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The Collection, Evaluation and Utilization of Wild Emmer (*Triticum Dicoccoides*) for Wheat Breeding

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J.G. Moseman, E.L. Sharp, C.F. Konzak

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The Collection, Evaluation and Utilization of Wild Emmer (*Triticum*
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1.

ABSTRACT

Some eight hundred lines of wild emmer, part of which were collected during the course of this research, as well as several hundreds of wild emmer x wheat derived wheat lines were evaluated for plant morphology, rust resistance, powdery mildew resistance, grain protein content and quality and drought resistance.

A detailed morphogenetic study of the wild emmer collection enabled to classify the Israeli populations of wild emmer into three major forms of recognized geographical distribution.

Resistance (major and minor gene) to stripe rust and major gene resistance to leaf rust was revealed in the wild emmer collection. Both major and minor gene resistance to stripe rust was transferred into cultivated wheat.

The geographical distribution of resistance genes and their association with eco-climatic attributes is under a final analysis.

Grain protein content in the wild emmer collection ranged from 14 to 28%. Low molecular protein sub-units (that are associated with poor baking quality) were very frequent in the wild emmers, but lines with a high proportion of high molecular weight protein sub-units were identified.

Large variation was found among the wild emmers and among their wheat derivatives in three physiological reactions to drought stress (seedling tolerance, cellular membranes' stability and dehydration avoidance).

Selected wild emmer hexaploid wheat derivatives combined a high protein content, excellent baking quality, stripe rust resistance and good yield performance in both Israel and the U.S.

THE COLLECTION, EVALUATION AND UTILIZATION OF WILD EMMER
(Triticum dicoccoides) for WHEAT BREEDING

2. Introduction

The improvement of wheat poses an increasing demand for new genetic resources. The genetic vulnerability of the wheat crop of today (14) and the continuous need for stability of yield performance, requires the broadening of the genetic basis of our wheat varieties.

The utilization of diversified genetic resources in plant breeding was thoroughly and repeatedly discussed (e.g. 7), providing ample evidence that the wild relatives of cultivated crop plants are an important genetic resource. The centers of origin or diversification of a particular crop plant prove to be a rich and diversified reservoir of genes (10,15).

The "fertile crescent" in the Middle East and Asia Minor is a center of diversification of wheat (11). Among the wild progenitors of wheat native to this region, wild emmer (Triticum dicoccoides) is the most readily accessible genetic resource. It is interfertile with tetraploid wheat (9) and it is morphologically and physiologically similar to cultivated wheat (6).

Wild emmer was discovered in Palestine by Aaronshon (1). It is distributed in Israel (12) across a wide range of environmental conditions, in terms of seasonal temperatures, rainfall and soil type. Very polymorphic and distinct populations of wild emmer are distributed from the wet and cool Mount Hermon in the north to the hot and dry Judean mountains further south. The wide range of ecological conditions over a small geographical scale should produce a considerable range of variation and ecological adaptation in the wild emmer.

The idea to use wild emmer as a genetic resource in wheat breeding is not new. Already at the beginning of this century the potential agronomic value of wild emmer populations was recognized (2). While the initial interest in wild emmer was sporadic, it was always recognized that an

organized comprehensive collection effort is most warranted - especially in view of the progressive urbanization and the danger of the eradication of these populations in Israel.

The history of the actual evaluation and utilization of wild emmer toward wheat improvement is short. Past work has concentrated in two major and important areas: disease resistance and grain quality.

Rust resistance

Wahl (16) proposed that prevalence of plant pathogens in the center of diversity of a given crop plant and their co-evolution with the host as an interactive system, produced a broad range of virulent strains, including some that were never recorded elsewhere. He concluded and has shown that resistance to those strains would also develop in the system (17).

Stripe rust (Puccinia striiformis) in Israel may break into an epidemic and Israeli wheat cultivars differ in their reaction to the disease.

Upon testing populations of wild emmer, Gerechter-Amitai and Stubbs (8) selected T. dicoccoides var. Aaronsohni sel. G-25 resistant to all the 21 test-races of stripe rust used in their work. Resistance to race 20A was transferred into durum and common wheat (9,10).

Leaf rust (Puccinia recondita) is a major disease of wheat in the Middle East. In Israel it occurs regularly and may assume epidemic proportions. In the U.S. wild emmer originating from Palestine was found to be resistant to most races of leaf rust and was used subsequently in wheat breeding ((18), page 217-218). Initial studies with thousands of plants from 50 populations of wild emmer in Israel failed to reveal good resistance (3), while more recent tests in naturally infected field nurseries revealed some resistant accessions to leaf rust.

Grain quality

In the last decade, the potential of wild emmer as a genetic source of high grain protein content was revealed (Results from these laboratory).

The interest in the high protein wild emmers as a genetic resource assumed two major avenues: the improvement of the nutritive quality and the improvement of the baking quality of wheat. The role of high grain protein content in wheat baking quality is widely established and genes for high protein content would constitute a major impact on the baking quality of wheat grown under conditions that are less than optimal for obtaining good baking quality. The impact of a high protein wheat in nutritive terms is, however, questionable. The wheat consuming population in the developed countries do not lack protein, neither in terms of quantity nor quality. The wheat consuming population in the developing countries is usually in the higher income level, which again has an access to diverse protein sources. The poorer population in the developing countries that may subsist on wheat is always using, as part of their diet, various non-cereal foods (e.g., grain legumes, etc.) that provide protein well above what may be available in a potentially protein-rich wheat. The hunger stricken part of the developing world is not concerned with wheat at all.

For these reasons the high-protein wild emmer populations were considered in this research only in terms of their potential for improving the baking quality of wheat. This avenue of research began in this laboratory in 1968 when several collections of wild emmer were analyzed for their grain protein content, disclosing a range of protein of 19.6 to 24.4%. Wild emmer Sel G-25 was crossed onto tetraploid and hexaploid Israeli wheat cultivars. While the progenies were selected for agronomic type and stripe rust resistance only, they ranged in their grain protein content from 14.1 to 24.5% with 1000 kernel weights of 25 to 54 g and sedimentation values of up to 45cc. These preliminary results confirmed the belief that the high protein genes may be readily transgressed into common wheat. However, the high frequency of high protein progenies with low sedimentation values suggested that protein baking quality should be also carefully observed upon the introgression of high protein genes from T. dicoccoides.

Drought Resistance

The prevalence of wild emmer populations in semi-arid regions in Israel and the wide range of diversity in the ecological conditions where wild emmer is found allow to conclude that drought adaptive genes may be revealed within this germplasm.

It has been however pointed out (4) that positive drought resistance attributes in crop plants do not necessarily corroborate with the drought adaptive traits in natural vegetation. Natural vegetation is subjected to the selection pressure for survival under stress, while manmade crop varieties are selected for productivity in stress environments. Thus, apart from the evaluation of drought resistance attributes, the study of drought resistance in the wild emmers should serve to shed some light on the relative importance of this germplasm for the improvement of drought resistance of wheat, as a single case of a cultivated crop plant.

2.1. Materials and Methods - General

The research was designed as a "three-pronged" plan, where three classes of wild emmer germplasm were investigated with respect to disease resistance, grain protein and drought resistance.

The germplasm used consisted of old collections of T. dicoccoides maintained at this laboratory, new collections made during the course of this investigation and various wild emmer-derived wheat progenies arising from crosses between wild emmer and cultivated wheat, made before and during this research.

Bulk collections of wild emmer seed were made in the grain ripening stage at the various locations, in the course of the three year period. The original seed accessions served both for pathological and grain protein studies. Some of the seed was also used for planting nurseries, maintained under optimal conditions (including fertilization, irrigation and disease control), at the Bet Dagan Experiment Farm. These nurseries were used for seed multiplication as well as morphological and phenological observations.

Wild emmer derivatives were grown under similarly optimal conditions at Bet Dagan, in nursery rows or in larger yield-test plots. Selection was performed within or among these materials, according to plant phenology, morphology, yield, grain quality and disease reaction.

Seed of the various wild emmers or their derivatives were supplied to and used by the various cooperators in this project.

The detailed 'materials and methods' for each phase of the project are described in the individual sections of this report. The various sections describing the results and discussion are submitted in the form of manuscripts submitted or accepted for publication.

All the data accumulated on the wild emmer collection is being organized as a computerized data base on a CMS file. The amount of data is huge and only part of it was entered into the data base at this time. A partial printout of the listed accessions and their collection sites is included in the Appendix. Further work to complete this data base is in progress. At the final stage the wild emmer data base will include information on plant morphology, plant phenology, disease reactions, protein content, classification of the grain protein sub-units, and reactions to drought stress. Essential climatic data are being included for each collection site and in the final analysis correlation studies (using SAS) will be performed to indicate associations between plant attributes and the environmental conditions at the collection sites.

2.2.

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3.

RESULTS AND DISCUSSION

A Morphological Study of the Israeli Populations of Triticum dicoccoides

by H. Goldenberg

(report enclosed herein)

Temperature-Sensitive Genes for Resistance to Puccinia striiformis in
Triticum dicoccoides

by Z.K. Gerechter-Amitai, E.L. Sharp and Mareika Reinhold

(report enclosed)

Transfer of additive 'Minor effect' Genes for Resistance to Puccinia striiformis
from Triticum dicoccoides into Triticum durum and Triticum aestivum

by M. Reinhold and E.L. Sharp and Z.K. Gerechter-Amitai

(enclosed)

Resistance of Triticum dicoccoides Collected in Israel to Infection with
Puccinia recondita tritici

by J.G. Moseman, E. Nevo, A.K. Gerechter-Amitai, M.A. El Morshidy and

D. Zohary

(enclosed)

Breeding Bread Wheat Cultivars for High Protein Content by Transfer of Protein
Genes from Triticum dicoccoides

by Adriana Grama, Z.K. Gerechter-Amitai, A. Blum and G.L. Rubenthaler

(enclosed)

Wild Emmer as a Donor of Genes for Resistance to Stripe Rust and for High
Protein Content

by Adriana Grama, Z.K. Gerechter-Amitai and A. Blum

(enclosed)

Computer Assisted Analysis of the Kernel Protein Genetic Variability in
Triticum dicoccoides Collections

by L. Mansur-Vergara, C.F. Konzak, Z.K. Gerechter-Amitai, A. Grama
and A. Blum

(enclosed)

Drought Resistance Reactions of Wild Emmer (T. dicoccoides) and Wild Emmer
x Wheat Derivatives

by A. Blum, A. Ebercon, B. Sinmena, H. Goldenberg, Z.K. Gerechter-
Amitai and A. Grama

(enclosed)

3.1. The Morphological Study of Israeli Wild Wheat

by

H. Goldenberg-Poiarkova

A complete detailed morphological description that reflects the extensive variability of the Israeli wild wheat Triticum dicoccoides Körn (T. turgidum L. emend. var. dicoccoides (Körn) Bowden) is lacking in spite of the high interest of cytologists, phytopathologists, biochemists and breeders in this species. The thorough morphological examination of any wild species or variety that could be used for crop improvement is essential. Certain morphological traits, e.g., seed shape and size, plant habit, etc. are important agronomically. The morphological plant structure is an expression of its cytogenetical peculiarity and thus should not be ignored.

The wild emmer was discovered in Israel by A. Aaronson in 1906.

The first detailed morphological description of T. dicoccoides was performed by Percival in his classical monograph "The Wheat Plant" (1921). Unfortunately, he did not examine specimens from the Israeli territory of today, but only from Syria and Western Iran (l.c., p. 178).

Israeli (Palestine) wild emmer was described by Yakubziner in 1932. The description was not carried out in sufficient detail regarding such essential features as growth habit, leaf width, etc. The next description published by Flaksberger in 1935 was scanty and even less successful. It is noteworthy that both authors used N.I. Vavilov's division of Syria-Palestine wild two-grained wheat into two groups: "judaicum" with broad spike and big grain and "horanicum" with narrow spike and smaller grain.

The two groups were divided by each author into many varieties according to spike pubescence and color. For a species with such a large variability as T. dicoccoides such an approach to variety definition is artificial and too formal.

Harlan and Zohary (1966) divided T. dicoccoides into two races that are distinguished by their character combinations and geographical distribution. The first race is the "Palestine race", that is characterized by vigorous growth with tall and thick stems, wide leaves, large spikes and grains. The second race is the "Turkish-Iraqi race", characterized by a small and slender plant, small spikes and grains. This division was confirmed by Rao and Smith (1968), Rawal and Harlan (1975). At the same time the other wild two-grained wheat species T. araraticum Jakubz., that formerly had been known only from Transcaucasia, has been found in the Turkish-Iran-Iraq area (Harlan and Zohary, loc. cit.; Johnson, 1975; Feldman, 1976 and others).

The present morphological study was performed on a total of about 800 different lines from the majority of the wild wheat population in Israel (see appendix). The accessions of various lines were planted at Bet Dagan through 4 years (1979 through 1982). Six hundred and eighty, 565, 262 and 712 accessions were planted in 1979, ¹⁹⁸⁰1981 and 1982, respectively. Each accession was planted in one row 1-m long, spaced 1.2 m apart with 25 seeds per row. Quantitative and qualitative morphological and phenological data were collected yearly on each accession. The main tillers were used for observation and measurements of spikes. Most of the lines were examined morphologically also on living specimens collected from their native habitats.

The morphological studies of accessions grown at Bet Dagan enabled

estimating the variability of the Israeli wild emmer in terms of the characters and the range in their variations (Table 1). Table 1 does not comprise all varying morphological characters. There was also appreciable diversity in shoot color, in ligule and auricle shape and dimensions, in glume shape and its surface variations, in beak form (straight or curved, acute or obtuse), in straw solidness (solid, semisolid, hollow), etc. These characters were scored, but the four-year observations indicated that they are completely unstable and vary at random within lines. Therefore, they were not taken into consideration. The variability of Israeli wild emmer is striking even without the consideration of these minor traits.

The comparative analysis of the data obtained in 4 years of growing the accessions and by examination of native plants allowed identifying three major groups of Israeli wild wheats, which are distinguished by more or less stable combinations of morphological characters.

The most homogeneous group is authentic to "Palestine race" of Harlan and Zohary (1966, loc. cit.) in its morphological aspects. This group consisted of approximately 180 lines and constitutes about 22% of the examined lines. It has well-defined mezomorphic character. After tillering, about a month before heading, all tillers bend through 2nd and 3rd basal nodes and stay erect through heading and maturity. Stems long, 90-135 cm and thick to 5 mm in 2nd basal internode. Leaves green or light bluish-green. Lamina of 2nd topmost leaf flat or slightly folded, largely varying in length, wide, 16-21 mm. Upper leaf sheaths frequently covered with waxy bloom. Lower leaf sheaths glabrous, glossy. Heading early, 110-129 days after emergence, begins in plants central part and spreads gradually to all tillers. Spikes elonged, large, 9-16 cm by 8-12 mm, naked,

shiny, white to reddish, sometimes $\pm$ brown to black, or pubescent (in 15% of total examined lines), white. Spikes with waxy bloom occurred in about 3% of all lines. Spikelets with normally developed 3rd flower and kernel were observed in about 43% of the examined lines. Glumes tough, moderately scabrid. Glume beak exclusively large, 2.5-5 mm x 1.5-2.5 mm at its base. Awns thick, moderately coarse, parallel, 17-23 cm long. Kernels of 2nd flowers of spikelets (the biggest) 9-12 mm long. Deviated forms of "Palestine race" were sometimes observed, such as forms with narrower leaves, shorter beaks of thicker and coarser awns, while other typical features were preserved.

The distribution of the "Palestine race" is shown in Table 2 and Figure 1. The area embracing the Sea of Galilee from its northern side is the most thickly populated with this race. Outside this area types of the "Palestine race" become sporadic. This group is not found on Mount Hermon and is rare in the southern areas of Israel.

The authentic specimen of T. dicoccoides found by Kötchy on the slope of Mount Hermon and named by Körnike, does not belong to "Palestine race". It is a representative of a different small-spiked group of two-grained wild wheat*. This small and slender Hermonian form is mentioned by D. Zohary (1969, p. 52). The herbarium specimens of T. dicoccoides collected and vouchered by A. Aaronson, that are maintained at the same museum in Vienna, are typical samples of "Palestine race".

A large spike is not an exclusive characteristic of the "Palestine race". Among other Israeli wild wheat lines there is one group that sometimes develops rather big spikes, but their classification is determined by additional different morphological character combinations.

*Confirmed by description, measuring and photograph of spikelets made by us in the "Naturwissenschaft Museum" in Vienna in February, 1983.

The second group consists of plants that are semiprostrate and loose, because tillers bend in each node. Heading begins from peripheral prostrate tillers and some tillers may not head or may not mature. Stems shorter and thinner than in "Palestine race". Leaves dark green, semi-folded or semirolled. Leaf sheaths missing waxy bloom. Basal sheaths bristly haired. Green spikes distinguished by their tapering towards apex. Spikes naked, strongly pigmented, bright red to black, rarely pubescent, reddish or blackish, their dimensions vary widely. Glumes very tough, coarse. Awns very thick, coarse, divergent, their length varying widely. Glume beaks usually smaller, than in the "Palestine race", varying in shapes and dimensions.

Several representatives of this group are included in Z.K. Gerechter-Amitai's "Elite" group that is characterized by high resistance to stripe rust. The data on the distribution of the above group have not been summarized. It is known that some populations occur in the same regions as the "Palestine race" (e.g., at Rosh Pinna).

The third group of Israeli wild emmer is the most frequent and variable. It differs from the other groups by narrow spike and conspicuous xeromorphic appearance.

Typical representatives of this group have thin stems, short, 35-90 cm, with prostrate or semiprostrate growth habit. Leaves dark green or blue-green. Lamina of 2nd topmost leaf narrow, 6.5-11 mm, semirolled to rolled. Lower leaf sheaths scabrid or bristled. Heading late, up to 160 days after emergence, frequently scanty. Spikes elongated, short to very long, narrow, 5.5-9 mm, naked, white to red-black and black, or pubescent, white to reddish. Glumes fine textured, slightly scabrid to smooth (in white forms) or more tough, scabrid (in pigmented forms). Glume beaks small, 0.25-2 mm by 0.5-1.5 mm at base. Awns mostly thin, flexible, widely

varying in length. Kernels of 2nd flowers of spikelets 7.75-10.75 mm long. Because of profuse tillering and scanty heading rosette of vegetative tillers is created at base of plant. Tiller rosette prostrate to erect. In the lines with latest heading (winter habit?) abundant tillers make tough, pillow-shaped rosette. Differences in degree of vegetative and generative tillers development is caused, evidently, by different level of vernalization and photo-period responses in various lines of T. diocoides (Kushnir and Halloran, 1982).

Within this 3rd group, there are numerous narrow-spiked forms with deviation in morphological structure, such as plants with taller stems, erect habit, wider leaves, longer beaks (characteristic, for instance, to the Hermonian lines) or rarely with paradoxally early heading (G-510, G-513).

This group on the whole, including its nontypical forms with many divergent characters, is widely distributed in Israel. It extends northwards* and southwards. It is common in the Samaria and Judea Mountains, but sometimes it occurs, like representatives of the former group, in sites where the "Palestine race" populations are growing.

Thus, the Israeli wild emmer lines display striking morphological variability. On the background of large and randomized variations, 3 different groups are revealed. Each has its more or less stable definite morphological features. One of these groups, identical with the "Palestine race", is morphological distinct and relatively early in flowering. It is geographically restricted within Israel. Does it belong to T. dicoccoides, described by Kőznicke, in spite of its obvious difference from the authentic specimen of T. dicoccoides? Johnson notes (1975) that "T. araraticum is

*A. Amitai has brought a typical specimen of this group in June 1983 from Lebanon.

most easily distinguished from T. dicoccoides by the presence of an awn on the third lemma". We observed the 3rd developed flowers with their awns and kernels not only in the nursery, but also in native Israeli habitats (lines G 555, G 614, G 623 and others). Is a part of Israeli wild wheat analogous to one of the some chromosome types of T. araraticum, selected by Kawahara and Tanaka (1977)? Does the group of wild wheat that has strongly pigmented tough glumes, very thick awns and bristled sheaths, belong under the same cytogenetical group as the "Palestine race"? Do the xeromorphic small-spiked narrow-leaved late forms have to be attributed to the "Turkish-Iraqi" race of T. dicoccoides? It could be possible that among the group of Israeli wild wheats diploid Triticum varieties that are sometimes undistinguished morphologically from tetraploid wild wheats in a common stand (Zohary, 1965; Rawal and Harlan, 1975) are concealed.

It is known that T. dicoccoides, as well as T. araraticum, are not homogenous cytogenetically (Wagenaar, 1966; Konarev et al., 1972; Migushova et al., 1975, etc.). But to answer all above questions on the taxonomical or intraspecific structure of Israeli wild wheat it is necessary to employ cytogenetical and electrophoretical methods combined with an accurate and detailed morphological analysis.

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Table 1. The range of phenotypic variability in the Israeli wild emmer collections

No.	Characters	Unit of Measurement	Range	Qualitative Variations
1.	Stem height (without spike)	cm	45-130	
2.	Length of 2nd topmost leaf lamina	cm	17-47	
3.	Width of 2nd topmost stem leaf lamina	mm	6.5-22	
4.	Attitude of topmost stem leaf			Flat; semifolded; semi-rolled; rolled
5.	Leaf color			Green; dark green; light bluish-green; blue-green
6.	Waxy bloom on upper leaf sheath			Missing; present; heavy
7.	Superface of lower leaf sheath			Glabrous; slightly scabrid; scabrid; bristled
8.	Spike length	cm	7-16	
9.	Spike width	mm	5.5-12.0	
10.	Spike pubescence			Missing; present
11.	Spike color			White; red; brown; red-black; black
12.	Waxy bloom on spike			Missing; present
13.	Spikelet width	mm	3.5-9.0	
14.	Awn length	cm	12-26	
15.	Awn thickness			Thin; intermediate; thick
16.	1st glume length	mm	9-17	
17.	Glume beak length	mm	0.25-5.00	
18.	Glume beak base width (=glume keel height)	mm	0.5-2.5	
19.	Reproductive tillers habit at maturity			Erect; semiprostrate; prostrate
20.	Vegetative tiller rosette type (if present) at maturity			Erect; prostrate; pillow-shaped
21.	Spikelet 2nd kernel length	mm	7.75-12.00	
22.	Heading time after emergence	days	110-160	

Table 2. Frequency of "Palestine race" lines in various locations in Israel, as per Fig. 1.

Location No.	Frequency of "Palestine race" lines	
	No.	%
1	2	1.1
2	92	51.1
3	22	12.2
4	3	1.7
5	5	2.8
6	36	20.0
7	2	1.1
8	1	0.6
9	1	0.6
10	1	0.6
11	6	3.3
12	3	1.7
13	2	1.1
14	2	1.1
15	2	1.1
Total	180	100

Fig.1. Locations of distribution (see Table 1) of "Palestine race" in Israel.

3.2. Temperature-Sensitive Genes for Resistance to Puccinia striiformis
in Triticum dicoccoides

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INDEX WORDS

Triticum dicoccoides, wild emmer wheat, Puccinia striiformis,
stripe rust of wheat, minor genes

1 SUMMARY

2 Twenty-six selections of wild emmer collected at different sites in
3 Israel and three entries obtained from Turkey were studied for the possible
4 presence of temperature-sensitive genes controlling reaction to Puccinia
5 striiformis. In tests carried out in Israel with a local P. striiformis
6 isolate at two temperature regimes, 16 selections showed a change in
7 infection type toward resistance at the higher temperature regime. In
8 comparable tests performed in the United States with a Montana P. striiformis
9 isolate of different virulence pattern - including 14 of the same selections
10 - ten entries displayed a temperature-sensitive reaction. Although slightly
11 different temperature regimes were used in Israel and the United States,
12 the results obtained were in general agreement.

13
14 INTRODUCTION

15 In view of the scarcity of genes for rust resistance in cultivated
16 wheat, screening for resistance has been extended to the wild relatives of
17 wheat (GERECHTER-AMITAI & LOEGERING, 1977; GERECHTER-AMITAI & STUBBS, 1970;
18 GERECHTER-AMITAI & WAHL, 1966).

19 AARONSOHN (1910,1913), who discovered wild emmer (Triticum dicoccoides
20 Koern.) in northern Israel, realized nearly 70 years ago its importance as
21 a potential source of rust resistance. GERECHTER-AMITAI & STUBBS (1970)
22 have shown that the Israeli populations of wild emmer represent a valuable
23 source of stripe rust resistance; one selection in particular, T. dicoccoides
24 G-25, proved to be highly resistant to all 21 races of Puccinia striiformis
25 West. used in their tests. GERECHTER-AMITAI & GRAMA (1974), who demonstrated
in this selection the presence of one dominant major gene, successfully

1 transferred this resistance both to Triticum durum Desf. (GERECHTER-AMITAI
2 & GRAMA, 1974) and to Triticum aestivum L. (GRAMA & GERECHTER-AMITAI, 1974).

3 Using specific temperature regimes, LEWELLEN et al. (1967) detected in
4 the wheat plant introduction PI 178383 three temperature-sensitive genes,
5 recessive in action, which they designated as 'minor genes'. One detectable
6 homozygous minor gene usually reduced the infection type from 4 or 3 to 3-,
7 2 or 1 in the classification system; with two or three of the genes, the
8 infection type was reduced from 4 or 3 to 1-, 0, 0- or 00, respectively
9 (SHARP, 1973). Temperature-sensitive, recessive, additive 'minor genes'
10 have been described for a number of spring and winter wheat cultivars
11 (KRUPINSKY & SHARP, 1978, 1979). This type of resistance, involving a
12 number of different genes, may be more durable than monogenic resistance,
13 since virulence in the pathogen would have to develop step by step.

14 The objective of the present study was to investigate whether such
15 temperature-sensitive genes, comparable to the 'minor genes' found in
16 cultivated wheat, exist in the natural populations of wild emmer.

17 MATERIALS AND METHODS

18 The seed samples of T. dicoccoides used in the tests included 26
19 accessions collected in Israel (Fig. 1) and three accessions obtained from
20 Turkey. Each of the 29 accessions originated from a different collection
21 site.

22 All the entries of wild emmer were progenies of single-plant selections,
23 which in prior seedling tests had been susceptible or intermediate in
24 reaction to stripe rust at 15°C.
25

Two isolates of P. striiformis were used in the experiments. One of these, GYR-22, had been isolated from wild emmer in Israel; the other - B-1 - was collected in the Gallatin Valley in Montana. The two isolates, used in the respective countries, were of distinctive virulence types, differing essentially on four differential varieties (Table 1). The evaluation of the test material was carried out in growth chambers, programmed at different temperature regimes.

In Israel, two similar sets of seedlings were grown simultaneously at a daily photoperiod of 13.5 hours, including 10.5 hours at a maximum light intensity (25,000 lux, combined incandescent and fluorescent light), and a stepwise light increase and decrease, respectively, for 1.5 hours each. Preinoculation temperature was 15°C. The seedlings were inoculated when the second leaf appeared. After inoculation the plants were kept in dew chambers at 9°C for a 24-hour dark period, followed by a stepwise increase in light and temperature. One of the sets was then maintained at 15°C day and night, the other at 18/24°C dark/light and for 16 hours at the higher temperature. Infection types on both sets of seedlings were rated 14 days after inoculation.

In the United States, the low-temperature regime consisted of 2°C at night and 18°C during the day, and the high-temperature regime of 15°C at night and 24°C during the day. These regimes simulated spring and summer conditions in Montana and are known to be effective for the detection of temperature-sensitive 'minor genes' (SHARP & FUCHS, 1982). The photoperiod used was 12 hours (26,000 lux, combined fluorescent and incandescent light) for each regime. The plants were inoculated when the second leaf appeared, 2

1 or 3 weeks after planting, using the inoculation technique described by
 2 SHARP (1965). The inoculated plants were exposed to a 24-h dew period at
 3 7°C before being returned to the respective temperature regimes. Infection
 4 types were rated 12 or 21 days after inoculation, depending on the tem-
 5 perature regime.

6 The following scale was used in infection type (IT) ratings:

7	0	= no visible infection
8	1	= very resistant
9	2	= resistant
10	3	= moderately resistant
11	4	= low intermediate
12	5	= intermediate
13	6	= high intermediate
14	7	= moderately susceptible
15	8	= susceptible
16	9	= very susceptible

17 Changes within the susceptible group, between 'susceptible' (IT 8) and
 18 'very susceptible' (IT 9), were not considered significant.

19

20 RESULTS

21 In Israel, 16 out of 29 single-plant selections were either susceptible
 22 or intermediate in reaction at 15°C and displayed a change toward resistance
 23 when tested at the 18/24°C dark/light temperature regime. In the 13 other
 24 entries, infection types were similar at both temperature regimes (Table 2).
 25 In those selections in which temperature-sensitive reactions occurred, the

1 changes in infection type were of various magnitudes. In two cases (no. 4
2 and 22), all the seedlings were uniformly moderately susceptible at 15°C
3 but displayed two (no. 4) or even three (no. 22) distinctly different lower
4 infection types (i.e., were more resistant) at 18/24°C. This reaction
5 pattern may be an indication of the presence of more than one temperature-
6 sensitive resistance gene in each of these two single-plant selections.

7 Fourteen of the wild emmer accessions were evaluated both in Israel and
8 in Montana, using the respective P. striiformis isolates from these areas
9 (Table 2). In the tests performed in the United States, ten entries
10 showed a shift toward resistance at the high temperature regime, whereas
11 the four other entries were similarly susceptible at both temperature
12 regimes. It is noteworthy that among the ten entries displaying a tem-
13 perature-sensitive reaction, eight showed this characteristic at both
14 locations. Similarly, three of the remaining entries (all the accessions
15 originating from Turkey) did not show a shift in infection type in either
16 country.

17 Among the 14 wild emmer accessions tested in both countries, three
18 displayed a temperature-sensitive reaction at only one location.

19
20 DISCUSSION

21 The shift in infection type that occurred in a number of wild emmer
22 selections when using different temperature-profiles proves the existence
23 of temperature-sensitive genes for stripe rust resistance in T. dicoccoides.

24 The fact that temperature-sensitive reactions were observed in 18 out
25 of 26 selections originating from different collection sites in Israel,

1 indicates that this phenomenon is rather common in the wild emmer popula-
2 tions indigenous to this country. The occurrence of temperature-sensitive
3 genes was not restricted to any particular geographic region - their
4 presence became evident in collections from Upper and Lower Galilee, Mt.
5 Hermon, the Golan Plateau and the Jordan Rift Valley (Fig. 1).

6 In most entries, temperature-sensitive reactions were observed, in the
7 tests made in Israel and the United States, in the same wild emmer
8 selections - regardless of the P. striiformis isolate used. However, in
9 some of the entries that were tested in both countries, significant shifts
10 in infection type were recorded at one location only but not at the other.
11 The exceptions could be due to either the somewhat different temperature
12 and light regimes used in the two laboratories or the existence of race-
13 specificity of the resistance genes in the wild emmer accessions studied.

14 The so-called temperature-sensitive minor genes, when occurring
15 apparently singly in cultivated wheat lines, were described as having a
16 minor effect on the resistance (SHARP, 1973). In the present study of wild
17 emmer, in at least one of the entries (no. 14), a very strong shift in
18 infection type was observed. Thus it is questionable whether all the
19 temperature-sensitive genes in T. dicoccoides can be considered to be minor
20 genes.

21 We have shown that temperature-sensitive genes occur in wild emmer. It
22 still remains to be proven whether these genes are of the same kind as those
23 found in cultivated wheat. Various crossing programmes, to study further
24 characteristics and combining ability of the temperature-sensitive genes in
25 wild emmer, are in progress. One of the characteristics of minor effect

1 genes in T. aestivum, namely additive gene action, has been investigated
2 also in T. dicoccoides (GRAMA et al., 1984).

3 In other studies (GERECHTER-AMITAI & STUBBS, 1970; VAN SILFHOUT &
4 GERECHTER-AMITAI, unpublished), it was found that major genes, effective
5 over a wide range of temperatures, are rather common in the populations of
6 T. dicoccoides in Israel. Since the temperature-sensitive minor effect
7 genes were shown to appear also quite frequently in wild emmer, it may be
8 expected that often both kinds of genes are present in individual plants in
9 nature. In one instance, involving sel. G 086-1 (no. 16), it was shown (in
10 other tests with different P. striiformis isolates) that both kinds of
11 genes indeed occurred together in the same wild emmer selection (unpublished
12 data). The presence of both kinds of genes in breeding lines may be of
13 particular protective value.

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1 Table 1. Reaction of differential varieties to two different virulence
 2 types of Puccinia striiformis.

4	Differential variety	Infection type ¹	
5		Israel isolate	U.S. isolate
6	Heines VII	2	6
7	Carstens V	1	2
8	Compair	2	1
9	Suwon 92 x Omar	1	2
10	Michigan Amber	8	9
11	Lee	8	4
12	Lely	1	2
13	Moro	1	1
14	Heines Kolben	2	2
15	Clement	2	1
16	Donata	1	1
17	<u>Triticum spelta saharens</u>	9	9
18	Hybrid 46	1	2
19	Selkirk	9	2
20	Chinese 166	1	1
21	Bon Fermier	2	7

22
 23 ¹For scale of infection types, see text.

24

25

Table 2. Selections of Triticum dicoccoides tested for the presence of temperature-sensitive resistance genes for Puccinia striiformis at two temperature-profiles

No.	<u>Triticum dicoccoides</u> Collection site Selection		Infection type ¹			
			Israel		United States	
			Low 15°C	High 18/24°C	Low 2/18°C	High 15/25°C
1	Almagor	G-192-1	9	9		
2	Almagor - Kefar Nahum	G-094-1	9	9	9	6
3	Ammiad	G-072-1	6	3		
4	Ammiad, north	G-085-1	7	4,6		
5	Bet Qeshet	G-121-1	9	6	6,8	4
6	Diyarbakir, Turkey	G-178-1	9	9	9	8
7	Faqqua	G-187-1	9	9		
8	Hazor	G-020-1	9	6	8	6
9	Jerusalem	G-186-1	9	9		
10	Karakadaj, Turkey	G-201-1	9	9	9	8
11	Kefar Giladi	G-012-1	7	6		
12	Kefar Hittim	G-044-1	7	6		
13	Korazim	G-092-1	9	8	7	6
14	Majdal Shams	G-158-1	9	4	9	7
15	Mapal Nehoshet	G-123-1	9	9		
16	Mizpe Yammim	G-086-1	9	6	9	6
17	Mt. of Beatitudes	G-131-1	9	6	8	6
18	Mt. of Beatitudes, south	G-070-1	9	8		
19	Nahal Oren	G-140-1	9	9		
20	Nahal Zavitan	G-125-1	9	9		
21	Nesher, Mt. Carmel	G-077-1	9	8		
22	Qarne Hittim	G-075-1	7	2,3,6		
23	Qiryat Shemona	G-013-1	7	6		
24	Sede Eliezer	G-014-1	9	6	8	8
25	Sheikh Hussein	G-128-1	9	6	9	6
26	Siverek, Turkey	G-210-1	9	9	9	8
27	Wered haGalil	G-076-1	8	6	8	6
28	Yavneel	G-050-1	6	2	8	6
29	Zefat	G-027-1	8	7		

¹For scale of infection-types, see text

Fig. 1. Geographic distribution of Triticum dicoccoides collections made in Israel and tested for the presence of temperature-sensitive genes.

○ = temperature-sensitive gene indicated; ● = temperature-sensitive gene not indicated.

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FIGURE CAPTIONS AND

TABLE HEADINGS

Figure 1. Geographic distribution of sites (Identified by numbers) where
Triticum dicoccoides collected in Israel.

Table 1. Reactions of Triticum dicoccoides accessions Collected at Sites
in Israel to Infection with Puccinia recondita tritici.

Table 2. Reactions of Triticum dicoccoides accessions Collected in Israel
to Infection with Puccinia recondita tritici.

Fig. 1. Geographic distribution of sampling localities of *T. di-coccoides*

Table 1. Reactions of Triticum dicoccoides accessions Collected at Sites
in Israel to Infection with Puccinia recondita tritici.

Site	Site No.	No. of Accessions	Reactions + /			Avg. Infection Types
			R	M	S	
Bet Meir	12	34		19	15	6.3
Qazrin	2	35		10	25	6.9
Bat Sheloma	6	32	1	4	27	7.3
Kokhov Hashahar	9	34		1	33	7.3
Mt. Gerizim	8	9		4	5	7.6
Mt. Hermon	1	25		2	23	7.8
Mt. Gilboa	7	26	1	3	22	7.8
Sanhedriyya	11	21			21	7.8
Taaiyiba	10	22		1	21	7.9
Rosh Pinna	4	28			28	7.9
Tabigha	5	32			32	8.0
Yehudiya	3	16			16	8.0
Total		334	2	44	288	7.5
%			0.6	13.2	86.2	

Reactions: R (Resistant)=IT 0-3; M (Moderately Resistant)=IT 4-6;
S (Susceptible)=IT 7-9.

Table 2. Reactions of Triticum dicoccoides accessions Collected in Israel
to Infection with Puccinia recondita tritici

Collector	Reactions						Total
	R		M		S		No.
	No.	%	No.	%	No.	%	
Nevo and Zohary	2	.6	44	13.2	288	86.2	334
Gerechter-Amitai	7	1.9	51	13.7	314	84.4	372
Total, Avg. %	9	1.3	95	13.4	602	85.3	706

INTERNATIONAL ATOMIC ENERGY AGENCY

: Research Co-ordination Meeting (RCM)
: The Use of Nuclear Techniques for Cereal Grain
Protein Improvement

: IAEA Headquarters Vienna 6-10, Dec. 1982.

RCM

3.5. Breeding bread wheat cultivars for high protein content by
transfer of protein genes from Triticum dicoccoides.

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Abstract

BREEDING BREAD WHEAT CULTIVARS FOR HIGH PROTEIN CONTENT BY TRANSFER OF PROTEIN GENES FROM Triticum dicoccoides

Triticum dicoccoides sel. G-25, a selection of wild emmer having a protein content of 20.5% and a kernel weight of 31.5 mg, was used as the donor of protein genes. Since this selection is highly resistant to stripe rust, the objective of the crossing programme was to transfer this resistance, together with the high protein potential, to durum and bread wheat cultivars susceptible to the disease.

In the tetraploid lines obtained from the T. dicoccoides/T. durum cross, the protein values ranged from 17-22%. These lines had the resistance to stripe rust from the wild emmer and to stem rust from the durum. Following two further crosses between these tetraploid lines and T. aestivum cultivars, several lines were selected which combined good yield, high protein level and resistance to rust diseases. These lines attained protein levels of 14-19% in the whole grain and 14-17% in the flour, combined with yields of 4.5-6.0 t/ha. They also had inherited resistance to stripe rust from the wild emmer progenitor and resistance to stem rust - and in some instances also to leaf rust - from the cultivated wheat parental lines.

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681-E. This investigation was supported by the United States - Israel Binational Agricultural Research and Development Fund (BARD).

INTRODUCTION

Research on wheat amelioration by the transfer of desirable genes from wild emmer (Triticum dicoccoides Koern.) to cultivated wheat was commenced at the Volcani Center of the Agricultural Research Organization (ARO) in 1965 (1,2,3). It is now an integral part of our wheat breeding programme.

The utilization of wild emmer as donor of advantageous genes for wheat breeding ensued from the findings by Gerechter-Amitai and Stubbs (4), in 1964, that wild emmer, indigenous to Israel, is a valuable source of stripe rust resistance. Soon after, in 1967, Gerechter-Amitai and Grama (3) discovered that the grain protein content in several collections of wild emmer was considerably higher than that in cultivated wheat - ranging from 20-24%. In 1976, Gerechter-Amitai and Grama (unpublished results) began a large-scale survey of protein in wild emmer, including hundreds of original collections made in the natural habitats of the plants, in which the protein values ranged from 13.9 to 28.9%. Similar results were reported by Avivi (5).

In studies of the inheritance of resistance to stripe rust in crosses between wild emmer and cultivated wheat, Gerechter-Amitai and Grama showed that valuable genes could be transferred readily from T. dicoccoides to both T. durum (1) and T. aestivum (2). In these initial crosses, made in 1965-66, genes for both stripe rust resistance and high protein content were successfully incorporated into cultivated wheat.

Since 1979, The Volcani Center has been conducting a cooperative study with Washington State University and the Western Wheat Quality Laboratory at Pullman, Wash., on quantity and quality of protein in wild emmer and the use of wild emmer for the improvement of protein in cultivated wheat.

In the last three decades, some 750 wild emmer accessions were collected in approximately 250 sites in Israel. These accessions present a wide diversity in many characteristics, including stripe rust resistance (4,6), grain protein content and kernel weight - traits which are of special interest in our breeding programme (TABLE I). As illustrated by a few examples in TABLE I, these traits are, in many instances, independent of one another in wild emmer.

The aim of this paper is to give a brief account on the methods and research results relating to our most advanced material, developed from T. dicoccoides sel. G-25, with special reference to high protein content.

MATERIALS AND METHODS

In our first crosses, carried out in 1965, T. dicoccoides sel. G-25 served as the wild gene donor. This selection was, at that time, the most valuable wild emmer material for our crossing programme, being endowed with excellent stripe rust resistance and an average grain weight of 31 mg. Its grain protein content ranged, in different years, from 20 to 24% - a high value when compared with cultivated wheats. However, as a wild progenitor, it also possesses certain undesirable

agronomic traits, such as brittleness of the rachis, poor threshability and low yielding capacity.

In these initial crosses, Nursit 163 - a formerly grown durum cultivar selected from a local land race - was used as the cultivated parent. This cultivar is resistant to stem rust, has good grain quality, and a protein content of 15-18%. Yet, Nursit 163 is a very tall variety, a poor yielder (2.0-3.5 t/ha) as compared with the new semi-dwarf durums, and is susceptible to stripe rust.

The T. dicoccoides/T. durum hybrid was then crossed in turn with two tall bread wheats formerly grown in Israel - Merav (=Gabo//Kenya 324/General Urquiza) and M 708 (=Aguilera/Kenya 324//Marroqui/Supremo/3/Gabo), once considered of good yield potential (4-5 t/ha) but low to medium in protein content (10-12%).

In the final phase, these triple crosses were crossed again to several bread wheat cultivars - dwarf and semi-dwarf varieties with improved yield potential (5.0-5.5 t/ha). The scheme of the stepwise breeding method used for the transfer of alien genes from wild emmer into cultivated bread wheats is shown in FIG. 1.

Throughout the breeding process, care was taken to discard plants possessing negative characters particular to the wild progenitor and, concurrently, to select for the valuable traits inherited in part from the wild emmer and in part from the cultivated parent.

From F_2 to F_8 , severe selection pressure for agronomic traits was exercised in the field. At the same time, single-plant selections and their offspring were tested for quality characters in the laboratory.

The agronomic traits on which selection pressure was placed at the Bet Dagan Experiment Farm were the following:

- Resistance to rust diseases (stripe rust, stem rust and leaf rust)
- Plant height (semi-dwarf type)
- Straw strength (non-lodging under optimal field conditions)
- Phenology (early maturity)
- Spike fertility (50-60 kernels in the main spike)
- Non-brittleness (avoidance of losses due to spikelet shedding)
- Threshability (suitable for mechanical harvesting)
- Yield performance (not less than 90% of the high-yielding standard).

The quality characters tested for in the laboratory at Bet Dagan were as follows:

- Whole grain protein content (analysed by NEOTEC Grain Quality Analyzer, calibrated for T. dicoccoides, T. durum and T. aestivum, respectively)
- Kernel weight (TKW not less than 38 g)
- Test weight (not less than 72 kg hectolitr weight)
- Zeleny Sedimentation Index (sedimentation values over 45)
- Mixogram (Bread Wheat Chart: 'High protein' group; use of 10 g flour sample).

The quality characters tested for in the Western Wheat Quality Laboratory at Pullman were as follows:

- Wheat type (hard or soft grain)

- Flour yield (percentage of extract)
- Flour protein content
- Mixogram type
- Water absorption
- Micro-loaf volume (10 g flour sample).

RESULTS

The grain protein content and the yield performance, both of the parents and of the derivatives, in the various steps of our wild emmer/cultivated wheat breeding programme, are given in FIG. 2.

The tetraploid progenies obtained from the initial cross between T. dicoccoides sel. G-25 and T. durum cv. Nursit 163, which were fully fertile, segregated for protein content, rust resistance, seed weight and seed color. While the grain protein content was most promising (17-22%), the agronomic traits were definitely unsatisfactory - the plants were heavily lodging, the spikes were brittle and the yields were very poor (2 t/ha).

To improve the agronomic traits, the F_1 plants of this initial cross were top-crossed with two bread wheat cultivars - Merav and M 708 - and the resulting pentaploid progenies were exposed, for several generations, to selection pressure. In F_9 , 29 hexaploid derived lines, selected for their stripe rust resistance and low incidence of spike shattering, were submitted to preliminary yield trials (10 m² plots); the distribution of their protein content and yield performance is included in FIG. 3. As shown, the values for protein content

in the 29 selected lines (indicated in FIG. 3 by a broken-line frame) ranged from 15 to 20%, with yields of 55-100% of the standard cv. Lakhish (5.5 t/ha). From their distribution it can be seen that, in general, there exists a negative correlation between grain yield and protein content. In order to maintain the high protein content, we had to give up some of the yield potential and settle for a satisfactory compromise. On this premise, four lines were selected from the F_9 population, in which the protein content came to 19-20% and the grain yield reached 88-93% of the standard cv. Lakhish. These four lines (marked P_4 in FIG. 3) are still used in our breeding programme as donors for high protein and stripe rust resistance.

However, although the protein contents and sedimentation values in these four F_9 selections were high, the baking quality - expressed both by mixograms and loaf volumes - was poor. In order to improve the baking quality, these four triple-cross lines were further crossed to high-yielding dwarf and semi-dwarf bread wheat cultivars (marked P_5 in FIG. 3), which had a low to medium protein content (11.5-13.5%) but good baking quality. From these crosses, a number of new lines, selected in F_6 - F_8 , had a high protein content and particularly promising baking quality characteristics (TABLE II). They excelled in flour protein, mixogram type and micro-loaf volume. Some of these lines (marked H.P.L. in FIG. 3) had grain protein

values of 18-19% and yields of 4.5-6.0 t/ha. Many lines outyielded the former standard cv. Lakhish by 5-10%, while some of the lines (e.g. T. dicoccoides derivative V761-9-4-2) even equaled in yield the newly released bread wheat cultivar Bet Lehem (TABLE II).

Moreover, the protein yield obtained per hectare was significantly higher in most of the wild emmer derivatives than the values attained by Bet Lehem. In line V761-9-4-2, in particular, the protein yield per hectare amounted to 1156 kg as compared with 794 kg/ha for Bet Lehem - outyielding the new bread wheat cultivar, in protein, by 45%. While the result of this selection is exceptional (due to both high yield and high protein levels), the average protein yield of the whole population tops Bet Lehem by approximately 13%.

In addition to their quality characters, these lines had also inherited from the wild emmer progenitor resistance to stripe rust and from the cultivated parents resistance to stem rust - and in some instances, also to leaf rust.

DISCUSSION

In our investigations on the utilisation of wild emmer for the improvement of cultivated wheat, high grain protein content and stripe rust resistance were transferred, together, from Triticum dicoccoides to T. durum and T. aestivum. In addition to these two characters, it was possible to select for a whole range of agronomic traits and, at the same time,

to eliminate all the negative traits inherited from the wild parent. This dual-process eventually resulted in the selection of commercially valuable bread wheat lines.

It is commonly accepted that in the cereal crops there exists a negative correlation between grain yield and protein content. This was found to be true, in general, also in our studies; however, among the segregating populations, lines could be detected which appeared to defy this limitation. As shown in FIG. 3, one group of hybrid derivatives (marked P_4 in the figure) had a high grain protein content (18-20%) together with acceptable yields (88-95% of the former standard bread wheat cv. Lakhish). In order to approach the yield potential of today's foremost varieties, and to improve further on quality characters, the hybrid derivatives were crossed once more to hexaploid wheat - new bread wheat cultivars with a high-yield potential and good baking quality. Again it was possible to select superior lines - sacrificing only 1-2% in protein content in order to attain the other objectives.

On the basis of the results obtained so far in our studies, it is our belief that by a judicious choice of the parents participating in the crossing programme for superior quality characters - such as high-protein content, high-yielding capacity, effective disease resistance and good

baking quality - followed by severe selection for the desired traits, it is possible to breed a variety combining all these traits.

In our initial study, where we used as donor of high protein a selection of wild emmer (sel. G-25) with a protein content of 20.5%, we eventually attained commercially valuable lines of bread wheat with protein contents up to 19%. In our wild emmer collection we now have accessions which, in nature, had protein contents up to 28%; conceivably, by using these high-protein wild emmer selections in the breeding programme, we can expect to obtain new hexaploid lines with a still higher protein content than that attained so far.

Likewise, today we have new cultivars with higher yield performance than the cultivars used in our work. Thus, with better selections of T. dicoccoides and better varieties of cultivated wheat, we can look forward to wild emmer derivatives with improved protein content and grain yield.

The importance of this new type of germplasm has already received a wide recognition.

Many breeders in the U.S. and Europe have requested seed samples of the outstanding lines and have introduced them in their breeding programme.

Four lines bred at the Volcani Center were introduced by the USDA in the 1983 International Spring Wheat Rust Nurseries (No. 312-315).

One high yielding line, bred at the Volcani Center, resistant to all three rusts and rich in protein content was already introduced in the variety trials conducted at the Washington State University, Pullman.

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TABLE I. Data on stripe rust resistance, whole grain protein content and grain weight, in several Triticum dicoccoides accessions

Accession no. and selection	Origin of seed	Stripe rust resistance	Grain protein %	Grain weight mg
G 25	Nursery	Major gene	20.5	31.5
G 35-1	Nursery	none found	20.0	44.3
G 121-1-1	Nursery	Minor gene	22.9	17.7
G 158-1-2-1	Nursery	Minor gene	22.0	47.3
G 314-4-6	Nursery	Major gene	20.0	14.9
G 725	Nature	Minor gene	25.5	20.3
G 728	Nature	Minor gene	25.4	40.0
G 787	Nature	Major gene	13.9	40.8

TABLE II. Quality data on several lines of hard grain bread wheat endowed with protein genes transferred from T. dicoccoides and two bread wheat check varieties

Selection	Grain protein ^a %	Flour yield ^b %	Flour protein ^b %	Mixogram type ^{ab}	Water absorption ^b %	Loaf volume ^b cm ³	Grain yield ^a kg/ha	Protein yield ^a kg/ha
V761-9-1-2	16.5	69.4	15.0	5H	69.5	108	5,053	833
V761-9-4-2	19.0	68.0	17.1	3H	66.0	107	6,084	1156
V761-10-1-1	17.1	73.3	16.0	2H	66.0	100	5,004	856
V761-28-4-2	18.1	68.4	16.8	5H	69.0	114	5,038	907
V763-2-2-1	16.5	69.0	15.4	1H	66.0	85	5,023	829
V766-7-1-2	17.3	70.7	16.5	6H	70.0	108	5,038	872
V879-3-1-2	16.5	71.8	15.3	2H	65.0	97	4,902	809
V882-22-2-3	15.8	68.2	14.9	4H	69.0	97	4,040	638
Betlehem ^c	13.1	70.4	12.0	4M	66.0	100	6,061	794
Wampum ^d	-	75.2	11.1	3M	60.0	87	-	-

^adata obtained at Bet Dagan

^bdata obtained in Pullman

^cBetlehem = Israeli check variety

^dWampum = Western Wheat Quality Laboratory check variety

FIG. 1. Scheme of the stepwise breeding method used in the transfer of alien genes from wild emmer into cultivated bread wheat.

FIG. 2 Grain protein content and grain yield obtained at various stages of the wild emmer/cultivated wheat crossing programme

FIG. 3. Distribution of grain protein content vs. grain yield (given as percentage of standard cv. Lakhish) of parents and of progenies endowed with high protein genes transferred from Triticum dicoccoides

- P_1 = T. dicoccoides sel. G-25
 P_2 = T. durum cv. Nursit 163.
 P_3 = T. aestivum cvs. Merav, M 708, Lakhish
 P_4 = $P_1/P_2//P_3$
 P_5 = T. aestivum high-yielding cultivars
 H.P.L. = P_4/P_5 (derived high-protein lines)
 L. = T. aestivum standard cv. Lakhish
 B.L. = T. aestivum cv. Bet Lehem

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36. WILD EMMER AS A DONOR OF GENES FOR RESISTANCE TO STRIPE RUST AND FOR HIGH PROTEIN CONTENT*

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SUMMARY

Stripe rust resistance and grain protein content were studied in 750 wild emmer accessions collected at 250 sites.

Reaction patterns to diverse stripe rust cultures, and F₂ data in crosses between resistant selections of wild emmer and susceptible durum, both suggest the existence of a number of different major genes in Triticum dicoccoides. In studies of minor effect genes in wild emmer, intercrossing of lines displaying temperature-sensitive reactions resulted in additive resistance in some of the progeny.

Protein values ranged from 13.9-25.5% in seed collected in nature and from 15.4-26.9% in seed grown in nurseries. The correlation factors for protein values in seed collected in nature and in nurseries indicate genetic control of the grain protein potential.

In a cross between a selection of wild emmer and a durum cultivar, lines were selected which combined the resistance and high protein content of the wild emmer and the large kernel weight of the durum parent.

* Contribution from the Agricultural Research Organization, Bet Dagan, Israel, 1983 series, No. 830-E. This investigation was supported in part by The Netherlands Ministry for Development Cooperation and in part by the United States - Israel Binational Agricultural Research and Development Fund (BARD).

Wild emmer (Triticum dicoccoides Koern.) in Israel grows chiefly in the mountains in the north, extending southward to the fringe of the Judean Desert.

In the wild populations of T. dicoccoides there exists an enormous genetic diversity with regard to many characteristics (NEVO et al., 1982; Mansur, 1983). This rich variability makes wild emmer a valuable gene source for wheat amelioration. The studies summarized in the present paper deal mainly with two characteristics, namely, resistance to the stripe rust fungus (Puccinia striiformis West.) and high grain protein content.

Wild emmer indigenous to Israel was found to be a valuable source of stripe rust resistance (GERECHTER-AMITAI and STUBBS, 1970). In subsequent work it was shown that this resistance, based on major genes, is transferable to both T. durum and T. aestivum (GRAMA and GERECHTER-AMITAI, 1974). In later studies, also temperature-sensitive genes for stripe rust resistance, probably minor effect genes, were detected in wild emmer (GERECHTER-AMITAI et al., 1981).

In their initial work, in 1967, on the utilization of wild emmer for improving cultivated wheat, GERECHTER-AMITAI and GRAMA (1977) discovered that the grain protein content in several of their wild emmer collections was considerably higher than that in cultivated wheat - ranging from 20-24%. Similar results were reported by AVIVI (1979).

The objectives of the present research were to conduct a genetic study of stripe rust resistance and high grain protein content in T. dicoccoides; and to transfer valuable genes for these two traits into T. durum and T. aestivum backgrounds, thus utilizing T. dicoccoides for developing rust-resistant, protein-enriched, high-yielding wheat cultivars.

In previous work the authors (GRAMA et al., in press) showed that genes for stripe rust resistance and for high protein content, together, can be successfully transferred from wild emmer into cultivated wheat, resulting in outstanding agronomic lines.

MATERIALS AND METHODS

The wild emmer collection included approximately 750 accessions from ca. 250 sites. Most seed samples are part of an original collection, throughout the distribution area of this species in Israel, made for the purpose of this study; a few samples were obtained from Lebanon and Turkey.

Major gene resistance for stripe rust. The collection was tested in the seedling stage in growth-chambers at 15°C and 22,000 lux, with one to six cultures of stripe rust isolated in Israel. The most resistant seedlings were grown to maturity in order to establish - often necessitating reselections - homogeneously resistant lines. These single plant selections were then crossed to the susceptible T. durum line D 447 and the resulting F₁ and F₂ were studied for the genetics of the resistance.

High grain protein content. Twelve hundred lines of wild emmer were assayed for protein content using a NEOTIC infrared analyzer. The material included both seed collected in nature and seed grown from the same collections, under uniform field conditions, at the Bet Dagan Experiment Farm.

Correlations were calculated between the protein content of (a) accessions grown in nurseries in two consecutive years; and (b) of original seed as compared with the nursery-grown material.

A preliminary study of the inheritance of grain protein content was made in a cross between T. durum line D 447 (11.8% protein) and T. diococcoides sel. G-168 (24.8% protein) - one of three accessions in which two major genes for resistance had been found.

RESULTS

Major gene resistance to stripe rust. In seedling inoculation tests with different cultures, the wild emmer accessions displayed a variety of infection-types. Many entries contained plants which proved resistant both as seedlings and in the adult stage. In a cooperative study with the Research Institute for Plant Protection (IPO), Wageningen, lines obtained from these resistant selections displayed diversified reaction patterns when inoculated with virulent isolates from North and East Africa, Asia and South America - numerous selections proving resistant to all cultures (van Silfhout, personal communication).

In order to study the genetics of resistance, 32 of the wild emmer selections were crossed with susceptible T. durum. The F_2 data indicate one dominant gene in 27 accessions, two dominant genes in three accessions, and one recessive gene in one accession.

Minor gene resistance to stripe rust. In the crossing scheme designed to test temperature-sensitive selections for additive resistance, the F_2 displayed - in most cross combinations - a transgressive segregation for higher resistance. In the F_3 populations, a marked shift toward resistance indicated a positive response to selection. In some combinations, additive

resistance selected for (in F_2) at the high temperature regime, was expressed (in F_3) also at the low temperature regime.

Grain protein content. In 1980 and 1981, the protein values ranged from 13.9% to 25.5% for the seeds collected in nature and from 15.4% to 26.9% for the nursery-grown seeds (Table 1). Frequency distributions for grain protein in 153 wild emmer accessions collected in nature in 1980 and of the same accessions grown in the nursery in 1981, show a shift toward higher protein content in the nursery-grown material (Fig. 1).

In the cross between T. durum (11.8% protein) and T. dicoccoides (24.8%), the protein values in the F_3 population ranged from 13.0% to 21.4%, with an average of 17.8% (Fig. 2A). In the same population the F_3 progeny had kernel weights between 22.6 mg and 58.0 mg, with a population average of 39.8 mg - as compared with 54.7 mg of the cultivated parent and 15.6 mg of the wild parent (Fig. 2B). As indicated, all the F_3 progenies had kernels larger than the wild progenitor; about 6% had kernels larger than the durum parent. Some progenies, which combined high protein content with large sized grains (Fig. 3, marked "A"), and also had good stripe rust resistance, were selected as outstanding breeding material.

DISCUSSION

The diversified reaction patterns observed in the seedling inoculation tests with various stripe rust cultures indicate the existence of different genotypes for resistance in wild emmer. The presence of different major genes in T. dicoccoides was corroborated by the F_2 data in our crosses between resistant wild emmer selections and susceptible T. durum.

Table 1. Range of grain protein values (%) in wild emmer and correlation coefficients calculated for (a) entries in common to nurseries in two consecutive years and (b) entries collected in nature and grown in the nursery the following year.

Origin	Year	Min.	Max.	Avg.	Entries	R ²
Nursery	1980	15.4	26.9	22.8	153	.644 (a)
"	1981	17.2	26.4	22.5	153	
Nature	1980	16.4	24.7	19.6	157	.487 (b)
"	1981	13.9	25.5	20.4	47	

Transgressive segregation for higher resistance displayed in the F_2 and F_3 populations of crosses between temperature-sensitive selections clearly demonstrates an additive effect of resistance. Since this enhanced resistance, conferred by minor effect genes, was shown in some combinations to be effective also at the low-temperature regime, it may be utilized in commercial wheat breeding.

The high protein potential of wild emmer in nature was expressed also under field conditions. It was also found that the protein values of wild emmer accessions were consistent when grown in nurseries for two consecutive years. Since the correlation coefficients in both comparative studies are significant (Table 1), a high degree of genetic control is indicated. Increased protein values observed in nursery-grown seed may be a response to nitrogen fertilization.

The distribution curve for protein content in the F_3 population (Fig. 2A) denotes a polygenic trait inheritance. All progenies had protein values higher than the cultivated parent but none of the lines tested attained the high protein level of the wild emmer. The lack of lines having this high value may be a result of losing some progenies due to the spike-shattering habit inherited by some progenies from the wild parent. Another reason could be a negative correlation between kernel weight and protein content due to the sharp increase in grain size (Fig. 3).

It is noteworthy that the expression of the high kernel weight of durum line D 447 (54.7 mg) was not impaired by the low kernel weight of wild emmer sel. G-168 (15.6 mg) - some progenies even excelling in kernel weight (up to 62.0 mg).

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Genetic diversity and environmental associations of wild wheat,
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Figure 1. Frequency distributions for grain protein in a wild emmer population. A. in nature. B. in the nursery

Figure 2. Frequency distributions in a F_3 population of the cross

T. durum D 447/T. dicoccoides G-168. A. for protein content;
B. for kernel weight

Figure 3. Correlation between protein content and kernel weight in a F_3 population of the cross T. durum D 447/T. dicoccoides G-168.

3.7 COMPUTER ASSISTED ANALYSIS OF THE KERNEL PROTEIN GENETIC VARIABILITY IN
TRITICUM DICOCCOIDES COLLECTIONS*

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Running Head: T. dicoccoides Protein Genetic Variability

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SUMMARY

Triticum dicoccoides Korn (wild emmer) is being used as a genetic resource for improving the protein content of common wheat (Triticum aestivum). Studies of the genetic variability in kernel protein subunits in T. dicoccoides are rare. The purpose of this study was to determine the genetic variability in kernel protein subunits of wild emmer accessions collected from various ecological regions. Total proteins were extracted from half seeds of 841 accessions of T. dicoccoides with a buffer containing SDS (sodium-dodecyl sulfate) and 2-mercaptoethanol. The reduced, dissociated polypeptides were fractionated according to molecular weight (MW) by one-dimensional high resolution polyacrylamide gel electrophoresis (SDS-PAGE). The gels were stained and dried. A computer-assisted analysis of the densitometric scans of the SDS-PAGE patterns was carried out. The pattern of each scan was characterized by the number of protein bands and their MW. The number and frequency with which protein subunit bands were present or absent in defined MW ranges was determined in order to estimate the genetic variability. The variability in number and MW of the proteins far exceeded that expected from previous reports. Results indicated the greatest genetic variability occurs for proteins in the high MW region (above 70000 MW) followed by those in the medium range (70000 to 33300 MW). Little genetic variability was revealed in protein subunits of below 33300 MW.

Key Words: - Electrophoresis - Endosperm
proteins - emmer - wheat.

INTRODUCTION

A large segment of the world's population depends on wheat (Triticum aestivum) as their primary source of nutrients. Because of this, and the known deficiency of lysine in wheat protein, higher levels of protein and lysine are needed, especially to improve the low income wheat consumer's diet. Wild emmer (T. dicoccoides Korn), a close relative of our cultivated wheats, was found to contain relatively high kernel protein content coupled with large grain size and good baking quality (Avivi 1979; Grama et al. 1983). It is now being used as a genetic source for the improvement of wheat kernel protein content and quality. The potential for exploitation of this exotic material to further improve wheat protein content and quality opens new possibilities to achieve this goal provided genetic variability can be identified among genes coding for kernel proteins in the wild emmer gene pool.

In earlier work, relatively few accessions of T. dicoccoides were examined electrophoretically for kernel protein genetic variability. An exception is recent work by Nevo et al. (1982) who examined allozyme genetic variability among soluble proteins of 457 individuals representing 12 populations from Israel. He found considerable genetic variability of these proteins as revealed by their differential mobility in non-denaturing starch gel electrophoresis.

Electrophoregrams of proteins can be used to assess genetic variability because a large number of studies show that the structure, production (presence or absence), and dosage of particular proteins are controlled almost entirely by the genotype of the plant and are therefore virtually unaffected by the growing conditions (Auriau et al.

1976; Fullington et al. 1980, 1983; Orth and Bushuk 1973; Zillman and Bushuk 1979; for a review see Kasarda et al. 1976, Konzak 1976).

Furthermore, electrophoresis of wheat proteins has been used to identify varieties, and this work indirectly provides evidence for the independence of the presence or absence of bands from environmental influences.

The purpose of this study was to estimate the extent of kernel protein genetic variability of Triticum dicoccoides.

MATERIALS AND METHODS

Wheat Samples

Mature seeds of 841 accessions of Triticum dicoccoides varying in protein content from 15 to 25% were used in this study. The genetic material originated from many sites in Israel and some from Turkey and Lebanon, representative of various environments differing in climatic and soil characteristics. The accessions include original seeds collected in nature as well as seeds increased at the Volcani Institute nurseries. Furthermore, some were bulk collections, whereas others were single-plant selections or even reselections carried on for several years.

Extraction of Proteins from Kernels

Total proteins can be extracted from wheat kernels using buffers containing sodium dodecyl sulfate and 2-mercaptoethanol (Cole et al. 1981; Fullington et al. 1980). In this study total proteins were extracted from the embryoless half of the kernel of the T. diccocooides accessions using the buffer system of Fullington et al. (1980).

The half seeds used were crushed using pliers with jaws covered by a small piece of paper. The volume of the buffer used for extraction was adjusted to 325 μ l of buffer/10 mg seed in all cases. The mixture was further ground and homogenized for one minute using a tissue-grinding pestle and mortar attached to a slow speed electric motor. The samples were then heated in boiling water for 5 minutes to aid solubilization and reduction. Then the insoluble material was spun down for 10 minutes at 8699xg. A 10 μ l aliquot of the supernatant was used for electrophoresis.

Electrophoresis

The discontinuous high resolution sodium-dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE) system used was similar to that devised by Laemmli (1970) and modified later by Fullington et al. (1980, 1983) and Cole et al. (1981) for wheat storage proteins with some minor but significant differences in apparatus, molecular weight standards, gel size, staining and destaining procedures.

Apparatus

A Hoeffer SE 500 vertical slab gel unit was used for SDS-PAGE throughout this work. A constant current of 15 ma. per gel for about 3.2 hrs was applied to 18 samples plus two molecular weight standards in each gel. The voltage varied from 70-80 V at the start of the run to 200-220 V at the end. The first 440 test samples were loaded in duplicate. However, on gaining experience, the gels proved sufficiently uniform and clear so that it was not necessary to run duplicate samples. Later unusual samples were run two or more times for confirmation.

Molecular Weight Standards

Molecular weight standards (MWS) obtained from Bio-Rad Laboratories, Richmond, California, consisted of the following proteins: lysozyme 14000 MW, soybean trypsin inhibitor 21500 MW, carbonic anhydrase 31000 MW, ovalbumin 45000 MW, bovine serum albumin 66200 MW, and phosphorylase B 92500 MW. The MWS were prepared by mixing one part of the standard proteins with 19 parts extraction buffer that included five percent 2-mercaptoethanol, as with the wheat samples. The MWS were included in two slots of all the gels, at the center and at the end. Faint impurities were observed in the MWS but they caused no difficulties in the determination or calculations.

Acrylamide Gels

Gel slabs with 20 slots were used. The separating gel (10 cm x 13.5 cm x 0.75 mm) contained 17.5% (w/v) acrylamide, 0.08% (w/v) bis (N,N'-methylene-bis-acrylamide), 25% of 1.5 M tris (tris hydroxymethyl aminomethane) buffer made to pH 8.8 with HCl. Of this solution, 47.2 ml were polymerized by adding 246 μ l of 10% ammonium persulfate freshly prepared 10 minutes before pouring the gels. In addition, immediately before pouring the gels, 16 μ l of TEMED (tetramethylene-diamine), 0.48 ml of a 10% SDS solution were added. The stacking gel (3 cm x 13.5 cm by 0.75 mm) contained 3.85% acrylamide (w/v), 0.104% bis (w/v), 25% of 0.5 M tris buffer adjusted to pH 6.8 with HCl. A 20.17 ml aliquot of this solution contained, in addition, 100 μ l of 10% ammonium persulfate, 10 μ l TEMED, and 0.2 ml of 10% SDS.

Staining and Destaining

Gels were stained using a solution of 2.5 g Coomassie Blue R-250 in 500 ml methanol, 150 ml glacial acetic acid, and 1850 ml glass-distilled water for at least 12 hours, but no more than 18 hours. The destaining solution was made up by mixing 500 ml methanol, 160 ml glacial acetic acid and 1340 ml glass distilled water. The destaining solution was changed daily until no color was visible in the background. The gels were subsequently dried on porous cellophane following the procedure described in the Bio-Rad manual for the Gel Slab Dryer Model 224.

Densitometry and Computer Analysis

A Beckman densitometer Model R-112 was interfaced to a Radio-Shack TRS-80 Model II 64K microcomputer equipped with an 8 mega bytes memory hard disk accessory. Gels were scanned at 570 nm, in the low speed setting (about 2 min/scan) of the densitometer with the slit size 0.3 x 2 mm. This information was directly digitized and transferred to the microcomputer. A series of computer program software for data acquisition and analysis in TRS-80 model II *BASIC was written. These programs include "Dense" to read and then store all the raw data in a file. Another program, designated "Geldump", produces a graph of each scan as well as numbers, and assigns a MW and a relative intensity value (relative to average intensity) to each peak and transfers all the data to a storage file for later access. This program also normalizes all graphs to equivalent areas for comparisons independent of amount of protein loaded onto the gel.

*Trade name of Tandy Radio Shack Corp. Fort Worth, Tx.

Program "Gel STD" was used to calculate the MW of each peak. The computer input information was the following: distance of migration from the origin to a high MW band (the first darkly stained band was regularly used) and a low MW band (usually the last band), the gel length, and the distance migrated by each MWS. Other computer programs were written to carry out qualitative analyses for assessing the genetic variability for protein subunit composition of the accessions. A description of these programs follows:

"GelFuzz": This program smoothed graphs to remove shoulders and very small peaks that cannot be distinguished from background noise. All analyses were carried out in both smoothed and raw data. Results (not presented) indicated that the smoothed data would be more reliable.

"GelBlob" searched through each scan and then printed a dot in a graph of relative intensity (RI) vs. MW for every peak. Other program options included the ability to specify the MW range, relative intensity range, and whatever samples one desires to analyze so that it is possible to focus on a particular area of the gels. Processing options allowed the use of the raw data or smoothed data, i.e., with shoulders and very small peaks removed. This program was the basis for the qualitative analysis discussed below.

Qualitative Analysis: The output that resulted from the processing of the gel scan data with the "GelBlob" program was a relative intensity (RI) vs. MW graph representing all the scans, thus a composite of all the samples. This is herein designated as a "dot graph". The dot graph was subdivided into three regions: the high MW (140000 to 70000), the medium MW (70000 to 33300), and the low MW

region (33300 to 8800). These divisions were chosen at the natural break points for grouping bands in the gels. These regions were further subdivided into their individual MW ranges which correspond to dot clusters or spaces between clusters. The high MW region was subdivided into seven MW ranges decreasing in MW by about 10% each time. This was done because no clusters or spaces between clusters existed within this region, unlike the case for the medium and low MW regions which were divided in terms of their clusters and spaces. The program "GelBar" was designed to analyze the make-up of these MW ranges. Three graphs of frequency vs. MW were produced, one for the high, one for the medium, and one for the low MW regions. For each MW range the graphs produced to show the number of peaks and their frequencies.

"GelFreq": This program was used to graph or produce tables of MW vs. frequency (presence or absence of bands) over specified MW regions, relative intensities, of any number of samples. Either the raw data or the data file previously processed through "GelFuzz" was used.

RESULTS

The results illustrated by the protein profiles of selected samples shown in the gel of Fig. 1 indicated that the lower MW region (33300 and under) was the least variable, and high MW region (140000 to 70000) had the greatest protein subunit variability with the medium MW region (70000 to 33000) in between.

The following lines of evidence support these conclusions:

1. Observations: Visual observations, and the review of the gels over many times suggested to the experienced observer that the order of variation was as stated above.

2. Dotgraph.

Fig. 2 is a computer-generated RI vs. MW composite of 841 samples, with each dot representing a peak from a single scan. In the low MW region dot/peaks (representing protein subunits) clustered around definite MWs. A relatively greater spread of the dots/peaks occurred in the medium MW region. However, in the high MW region, no dot/peak clustering occurred. Complementing the observations made of the gels, it was deduced from this graph that the clustering of dots/peaks occurred around a given MW when a band was present in most samples at the MW in question. If the MW measurements were 100% accurate and the same band appeared in all the samples, differing only in intensity, then the dot graph (Fig. 2) would show this as a line made up of dots at the corresponding MW. Given that SDS-PAGE MW calculations from gel to gel carry an error, a cluster rather than a line of dots appears around, rather than exactly at, a given MW. Fig. 3 illustrates how the composite represents individual scans.

3. A final line of evidence is the computer-generated graphs of Figs. 4, 5, and 6. These graphs were obtained by dividing the dot graph (Fig. 2) into the MW ranges that make up its clusters and the spaces between them which had fewer dot peaks (Fig. 7). A close examination of Figs. 4, 5, and 6 reveals the heterogeneity in the makeup of each cluster, and hence the protein subunit variability in the 841 accessions of T. dicoccoides studied. In the low MW region (Fig.

4) one band predominates in most of the MW ranges. However, in the

medium and high MW regions (Figs. 5 and 6) ranges almost always have a diverse composition.

As an example, the variation in protein composition in the 47800 to 39600 MW range differs markedly from that in the 8800 to 10000 MW range. In the 47800 to 39600 MW region 4% of the samples had one peak in this region, 36% had two peaks, 40% had three peaks, 20% had four peaks or more in this range. In contrast, in the range between 8800 and 9800, 95% of the samples had one peak and only 2% of the samples had no peak. The less compact cluster of these higher MW range is thus more heterogeneous compared to the compact cluster in the 8800-9800 MW. Consequently, these results indicate that the low MW region (33300 and under) is highly conserved while extensive protein subunit genetic variability is present in the medium (70000 to 33300 MW) and in the high MW region (140000 to 70000 MW).

DISCUSSION

The data showed that the low MW region is the least variable, probably because this region is mostly composed of low MW albumin and globulins, many of which are essential enzymes or structural proteins. One would not expect such proteins to vary much in their size because a slight change in size could render them nonfunctional. However, it is entirely possible that genetic variation may be revealed for low MW soluble proteins using another electrophoretic system that detects protein on the basis of charge or other property than MW. The work of Nevo et al. (1982) supports this hypothesis. They found considerable allozyme variation for soluble enzymes extracted from leaf tissue of seedlings of T. diccoides using nondenaturing starch gel

electrophoresis. It must be kept in mind that SDS-PAGE of total protein probably masks part of the genetic variation existing in a population, because protein subunits of different pI, and amino acid composition but of same MW would migrate to the same place in the gel. This may explain the relatively little variation observed for the low MW subunits in this study.

The medium and high MW regions, in contrast, showed extensive protein subunit variability in their migration in SDS-PAGE gels, and are mostly storage proteins, i.e., gliadins and glutenins (Cole et al. 1981; Fullington et al. 1980). The functions of these proteins is to serve as a nutrient reserve for the young seedling. It is reasonable to speculate that variation in the size of these proteins would not be deleterious to the plant, and therefore great variability can exist.

The nature of this variation is not yet certain, but a number of explanations have been offered. Lawrence and Shepherd (1980) suggested that variations in high MW glutenins, for bands which appear as alternatives of each other (which may be the case in some of the I. dicoccoides accessions), can be explained in simplest terms as due to alternative forms of the same allele. Another possibility is that post-translational cleavage of a protein precursor causes variation in size, provided that variation occurs on the location of the point of cleavage (Lawrence and Shepherd 1980). Regarding this point, Larkins and Hurkman (1978) presented evidence in maize that some of the storage proteins are synthesized as precursors which are later processed by proteolytic cleavage of a small sequence of amino acids. Recent work by Greene (1981) provides evidence that the same phenomena occur in wheat. He observed that gliadin polypeptides synthesized in vitro

were larger than their in vivo counterparts. He suggested that the former may be precursors which, in vivo, undergo processing to yield the smaller final product.

It has been observed that the transcriptional unit of the eukaryotic genome can be made up of exons, which are the DNA sequences that are actually transcribed into mRNA for protein synthesis, and introns or DNA sequences which are transcribed into RNA but later are excised and not made into mRNA and therefore do not end up as protein (Gilbert 1978). Based on this, Thomson and Doll (1979) speculated that single nucleotide substitutions could affect the "splicing pattern of a transcribed unit", causing additions or deletions of whole amino acid sequences. It is noteworthy this event could arise from a single mutation.

Another explanation is that variation in protein subunit migration in SDS-PAGE may be due in part to variation from the assumed constant ratio of SDS binding to the proteins (1.4 g SDS/g protein). If considerable variation occurs from this theoretical value, then proteins of the same size can vary in mobility. Fortunately, Bietz and Wall (1972) found that gluten subunits (mostly glutenins and gliadins) bind SDS in proportions close to the theoretical value.

Phosphorylation, glycosylation or conjugation also are known to cause anomalous behavior of proteins in SDS-PAGE (Chrambach et al. 1976), so these types of modification must be taken into consideration as a possibility. However, the low MW region is so stable that it served as an internal control. Thus, it is certain that most of the protein subunit variability observed in the high and medium MW weight regions is due to genetic factors, with the possibilities that 1) the

presence or absence or the size of a carbohydrate moiety attached to a protein could have caused some of the variability and 2) although results indicated that the HMW region had the greatest protein subunit variability it is possible that part of the variability may be more apparent than real. The relatively high concentration of acrylamide used (17%) tends to bunch up the HMW bands rather closely near the top of the gel, therefore slight variability even within single gels relative to the MWS might result in appreciable variation in apparent mobility of bands with identical mobilities. This may have contributed to the apparent absence of peaks in the HMW region of the dot graph.

Unequal crossing-over of chromosomes containing repeated DNA sequences is another possible genetic factor accounting for the protein subunit variability. This event would give rise to allelic genes or gene complexes whose end products are polypeptides of varying length. The occurrence of repeated DNA sequences in wheat is well documented (Peacock et al. 1981), however it is not yet certain that such regions code for storage proteins.

The examples offered above can be considered as events that may have occurred in the early stages of diploid wheat progenitor evolution. Therefore, the variation in protein subunits observed today in the case of T. dicoccoides may be a product of differential diploid parent contribution to the formation of the tetraploid T. dicoccoides. Kasarda (personal communication, 1982) favors this idea. His opinion is that the variable contribution could have occurred either through multiple formation of tetraploids involving interactions of different A and B genome donors or through

introgressive events at a later stage, mainly with the independently formed AB combinations. Zohary and Feldman (1962) explained genetic variability in morphology and other characters of the polyploid species of Aegilops-Triticum by suggesting that formation of initial amphidiploids was followed by extensive hybridization between them.

On the other hand, ample time has elapsed for a major portion of the variability resulting from the recombinations of genes from polyphyletic origins to have evolved within T. dicoccoides as races become established in separated local environments. More research on protein molecular evolution and wheat genetics will be needed to ascertain the true nature of the variability observed in the protein subunits. Also, an extensive analysis needs to be made of the diploid progenitors, and comparisons made with those from locations nearby the sites of T. dicoccoides swarms. Moreover, if appreciable variation is observed in SDS-PAGE gels, which differentiate proteins solely on the basis of size and not charge, isoelectric point or amino acid sequence, then the variability observed in 2-D and other electrophoretic systems must be even greater. Efforts are now under way to select and exploit those accessions of greatest breeding value for increasing the quantity and quality of proteins in high yielding modern wheats. Grama et al. (1982) provided details as to how this is being accomplished.

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FIGURE LEGENDS

- Fig. 1. SDS-PAGE of 13 selected I. dicoccoides accessions chosen on the basis of uniqueness from several different gels and reproduced in a single run. The variety Chinese Spring is included for comparison. Slot 1 = BP11, 2 = BP13, 3 = BP17, 4 = BP150, 5 = BP156, 6 = BP374, 7 = BP376, 8 = BP388, CS = Chinese Spring, S = Molecular Weight Standards, 9 = BP462, 10 = BP574, 11 = BP573, 12 = BP783, 13 = BP1010.
- Fig. 2. Composite of all samples showing divisions for high (70000 MW and above), medium (70000 MW to 33300 MW), and low MW regions (33300 to 8800 MW).
- Fig. 3. Composite of all samples and three individual scans.
- Fig. 4. Computer-generated graph of frequency (presence or absence) for peaks in the low MW region.
- Fig. 5. Computer-generated graph of frequency (presence or absence) vs. MW for peaks in the medium MW region.
- Fig. 6. Computer-generated graph of frequency (presence or absence of peaks) vs. MW range for peaks in the high MW region.
- Fig. 7. Composite of all samples partitioned into individual clusters and spaces between clusters.

SDS - PAGE TOTAL PROTEIN

Fig. 1

Fig 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

Fig. 7

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3.8. DROUGHT RESISTANCE REACTIONS OF WILD EMMER (T. dicoccoides)
AND WILD EMMER X WHEAT DERIVATIVES¹

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Summary

Wild emmers (T. dicoccoides) collected from various sites in Israel and wheat selections derived from wild emmer x wheat crosses were subjected to three tests for drought resistance in terms of dehydration avoidance, seedling tolerance and stability of the cellular membranes under stress.

Relatively high rates of drought resistance were revealed for each trait within the wild emmers and their derivatives. Drought resistance in terms of the tests performed in the wild emmers was not correlated with collection-site aridity.

Introduction

The genetic improvement of drought resistance in wheat requires the exploration of potential genetic resources for drought resistant attributes. While significant genetic variation for defined drought resistant attributes appears to exist in well-adapted high-yielding wheat breeding germplasm (Blum et al, 1981), alien wheat genetic resources should not be overlooked as a potential gene pool for future utilization.

Wild emmer (T. dicoccoides), the tetraploid progenitor of cultivated wheat, has been shown to be reasonably compatible to wheat in terms of the introgression of genes into wheat (Gerechter-Amitai and Grama, 1974; Grama and Gerechter-Amitai, 1974). Transfer of genes for several plant characters (e.g., disease resistance, high kernel protein content) from wild emmer into cultivated wheat was found possible with only minor or no deterioration in the agronomic perform-

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1 ance of the progeny (Grama et al, 1982).

2 Wild emmer is widely distributed in various habitats over parts of
3 Central and Northern Israel. Wild emmer habitats in Israel vary in
4 precipitations, temperature and soil type. Continuous exploration and
5 collection of wild emmer resulted in a large and variable collection
6 maintained at this laboratory. It was considered important to explore
7 the variation for several drought resistant attributes in the wild
8 emmer collection, as well as in a sample of wild emmer x wheat derived
9 wheats, in order to establish the usefulness of the wild emmer gene
10 pool for the genetic improvement of drought resistance in wheat.

11 Materials and Methods

12 Work was performed with wild emmer accessions previously collect-
13 ed in Israel. Collection sites ranged within a latitude of 31' 40⁰N to
14 33' 20⁰N, an altitude of -200 to 1600 m and a mean total annual
15 rainfall of 270 to 1150 mm. Seed used in this study was obtained by
16 bulking or by selecting heads within rows of the collected wild emmers
17 grown under favourable conditions at Bet Dagan.

18 The wild emmer x wheat derivatives used in this study were F₉ to
19 F₁₁ lines selected from the cross [T. dicoccoides G-25/ Nursi-
20 163//Merav]. T. dicoccoides G-25 was an accession collected at Rosh
21 Pinna, carrying resistance to stripe rust. 'Nursi-163' was a selection
22 out of a durum land race and 'Merav' was a local bread wheat cultivar.

23 All the ^{DERIVATIVES} selections used were well-adapted and agronomic hexaploid
24 wheats, that were selected mainly for stripe rust resistance.

25 Three tests for drought resistance were performed, using estab-

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lished methodology. These tests were chosen largely due to their relative ease of performance in large populations and their current employment in wheat breeding in Israel.

'Dehydration avoidance' (the relative ability to maintain high leaf water potential under conditions of soil moisture stress) was evaluated indirectly by remote infra-red thermal sensing of plant canopies under water stress (Blum et al, 1982). The test was performed at the Gilat experiment station, where mean total annual rainfall is 220 mm. Materials were planted in rows 1 m long and 90 cm apart, arranged in blocks of 50 rows. Five check cultivars were planted in each block. When water stress occurred (at about the early boot stage), midday canopy temperatures were recorded with a hand-held Barnes "Instatherm" infra-red thermometer. All the necessary precautions were employed, as detailed elsewhere (Blum et al, 1982). Four readings were made on four separate dates during the drying cycle, when leaf water potentials (measured with a pressure chamber) in a check cultivar ('Barkee') ^{de} increased from -19.1 to -23.7 bars. Canopy temperatures were converted to percent of the mean of the block, in order to isolate site variation among blocks, and were then averaged over the four readings for each entry.

'Desiccation tolerance' was evaluated in terms of cellular membrane stability after exposure of leaf discs to water stress in vitro, using a 40% solution of polyethylene glycol-6000 as the stress medium (Blum and Ebercon, 1981). The rate of injury to cellular membranes by desiccation was estimated by measuring (conductometrically) the elec-

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1 electrolyte leakage from stressed and non-stressed leaf discs. Plant
2 materials used in the test were obtained from a nursery grown under
3 favourable conditions at Bet Dagan. Five samples (replicates) of 20
4 leaf discs each were taken in each entry upon flowering. Five check
5 cultivars were included in this test.

6 'Seedling tolerance' to water stress was evaluated only in the
7 wild emmers, in terms of the reduction in growth rate under water
8 stress. Seedlings were grown in the growth chamber in nutrient
9 solutions with ("stress") or without ("control") polyethylene glycol-
10 6000 (25%). Growth rates were evaluated by sampling seedlings for
11 their top dry matter weight over a seven day interval. Five seedlings
12 were sampled for each sampling date x medium x entry combination. Full
13 details on the procedure are given elsewhere (Blum et al, 1980). The
14 rate of injury to seedling growth rate (mg/plant/day) was calculated
15 from stress and control data. Two check cultivars were included in the
16 test.

17 Heading date and plant height were recorded for the wild emmers
18 grown under favourable conditions at Bet Dagan.

19 Results and Discussion

20 For the 172 wild emmer accessions tested, leaf canopy tempera-
21 tures as percent of the mean of the block (Fig. 1) ranged from 85%
22 (cooler and more resistant) to 120% (warmer and more susceptible). For
23 a typical mean block canopy temperature of 30°C, this range would
24 represent a difference of 7.3°C between extreme accessions. Previous
25 results from replicated wheat tests grown at the same site (Blum et al,

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1 1982) indicated that 1.1 to 1.9°C constituted a significant ($P = 0.05$)
2 difference among entries.

3 The distribution of the 141 wild emmer x wheat derivatives for
4 canopy temperatures did not differ much from that of the wild emmers,
5 with just a slight possible shift towards lower temperatures in the
6 former. The variation in canopy temperature for both the wild emmers
7 and their derivatives exceeded that among the check cultivars. Some of
8 the wild emmers and their derivatives apparently carried a higher level
9 of dehydration avoidance than any of the check cultivars.

10 For the 206 wild emmer accessions tested, the rate of injury to
11 cellular membranes by desiccation (Fig. 2) ranged from 0 to 70%, with
12 distinct skewness of distribution towards low injury rates. The
13 distribution of the 91 wild emmer x wheat derivatives, in this respect,
14 was more normal, ranging from 10 to 90%. For both the wild emmers and
15 their derivatives, a high proportion of the entries tested were more
16 tolerant, in this respect, than the check cultivars.

17 For both 'dehydration avoidance' and 'desiccation tolerance',
18 appreciable levels of resistance were revealed in the wild emmer x
19 wheat derivatives, although they were selected only for stripe rust
20 resistance and agronomic performance under normal to favourable grow-
21 ing conditions.

22 For the 39 wild emmer accessions tested, the rate of injury to
23 seedling growth (Fig. 3) ranged from 0 to 100%. This range exceeded
24 that between the resistant ('Inbar') and the susceptible ('Cajeme')
25 (Blum et al, 1980) check cultivars.

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1 The wild emmers' data for each drought response (except for
2 seedling growth) were grouped according to collection sites. Results
3 for 17 sites, each represented by at least nine accessions, are
4 presented in table 1.

5 Within most sites the variance among accessions for each of the
6 two drought responses was large. For several sites, the variance
7 within a site was as large as the variance among sites. For example,
8 the range in desiccation injury among accessions at Korazim represents
9 the full range among all tested accessions as per Fig. 2.

10 The possible reasons for the extensive variation in these drought
11 responses within certain sites cannot be seen in the data. For the two
12 drought responses, there were no significant correlations across sites
13 between the within-site variance and site mean annual rainfall, site
14 mean daily temperature on site altitude. Nor were the two drought
15 responses, or their within-site variances correlated across sites.
16 These two drought responses appear to be independant of each other and
17 independant of the main meteorological variables of the collection
18 sites.

19 Correlations were also calculated across accessions, between each
20 of the three drought responses and several meteorological and plant
21 variables (Table 2).

22 None of the drought responses were significantly correlated with
23 site aridity, in terms of total annual rainfall. Dehydration avoidant
24 accessions (having relatively lower canopy temperatures) appeared to
25 originate at low altitudes in relatively warmer conditions - typical of

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1 sites in the Jordan Valley. These accessions tended to be character-
 2 ized by small plants of short growth duration. While the correlation
 3 coefficients for the above associations were very small (although
 4 statistically significant), the possible advantage of small and early
 5 maturing wild emmer ecotypes in terms of dehydration avoidance is
 6 physiologically quite reasonable. However, when the data presented
 7 are taken as a whole, drought resistance in wild emmer, in terms of the
 8 three tests performed, appears to be almost randomly distributed among
 9 sites with little if any relations to site aridity. It may be argued,
 10 therefore, that these drought responses do not confer any selective
 11 advantage in T. dicocoides growing in arid environments. These drought
 12 resistance tests were developed and are considered important in the
 13 selection of cultivated wheat for higher productivity in arid condi-
 14 tions. Likely, these drought resistance attributes may not be signifi-
 15 cant in the evolution of T. dicoccoides, where survival mechanisms and
 16 not productivity are preferred by natural selection. If this is the
 17 case, then these drought resistance attributes are essentially "neu-
 18 tral" (Kimura, 1979) with respect to natural selection and would indeed
 19 be randomly distributed in T. dicoccoides.

20 Assuming that the above interpretations are realistic, a final
 21 speculation is proposed. When the wild progenitors of crop plants are
 22 explored as genetic resources for the improvement of crops' drought
 23 resistance, useful genes are not necessarily found mostly in stress
 24 environments - since the drought resistance genes that confer a
 25 selective advantage in natural habitats are not necessarily those that

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1 confer on advantage in man-made selected plants in agricultural eco-
2 systems.

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Figure captions

Fig. 1. Distribution of 172 wild emmers ('DIC') and 141 wild emmer x wheat derivatives ('DER') with respect to leaf canopy temperature (as percent of the mean of the block), as compared with five check wheat cultivars.

Fig. 2. Distribution of 206 wild emmers ('DIC') and 41 wild emmer x wheat derivatives ('DER') with respect to desiccation injury to cellular membranes, as compared with five check wheat cultivars.

Fig. 3. Distribution of 39 wild emmers with respect to the rate of injury to seedling growth rate by water stress, as compared with two check wheat cultivars.

Table 1. Mean, range and variance for leaf canopy temperature and desiccation injury of wild emmer accessions collected from 17 sites.

Site	Leaf temperature (as percent of the mean of the block)			Desiccation injury (%)		
	Mean	Range	Variance	Mean	Range	Variance
Rosh Pinna	106.9	100.2-115.6	41.6	17.8	9.3-44.6	226
Mt. Beatitude	100.8	96.6-107.0	15.1	27.5	16.8-48.4	160
Nahal Oren	101.0	93.2-110.5	37.7	22.4	13.8-44.3	185
Kefar Shammai	106.8	89.9-114.0	97.6	28.3	17.0-49.6	154
Mt. Hermon	107.7	97.9-117.8	40.3	27.3	17.6-50.4	241
Maale Gilboa	103.9	99.3-114.0	33.6	32.4	15.2-42.4	137
Korazim	98.5	97.8-102.1	28.1	29.4	4.8-64.6	472
Mt. Kennaan	101.6	95.8-108.3	13.9	24.5	14.6-59.9	263
Arbel	106.6	101.5-111.7	21.0	27.9	21.7-33.6	102
Berekhet Ram	101.7	91.8-107.2	21.1	32.0	20.8-42.3	144
Zefat	100.3	93.8-110.7	51.7	15.3	6.2-24.3	56
Ramot	102.4	99.3-105.3	6.8	30.9	26.5-45.7	157
Kefar Giladi	96.8	91.1-112.1	54.2	16.1	5.2-30.6	141
Gonen	104.5	99.3-109.9	16.1	23.1	4.2-47.3	440
Kasrin	104.1	99.3-109.1	42.0	54.7	28.1-88.9	676
Maale Gamla	97.4	93.2-104.6	17.8	28.9	7.4-61.4	623
Gesher Ariq	104.0	98.4-105.9	14.0	56.0	46.5-66.0	59
Variance among sites			89.5			574.4
F among sites			2.5			2.5

Table 2. Correlation coefficients (r) between each of the drought responses and several meteorological and plant variables, across the various wild emmers tested.

Drought response	No. of accessions	Altitude	Mean		Days to heading	Plant height
			annual rainfall	daily temperature		
Canopy temperature	172	0.141*	0.106	-0.142*	0.129*	0.134*
Desiccation injury	206	-0.098	-0.099	0.100	0.030	0.101
Seedling injury	39	-0.063	-0.118	0.054	-0.194	0.065

(*) Significant at $P = 0.05$.

Fig. 2

(Blum et al.)

Fig. 3

(Blum et al.)

4.

DESCRIPTION OF COOPERATIONIsraeli Team

The research responsibilities for the part of the work done in Israel were divided among four individuals, as follows:

Dr. Z.K. Gerechter-Amitai and Dr. Helena Goldenberg performed field trips and carried out the collection work. The latter was responsible for growing the collections at Bet Dagan and carried out all the plant morphological and phenological observations towards their final analysis. Dr. Z.K. Gerechter-Amitai was responsible for the evaluation of stripe rust resistance in the collections and the derived wheat materials. Dr. Adriana Grama was responsible for protein analysis work in the collections as well as all the evaluations of the derived wheat materials, in the field and laboratory. Dr. A. Blum carried out the observations on drought resistance in the various materials and is developing, together with all others, the final computerized data base of the wild emmer collection.

U.S. Team

Each year seed of the new collections of wild emmer was sent to the U.S. investigators, as soon as possible. Likewise, seed grown at the Bet Dagan Farm, both of wild emmer and derived wheat materials, was forwarded to the cooperators. For some studies, single plant selections of previous collections were also supplied.

Dr. E.L. Sharp and Dr. M. Reinhold (Montana) carried out work on minor (temperature sensitive) genes resistance to stripe rust in wild emmers and the progeny of their crosses onto tetraploid and hexaploid wheats. Selected progenies were sent to Israel for agronomic and grain quality evaluations. Their work on stripe rust was closely associated to respective work done by Dr. Z.K. Gerechter-Amitai in Israel.

Dr. C.F. Konzak and Mr. L. Manzur-Vergara (Washington State) carried out the electrophoretic work for the identification of the relative frequency of the grain protein sub-units in the wild emmers. Dr. G.L. Rubenthaler

(Washington State) evaluated the baking quality of the various derived hexaploid wheat lines selected in Israel and grown in both Israel and Washington State.

Dr. J.G. Moseman (Beltsville) tested the various wild emmer collections for leaf rust and powdery mildew.

A large part of the collection is now being maintained by the USDA germplasm bank at Beltsville.

5.

BENEFIT TO AGRICULTURE

1. The great value of the Israeli wild emmer population as a genetic resource for wheat breeding has been established. The information gained and its catalogueing in the form of a computerized data base (in work at this date) will enable a rapid and easy access to defined genetic resources within this germplasm. The full record of the geographical distribution of these genetic resources will reduce the future efforts in re-collections for specific purposes. The maintenance of this collection at both Bet Dagan and Beltsville reduce the risk involved in a possible extinction of wild emmer in its native habitats.
2. Genes for resistance to stripe rust were transferred from the wild emmer into cultivated wheats grown in Israel and Northern U.S. These genes are now available in a background of adapted and agronomic wheat materials and its further utilization does not require any crosses with wild emmer.
3. The understanding of the relative frequencies of the grain protein subunits in wild emmer will make any future attempts to use this germplasm for wheat protein improvement more comprehensive, cheaper and easier. It has been shown that the use of high protein genes of the wild emmers requires the judicious testing of segregates for protein quality in terms of baking performance.
4. Wild emmers were found to be a potential genetic resource for drought resistance attributes that are compatible with a normal high yielding wheat germplasm. This phase of work demonstrated that agronomic drought resistance attributes are frequent in almost any population of wild emmer.

As a direct result of this work two wild emmer derived common wheat lines selected in Israel and tested in Washington State are being seriously considered as cultivars for commercial release in Washington State. Preliminary results have shown these lines to perform as well or better than local cultivars, while having a significantly greater baking quality.

Several such selections were also good enough to justify advanced testing in the regional wheat variety trials in Israel, and they constitute a future potential release to growers in Israel.

Some of the derived wheat lines, that carry the wild emmer stripe rust resistance were requested for the inclusion in the International Spring Wheat Rust Nursery. Their inclusion in this nursery opens the way for a worldwide utilization of some of the results of this research.

Numerous requests for seed of this germplasm were received from many countries, including various States in the U.S. These requests point out the importance that wheat breeders throughout the world ascribe to this important germplasm.

APPENDIX

A Listing of Triticum dicoccoides Collections in Israel and their collection sites, designated by name, longitude, latitude and altitude.

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-4M	ROSH PINNA	2000	2640	440
G-7MB	KEFAR GILADI	2030	2940	500
G-12-1M	KEFAR GILADI	2030	2940	500
G-13-1M	BIRYAT SHEMONE	2030	2900	220
G-14-1M	SEDE ELIEZER	2030	2730	130
G-15M	SEDE ELIEZER	2030	2730	130
G-20M	HATSOR	2010	2650	300
G-21M	ROSH PINNA	2000	2640	440
G-23M	ROSH PINNA	2000	2640	440
G-25M	ROSH PINNA	2000	2640	440
G-27M	ZEFAT	1980	2630	550
G-28M	MERON	1870	2660	880
G-29-1M	MT. MERON	1870	2600	920
G-32-1M	AMMIAD	2010	2600	300
G-34-1M	AMMIAD	2010	2600	300
G-35-1M	AMMIAD	2010	2600	300
G-39-1M	ALHAGOR	2060	2580	50
G-40M	MT. OF BEATITUDE	2020	2540	-75
G-41-1M	MT. OF BEATITUDE	2020	2540	-75
G-43-1M	MT. OF BEATITUDE	2020	2540	-75
G-44-1M	KEFAR HITTIH	1920	2460	50
G-48-1M	PORRIYA	2020	2380	-40
G-50M	YAVNEEL	1930	2350	50
G-52M	BAT SHELOMO	1510	2230	150
G-57M	AMMIAD	2010	2600	300
G-58M	DISHON	2030	2780	450
G-59-2B	JERUSALEM	1700	1340	800
G-64M	MT. OF BEATITUDE	2020	2540	-75

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-68-1M	HERON	1870	2600	900
G-70M	MT. OF BEATITUDE	2020	2540	-75
G-71M	ALHAGOR	2060	2580	50
G-72-1M	AMMIAD	2010	2600	300
G-74-1M	KEFAR GILADI	2030	2940	350
G-75-1M	GARNE HITTIM	1900	2450	390
G-76M	MT. OF BEATITUDE	2020	2540	-75
G-77-1M	MT. CARMEL	1550	2390	300
G-78-1M	ALHAGOR	2060	2580	50
G-79-1M	KORAZIM SILL	2000	2570	200
G-81-1M	KORAZIM SILL	2000	2570	200
G-82-1M	BET BESHET	1830	2360	195
G-83-1M	BET BESHET	1830	2360	195
G-84-1M	ROSH PINNA	2000	2640	440
G-85-1M	AMMIAD	2010	2600	300
G-86-1M	AHIRIM	1930	2600	525
G-87M	BET BESHET	1830	2360	195
G-88-1M	JABA	1750	1400	650
G-89M	KEFAR SHAHHAY	1940	2620	630
G-90M	ROSH PINNA	2000	2640	440
G-91M	WERED HAGALIL	2020	2560	100
G-92M	WERED HAGALIL	2020	2560	100
G-93-1M	WERED HAGALIL	2020	2560	100
G-94-1M	KEFAR NAHUM	2040	2540	200
G-95M	WERED HAGALIL	2020	2560	100
G-96-2BGR.	KEFAR NAHUM	2040	2540	200
G-97M	KORAZIM SILL	2000	2570	200
G-98-1M	KORAZIM SILL	2000	2570	200

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-99M	KEFAR NAHUM	2040	2540	200
G-100M	HERED HAGALIL	2020	2560	100
G-104A-2M	KEFAR SHAMMAY	1940	2620	630
G-108-1BM	GOLAN	2260	2780	1010
G-109MB	GOLAN	2150	2480	230
G-110-1BM	HITSPE GADOT	2110	2690	280
G-111-1BM	KOKHAV HAYARDEN	2000	2230	310
G-112M	MAALE GILBOA	1900	2120	200
G-113-1B	MAALE GILBOA	1900	2120	200
G-114M	MAALE GILBOA	1900	2120	200
G-115M	TAIYBE	1830	1460	400
G-116-1M	YABAD	1840	2120	180
G-117M	KEFAR SHAMMAY	1940	2320	630
G-118M	KEFAR SHAMMAY	1940	2320	630
G-119M	ALHAGOR	2040	2540	200
G-120M	KORAZIN SILL	2000	2570	200
G-121-1M	BET BESHEH	1830	2360	195
G-122M	ROSH PINNA	2000	2640	440
G-123M	N. ZAVITAN	2150	2640	225
G-124M	S. HUSSEIN	2150	2640	225
G-125M	MESHUSHIM	2220	2740	775
G-126-1M	MESHUSHIM	2220	2740	775
G-127-1M	MESHUSHIM	2220	2740	775
G-128M	S. HUSSEIN	2110	2640	175
G-129-1M	HT. OF BEATITUDE	2020	2540	-75
G-130-1M	HT. OF BEATITUDE	2020	2540	-75
G-131-1M	HT. OF BEATITUDE	2020	2540	-75
G-132-1M	HT. OF BEATITUDE	2020	2540	-75

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-133H	MT. OF BEATITUDE	2020	2540	-75
G-134-1H	MT. OF BEATITUDE	2020	2540	-75
G-135-1H	MT. OF BEATITUDE	2020	2540	-75
G-136-1H	MT. OF BEATITUDE	2020	2540	-75
G-137-1H	MT. OF BEATITUDE	2020	2540	-75
G-138-1H	NAHAL OREN	1490	2360	475
G-139-1H	NAHAL OREN	1490	2360	475
G-140-1H	NAHAL OREN	1490	2360	475
G-141H	HITSPE HAYAHIN	1930	2620	700
G-142H	KEFAR SHAMHAY	1940	2620	630
G-143H	KEFAR SHAMHAY	1940	2620	630
G-144H	KEFAR SHAMHAY	1940	2620	630
G-145H	KEFAR SHAMHAY	1940	2620	630
G-146-1H	KEFAR SHAMHAY	1940	2620	630
G-147H	KEFAR SHAMHAY	1940	2620	630
G-148H	KEFAR SHAMHAY	1940	2620	630
G-149H	ROSH PINNA	2000	2640	440
G-150H	ROSH PINNA	2000	2640	440
G-152-1H	ROSH PINNA	2000	2640	440
G-153-1H	ROSH PINNA	2000	2640	440
G-154H	ROSH PINNA	2000	2640	440
G-156H	NEHE ATIH	2190	2960	900
G-158-1H	HAJDAL SHAMHS	2220	1970	1200
G-159-1-18H	HAJDAL SHAMHS	2220	1970	1200
G-161-1H	HAJDAL SHAMHS	2220	1970	1200
G-165-1H	HESHUSHIN	2220	2740	775
G-166-1H	ROSH PINNA	2000	2640	440
G-167H	EILABUN	1920	2500	200

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-168-1M	MT. HERMON	2220	2980	1575
G-170-1M	HAR DOV	2170	3030	1420
G-179-1M	HAR DOV	2170	3030	1420
G-183-1M	?			
G-186M	JERUSALEM	1690	1310	800
G-187-1M	FABGUA	1890	2110	425
G-188M	MAALE GILBOA	1890	2090	450
G-189M	?			
G-190-1M	AMMIAD	2010	2600	300
G-191-1M	KORAZIM SILL	1990	2580	200
G-192M	KORAZIM SILL	1990	2580	200
G-193M	MT. KENAAN	1990	2660	850
G-194-1M	LEBANON-RASHAYA			
G-195M	LEBANON-RASHAYA			
G-197-1M	LEBANON-AIHA			
G-198M	LEBANON-AIHA			
G-200-1M	LEBANON-RASHAYA			
G-211-18M	HE-AMI	1640	2120	475
G-212M	BET GESHET	1830	2360	195
G-213M	BET GESHET	1830	2360	195
G-214M	BET GESHET	1830	2360	195
G-216-5M	EILABUN	1890	2430	200
G-217M	EILABUN	1890	2430	200
G-218M	HAR NETOFA	1850	2500	525
G-219M	HAR NETOFA	1850	2500	525
G-220-18-18M	SEGEV	1750	2530	180
G-221M	SEGEV	1750	2530	180
G-222-18-1M	SEGEV	1750	2530	180

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-223-2H	HIGDAL	1910	2530	50
G-224H	HIGDAL	1910	2530	50
G-225H	HIGDAL	1910	2530	50
G-226-2H	HIGDAL	1910	2530	50
G-227-3H	HIGDAL	1950	2500	140
G-228H	YAVNEEL	1970	2340	150
G-229H	KEFAR HITTIN	1970	2440	25
G-230-1BH	KEFAR HITTIN	1970	2440	25
G-231H	ARBEL CLIFF	1960	2470	110
G-232H	ARBEL CLIFF	1960	2470	110
G-233H	ARBEL CLIFF	1960	2470	110
G-234H	KEFAR ZEITIN	1940	2460	40
G-235H	PORRIYA	2020	2380	-40
G-236H	BAT SHELOMO	1510	2240	110
G-237H	BAT SHELOMO	1510	2240	110
G-238H	NAHAL OREN	1540	2360	375
G-239H	NAHAL OREN	1540	2360	375
G-240H	NAHAL OREN	1540	2360	375
G-241H	NAHAL OREN	1540	2360	375
G-242H	NAHAL OREN	1540	2360	375
G-243H	NESHER	1550	2390	300
G-244H	JERUSALEM	1690	1310	800
G-246H	JERUSALEM	1690	1310	800
G-247H	JERUSALEM	1690	1310	800
G-248H	JERUSALEM	1690	1310	800
G-249H	JERUSALEM	1690	1310	800
G-251H	BET HEIR	1540	1340	540
G-252-1BH	BET HEIR	1540	1340	540

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-253-7M	BET HEIR	1540	1340	540
G-254M	GIVAT HAHORE	1820	2240	400
G-255M	GIVAT HAHORE	1820	2240	400
G-256M	GIVAT HAHORE	1820	2240	400
G-257M	LAVI	1920	2440	310
G-258M	LAVI	1920	2440	310
G-259M	BARNE HITTIN	1900	2450	395
G-260-1M	BARNE HITTIN	1900	2450	395
G-261M	PORRIYA	1960	2430	155
G-262M	MAALE GILBOA	1890	2110	425
G-263-18M	MAALE GILBOA	1890	2110	425
G-264-1M	MAALE GILBOA	1890	2110	425
G-265M	HAR TURAN	1850	2450	550
G-266M	HAR TURAN	1850	2450	550
G-267M	MT. OF BEATITUDE	2020	2540	-75
G-268M	MT. OF BEATITUDE	2020	2540	-75
G-269-18M	MT. OF BEATITUDE	2020	2540	-75
G-270-18M	MT. OF BEATITUDE	2020	2540	-75
G-271-18M	MT. OF BEATITUDE	2020	2540	-75
G-272M	MT. OF BEATITUDE	2020	2540	-75
G-273M	KORAZIM SILL	2000	2570	200
G-274-2M	KORAZIM SILL	2000	2570	200
G-275M	KORAZIM SILL	2000	2570	200
G-276-18M	KORAZIM SILL	2000	2570	200
G-277-18M	KORAZIM SILL	2000	2570	200
G-278M	N. ZAVITAN	2150	2660	300
G-279M	HUSHNIYYA	2560	2110	100
G-280-18M	CUSTOMS HOUSE	2150	2440	300

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-281H	BEREKHET RAH	2220	2940	1030
G-282H	BEREKHET RAH	2220	2940	1030
G-283H	HAJDAL SHAHHS	2220	2970	1200
G-284H	ROSH PINNA	2000	2640	440
G-285H	ROSH PINNA	2000	2640	440
G-286H	ROSH PINNA	2000	2640	440
G-287H	MT. KENAAN	1990	2660	850
G-288H	MT. KENAAN	1990	2660	850
G-289H	MT. KENAAN	1990	2660	850
G-290H	ZEFAT	1980	2620	700
G-291H	ZEFAT	1980	2620	900
G-292H	ZEFAT	1980	2620	700
G-293H	ZEFAT	1980	2620	700
G-294H	MT. KENAAN	1980	2620	700
G-295H	ALHA	1970	2740	650
G-296H	ALHA	1970	2740	650
G-297H	ALHA	1970	2750	530
G-298H	ALHA	1970	2750	530
G-300H	ALHA	1970	2750	530
G-301H	DISHON	1980	2760	460
G-302H	DISHON	1980	2760	460
G-303H	DISHON	1980	2760	460
G-304H	HERON	1870	2670	1020
G-305H	EN ZEITIH	1880	2660	950
G-306H	KEFAR SHAKHAY	1940	2620	630
G-307H	KEFAR SHAKHAY	1940	2620	630
G-308H	HAJDAL SHAHHS	2200	2950	870
G-309H	HAJDAL SHAHHS	2200	2950	870

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-310-3M	HAJDAL SHAMHS	2200	2950	870
G-311M	HAJDAL SHAMHS	2200	2950	910
G-312M	HAJDAL SHAMHS	2200	2950	910
G-313M	HAJDAL SHAMHS	2200	2950	910
G-314-3M	MT. HERMON	2200	3000	1200
G-315M	MT. HERMON	2200	3000	1250
G-316M	MT. HERMON	2200	3000	1300
G-318M	MT. HERMON	2200	3000	1300
G-319M	ARBEL CLIFF	1950	2450	50
G-320M	BET MEIR	1540	1340	540
G-321M	AMIRIM	1930	2600	550
G-322M	AMIRIM	1930	2600	550
G-323M	AMIRIM	1930	2600	550
G-324	AMIRIM	1930	2600	550
G-325M	AMIRIM	1930	2600	550
G-326M	HITSPE HAYAMMIN	1930	2600	550
G-327-28M	HITSPE HAYAMMIN	1930	2600	550
G-328M	KEFAR SHAMHAY	1940	2620	640
G-329M	KEFAR SHAMHAY	1940	2620	640
G-330M	KEFAR SHAMHAY	1940	2620	640
G-331M	HERON	1950	2610	650
G-332M	HERON	1950	2610	650
G-333M	MT. KENAAN	1980	2620	550
G-334M	MT. KENAAN	1980	2620	550
G-335M	MT. KENAAN	1940	2610	590
G-336M	MT. KENAAN	1940	2610	590
G-337M	MT. KENAAN	1940	2610	590
G-338M	MT. KENAAN	1940	2610	590

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-339M	MT. KENAAN	1940	2610	590
G-340M	MT. KENAAN	1940	2610	590
G-341M	MT. KENAAN	1930	2600	530
G-342M	MT. KENAAN	1930	2600	550
G-343M	BIRIYYA	1970	2650	930
G-344M	DALTON	1960	2690	800
G-345M	DALTON	1960	2690	800
G-346M	HERON	1910	2690	750
G-347M	KEFAR SHAMHAY	1690	1310	800
G-348M	KEFAR SHAMHAY	1690	1310	800
G-349M	KEFAR SHAMHAY	1690	1310	800
G-350M	EN ZEITIM	1950	2670	730
G-351M	EN ZEITIM	1950	2670	730
G-352M	HERON	1700	1310	790
G-353M	EN ZEITIM	1950	2670	750
G-354M	EN ZEITIM	1950	2670	750
G-355M	MT. KENAAN	1960	2640	830
G-356M	HERON	1890	2660	1210
G-357M	HERON	1890	2660	1210
G-358M	HASSADA	2210	2940	940
G-359M	HASSADA	2210	2940	940
G-360M	MT. HERHON	2200	3000	1250
G-361M	MT. HERHON	2200	3000	1250
G-362M	MT. HERHON	2200	3000	1250
G-363M	MT. HERHON	2200	3000	1250
G-364M	AHIRIM	1690	1310	810
G-365M	KOKHAV HAYARDEN	2000	2230	-100
G-366M	GIVAT KOAH	1469	1600	100

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-367-18M	GIVAT KOAH	1469	1600	100
G-368M	GESHER	1280	2100	150
G-369M	GESHER	1280	2100	150
G-370M	NEWE UR	2020	2240	-160
G-371M	NEWE UR	2020	2240	-160
G-372M	NEWE UR	2020	2240	-160
G-373M	MAALE GILBOA	1900	2120	200
G-374M	MAALE GILBOA	1900	2120	200
G-375M	MAALE GILBOA	1900	2120	200
G-376M	MAALE GILBOA	1900	2120	200
G-377M	MAALE GILBOA	1900	2120	200
G-378M	RAMOT	2130	2520	50
G-379M	RAMOT	2130	2520	50
G-380M	RAMOT	2130	2520	50
G-381M	RAMOT	2130	2520	-40
G-382M	HULA RESERVATION	2050	2760	125
G-383M	HULA RESERVATION	2050	2760	125
G-384M	KEFAR GILADI	2040	2940	347
G-385M	KEFAR GILADI	2040	2940	345
G-386M	KEFAR GILADI	2040	2940	345
G-387M	KEFAR GILADI	2040	2940	345
G-388M	KEFAR GILADI	2040	2940	345
G-389M	KEFAR GILADI	2040	2940	345
G-390M	YIFTAH	2020	2820	455
G-391M	GONEN	2100	2810	100
G-392M	GONEN	2100	2810	100
G-393M	GONEN	2100	2810	100
G-394M	GONEN	2100	2810	100

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
		DEG	DEG	METER
G-395M	GONEN	2100	2810	100
G-396M	GONEN	2100	2810	100
G-397M	GASRIN	2040	2570	75
G-399M	GASRIN	2040	2570	75
G-400M	GASRIN	2040	2570	75
G-401M	GASRIN	2040	2570	75
G-402M	GASRIN	2040	2570	75
G-403M	GASRIN	2040	2570	75
G-404M	GASRIN	2040	2570	75
G-405M	GASRIN	2040	2570	75
G-406M	SIFSUFA	1910	2690	750
G-408M	WADI MAKHOKH	1800	1430	575
G-409-2M	WADI MAKHOKH	1800	1430	575
G-410M	NAHAL RIMMONIM	1820	1490	650
G-411-1M	NAHAL RIMMONIM	1820	1490	650
G-412M	TAIYBE	1830	1460	400
G-413M	SHADMOT DEVORA	1910	2340	175
G-414M	KAFR KAMA	1920	2340	225
G-415M	KAFR KAMA	1920	2340	225
G-416M	NAHAL OREN	1510	2370	380
G-417M	NAHAL OREN	1510	2370	380
G-418M	NAHAL OREN	1510	2370	380
G-419M	NAHAL OREN	1510	2370	380
G-420M	NAHAL OREN	1510	2370	380
G-421M	NESHER	1550	2390	325
G-422-1M	NESHER	1550	2390	325
G-423M	TEKHNION	1520	2440	185
G-424M	HA'ALE GANLA	2150	2560	105

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-424M	MAALE GAMLA	2150	2560	105
G-425M	MAALE GAMLA	2150	2560	105
G-427M	MAALE GAMLA	2150	2560	105
G-428M	MAALE GAMLA	2150	2560	105
G-429M	MAALE GAMLA	2150	2560	105
G-430M	MAALE GAMLA	2150	2560	105
G-431M	MAALE GAMLA	2150	2560	105
G-432M	MAALE GAMLA	2150	2560	105
G-433M	MAALE GAMLA	2150	2560	105
G-434M	MAALE GAMLA	2150	2560	105
G-435M	MAALE GAMLA	2150	2560	105
G-436M	MAALE GAMLA	2150	2560	105
G-437M	MAALE GAMLA	2150	2560	105
G-438M	MAALE GAMLA	2150	2560	105
G-439M	YAHUDIYA	2140	2590	100
G-440M	HADI MEKHOKH	1800	1430	575
G-441-1M	TAIYBE	1830	1460	650
G-442-2M	TAIYBE	1830	1460	650
G-443M	NAHAL RIMMONIM	1820	1490	650
G-444M	NAHAL RIMMONIM	1820	1490	650
G-445M	NAHAL RIMMONIM	1820	1490	650
G-446M	KOKHAV HASHAHAR	1830	1520	600
G-447M	KOKHAV HASHAHAR	1830	1520	600
G-448M	DUMA	1870	1470	240
G-450M	HAJDAL BANI FADIL	1845	1655	300
G-451M	GESHER ARIQ	2080	2570	-175
G-452M	GESHER ARIQ	2080	2570	-175
G-453-1M	GESHER ARIQ	2080	2570	-175

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-454M	CUSTOMS HOUSE	2090	2580	-85
G-455M	CUSTOMS HOUSE	2090	2560	-85
G-456M	SANABIR	2100	2590	75
G-457M	SANABIR	2100	2590	75
G-458M	HAPAL DEVORA	2140	2730	400
G-459M	HAPAL DEVORA	2140	2730	400
G-460M	HAPAL DEVORA	2140	2730	400
G-461M	GUSBIYA	2140	2730	400
G-462M	RAMOT NAFTALI	2020	2790	400
G-463M	RAMOT NAFTALI	2020	2790	400
G-464M	MEVOT HAHERMON	2020	2780	450
G-465M	MEVOT HAHERMON	2020	2780	450
G-466M	MEVOT HAHERMON	2020	2780	400
G-467M	RAMOT NAFTALI	2020	2790	400
G-468M	RAMOT NAFTALI	2020	2790	400
G-469M	DISHON	1940	2760	690
G-470M	DISHON	1940	2760	690
G-471M	DISHON	1940	2760	690
G-472M	DISHON	1940	2760	690
G-473M	DISHON	1940	2760	690
G-474M	DISHON	1940	2760	690
G-475M	DISHON	1940	2760	690
G-476-10M	BEREKHET RAH	2210	2940	975
G-477-2M	BEREKHET RAH	2210	2940	975
G-478-2M	BEREKHET RAH	2210	2940	975
G-479-1M	MT. HERMON	1030	2220	1575
G-480-6M	MT. HERMON	1030	2220	1575
G-481-3M	MT. HERMON	1030	2220	1575

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-482-5M	MT. HERMON	1030	2220	1575
G-483M	MT. HERMON	1030	2220	1575
G-484M	MT. HERMON	1030	2220	1575
G-485M	MT. HERMON	1030	2220	1575
G-486-5M	MT. HERMON	1030	2220	1575
G-487M	MT. HERMON	1030	2220	1575
G-488M	HAR SHAUL	1910	2070	350
G-489M	AMMIAD	2010	2600	300
G-491M	BEREKHET RAH	2210	2940	975
G-492M	BEREKHET RAH	2210	2940	975
G-493M	BEREKHET RAH	2210	2940	975
G-494M	BEREKHET RAH	2210	2940	975
G-495M	BEREKHET RAH	2210	2940	975
G-496M	BEREKHET RAH	2210	2940	975
G-497M	BEREKHET RAH	2210	2940	975
G-498M	BEREKHET RAH	2210	2940	975
G-500M	NAHF	1800	2600	100
G-502M	MT. HERMON	1030	2220	1575
G-503M	MT. HERMON	1030	2220	1575
G-504M	MT. HERMON	1030	2220	1575
G-506M	MT. HERMON	1030	2220	1575
G-507M	MT. HERMON	1030	2220	1575
G-509M	MT. HERMON	1030	2220	1575
G-510M	NAHAL GITIT	1870	1670	300
G-511M	NAHAL GITIT	1870	1670	300
G-513M	NAHAL GITIT	1870	1670	300
G-515M				
G-516	?			

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ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-517	?			
G-518	?			
G-519	?			
G-520	?			
G-521	RAHALLAH	1718	1557	575
G-522	RAHALLAH	1718	1557	575
G-523	RAHALLAH	1718	1557	575
G-524	RAHALLAH	1805	1809	500
G-525	MEKHORA	1917	1744	50
G-526	MEKHORA	1897	1743	200
G-527	MEKHORA	1891	1727	150
G-528	HALE EFRAYIM	1867	1642	300
G-529	HALE EFRAYIM	1867	1642	300
G-530	NURIT	1825	2169	75
G-531	NURIT	1825	2169	75
G-532	NURIT	1835	2154	175
G-533	NURIT	1835	2154	175
G-534	NURIT	1835	2154	175
G-535	JERUSALEM	1708	1336	800
G-536	HALE GILBOA	1882	2118	275
G-537	HALE GILBOA	1882	2118	275
G-538	HALE GILBOA	1882	2118	275
G-539	HALE GILBOA	1882	2118	275
G-540	HALE GILBOA	1882	2114	225
G-541	HALE GILBOA	1894	2106	325
G-542	HALE GILBOA	1894	2106	325
G-543	HALE GILBOA	1897	2105	300
G-544	HALE GILBOA	1897	2105	300

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-545	MAALE GILBOA	1904	2120	200
G-546	MAALE GILBOA	1904	2120	200
G-547	GIVAT HAHORE	1826	2247	400
G-548	GIVAT HAHORE	1826	2247	400
G-549	GIVAT HAHORE	1831	2246	450
G-550	GIVAT HAHORE	1831	2246	450
G-551	SHARONA	1942	2356	225
G-552	SEMADAR	1963	2362	75
G-553	PORRIYA	2025	2385	1
G-555	PORRIYA	2027	2385	-40
G-556	PORRIYA	2027	2385	-40
G-557	PORRIYA	2027	2385	-60
G-558	PORRIYA	2027	2385	-60
G-559	KEFAR HITTIN	1983	2446	50
G-560	KEFAR HITTIN	1971	2447	25
G-561	KEFAR HITTIN	1971	2447	25
G-562	ARBEL	1954	2452	50
G-563	KEFAR ZEITIN	1929	2466	50
G-564	ARBEL	1950	2453	60
G-565	ARBEL	1950	2453	60
G-566	HAZOREIN	1974	2416	100
G-567	HIGDAL	1914	2537	50
G-569	KARE DESHE	2015	2541	-125
G-569	KARE DESHE	2015	2541	-125
G-570	KARE DESHE	2015	2541	-125
G-571	KARE DESHE	2015	2541	-125
G-572	KARE DESHE	2016	2545	-100
G-573	KARE DESHE	2016	2545	-100

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-574	KARE DESHE	2016	2545	-100
G-575	ZOHET GOLANI	1943	2436	175
G-576	ZOHET GOLANI	1943	2436	175
G-577	ZOHET GOLANI	1943	2436	175
G-578	ZOHET GOLANI	1943	2436	175
G-579	ZOHET GOLANI	1943	2436	175
G-580	HUGOG	1971	2542	50
G-581	HUGOG	1971	2542	50
G-582	HUGOG	1971	2542	50
G-583	HUGOG	1973	2528	-125
G-584	TEL KINNEROT	2004	2541	1
G-585	TEL KINNEROT	2004	2541	1
G-586	TEL KINNEROT	1998	2542	1
G-587	TEL KINNEROT	1998	2542	1
G-588	MT. OF BEATITUDE	2023	2545	-75
G-589	ALHAGOR	2054	2580	25
G-590	ALHAGOR	2054	2580	25
G-591	ALHAGOR	2054	2580	25
G-592	ALHAGOR	2064	2588	50
G-593	ALHAGOR	2082	2600	-25
G-594	ALHAGOR	2082	2600	-25
G-597	HERED HAGALIL	2024	2568	100
G-598	HERED HAGALIL	2024	2568	100
G-599	KORAZIN-ZOHET	2014	2576	200
G-600	KORAZIN-ZOHET	2014	2576	200
G-601	KORAZIN-ZOHET	2014	2576	200
G-602	KORAZIN-ZOHET	2014	2576	200
G-603	KORAZIN-ZOHET	2004	2573	200

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-604	KORAZIM-ZOHET	2004	2573	200
G-605	KORAZIM-ZOHET	2004	2573	200
G-606	KORAZIM-ZOHET	2004	2573	200
G-607	KORAZIM-ZOHET	2004	2573	200
G-608	HUGOG-NORTH	1935	2564	125
G-609	HUGOG-NORTH	1935	2564	125
G-610	HUGOG-NORTH	1935	2564	125
G-611	HUGOG-NORTH	1981	2565	150
G-612	KORAZIM-ZOHET	1999	2582	200
G-613	KORAZIM-ZOHET	1999	2582	200
G-614	AMMIAD	2017	2606	300
G-615	KEFAR HANASI	2069	2647	275
G-616	KEFAR HANASI	2069	2647	275
G-617	KEFAR HANASI	2069	2647	275
G-618	GESHER BENOT YABOV	2097	2689	125
G-619	GESHER BENOT YABOV	2106	2684	225
G-620	GESHER BENOT YABOV	2110	2686	275
G-621	GESHER BENOT YABOV	2110	2680	275
G-622	GESHER BENOT YABOV	2110	2680	275
G-623	GESHER BENOT YABOV	2110	2680	275
G-624	ELKANA-SHOMRON	1537	1688	250
G-625	ELKANA-SHOMRON	1537	1688	250
G-626	SALFIT-SHOMRON	1734	1696	630
G-627	SALFIT-SHOMRON	1734	1696	630
G-628	TAIYBE	1815	1503	625
G-629	TAIYBE	1815	1503	625
G-630	TAIYBE	1815	1503	625
G-631	TAIYBE	1835	1466	400

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-632	TAIYBE	1835	1466	400
G-633	NESHER	1552	2399	325
G-634	NESHER	1554	2397	300
G-635	AHIHUD	1691	2578	100
G-636	AHIHUD	1667	2116	325
G-637	PARK HAYARDEN	2106	2657	200
G-638	MEVO HANNA	2116	2378	350
G-639	AFIQ	2176	2432	350
G-640	AFIQ	2176	2432	350
G-641	AFIQ	2176	2432	350
G-642	ELI AL	2189	2456	350
G-643	ELI AL	2189	2456	350
G-644	ELI AL	2189	2456	350
G-645	ELI AL	2189	2456	350
G-646	AVNE ETAN	2216	2472	375
G-647	AVNE ETAN	2216	2472	375
G-648	NOV	2239	2482	400
G-649	NOV	2239	2482	400
G-650	NOV	2239	2482	400
G-651	NOV	2239	2482	400
G-652	ELI AL	2174	2459	390
G-653	ELI AL	2174	2459	390
G-654	DALIYYA	1572	2204	200
G-655	DALIYYA	1572	2204	200
G-656	DALIYYA	1572	2204	200
G-657	KINNERET	2029	2359	-125
G-658	KINNERET	2032	2366	-150
G-659	HIZPA	1962	2438	150

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-660	KEFAR HITTIN	1959	2445	100
G-661	KEFAR ZEITIN	1945	2466	40
G-662	KEFAR ZEITIN	1945	2466	40
G-663	MAALE GANLA	2142	2560	1
G-664	MAALE GANLA	2142	2560	1
G-665	MAALE GANLA	2142	2560	1
G-666	MAALE GANLA	2164	2557	150
G-667	MAALE GANLA	2164	2557	150
G-668	MAALE GANLA	2157	2540	225
G-669	GANLA	2217	2572	450
G-670	RAMAT MAGSHINIM	2237	2546	450
G-671	RAMAT MAGSHINIM	2254	2510	440
G-672	GUSBIYA	2184	2652	400
G-673	GUSBIYA	2184	2652	400
G-674	NAHAL BET RIMON	1823	2423	300
G-675	NAHAL BET RIMON	1806	2429	400
G-676	TURAN	1867	2440	325
G-677	NAHF	1807	2600	275
G-678	NAHF	1807	2600	275
G-679	NAHF	1807	2600	275
G-680	ZEFAT	1988	2626	700
G-681	ZEFAT	1988	2626	700
G-682	ZEFAT	2000	2623	550
G-683	ZEFAT	2000	2623	550
G-684	SANABIR	2116	2684	300
G-685	SANABIR	2116	2684	300
G-686	BAZRIN	2132	2700	385
G-687	BAZRIN	2132	2700	385

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-688	GAZRIN	2173	2854	375
G-689	GAZRIN	2173	2854	375
G-690	GAZRIN	2138	2703	400
G-691	GAZRIN	2135	2702	400
G-692	KAFR NAFFAH	2189	2737	650
G-693	MT. HERMON	2211	2982	1450
G-694	RAHIYA	2140	2013	600
G-695	RAHIYA	2147	2843	625
G-696	RAHIYA	2147	2843	625
G-697	RAHIYA	2149	2850	600
G-698	RAHIYA	2149	2850	600
G-699	RAHIYA-BANIAS	2150	2883	550
G-700	RAHIYA-BANIAS	2152	2925	425
G-701	RAHIYA-BANIAS	2152	2925	425
G-702	KAFR NAFFAH	2176	2759	700
G-703	KAFR NAFFAH	2176	2759	700
G-704	KAFR NAFFAH	2168	2771	675
G-705	KAFR EL MA	2265	2466	400
G-706	KAFR EL MA	2265	2466	400
G-707	NAHAL GOLAN	2217	2445	350
G-708	NAHAL GOLAN	2217	2445	350
G-709	NAHAL GOLAN	2217	2445	350
G-710	JERUSALEM	1696	1315	300
G-711	MT. HERMON	2220	2980	1575
G-712	MT. HERMON	2220	2980	1575
G-713	MT. HERMON	2220	2980	1575
G-714	MT. HERMON	2220	2980	1575
G-715	MT. HERMON	2220	2980	1525

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-716	MT. HERMON	2220	2980	1525
G-717	MT. HERMON	2220	2980	1525
G-718	GAMLA	2207	2571	410
G-719	GAMLA	2198	2567	275
G-720	GAMLA	2198	2567	275
G-721	HAR DOV	2170	3030	1350
G-722	HAR DOV	2170	3030	1350
G-723	HAR DOV	2170	3030	1450
G-724	HUGOG	1971	2547	1
G-725	KEFAR HITTIN	1971	2447	25
G-726	KINNERET	2034	2369	-160
G-727	KINNERET	2034	2369	-160
G-728	HUGOG	1973	2528	-125
G-729	HUGOG	1973	2528	-125
G-730	HUGOG	1998	2524	-180
G-731	HUGOG	1998	2524	-180
G-732	HUGOG	1996	2527	-150
G-733	HUGOG	1996	2527	-150
G-734	HUGOG	1996	2527	-150
G-735	TEL KINNEROT	2004	2541	1
G-736	TEL KINNEROT	1998	2542	1
G-737	ALHAGOR	2082	2600	-25
G-738	ALHAGOR	2065	2566	-100
G-739	ALHAGOR	2065	2566	-100
G-740	ALHAGOR	2065	2566	-100
G-741	RESHAFIG	1987	2091	-80
G-742	RESHAFIG	1927	2091	-80
G-743	KOKHAV HAYARDEN	2006	2236	-100

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-744	KOKHAV HAYARDEN	2006	2236	-100
G-745	HAALE GAHLA	2133	2552	-75
G-746	HAALE GAHLA	2129	2544	-125
G-747	HASPIN	2252	2487	425
G-748	SUSITA	2127	2422	125
G-749	SUSITA	2124	2423	100
G-750	ALHAGOR	2065	2562	-120
G-751	ALHAGOR	2065	2562	-120
G-752	KEFAR NAHUM	2061	2556	-175
G-753	ALHAGOR	2062	2563	-125
G-754	GESHER BENOT YABOV	2106	2684	225
G-755	PARK HAYARDEN	2106	2657	200
G-756	PARK HAYARDEN	2101	2632	150
G-757	PARK HAYARDEN	2101	2632	150
G-758	YAHUDIYA	2111	2563	-140
G-759	YAHUDIYA	2111	2563	-140
G-760	YAHUDIYA	2144	2592	100
G-761	YAHUDIYA	2144	2592	100
G-762	YAHUDIYA	2144	2592	100
G-763	BAZRIN	2176	2648	375
G-764	GESHER BENOT YABOV	2100	2693	150
G-765	GIVAT HAMORE	1841	2246	500
G-766	GIVAT HAMORE	1841	2246	500
G-767	GIVAT HAMORE	2227	2250	425
G-768	GIVAT HAMORE	2225	2252	400
G-769	GIVAT HAMORE	2225	2252	400
G-770	EILABUN	1893	2492	275
G-771	EILABUN	1923	2504	200

ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
		DEG	DEG	METER
G-772	EILABUN	1927	2493	200
G-773	EILABUN	1927	2493	200
G-774	EILABUN	1927	2493	200
G-775	EILABUN	1927	2493	200
G-776	HADI HAMAM	1966	2484	-75
G-777	RAHIYA-BANIAS	2146	2838	650
G-778	RAHIYA-BANIAS	2146	2838	650
G-779	RAHIYA-BANIAS	2148	2862	475
G-780	RAHIYA-BANIAS	2148	2862	475
G-781	RAHIYA-BANIAS	2156	2917	525
G-782	HUGOG	1936	2571	175
G-783	NAHAL BET RIFON	1823	2423	300
G-784	AVNE ETAN	2224	2470	400
G-785	AVNE ETAN	2224	2470	400
G-786	KAFR NAFFAH	2226	2684	675
G-787	KAFR NAFFAH	2216	2697	675
G-788	RAHIYA	2146	2830	650
G-789	RAHIYA	2146	2830	650
G-790	EPHRAT-TEBDA	1668	1174	900
G-791	ALLON SHEVUT	1609	1191	900
G-792	ROGELIT	1540	1201	500
G-793	BET QESHET	1990	2363	150
G-794	GOREN	1716	2727	300
G-795	GOREN	1709	2725	300
G-796	GOREN	1709	2725	300
G-797	GILON	1722	2564	275
G-798	ZURIT	1731	2565	325
G-799	ZURIT	1731	2565	325

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ENTRY NAME	SOURCE (PLACE)	LONGTIT	LATITUD	ALTITUD
ALPHA	ALPHA	DEG	DEG	METER
G-800	HARARIT	1817	2487	425
G-801	RIHANYIA	1957	2726	675
G-802	RIHANIYA	1957	2726	675
G-803	GOREN	1709	2725	300
G-804	HUGOG	1965	2571	-100
G-805	ALLON ROAD	1809	1411	475

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