Genetics of Pathogenicity in *Puccinia coronata:* Pathogenic Specialization at the Host Genus Level

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ABSTRACT

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Physiologic forms of *Puccinia coronata* in Israel were isolated and characterized as a prelude to genetical studies of their pathogenicity. Seven forms were identified from representative species of grass genera recognized as primary hosts for crown rust forms elsewhere. Four additional forms were isolated from oats. The host range of these 11 forms on the original eight gramineous species was determined and found to be overlapping to a greater or lesser degree. The host range of single-spore cultures of certain forms isolated from grasses in Israel was wider and exhibited greater overlap than the host ranges combined from representatives of the same forms elsewhere in the world. This is a clear reflection of the dynamic host-parasite relationships existing in an area where hosts and parasites have co-evolved. The forms could be distinguished from each other when their main hosts were used as differentials. Apart from the fact that races are identified on crop plant cultivars and forms are identified on plant genera, there was no difference between races and forms. Isolates from one host were as different from each other as from isolates from other hosts. Strict specificity could not be detected by applying the criterion that a species is susceptible when some individuals in it are susceptible. The simultaneous inoculation technique revealed plants among the individuals within the host species that could serve as classical, very specific differential hosts. On the other hand, this method also revealed reliable common hosts that were useful for the propagation of hybrid rusts.

Additional key words: crown rust, host range, *formae speciales,* wild plants.

Most of the investigations on the genetics of pathogenicity and of host:parasite relationships deal with systems of pathogen races vs host cultivars. Only a few deal with more complicated systems like *formae speciales* vs host genera (eg, 9,11,12,16,23).

Earlier literature on pathogenic specialization of crown rust fungi is surveyed by Simons (19). He stresses the confusion and ambiguity among pathologists about terminology and classification of the subunits of the species *Puccinia coronata.* Most forms were not found to be specific to the host of origin and there was some overlapping in the host ranges of some of them. The criterion to distinguish between forms is their host range among host species, genera, or families (18). The extent of host range overlap led Simons (19) to the conclusion that the use of the term forms is more a matter of habit or convenience than adherence to reliable taxonomy.

About 16 *formae speciales* are recognized in *P. coronata* and these are named after the hosts from which they were isolated. The most common ones investigated were: f. spp. *agropyri* Erikss., *agrostis* Erikss., *alopecuri* Erikss., *arrhenatheri* Kleb., *avenae* Erikss., *calamagrostis* Erikss., *festucae* Erikss., *holci* Kleb., *lolii* Erikss., *phalaridis* Kleb., and *secalis* (f. sp. nov.) (3,7,14,17,21, and different reports according to 7,19, and others). In Israel only one *forma specialis, avenae,* has so far been investigated (5).

The purpose of our investigation was to determine the genetics of host:parasite relationships at the level of host genus vs pathogenic form. Our model for this investigation was the system of crown rust

with its subunits vs many species of wild grasses. The first step in our investigation was the identification and characterization of these rust subunits. In the text that follows the terms *forma specialis* and *formae speciales* are abbreviated to form and forms, respectively.

MATERIALS AND METHODS

Cultures of *Puccinia coronata.* *Cultures from wild host species.* Samples of orange-colored rust fungus urediospores were collected from hosts known from abroad to be principle hosts of crown rust. The samples were removed from the hosts aseptically, and only those that produced coronate teliospores, either naturally or by induction (1), and that also failed to parasitize cultivated oats (to avoid random collection of form *avenae* which is wide-spread in Israel and capable of parasitizing hosts of origin of other forms) were saved. All cultures, except the one from *Arrhenatherum,* were purified by single sporing.

Cultures were isolated from the following host species and named according to host genera: *Agrostis verticillata*—f. sp. *agrostis; Alopecurus utriculatus*—f. sp. *alopecuri; Arrhenatherum palaestinum*—f. sp. *arrhenatheri; Avena sativa & Avena sterilis*—f. sp. *avenae; Festuca arundinacea*—f. sp. *festucae; Holcus annuus*—f. sp. *holci; Lolium perenne*—f. sp. *lolii;* and *Phalaris bulbosa*—f. sp. *phalaridis.*

Races of the avenae form. Seven isolates representing the most common oat crown rust races in Israel were selected from our culture collection and were named according to the races to which they belong: 202, 203, 263, 264, 276, 277, and 286 (20). Two

additional cultures were obtained from selfing of a single-spore isolate of race 203 (A. Dinoor, *unpublished*): A-8-1 (a culture of race 264 for which six of the grass genera were hosts) and A-4-1 (a culture of race 202 for which three of these genera were hosts).

Propagation of rust fungus cultures. The cultures were propagated on seedlings of the host species from which they were isolated (with the exception of f.spp. *alopecuri* and *lolii* which were propagated on other species of their original host genera). Upon bursting of pustules, the leaves were cut and maintained in petri plates on filter paper soaked with 200 ppm benzimidazole.

Long-term preservation of cultures. Cultures were maintained at 4–6 C in Pyrex tubes sealed under partial vacuum with $CaCl_2$ compartmented within each tube.

Plants for host-range determination. Seeds of plants to be tested in host-range experiments were planted in sterilized soil and maintained under isolation. Seed of grasses were collected from different locations and propagated without controlled selfing.

Inoculation. Prior to inoculation, the hosts' leaves were sprayed with water and surfactant (Tween-20, Rohm & Haas, Philadelphia, PA 19105 USA, 5–10 drops per liter). The inoculum of spores was either brushed from infected leaves onto the wet uninfected leaves to be tested, or transferred and spread with a tiny spatula. Inoculated plants were kept in moist chambers for 24 hr and then moved to an air-conditioned glasshouse (20 ± 2 C). Since there are very few or no stomates on the abaxial sides of the leaves of some grass species, the leaves were inoculated on the adaxial side.

Many of the inoculations were done by using the simultaneous inoculation technique (2). Up to seven cultures were inoculated side by side on each leaf. The segment inoculated was carefully marked with India ink. The sequence of cultures on the leaves was altered between leaves to expose any unexpected position effect. No position effect had been previously detected (Khair and Dinoor, *unpublished*).

Determination of hosts' responses and host range. Host responses were recorded 14 and 21 days after inoculation. The higher reaction of the two was used. A special key to designate hosts' response was established, based on the classical key (15) but with some modifications. The modified key reads as follows:

Type 4. High susceptibility. Medium to large pustules surrounded by greenish (and sometimes yellowish) background develop on each and every individual of the hosts' sample.

Type 3. Medium susceptibility. Individual plants of a host species are not uniform in their reactions and/or pustules develop late (by 21 days after inoculation).

Type 2. Low susceptibility. The postules are small and surrounded by necrosis, but reinoculation of the original susceptible host results in type 4 reaction.

Type 1. Very low compatibility between host and parasite. Pustules are very small, surrounded by necrosis, and sometimes there is direct production of teliospores. Reinfection of the original, susceptible host, is unsuccessful.

Type 0. Highly resistant or immune host. All individuals of the host sample show no symptoms or there is necrosis without any sporulation.

TABLE 1. The interactions between *Puccinia coronata* isolates and selected grass species

| Grass species in family groups[b] | ag | al | ar | av | | | | | | | | | h | p | f | l |
				202	203	263	264	276	277	286	A-4-1	A-8-1				
Agrostideae																
Agrostis verticillata	4	0	0	0	0	0	0	0	0	0	0	0	3C	0	3C–	3C
Alopecurus myosuroides	1C*	4	0	0	0	0	0	3C*	3B	0	0	0	2C*	3B–	3B	0
Alopecurus utriculatus	3B	4	0	3B	0	3C*	3C	3B	3B	3B–	0	0	3A	0	3B+	3B–
Alopecurus ventricosus	2B*	4	0	4	3B*	3C	2B–	0	2	3B–	0	3B*	3B	0	3C	3C
Aveneae																
Arrhenatherum palaestinum	3B–	2C*	4	3B	4	3A+	4	3B	4	4	3A+	3B	3C	2C*	3C	3C
Avena barbata	0	3C*	3A	4	4	4	4	4	4	4	4	4	0	0	0	0
Avena longiglumis	4	4	0	4	4	4	4	4	4	4	4	4	3C*	3C–	3C*	3C–
Avena sativa	0	0	0	4	4	4	4	4	4	4	4	4	0	0	0	0
Avena sterilis	0	0	0	4	4	4	4	4	4	4	4	4	0	0	0	0
Avena wiestii	0	0	0	4	4	4	4	4	4	4	3C	3C–	2C*	0	0	0
Holcus annuus	0	1C*	0	0	0	0	0	0	0	0	0	0	4	0	4	4
Phalarideae																
Phalaris brachystachys	0	0	0	0	0	0	0	0	0	0	0	0	3A+	1C*	3C–	2A+
Phalaris bulbosa	3C–	0	0	0	0	0	0	0	0	0	0	0	0	4	3A–	0
Phalaris canariensis	0	0	0	0	3C*	0	0	1C*	2B–	0	0	0	3A	3C	3A	2C*
Phalaris minor	4	4	0	4	2C	2C*	3A*	3B	4	4	0	2C*	2C*	4	3A–	2
Phalaris paradoxa	4	4	0	4	4	4	4	4	4	4	3A+	3A+	3A–	4	4	4
Festuceae																
Festuca arundinacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	3B
Lolium gaudinii	3B	3C	0	0	3B*	0	0	0	0	0	0	3B*	4	0	4	4
Lolium multiflorum	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4	4
Lolium perenne	0	4	0	0	0	0	0	0	0	3B	0	0	4	0	3A	4
Lolium rigidum	3B+	2C*	0	2C*	0	0	0	2C*	0	3B–	0	3C*	4	3C*	4	4
Lolium subulatum	4	3C+	3A	0	0	0	0	0	0	0	0	1C*	4	0	4	4
Lolium temulentum	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4	4

[a] abbreviations of names for the rust forms: ag — f. sp. *agrostis*; al — f. sp. *alopecuri*; ar — f. sp. *arrhenatheri*; av — f. sp. *avenae*; h — f. sp. *holci*; p — f. sp. *phalaridis*; f — f. sp. *festucae*; l — f. sp. *lolli*. Symbols are defined in Materials and Methods.
[b] Host species from which the cultures were first isolated, and their reactions to the eight crown rust forms are underlined. A species with a reaction of 2 and above was classified as a host.

Two additional classifications were needed to describe the variation in types 1, 2, and 3, between individuals of the same host sample, or the variation of infection types on the same individual. *Classification 1:* A — Mixture of infection types on the same leaf, similar to the "X" reaction (19). B — Individual plants of a host species segregate in response to a single-spore culture. C — Both A and B. *Classification 2:* + — susceptibility is predominant in the host sample; − — resistance (types 0 and 1) is predominant; * — susceptibility is expressed by formation of only a few pustules.

TABLE 2. Results of simultaneous inoculation of individual seedlings of the principal host species and of two "universal hosts" with forms of *Puccinia coronata*[b]

Host species[a]	Category	Percentage of plants in each category	Reaction to form[b]						
			ag	al	av	h	p	f	l
Agrostis verticillata	a	87.5	4	0	0	0	0	0	0
	b	12.5	4	0	0	4	0	0	4
Alopecurus myosuroides	a	75	0	4	0	0	0	0	0
	b	12.5	0	2	0	0	0	0	0
	c	12.5	1	4	0	0	0	4	0
Avena sativa	a	100	0	0	4	0	0	0	0
Holcus annuus	a	62.5	0	0	0	4	0	4	4
	b	25	0	0	0	4	0	4	0
	c	12.5	0	0	0	4	0	0	0
Phalaris bulbosa	a	70	0	0	0	0	4	0	0
	b	20	3	0	0	0	4	3	0
	c	10	4	0	0	0	4	0	0
Festuca arundinacea	a	88.8	0	0	0	0	0	4	0
	b	11.1	0	0	0	0	0	4	3
Lolium rigidum	a	11.1	4	2	0	4	2	4	4
	b	44.4	4	0	0	4	0	4	4
	c	11.1	0	0	4	4	0	3	4
	d	11.1	0	0	0	4	0	4	4
	e	22.2	0	0	0	4	0	0	4
Vulpia membranacea	a	100	4	4	4	4	4	4	4
Avena longiglumis	a	9.1	4	4	3	3	4	3	2
	b	9.1	4	4	4	2	3	3	3
	c	9.1	4	4	4	2	3	3	2
	d	9.1	4	4	4	1	3	3	3
	e	27.3	4	4	4	0	3	4	0
	f	18.2	4	4	4	0	2	4	0
	g	9.1	4	2	4	0	4	0	0
	h	9.1	3	1	4	0	3	3	0

[a] Each host species is categorized according to reactions of individual plants. (In each host 8–12 seedlings were tested.)
[b] For abbreviations of names for the rust forms see Table 1.

A grass species was considered to be a host when at least one individual showed a type 2 or higher reaction. Spores from such type 2 reactions always reinfected the susceptible original host. Basically, the capability of the rust fungus to reproduce on the grass species concerned was the criterion we used to decide whether a species should be considered to be a host.

RESULTS

Characterization of fungal isolates from species of different host genera. Spores of seven crown rust cultures isolated from seven genera of grasses and nine cultures from oats were used to inoculate seedlings of 22 grass species and one oat cultivar belonging to these eight genera. The results are presented in Table 1.

The reactions of the respective original host species to the eight cultures representing the eight forms (underlined in Table 1) may first be considered separately from the rest of the table to discuss pathogenic specialization at the level of host genus. According to the literature the classification of the parasite's cultures into forms is no longer based on strict specificity to the original host. The underlined data in Table 1 show a similar situation. Only form *arrhenatheri* (ar) is highly specific, infecting only the original host. The other forms are capable of infecting one-to-six additional hosts. Nevertheless, the infection of hosts other than the original usually was of a lower grade and not all the individual plants in a sample of a host species were susceptible. The proportion of susceptible individuals in a given sample could be higher than, equal to, or lower than the proportion of resistant individuals.

Among the hosts, only *Avena* was susceptible to only a single form, form *avenae*. The other hosts were susceptible to one-to-seven additional forms.

There is no reciprocal symmetry in the data of Table 1. When an isolate from one host is capable of infecting another host it does not necessarily mean that an isolate from the second host will also infect the first host. The extreme examples are the rust isolated from *Festuca* that was infectious to six other hosts while *Festuca* itself was susceptible to only one additional rust form. On the other hand, the rust isolated from *Arrhenatherum* was innocuous to any of the other hosts while *Arrhenatherum* itself was susceptible (at least to some degree) to all the other rust forms. Despite the asymmetry and the overlapping of host ranges, the eight cultures isolated from the eight different hosts can be readily distinguished from each other when their pathogenicity towards even some of these eight hosts is examined. In addition and apart from the major differences in pathogenicity between these cultures, there are many more subtle differences in performance that corroborate the basic classification.

Interaction between forms of *P. coronata* and different species of the main grass genera. Table 1 includes the interactions between 16

TABLE 3. Comparison of the findings in Israel (Is) with those of other studies elsewhere (Ew)

Host genus	Rust form[a]																Total no. of forms attacking the host genus	
	ag		al		ar		av		h		p		f		l			
	Is[b]	Ew[b]	Is	Ew	Is	Ew	Is	Ew	Is	Ew	Is	Ew	Is	Ew	Is	Ew	Is	Ew
Agrostis	S	S	R	R	R	R	R	R	MS	R	R	R	MS	M	MS	R	4	2
Alopecurus	MS	R	S	S	R	M	S	S	MS	R	MS	R	MS	M	MS	S	7	5
Arrhenatherum	MS	R	MR	R	S	S	S	S	MS	R	MR	R	MS	M	MS	R	8	3
Avena	S	S	S	M	MS	R	S	S	MS	MR	MS	R	MS	R	MS	MS	8	5
Holcus	R	R	R	R	R	R	R	MR	S	S	R	R	S	R	S	M	3	3
Phalaris	S	R	S	MR	R	M	S	MS	MS	R	S	S	S	M	S	S	7	6
Festuca	R	R	R	R	R	R	R	S	R	R	R	R	S	R	MS	S	2	3
Lolium	S	R	S	R	MS	R	MS	MR	S	M	MS	R	S	MS	S	S	8	4
Total no. of genera susceptible to each form	6	2	5	3	3	3	5	7	7	3	5	1	8	6	8	6		

[a] For abbreviations of names for the rust forms see Table 1. Our scale of reactions was adapted to the common description of reactions as follows: 4 = S, 3 = MS, 2 = MR, 1 and 0 = R. There is no equivalent to M.
[b] Source of information.

cultures of *P. coronata* and 23 grass species. The cultures include the original eight which represent the eight different forms and additional eight cultures of form *avenae*. The grass species include the eight original host species from which the forms were isolated and 15 additional species from four of the genera of the original hosts. From the results it is clearly seen that species of one host genus may differ in their reactions to the various cultures. It is also shown that cultures belonging to one form differ in their performance on the various hosts. For example:

a. Species within the genus of the original host may all be highly susceptible to the culture from that original host (*Alopecurus, Avena,* and *Lolium*) or some species within the genus would be less susceptible than the original host species and even highly resistant (*Phalaris*).

b. Within one host genus some species would be specific hosts to the rust isolated from one species of that genus and some species will also be susceptible to other cultures and even to all the eight different forms (*Avena*).

c. Within one host genus, one species was susceptible to 7 forms while another species was resistant to the form isolated from the same genus but susceptible to other forms (*Phalaris*).

d. Races of the *avenae* form differ in their performance on certain species. Most of them attack *P. minor* while in the other extreme only one attacks *L. perenne*.

e. Isolates of the same race differ in their performance on the host species (see isolate 264 vs A-8-l and isolate 202 vs A-4-1).

When the host range over genera is determined according to the finding of at least one susceptible species within that genus, we find that differences between forms diminish. For example, it would be impossible to distinguish between forms *festucae* and *lolii* on the basis of the reactions of genera. From all the hosts tested these forms differ only on one species of *Alopecurus* and *Phalaris*.

Intraspecific variation in the reactions of hosts to the parasite. In many cases individual plants from one sample of a host species did not react uniformly to a particular rust culture. Therefore the conclusions regarding hosts being common to several rusts (namely being susceptible to different rust cultures) may not necessarily mean that the specified rust cultures could be propagated on the same individual host plant. A proper common host is a necessity for genetic studies on host:parasite relationships. Therefore we extended our studies to include the simultaneous inoculation technique, by which several rust cultures could be inoculated and examined side by side on individual host plants.

Some selected data are presented in Table 2. Despite the fact that only a small sample of seedlings from each host was sampled, variation in response to the rust was very common. The main findings are: a. In six of the seven principal hosts there was a type of seedling that was susceptible only to the original rust culture isolated from this species. These types of seedlings can serve as classical differentials to distinguish between forms. b. Most of the individual host plants behaved as "classical differentials." In addition, some individuals which were susceptible to more than their original form were more highly susceptible to this original form. c. In each of the principal hosts there were individuals susceptible to more than one form and even to five different forms. Two additional hosts that were found to be susceptible to all the seven forms were included here. *Vulpia* may serve as a universal suscept for local forms of *P. coronata* while in *Avena longiglumis* some individuals are useful for this purpose and some are not.

Comparison of our findings with those of other studies elsewhere. This comparison is presented in Table 3. Since the information in different countries relates to different host species, the results were grouped according to host genera. The criterion for classification as a host genus was when at least one species of this genus was susceptible to an isolate from a species in this genus. This comparison deals with a wider host range than when each species is considered separately.

The comparisons in Table 3 show that the host ranges of the forms in Israel (although they were single-spore isolates) are even wider than the grouped host ranges of forms from other parts of the world. This polyphagous expression suggests the complexity of host:parasite relationships between *P. coronata* and its hosts in

Israel. Our results also show that even some of the more conspicuous differences between forms shown elsewhere become obscure in our surroundings.

DISCUSSION

In the past, the principles of the genetics of host:parasite relationships have been mainly studied in systems of physiological races of one pathogen species and varieties of one host species. The genetics of host:parasite relationships at the level of pathogenic forms vs host genera was rarely examined, not only because of the inability to intercross different host species, but also because of the conclusion in some studies (9,12) that hybrids between forms were weak, and could not be propagated and carried on into further generations.

We assumed that an isolate of *P. coronata*, hybrid between pathogenic forms, might be successfully propagated and carried to further generations if inoculated and maintained on hosts common to both parental rust forms. Therefore, we set out to first identify the pathogenic forms and to look for common hosts. It is evident from the literature that the concept of pathogenic forms has developed and changed since it was first established. The early definition maintained that pathogenic forms are specific to host genera. Further reports, articles and review papers described some overlapping of host ranges between forms, blurring of distinct differences, and extension of host ranges to other species not so taxonomically closely related (eg, 11,13,19). The most generalized definition of pathogenic forms relates to differences in host ranges "at the species level or higher" (18).

Distinction between forms. Starting with eight cultures from eight grass genera, known from other countries to be hosts of specific forms, we extended our studies to more species within these eight genera, and an additional eight cultures from cultivated oats.

Our findings have shown extensive overlapping of host ranges between rust isolates that might have been classically considered as pathogenic forms. No relation whatsoever was found between susceptibility of a host species and the genus to which it belongs. At the extremes were species of different genera that were more similar to each other in their susceptibility to different cultures than to other species within the same genus (eg, *A. longiglumis* vs *P. paradoxa* compared to *A. sterilis* or *P. bulbosa*). The distinction between the eight isolates, which we named forms, was quite clear when they were compared on the eight host species. Some of the forms differed qualitatively from one another on six of the hosts (like form ar vs form f) and some differed only on one host (like form l vs form f). Some forms differed from others also quantitatively (like form h vs form al).

As we advance with the taxonomic hierarchy of the hosts, differences between isolates become less and less distinguishable. Thus, some of the forms differ on some of the host species, but not on the host genera (like forms al, av, and p). It does not seem logical that differences in host range at the host genus level will not show up at the species level. Therefore, unlike Robinson (18), we think that differences between forms in host range must be at the species level and those at a higher level does not make any differences. The choice of appropriate differentials to differentiate between forms is still a matter of trial and error.

As for taxonomical and evolutionary implications of host ranges we maintain that a host range in *P. coronata*, and probably in other pathogens, reflects proximity of co-existence between hosts and parasites rather than phylogenetic relationships (13). This conclusion is also illustrated in the much wider host range demonstrated for forms of *P. coronata* on grasses in Israel compared to those demonstrated by studies elsewhere. The botanical wealth of grasses in our region and the natural activity of *P. coronata* exposed many more variants of hosts and parasites to each other and brought about more and more cases of additional adaptation and therefore a wider host range. The same also has been found in Israel for other plant parasites (6,8).

The taxonomic hierarchy within *Puccinia coronata*. The nine cultures isolated from oats should belong to the form *avenae*. When inoculated onto differential oat cultivars they were classified into

seven races. But, when inoculated onto the grass differential species, these nine cultures can be grouped into four different forms. There was no greater similarity between these four forms than there is between the other forms from the other host genera. Therefore, it seems that there is no essential difference between a race and a form and it is only the matter of whether they were classified on oat cultivars or, alternatively, on grass species. From our results, we conclude that forms and races are parallel taxonomic entities rather than a form being a higher entity in the taxonomical hierarchy.

Names of the forms. When first determined, the forms were named according to the principal hosts from which they were isolated. Data like ours question this nomenclatural method. How would one name *P. coronata* from *L. perenne*, when the same host can be infected also by rust fungi from *Holcus* and *Alopecurus*? What would be the name of an isolate from *P. paradoxa* or *A. longiglumis*, when these hosts also are susceptible to rust fungus isolates from six other hosts?

Intraspecific variation in the grasses. Grasses were found to be variable in response to pathogens (eg, 3,10,19). In most cases groups of individuals from a particular host were inoculated each with a separate culture. Several investigators have noted the problem of deciding how many individuals of a species should be tested to determine whether or not it is a host. The frequency of susceptible individuals was sometimes very low (4,10) and this was also the case in some of the species tested by us. What should be the criterion for determining the susceptibility of a host? Any decision would be arbitrary. Cotter and Levine (4) determined the host response according to the proportion of susceptible individuals. We preferred the common approach (3,16): a species may be considered as a host even if one of its individuals is susceptible to the particular pathogen. This approach relates to the capacity of the species to harbor the pathogen. Many of the grasses are cross pollinated to some extent and it should therefore be realized, a priori, that we are dealing with a heterogeneous sample of individuals in each species. Research on host range will, of course, be much more accurate if efforts are made to establish homogeneous samples by special breeding procedures (like the work done in rye [22]) or clonal propagation.

Another way to overcome the problem of heterogeneity would be to inoculate each individual with several cultures separately. The only attempt at this approach with *P. coronata* was made by Brown (3) who inoculated each individual with two cultures but on two different leaves. We made use of the multiple inoculation technique to inoculate each individual plant with seven forms. This procedure was an important refinement for the identification of forms on one hand and the finding of common hosts on the other hand. Table 2 shows that, in six out of the seven original hosts tested, we may identify classical differential plants. These classical differentials were susceptible only to the form isolated from that particular host species. Based on another criterion, several species could be considered as common hosts inaccurately, because some individuals of that species were susceptible to one form and other individuals were susceptible to another form. With the simultaneous inoculation technique we could point out individual plants as common hosts on which the propagation of hybrid rusts would be facilitated.

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