. dicoccum* and *T. durum* are not exclusively confined to Palestine and South Syria. They also occur in Southern Turkey and possibly also in adjacent Iraq. We need, of course, further clarification of the spatial, ecological and genetic relationships between *araraticum* and *dicoccoides* types in Turkey, Iraq and Iran before a final decision can be made on whether *dicoccoides* wheats in these areas are genuinely wild, or secondarily derived. But all in all Rao and Smith's data raise grave doubts whether Palestine and South Syria are the sole location in which domestication of emmer wheats could have taken place. The north and north-east parts of the arc again become candidates.