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Resistance to yellow rust in Triticum dicoccoides. I. Crosses with susceptible Triticum durum

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Abstract

Out of 71 selections of wild emmer wheat which were involved in this study on the inheritance of resistance to yellow rust, 45 selections gave conclusive results. The most common finding was that the observed segregation ratios in the F_2-progenies indicated that the resistance is based on one or more dominant genes (67%). Less frequently, resistance may be conferred by one or more recessive genes (18%), or a combination of both dominant and recessive genes (15%). At least eight different genes have to be involved in the 45 wild emmer selections in order to account for our findings.

Additional keywords: Puccinia striiformis, stripe rust, wild emmer wheat, genetics, inheritance, major genes.

Introduction

For breeding bread wheat cultivars resistant to yellow rust (*Puccinia striiformis* Westend.), the need for yet unused genes has been emphasized (Van Silfhout and Groenewegen, 1984). Since cultivated wheat as a donor of effective resistance genes appears to be greatly exhausted, the necessity for a new source was indicated.

Gerechter-Amitai and Stubbs (1970) found a valuable source of resistance to yellow rust in Israeli populations of wild emmer wheat (*Triticum dicoccoides* Körn.). In these initial screening tests including 55 entries, 17 were found to contain resistant seedlings; two in particular, G-7 and G-25, proved to be resistant to many races and field-races, both in the seedling and in the adult plant stages. The inheritance in one of these accessions, sel. G-25, was subsequently studied in crosses with a susceptible *T. durum* cultivar, revealing that the resistance in this wild emmer selection is probably conferred by one dominant gene (Gerechter-Amitai and Grama, 1974). Using *T. durum* as a bridge, and also by direct crosses with *T. aestivum*, it was shown that the resistance can be transferred to bread wheat (Grama and Gerechter-Amitai, 1974). In further work, Grama et al. (1984) demonstrated that the resistance could be incorporated into an agronomically desirable type of bread wheat, with good baking quality.

The initial study of a limited number of wild emmer accessions was expanded into a comprehensive research project, including country-wide collections of *T. dicoccoides* in Israel, and screening of this material with local isolates of yellow rust. Eighty-two selections which had proved resistant in this research were further analyzed with 20 isolates of yellow rust from different countries and continents. Concurrently, 71 of these resistant selections were subjected to genetic analysis. In 26 of these selections, the F_2-progenies presented a wide range of infection-types and the segregation ratios indicated the presence of modifier, suppressor or minor-effect genes, a complexity requiring further study. The present analysis deals with the 45 selections for which conclusive results were obtained.

The objective of the present investigation was to study the mode of inheritance of yellow rust resistance in wild emmer, and to make the resistance genes accessible for wheat breeding.

Materials and methods

The seed of wild emmer used in the present study consisted of 45 selections from 38 collection sites in Israel and two in Lebanon. The collection was of wide geographic origin, extending from Mt. Hermon in the north to the Judean Desert in the south. Topographically, the seed had been collected from sea-level at the Mt. of Beatitudes to approximately 1400 m alt. on Mt. Hermon. The entries showed a wide range of variability for morphological traits and for colour characteristics.

In the crossing programme, *T. durum* Desf. cv. D447 (= LD393/2 Langdon ND58-322) was used as the susceptible parent. When crossed with the resistant wild emmer selections, the durum cultivar served usually as the female parent. The crosses were carried out in a wire-screen-protected nethouse.

Parents and progenies were tested in the seedling stage for yellow rust reaction in growth chambers under controlled light and temperature conditions. The seedlings were grown at 15 °C and a daily photoperiod of 14 h, including 12 h at a maximum light intensity (22 000 lux, combined fluorescent and incandescent light) and a step-wise light increase and decrease, respectively, of one hour each. Each of the F_2-progenies was inoculated with one of the following isolates; GYR-22 and WYR-295, belonging to race 2E0, and WYR-004, belonging to race 2E18, which were avirulent to all parents. The seedlings were inoculated when the second leaf appeared. For incubation the plants were kept in dew chambers at 9 °C for a 24 h dark period and afterwards grown under the same conditions as before inoculation. Notes on the infection-types (Gassner and Straib, 1928, 1932) were taken during the third week, usually 16-18 days after the inoculation.

In the segregating F_2-populations, non-sporulating (I.T. 00-0²) plants were considered to be resistant and sporulating (I.T. 1-4) plants to be susceptible. This borderline between resistance and susceptibility was chosen because it coincided with the infection-type of the resistant parent or of the F_1-population, if the F_1 was resistant. Expected ratios as well as the respective chi-squares were calculated for each of the crosses.

Results

The observed and expected F_2 segregation ratios in the 45 crosses between selections of resistant wild emmer and susceptible durum wheat are given in Table 1. In several of the crosses studied, two or more genotypes could be postulated on the basis of the observed segregation ratios. In these instances, the theoretical segregation for the simplest genotype was shown in Table 1, unless additional data would suggest otherwise. More complex genotypes were postulated when three or more distinct infection-types, in particular of the intermediate range, were observed in the F_2-populations. In a few cases also the data obtained in crosses with resistant sel. G-25 were taken into consideration in postulating the genotypes.

On the basis of the theoretical segregation ratios, nine different groups could be discerned. The largest of these (group 1) consists of 22 entries, each of which does not deviate significantly from what is expected under the hypothesis that the resistance is based on one dominant gene (3 : 1). Next (group 7), the F_2-populations of six entries showed segration ratios indicating the presence of one dominant and one recessive gene (13 : 3) and in five entries (group 6) the resistance seems to be based on two recessive complementary genes (1 : 15). These are followed by two groups (nos. 3 and 4), each including three entries, which probably have two dominant genes; in the former independently inherited (15 : 1), and in the latter complementary (9 : 7). Two entries (group 5) may be carrying two recessive genes each (7 : 9). The three remaining groups were represented by single entries only; in one of these (group 2), one recessive gene seems to be present (1 : 3), whereas in the other (group 8), one dominant and two recessive genes were indicated (55 : 9). In one cross (group 9), all 256 plants proved to be resistant, showing that probably at least three dominant genes are involved.

In all 45 crosses, the chi-square values (Table 1) were not significant at the 5% level.

Discussion

Although in our genetic study of resistance in wild emmer F_3-populations could not be tested due to the large number of selections included, additional studies of some of the same selections furnished supporting evidence on our hypothetical genotypes. By crossing 17 of the same selections with the resistant wild emmer sel. G-25, in 13 of these crosses confirmatory results were obtained (Gerechter-Amitai et al., 1989). Only in four of the crosses different genotypes were indicated in the two tests.

Each plant in an F_2-population with an infection-type lower than I.T. 3 has inherited part of the genes which are involved in the resistance of the parent. Therefore the borderline between the susceptible class and the resistant class can be set between any two consecutive infection-types. If the border is set between I.T. 00 and I.T. 0^2 one can expect segregation ratios which indicate the highest number of genes and indications for interaction between the genes. With a border at higher infection-types one will find a lower number of genes and fewer interactions between the loci. By using this method of shifting border-lines, supporting evidence can be found for the conclusions which were drawn at the lower infection-types (Van Silfhout and Drenth, 1987). Because in this paper too many crosses were analyzed to go into detail, one fixed border-line between I.T. $0^=$ and I.T. 1 was chosen for all entries. In most cases this will give a good estimate of the number of genes and the mode of inheritance.

Table 1. Genetic analysis of resistance to yellow rust in 45 crosses between resistant wild emmer selections and susceptible *Triticum durum* cv. D447.

Group	Wild emmer selection	F_2 segregation ratio (R : S)			Chi-square	P value
		observed	theoretical	expected		
1	G 025-5B	36: 9	3: 1	33.75: 11.25	0.600	0.30-0.50
	G 029-1	59: 17	3: 1	57.00: 19.00	0.281	0.50-0.70
	G 197-2-1B	111: 28	3: 1	104.25: 34.75	1.748	0.10-0.20
	G 240-5	64: 25	3: 1	66.75: 22.25	0.453	0.50
	G 288-3-5	80: 19	3: 1	74.25: 24.75	1.781	0.10-0.20
	G 298-8-1	90: 30	3: 1	90.00: 30.00	0	1.00
	G 303-1-4-3-2	32: 7	3: 1	29.25: 9.75	1.034	0.30-0.40
	G 305-1B	117: 41	3: 1	118.50: 39.50	0.076	0.70-0.80
	G 313-9-1-1	25: 11	3: 1	27.00: 9.00	0.593	0.30-0.40
	G 314-4-7	106: 36	3: 1	106.50: 35.50	0.009	0.90-0.95
	G 315a-3	141: 48	3: 1	141.75: 47.25	0.016	0.90
	G 332-1-2	21: 11	3: 1	24.00: 8.00	1.500	0.20-0.30
	G 351-3-1	68: 26	3: 1	70.50: 23.50	0.355	0.50-0.70
	G 360-1-3-2	111: 29	3: 1	105.00: 35.00	1.371	0.20-0.30
	G 363-4-3-1	38: 12	3: 1	37.50: 12.50	0.027	0.80-0.90
	G 368-6-1	18: 7	3: 1	18.75: 6.25	0.120	0.70-0.80
	G 436-4	48: 21	3: 1	51.75: 17.25	1.087	0.30
	G 476-10	34: 12	3: 1	34.50: 11.50	0.029	0.80-0.90
	G 484-6	96: 30	3: 1	94.50: 31.50	0.095	0.70-0.80
	G 485-5	100: 30	3: 1	79.50: 32.50	0.256	0.50-0.70
	G 487-11-3-3	32: 12	3: 1	33.00: 11.00	0.121	0.70-0.80
	G 498-2	19: 12	3: 1	23.25: 7.75	3.108	0.05-0.10
	G 503-2-1-1	59: 24	3: 1	62.25: 20.75	0.679	0.40-0.50
2	G 411-1-4-1-2	9: 46	1: 3	13.75: 41.25	2.188	0.10-0.20
3	G 117-1-1-1-3	32: 4	15: 1	33.75: 2.25	1.452	0.20-0.30
	G 168-1-2	63: 6	15: 1	64.69: 4.31	0.704	0.30-0.50
	G 309-8-1B-1	95: 11	15: 1	99.38: 6.62	3.082	0.05-0.10
4	G193-1	49: 34	9: 7	46.69: 36.31	0.262	0.60-0.70
	G 327-6	116:103	9: 7	123.19: 95.81	0.959	0.30-0.40
	G 340-3	52: 34	9: 7	48.38: 37.62	0.621	0.40-0.50
5	G 121-1-3-1-1-5-3	12: 25	7: 9	16.19: 20.81	1.926	0.10-0.20
	G 493-1-2	26: 31	7: 9	24.94: 32.06	0.080	0.70-0.80
6	G 213-2-8	7:132	1:15	8.69:130.31	0.350	0.50-0.60
	G 281-3-4	3:100	1:15	6.44: 96.56	1.958	0.10-0.20
	G 474-4-1-4	5: 92	1:15	6.06: 90.94	0.199	0.60-0.70
	G 507-6-3	11:100	1:15	7.56:113.44	1.667	0.20
	G 695-1	2: 19	1:15	1.31: 19.69	0.384	0.50-0.60
7	G 028-3-1-3	119: 25	13: 3	117.00: 27.00	0.182	0.60-0.70
	G 040-1-2	106: 21	13: 3	103.19: 23.81	0.409	0.50-0.60
	G 156-2	159: 31	13: 3	154.38: 35.62	0.739	0.30-0.50
	G 194-3	79: 17	13: 3	78.00: 18.00	0.068	0.80

Table 1. Continued.

Group	Wild emmer selection	F_2 segregation ratio (R : S)			Chi-square	P value
		observed	theoretical	expected		
7 (cont.)	G 316-2-5	120: 29	13: 3	121.06: 27.94	0.050	0.80-0.90
	G 345-1	152: 36	13: 3	152.75: 35.25	0.020	0.80-0.90
8	G 156-3	126: 19	55: 9	124.61: 20.39	0.110	0.70-0.80
9	G 303-3	256: 0				

From our study of the 45 selections of wild emmer it became evident that we are dealing with a number of different resistance genes. On the basis of only four of the postulated genotypes, namely, two dominant genes, two complementary dominant genes, two recessive genes and two complementary recessive genes, it can be concluded that at least eight different genes must be involved.

Based on these results, a backcross breeding programme was initated by us to transfer the resistance genes from wild emmer to high-yielding spring wheat cultivars.

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Samenvatting

Resistentie van wilde-emmer tarwe tegen gele roest. I. Kruisingen met een vatbare durum tarwe

In dit onderzoek werden 45 resistente wilde-emmer selecties (*Triticum dicoccoides*) gekruist met de vatbare *Triticum durum* cv. D447 om na te gaan hoe de resistentie van de wilde-emmer selecties overerft. De ouders, de F_1- en F_2-populaties van een bepaal-

de selectie werden in het kiemplantstadium getoetst met één Israëlisch gele-roest isolaat van fysio 2E0 of van fysio 2E18. In de uitsplitsende F_2-populaties werden de niet-sporulerende planten als resistent beschouwd en de sporulerende als vatbaar.

De waargenomen uitsplitsingsverhoudingen komen overeen met 9 verschillende theoretische uitsplitsingsverhoudingen in de F_2. Het meest voorkomend (23 herkomsten) was een R : S = 3 : 1 uitsplitsing, wijzend op één dominant gen. In zes herkomsten lijken twee dominante genen aanwezig te zijn, die in drie gevallen onafhankelijk overerven (15 : 1) en in de andere drie complementair (9 : 7). In één herkomst lijkt de resistentie op tenminste drie dominante genen te berusten, daar alle 256 getoetste planten resistent waren. Een uitsplitsing wijzend op één dominant gen samen met één of twee recessieve genen (13 : 3 of 55 : 9) werd in zeven herkomsten gevonden. Resistentie berustend op uitsluitend recessieve genen werd aangenomen in acht herkomsten. In drie gevallen erven deze genen onafhankelijk over (1 : 3 of 7 : 9), in de overige vijf complementair (1 : 15).

Concluderend kan worden gesteld dat de resistentie in dit wilde-emmer materiaal in de meeste herkomsten (67%) op uitsluitend dominante genen lijkt te berusten, of op een combinatie van dominante en recessieve genen (15%). In de overige herkomsten (18%) lijkt de resistentie te berusten op uitsluitend recessieve genen. Om de gevonden resultaten te kunnen verklaren moet worden aangenomen dat er tenminste acht genen zijn betrokken bij de resistentie in deze wilde-emmer herkomsten.

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