Prevalence and Geographic Distribution of Resistance to Crown Rust in Avena sterilis

I. Wahl

Division of Mycology and Plant Pathology, the Tel-Aviv University, Israel.

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ABSTRACT

Both seedling and adult plant resistance to the race group 264-276 of *Puccinia coronata avenae* were prevalent and widespread in populations of *Avena sterilis* in Israel. Seedling and adult plant resistance were found in about 32% of the oats collected in 446 locations.

Though resistance to crown rust is widespread, the frequency of its occurrence in different regions varies considerably. Seedling as well as adult plant resistance was common in the Plateau of Menashe, Coast of Carmel, Mt. Carmel, Haifa Bay, and the northern portion of the Central Coastal Plain. In the southern regions, resistant plants were less prevalent. Phytopathology 60:746-749.

In 1958 the writer reported the existence of resistance and tolerance to recurring crown rust outbreaks in Israel within the indigenous wild oat species, *Avena sterilis* L., a presumed ancestor of cultivated oats (15). He postulated that this protection is a result of natural selection associated with the long-lasting coexistence of *A. sterilis-Puccinia coronata* Cda. var. *avenae* Fraser & Ledingham host-parasite system in the center of origin of the host. Significantly, in this region the alternate hosts of *P. coronata avenae*, *Rhamnus* spp., are an important component of the natural vegetation (17).

This hypothesis was substantiated by studies conducted with *A. sterilis* in Israel (16), U.S.A. (6, 7, 11), Puerto Rico (7), and Canada (1, 2, 3, 5). These investigations proved that populations of *A. sterilis* in Israel constitute a rich and heterogenous reservoir of new and readily usable genes for resistance to crown rust in the seedling and adult plant stages. Wild oat species in the Mediterranean countries "represent a vast living gene pool, extremely variable" (Zillinsky & Murphy [19]); they also found that considerable variation exists among locations in distribution of specific gene frequencies.

Our purpose was to obtain a quantitative approximation of the prevalence of resistance to crown rust in populations of *A. sterilis* in Israel, and to determine whether or not the geographic distribution of these resistance factors in the country shows a specific pattern.

MATERIALS AND METHODS.—The reported studies were conducted over the years 1962-67. Initially, seed was harvested from plants of *A. sterilis*, regardless of their reaction to crown rust in nature, at or near locations corresponding to interstices on a 5-km grid drawn over the map of Israel. At a later stage of research, seed collections were secured by resorting to three other methods: (i) collection of bulk seed samples in countrywide surveys at random chosen sites; (ii) collection of bulk seed samples from a number of plants in locations where seedling resistance to crown rust had been discovered in preceding years; and (iii) harvesting of seed collections from plants displaying resistant reaction to crown rust in natural habitats.

Reaction of seedlings at the 1-leaf stage was investigated in the greenhouse by artificially inoculating them with races 264 or 276 of *P. coronata avenae*. The inoculation techniques were those of Stakman et al. (12). The rust performance on adult plants of *A. sterilis* was studied in field plots surrounded by spreader rows consisting of two standard susceptible varieties Fulghum and Mulga inoculated with races 264 or 276 of *P. coronata avenae*.

RESULTS.—*Avena sterilis flora*.—The hexaploid species ($2n = 42$) *A. sterilis* is a most common and valuable wild oat in Israel. It is distributed over the whole Mediterranean region of the country (4) (Fig. 1, 2), and penetrates to favorable niches far into the Negev desert. Ecologically, *A. sterilis* is a major component of herbaceous formations in the oak park-forest vegetation of the Mediterranean region. In addition, it is an aggressive weed that massively colonizes roadsides, edges of cultivation, and cultivated fields.

Genetically, *A. sterilis* belongs to the group of *A. sativa* L. and *A. byzantina* C. Koch. These close genetic affinities become apparent in the field. In places of their contact, such as edges of fields and roadsides, hybrids between cultivated *A. byzantina* (or *A. sativa*) and *A. sterilis* are common (D. Zohary, *personal communication*).

Physiologic specialization of P. coronata avenae.—In an attempt to gain a better understanding of evolution of resistance to crown rust in *A. sterilis* and its potential applicability, detailed studies were conducted on race composition and distribution of *P. coronata avenae*. In the years 1962-66, the racial identity of about 1,900 isolates of the fungus was studied. The isolates were collected annually from 118 to 150 locations throughout the country and identified by employing the keys provided by M. D. Simons and that published by Simons & Michel (10). The virulent race group 264-276 was widespread and prominent both on cultivated and wild oats, averaging 40% for the entire

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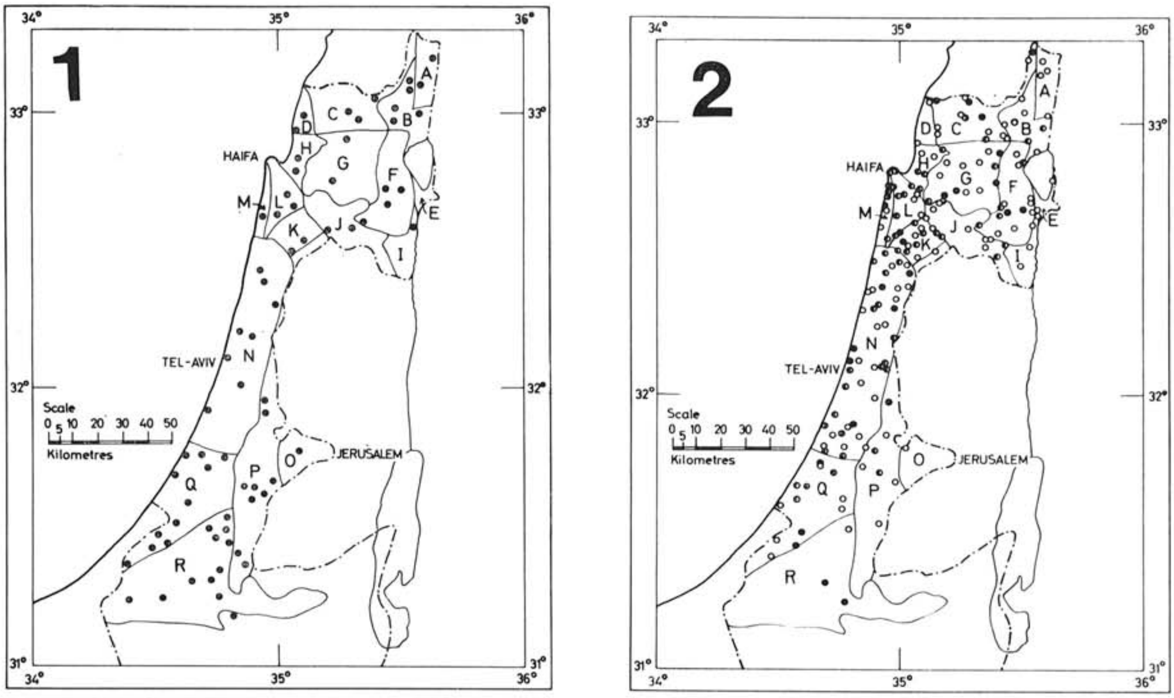

Fig. 1-2. **1)** Countrywide distribution of the crown rust race group 264-276 in 1964-1965. For designation of regions, see Table 1. **2)** Geographic distribution of seedling and adult plant resistance in *Avena sterilis* to races 264 and/or 276. ○ = Sources of seedling resistance. ● = Sources of mature plant resistance. ◐ = Sources of both seedling and mature plant resistance.

time period and comprising over 50% of the isolates in some years. Geographic distribution of the race group 264-276 in 1964-65 gives a good picture of the situation during the years 1962-66 (Fig. 1).

Prevalence of resistance to crown rust in Avena sterilis.—Frequency of occurrence of seedling resistance to crown rust in *A. sterilis* was assessed by inoculating 8,514 plants with races 264 or 276. These plants were derived from 1,342 seed collections harvested in 446 locations across the country (Table 1). Resistance was found in about 6% of the seedlings obtained from 14.6% of the parental seed collections which had been harvested in 144 locations. About 16% of 3,081 adult plants tested and found infected in experimental field plots displayed resistance to *P. coronata avenae*. They were derived from 151 of the total of 982 seed collections employed in these trials. Progenitors of the resistant plants were secured from 35.7% of the 227 places where our seed collections were originally harvested (Table 1). Apparently both seedling and adult plant resistance to crown rust in *A. sterilis* is widely distributed over the country.

Geographic distribution of resistance to crown rust.—Some regions abound in resistant plants, while in other regions resistant plants are rare (Table 1, Fig. 2). Both seedling and adult plant resistance is concentrated in the Mt. Carmel region, Coast of Carmel, Haifa Bay, Plateau of Menashe, the northern part of the Central Coastal Plain, and to a lesser degree in Eastern Esdraelon Valley. In Plateau of Menashe, seedling resistance was found in all 10 places of seed collection and in 62.8% of seed collections harvested. One hundred twenty-nine of the total of 440 seedlings derived from these collections displayed resistance to *P. coronata avenae*. In the southern regions, like the Judean Foothills, S. Coastal Plain, and N. Negev, seedling and adult plant resistance are less common.

A. sterilis selections reported by Murphy et al. (7) as being resistant to crown rust in field trials in Puerto Rico, Texas, Florida, and Georgia originated from northern and central Israel. Most of the selections resistant to *P. coronata avenae* in field tests in at least one of these States or in Puerto Rico were also derived from northern and central parts of the country.

DISCUSSION.—Accumulation of resistance to diseases caused by parasitic fungi in the endemic center of origin of species of cultivated plants or of allied species is presumably an outcome of natural selection. The above-reported differences in frequency of occurrence of resistance to crown rust in populations of *A. sterilis* in various parts of Israel obviously reflects distinct fluctuations in the impact of selection pressure over small areas in a small country. Conceivably, the following factors might have influenced such fluctuations: (i) race composition of *P. coronata avenae* in the regions concerned; (ii) occurrence of the alternate host represented in these regions by *Rhamnus* spp.; and (iii) climatic conditions. However, the ubiquity of the race group 264-276 used in our screening trials, and of susceptible oat plants suitable for inoculum increase,

TABLE 1. Frequency of occurrence of seedling and adult plant resistance[a] to crown rust in collections of *Avena sterilis* in the indicated parts of Israel. Seedlings inoculated with races 264 or 276 in the greenhouse. The same races were used for inoculation of spreader rows in field plots

	Seedling tests						Adult plant tests					
	Places of origin		Collections		No. seedlings		Places of origin		Collections		No. of plants	
Geographic region	Total	No. with resistant plants	Tested	No. with resistant plants	Tested	Resistant	Total	No. with resistant plants	Tested	No. with resistant plants	Tested	Resistant
A. Hula Valley	14	5	35	5	146	9	4	0	16	0	17	0
B. E. Upper Galilee	15	5	33	5	248	5	8	2	37	2	68	3
C. Upper Galilee	35	11	121	12	672	24	15	5	91	7	189	15
D. Coast of Galilee	11	3	17	3	128	4	2	0	7	0	15	0
E. Sea of Galilee	12	4	30	4	197	6	5	1	12	2	12	2
F. E. Lower Galilee	29	9	84	9	499	12	14	4	43	4	86	5
G. Lower Galilee	27	10	101	13	475	16	14	6	43	10	73	18
H. Haifa Bay	11	9	29	11	392	29	10	7	46	12	261	57
I. Bet Shan Valley	15	3	47	5	270	6	7	0	24	0	70	0
J. Valley of Esdraelon	23	8	74	8	553	17	11	5	28	7	138	17
K. Plateau of Menashe	10	10	43	27	440	129	8	6	100	30	405	139
L. Mt. Carmel	13	6	69	19	365	27	11	7	61	23	190	49
M. Coast of Carmel	10	7	28	11	353	43	8	5	19	8	218	58
N. Central Coastal Plain	83	34	203	42	1,484	113	54	20	230	32	859	98
O. Judean Mountains	14	1	23	1	112	1	2	0	8	0	10	0
P. Judean Foothills	54	9	182	9	970	28	27	5	90	5	256	18
Q. S. Coastal Plain	49	9	131	11	742	22	17	6	82	7	163	17
R. N. Negev	21	1	92	1	468	1	10	2	45	2	51	2
Total	446	144	1,342	196	8,514	492	227	81	982	151	3,081	498

[a] As expressed by infection types characteristic of resistant reaction, and described by Stakman et al. (12).

render the first factor unimportant. The same is true of the second factor, for the following reason. Although concentration of crown rust resistance in *A. sterilis* is usually associated with the presence of *R. palaestina* bushes harboring the gametophytic stage of the crown rust fungus (16), alternate host plants are not uncommon even in regions where resistance in stands of *A. sterilis* is relatively scanty.

Vavilov (14), in a most interesting discussion of evolution of resistance to rusts in cultivated and wild wheats, emphasizes that in arid environments *Triticum* populations are deficient in resistance to these diseases. He states, "Dry air and high temperature usually interfere with rust development. Therefore, neither natural nor artificial selections are likely to operate". Only in stands exposed sufficiently long to selection pressure could protection against rusts develop; such conditions favored evolution of "group resistance" to crown rust in Mediterranean oats, *A. byzantina* (close kin and derivative of *A. sterilis*) (14).

However, Vavilov (14) and Rudorf (8), both strong supporters of the idea that "natural selection for resistance . . . explains the occurrence and frequency of genes for resistance (in) the habitat of origin of species" (8), recognize, nonetheless, that not only disease resistance but also disease escaping are important for saving wild plants from disease hazards.

These ideas seem to explain to some extent the distribution of crown rust resistance in *A. sterilis* over a country with a variable climate (4). Scarcity of resistance in the arid N. Negev is attributable to meager rust development under very low humidity. In southern regions, such as Judean Foothills and S. Coastal Plain, populations of *A. sterilis* probably escape the full impact of crown rust incidence, which commences early in the season. On the other hand, in the central and some of the northern areas, the development of *A. sterilis* hosts and the crown rust parasite coincide. Consequently, selection pressure is exerted by the fungus. Accumulation of resistance genes in these regions can thus be expected.

Delineation of centers of resistance to *P. coronata avenae* may guide future oat collection work, since these centers appear to be permanent and constitute rich and heterogenic resources of genes (16).

Resistance to crown rust selected from *A. sterilis* is race-specific (1, 6, 9) and, thus, "vertical" by definition (13). This clearly implies that "vertical" resistance in oats is not necessarily a result of modern agricultural practice, as suggested (13), but has developed in the course of prolonged evolution. Nevertheless, the writer's work with *A. sterilis* for over 20 years convinced him of the abundant occurrence of "horizontal" resistance sensu van der Plank in this oat species. He agrees with van der Plank (13) that the availability of this type of resistance in oats needs to be determined.

Prominence of the highly versatile race group 264-276 of *P. coronata avenae* across the country in regions rich in plants susceptible also to other races and in regions where resistance to *P. coronata avenae* is altogether rare (Fig. 1, 2), obviously cannot be ascribed to screening effect of preferential host resistance. Therefore, races with a wide range of virulence should not be a priori considered as inferior in their fitness to survive when their virulence is "unnecessary", as frequently postulated (13). The behavior of parasitic fungi in the centers of origin of their hosts and of their own evolution may differ from their performance "out of place" (18).

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