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A VALUABLE SOURCE OF YELLOW RUST RESISTANCE IN ISRAELI POPULATIONS OF WILD EMMER, *TRITICUM DICOCCOIDES* KOERN.[1]

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SUMMARY

An extensive collection of wild emmer was screened for yellow rust resistance in a joint project by research institutes in Israel and The Netherlands.

In inoculation experiments performed both in seedling stage and at maturity, the wild emmer accessions displayed a diversity of responses to yellow rust infection, ranging from immunity to complete susceptibility.

Selection *Triticum dicoccoides* var. *aaronsohni* G-25 was most promising proving highly resistant to all 21 races and field races used. Selection G-7, which was also very resistant in the trials, differed slightly from G-25 in infection types produced on inoculation with one of the isolates; this may be an indication that the genetic factors controlling resistance in these two selections are not identical.

It is concluded that the diversified populations of wild emmer indigenous to Israel possess genes which confer high resistance to a very wide spectrum of yellow rust races, including all common races in Western Europe and the Middle East. As resistance factors can be transferred easily from *T. dicoccoides* to durum and common wheat, this source may be utilized in producing varieties of cultivated wheat with improved yellow rust resistance.

INTRODUCTION

In Western Europe, especially in The Netherlands, the problem of yellow rust of wheat (*Puccinia striiformis* WESTEND. f. sp. *tritici*) is closely associated with the phenomenon of continuous adaptation of the pathogen to its host, resulting in the appearance of new races. In The Netherlands, where the race population is determined annually, ten new races appeared during the period from 1955 to 1967 inducing epiphytotics on recently developed varieties that until then had been resistant (ZADOKS, 1961; UBELS et al., 1965; STUBBS, 1967). In 1968 another new race (race 60A) appeared, overcoming the resistance of the variety Flevina (Hope/Timstein//Heine's VII), which was one of the few remaining resistant varieties in The Netherlands.

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One of the causes, and possibly the main cause, of this easy adaptation of the pathogen to its host could be the fact that in the past – and even now – breeding for resistance to yellow rust has been founded on too narrow a genetic basis. In general, new commercial wheat varieties with improved resistance to yellow rust were obtained by combining genes, conditioning race specific resistance. Experience has shown that this kind of resistance could easily be overcome by the pathogen. Besides, the European wheat varieties are quite related to each other, as shown by VAN DER VAART (1951) and WIENHUES and GIESSEN (1957). It is now realized that a more lasting protection could be expected by incorporating into a variety one or preferably more genes, each conferring resistance to all known races of yellow rust. Unfortunately, the search for such factors in varieties of cultivated wheat has so far been moderately successful.

Until recently scientists in Israel considered yellow rust to be of less economic importance than leaf rust or stem rust of wheat. As yellow rust is particularly sensitive to environmental conditions, it was generally believed that irregular appearance and low prevalence of this disease were due to climatic conditions adverse to its development in this geographic area. Nevertheless, high yellow rust incidence has repeatedly been observed on wild native grasses and foreign entries in wheat nurseries in different regions of Israel, including the arid south, where precipitation averages less than 100 mm annually. There also are records of occasional severe outbreaks of yellow rust on local wheat varieties that had been cultivated in this country several decades ago (MINZ, 1945), but on substitution of those for more promising varieties, this disease was no longer a problem for some time. The potential danger of *P. striiformis* to the wheat crop in Israel was eventually realized in 1961, when the high-yielding stem rust-resistant variety M 708 (=Aguilera/Kenya 324//Marroqui/Supremo/3/Gabo) introduced from Mexico was so heavily attacked by yellow rust that it had to be withdrawn from cultivation within 2 years after its release to the farmers. In 1967, yellow rust again caused severe damage to a second superior wheat variety, Merav (= Gabo// Kenya 324/General Urquiza), which was first cultivated in 1962, resulting in yield losses up to about 25%.

Yellow rust specimens collected in Israel and sent to the Biologische Bundesanstalt für Land- und Forstwirtschaft at Braunschweig, Germany since 1959, for race determination, belong predominantly to race-group 20A, which prevails in the Mediterranean Basin and the Middle East (FUCHS, 1965). This race group, which apparently includes several variants, has proved virulent on a wide range of cultivated wheat varieties and native grass species (GERECHTER-AMITAI, unpublished). Characteristically enough, race 20A is capable of attacking the varieties Lee and Selkirk, which are resistant in northwestern and most parts of central Europe, where they have served as important sources for resistance to yellow rust in breeding programs. Conversely, wheat varieties grown in Israel and displaying various degrees of incompatibility to race 20A, ranging from high resistance to moderate "field resistance", all proved susceptible to at least one of the common races in Western Europe, when inoculated in the greenhouse (I. WAHL, personal communication). As variations in the racial composition of the pathogen have to be anticipated, and the wheat improvement program in Israel frequently necessitates incorporation of new breeding material lacking the desired resistance to yellow rust, the need for a promising source of resistance on a broad genetic basis has also been recognized in this country.

In view of the scarcity of effective genes for disease resistance in some of the cereals it is necessary to search for new genes in related wild species. With reference to the rust diseases of wheat, screening for resistance has been extended to the wild and semi-wild species of the Triticinae and attempts have been made to utilize resistance factors thus found in the wild forms by incorporating them into the cultivated wheats. By complex cytogenetic manipulations, RILEY et al. (1968) transferred yellow rust resistance from *Aegilops comosa* SIBTH. et SM. to *Triticum aestivum*, variety Chinese Spring; in a few European wheat varieties, which originated from intergenetic crosses, yellow rust resistance was derived from *Agropyron* species and rye (*Secale cereale* L.)

A search for new genes of resistance to wheat diseases would appear most rewarding in the "fertile crescent" belt, to which many of the close relatives of cultivated wheat are indigenous, and where the domestication of wheat is believed to have taken place millennia ago. On this premise, an extensive study has been undertaken to explore a number of wild species of the wheat group native to the Middle East and Asia Minor as potential sources of resistance to the rust diseases of cultivated wheat (GERECHTER-AMITAI and WAHL, 1966; GERECHTER-AMITAI, 1967). The present paper is confined to yellow rust resistance in wild emmer, *Triticum dicoccoides* KÖRN., indigenous to Israel.

T. dicoccoides, in many of its diversified forms, was discovered in northern Palestine by AARONSOHN (1910), who also reported a specific case where wild emmer excelled in resisting attack by rust – without indicating the kind of rust involved (AARONSOHN, 1913). Even then he realized the importance of having strains of wheat with the high rust resistance of wild emmer in addition to the properties of varieties grown by the farmer. More specifically, CREPIN (1924) observed that near Paris *T. dicoccoides* repeatedly proved immune to yellow rust.

The natural distribution of wild emmer is centered in the upper Jordan Valley, occurring in massive stands in basaltic soils and hard limestone slopes, from eastern Galilee to Mount Hermon, Jebel Druz and the Gilead Mountains (HARLAN and ZOHARY, 1966). In the south, its occurrence extends to the Judean Mountains in central Israel and the Es-Salt plateau northeast of the Dead Sea in Jordan; in the north, it reaches the Lebanon and Anti-Lebanon mountain ranges in Lebanon and southwest Syria. Ecologically, *T. dicoccoides* shows a rather wide altitudinal range, from early forms growing in the basin of the Sea of Galilee at 100 m below sealevel, to later forms which occur on the much cooler slopes of Mt. Hermon at 1200–1400 m (D. ZOHARY, personal communication).

Apart from wild emmer proper, a second type – often regarded as *T. araraticum* JAKUBZ. – occurs in Soviet Armenia and Georgia and in adjacent parts of eastern Turkey, Iran and Iraq. Morphologically, the two types of wild tetraploid wheats look very similar but cytogenetically they are decidedly distinct. In contrast to the Turco-Iraqi type, which shows strong sterility barriers when crossed with durum wheat, the Syro-Palestinian type of *T. dicoccoides* and *T. durum* are fully interfertile (WAGENAAR, 1966; A. GRAMMA and Z. K. GERECHTER-AMITAI, unpublished results).

The relative abundance of diversified populations of *T. dicoccoides* in the Middle Eastern distribution centre, and the variety of physiologic races of yellow rust that threaten the wheat cultivation in Western Europe, have brought about a close cooperation between the Volcani Institute of Agricultural Research at Bet Dagan, Israel, and the Institute of Phytopathological Research at Wageningen, The Netherlands, in screening wild emmer wheat as a potential source of resistance to yellow rust. This joint investigation was commenced in 1963 and is still in progress. The aim of this paper is to present an account of the diversity of wild emmer populations in respect to yellow rust performance, with emphasis on one or two selections which appear most promising as sources of resistance to this disease.

MATERIALS AND METHODS

The seed samples of wild emmer used in the screening tests are original collections, or their progeny, secured in Israel by Professor D. Zohary of the Hebrew University of Jerusalem, and by one of the authors (Z. G.-A.). Altogether, the test material consisted of 58 accessions obtained from 32 collection sites. It included several morphological forms of *T. dicoccoides*, mainly var. *kotschyanum* PERC., var. *spontaneonigrum* PERC. and intermediates between these two, and a few samples belonging to var. *fulvovillosum* PERC., var. *aaronsohni* PERC. and var. *spontaneovillosum* PERC. Ecogeographically, the collection is representative of the major distribution area of this species in Israel (ZOHARY and BRICK, 1961). In particular, the two accessions studied most extensively both originated from the eastern slopes of Upper Galilee facing the Jordan Rift Valley, on terra rossa overlying hard Ecocene limestone. One of these, designated *T. dicoccoides* G-7, was collected near Kefar Giladi at 350 m, as a mixed population composed mainly of var. *spontaneonigrum;* the other, *T. dicoccoides* G-25, is a field selection of var. *aaronsohni* which grew intermixed with other forms near Rosh Pinna at 500 m, approximately 32 km south of the former site.

Cultures of *P. striiformis* WEST. used in the course of the experiments belonged to 21 physiologic races and field races; these include all the major yellow rust races of Western Europe and the Middle East isolated in recent years.

In Israel, screening for yellow rust resistance was done in the greenhouse by seedling inoculation with race 20A. All accessions of wild emmer were first tested in the one-leaf stage; seedlings with resistance reactions or with no visual symptoms of infection were re-inoculated, in most instances at the 3–4 leaf stage. Several selections which proved resistant as seedlings were transplanted into a field plot for observation in the mature plant stage. One of the promising accessions was tested further under conditions of naturally occurring rust epiphytotics in the 1963/1964 Uniform Rust Observation Nurseries in different regions of the country. In all the experiments, both in the greenhouse and the field, the susceptible common wheat variety M 708 was used as control.

In The Netherlands, initial screening for resistant plants of *T. dicoccoides* was carried out in 1964 at Wageningen in an experimental field plot under conditions of severe artificially induced epiphytotics. In this trial, the whole collection of wild emmer was exposed to twelve West European races of yellow rust, viz. field races Heine's VII, Leda and Dippes Triumph, belonging to race group 8, and field races Etoile de Choisy, Falco, Opal and Cleo, belonging to race group 3/55.

The following year, the progeny of plants that had appeared resistant in the field experiment were screened further in the greenhouse at 15° ± 2 °C. Seedlings were first tested with one isolate of race 26; selections which proved highly resistant to this race were subsequently inoculated with several additional races, each race separately.

One of the most promising selections of wild emmer was also tested in the mature plant stage with several races of yellow rust in race nurseries, each nursery inoculated with one individual race. These nurseries, each 6 × 6 m, were established 50 m apart in a field of winter swede rape in the IJsselmeer polder of Oostelijk Flevoland. In each of the race nurseries, *T. dicoccoides* was sown next to the highly susceptible spring wheat *T. spelta* var. *saharense*. In addition, the likewise very susceptible *T. aestivum* variety Michigan Amber served as control in all tests, both in the greenhouse and in the field.

Yellow rust performance on inoculated seedlings was expressed in terms of infection types; in field nurseries, yellow rust incidence was recorded both in terms of infection type (I.T.) and percentage of leaf area attacked (P.A.). In the accompanying tables, the following infection types were recorded: i (no visible signs of infection) = immune[1]; 00 (no pustules, only chlorotic and/or necrotic flecks) = highly resistant; 3 (normal pustule formation with chlorosis) = moderately susceptible; 4 (normal pustule formation without chlorosis or necrosis) = very susceptible. The P.A. in the field trials ranges from 0 (no infection observed) to 100 (highest possible coverage).

RESULTS

The inoculation experiments carried out in the course of this investigation disclosed that *T. dicoccoides* displays a diversity of responses to yellow rust infection, ranging from complete susceptibility to high resistance. This heterogenous performance is found not only among collections of wild emmer from different geographic regions but also within individual populations inoculated with a single isolate of the rust.

In the screening tests performed at Bet Dagan involving 55 seed samples of *T. dicoccoides*, 17 contained seedlings which were resistant in the one-leaf stage, while the remaining 38 were entirely susceptible. Characteristically, none of the seventeen accessions was uniform in composition; the proportion of resistant plants in the samples ranged from a few individual seedlings to nearly 100% (G-25). Resistance was found in collections from the very north of Israel (G-7) to the Judean Mountains (G-8). In most instances, resistance in the one-leaf stage approached immunity; on re-inoculation of resistant selections in more advanced seedlings stages, the reactions varied with different collections and with individual plants from immunity to complete susceptibility. In several seed samples, the first seedling leaf was resistant to the test isolate, but the second was susceptible; in others, susceptible types of lesions developed only from the third or fourth leaf on, and in one case, symptoms of susceptibility did not show up until the fifth leaf. In a few collections, highly resistant plants in the one-leaf stage turned moderately resistant in subsequent seedling phases. Still another reaction pattern was observed on some plants from several localities, in which the expression of susceptibility was markedly delayed. While reactions could usually be differentiated clearly about 2 weeks after inoculation, these plants formed at first necrotic or chlorotic lesions, thus appearing resistant at the time when the first recording was made. These lesions, however, in turn gave rise to well-developing uredopustules, which by the fourth week after inoculation indicated a susceptible reaction of the tested plants.

[1] In nursery trials under conditions of natural infection, "i" may also denote "escape" if the intensity of attack is very low.

In one instance (G-7), only necrotic lesions were observed during the third week after inoculation, but some poorly developed pustules had formed by the fourth week (infection type 1).

Selections consistently resistant in different phases of the seedling stage were recorded in ten collections from five geographic regions. When six selections, from different collections, were transplanted into a field plot, the plants of one selection became heavily infected with yellow rust in the adult stage. In contrast, all plants of the other five selections, originating from three geographic regions, remained free of attack till maturity.

In all these trials, one of the most promising selections was *T. dicoccoides* G-25. When tested further in Uniform Wheat Rust Observation Nurseries next to the very susceptible *T. dicoccoides* G-39, selection G-25 proved immune from yellow rust attack, while the other accession and the *T. aestivum* control became severely rusted (Table 1). Yellow rust specimens collected in nine of these nurseries and sent to the *Biologische Bundesanstalt*, Braunschweig, for race determination, all belonged to race-group 20 A, predominantly to variant 20 A_2 and secondarily to variant 20 A_1 (FUCHS, 1965).

In the screening trial carried out in an experimental plot at Wageningen, 21 of the 57 collections tested exhibited resistance to yellow rust. Some of these were uniform in performance, while others segregated into resistant and susceptible plants.

In the greenhouse test on the progeny of plants that had appeared resistant in the field experiment, selections from ten collections were susceptible, from three moderately resistant, from six resistant and from two highly resistant. The latter two, viz. *T. dicoccoides* G-7 and G-25, were investigated further; the selection of G-7, however, could not be studied so extensively because of the scarcity of seed.

T. dicoccoides G-25, when inoculated in the seedling stage with 17 individual races of yellow rust, proved highly resistant to each; similarly, the selection G-7 displayed

Table 1. Performance of *T. aestivum* M 708 and *T. dicoccoides* G-39 and G-25 in the mature plant stage under conditions of natural infection with yellow rust in Uniform Wheat Rust Observation Nurseries in different regions of Israel in 1963/1964.
I.T. = infection type; P.A. = percentage of leaf area attacked.

Nursery location	Region	Races isolated from nurseries	*T. aestivum* M 708		*T. dicoccoides* G-39		*T. dicoccoides* G-25	
			I.T.	P.A.	I.T.	P.A.	I.T.	P.A.
Amir	Upper Jordan Valley	$20A_2$	4	20	3	10	i	0
Hula	Hula Valley	$20A_2$	3	1	3	2	i	0
Yiftah	Upper Galilee	? $20A_2$	3	20	4	50	i	0
‘En Dor	Lower Galilee	$20A_1$	4	60	4	100	i	0
Newe Ya’ar	Esdraelon Plain	$20A_2$	3	1	4	20	i	0
‘En HaShofet	Samarian Hills	–	3	2	3	5	i	0
Bet Dagan	Central Coastal Plain	$20A_2$	4	20	3	10	i	0
Jerusalem	Judean Mountains	$20A_2$	–	–	4	50	i	0
Qiryat Gat	Shefela Foothills	$20A_2$	4	20	4	80	i	0
Gilat	Northern Negev	$20A_1$, $20A_2$	3	20	3	50	i	0

Table 2. Infection types produced by seventeen races of yellow rust on *T. dicoccoides* G-25 and G-7 in the seedling stage; results obtained at Wageningen.

Race or race group	Field race	Michigan Amber	*T. dicoccoides* G-25	*T. dicoccoides* G-7
1		4	00	
2A		4	00	
3/55	Etoile de Choisy	4	00	
3/55	Falco	4	00	
3/55	Cleo	4	00	00
3/55	Opal	4	00	
8	Heine's VII	4	00	00
8	Alba	4	00	
20A (Israel)		4	00	
26		4	00	
27/53		4	00	00
32A		4	00	
42A (Japan)		4	00	
54	Peko	4	00	
54	Flamingo	4	00	00
60		4	00	
III (Chile)		4	00	

Table 3. Reaction of *T. dicoccoides* G-25 and G-7 in the mature plant stage to fourteen races of yellow rust in comparison with *T. aestivum* Michigan Amber and *T. spelta* var. *saharense* in race nurseries at Oostelijk Flevoland, The Netherlands, in 1965 and 1969.
I.T. = infection type; P.A. = percentage of leaf area attacked.

Race or race-group	Field race	Michigan Amber		*T. spelta* var. *saharense*		*T. dicoccoides* G-25		*T. dicoccoides* G-7	
		I.T.	P.A.	I.T.	P.A.	I.T.	P.A.	I.T.	P.A.
1		4	100	4	100	i	0	–	–
3/55	3/55	4	100	4	100	i	0	i	0
3/55	E. de Choisy	4	100	4	100	i	0	i	0
3/55	Falco	4	100	4	100	i	0	–	–
3/55	Cleo	4	100	4	100	i	0	i	0
3/55	Opal	4	100	4	100	i	0	i	0
8	Heine's VII	4	100	4	100	i	0	i	0
8	Leda	4	100	4	100	i	0	–	–
8	Alba	4	100	4	100	i	0	–	–
8	Dippes Triumph	4	100	4	100	i	0	i	0
27/53		4	100	4	100	i	0	–	–
54	Peko	4	100	4	100	i	0	–	–
54	Flamingo	4	100	4	100	i	0	i	0
60A		4	100	–	–	i	0	i	0

high resistance to each of the four races with which it was tested (Table 2). In contrast, the variety Michigan Amber used as control was susceptible in all inoculation trials.

In the race nurseries at Oostelijk Flevoland, where the reaction of wheat varieties to individual races of yellow rust was tested in the mature plant stage, *T. dicoccoides* G-25 was immune from infection with any of the 14 races included in the trial; the selection G-7 showed a similar reaction to the eight races, with which it was tested (Table 3). At the same time, both Michigan Amber and *T. spelta* var. *saharense* were very severely attacked in each of the race nurseries.

While *T. dicoccoides* G-25 has been studied so far primarily with regard to its performance on exposure to yellow rust races of Western Europe and the Middle East, some information has become available on the reaction of this selection to races prevalent in other geographic regions.

In greenhouse tests performed at Wageningen it was shown that *T. dicoccoides* G-25 is highly resistant to the very virulent race III of South America and race 42A of Japan (Table 2). In North America, *T. dicoccoides* G-25 developed only chlorotic flecks when inoculated in the seedling stage with four races of *P. striiformis*, viz. PNW-1, PNW-2, PNW-3 and PNW-4, prevailing in the Pacific northwest of the United States (L. H. PURDY, personal communication). Likewise, selection G-25 was resistant in greenhouse tests to race 59 and race 20A from Kenya (E. FUCHS, personal communication).

DISCUSSION AND CONCLUSIONS

The results of the present investigation indicate that the diversity in wild emmer is not restricted to morphologic characters but also applies to yellow rust performance. Resistant plants of *T. dicoccoides* have been found chiefly in var. *aaronsohni* and var. *kotschyanum*. In some instances, populations of wild emmer uniform in appearance have segregated on inoculation with yellow rust into resistant and susceptible seedlings. In one particular case, where several distinct morphologic forms had been found growing intermixed in their natural habitat, nearly all seedlings of var. *aaronsohni* (G-25) proved highly resistant to race 20A, while those of var. *spontaneonigrum* (G-22) were all susceptible. Resistance to yellow rust in *T. dicoccoides* may be confined to the seedling stage or may be effective in all phases of plant growth. In various instances, infection types in resistant plants were very low, seedlings being highly resistant and mature plants proving immune.

Promising populations of wild emmer are not limited to a narrow geographic area. Resistance to yellow rust in all growth phases has been observed in collections from Upper Galilee at elevations between 500 and 700 m and in the Samarian Hills at 150 m. Further selections with good seedling resistance – but not yet tested in the adult stage – were made in several additional collections, extending from Kefar Giladi in the northern-most part of Israel to Jerusalem at the southern fringe of wild emmer distribution. The complementary seedling inoculation tests performed in Israel with race 20A and in The Netherlands with race 26 indicate that some collections have a race specific resistance, while others show resistance to both races. This diversity in wild emmer with regard to yellow rust performance makes the natural populations of this species valuable as screening material for the desirable resistant types.

One of the most promising sources of resistance to yellow rust in wheat appears to be *T. dicoccoides* G-25. In the present investigation this selection proved highly resistant to all 21 races and field races with which it was tested (Table 2 and 3). These include practically all the common and most virulent races of Europe and the Middle East isolated in recent years. Furthermore, *T. dicoccoides* G-25 was resistant in various tests with yellow rust isolates from Chile, Kenya, Japan and the United States of America.

The very broad resistance of *T. dicoccoides* G-25 appears to be unique among the tetraploid and hexaploid wheats. As for Europe, the only wheat varieties with this kind of resistance were derived from intergeneric crosses. Although the genetic background of resistance has still to be analyzed, it seems unlikely that the genes for yellow rust resistance in *T. dicoccoides* are identical with those in other genera. The evolution of this kind of resistance in the wild relatives of cultivated wheat is probably the result of natural selection.

From the practical point of view it is most significant that the Syro-Palestinian type of wild emmer is easily crossable with domesticated wheats. In particular, it has been shown that the high resistance to yellow rust in *T. dicoccoides* G-25 can be transferred successfully to *T. durum* as well as to *T. aestivum* (Z. K. Gerechter-Amitai and A. Gramma, unpublished data).

Although *T. dicoccoides* G-7 has been tested so far with fewer races than G-25, the former selection has also proved very resistant, in all experiments, to representative isolates of the most common races in Europe and the Middle East. Yet, differences in infection types produced by seedlings on inoculation with race 20A (Israel) may be an indication that the resistance factors in these two selections are not identical. Preliminary studies on several more wild emmer collections of diverse origin suggest that resistance to *P. striiformis* in *T. dicoccoides* may be less sporadic than first indicated.

From the results of this investigation it may be concluded that the diversified populations of *T. dicoccoides* indigenous to the Middle East possess genes which confer high resistance to a very wide spectrum of yellow rust races. As resistance factors discovered in wild emmer can be transferred easily to durum and common wheat, *T. dicoccoides* may be utilized in producing varieties of cultivated wheat with improved yellow rust resistance.

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