Infection Structures of Host-Specialized Isolates of *Uromyces viciae-fabae* and of Other Species of *Uromyces* Infecting Leguminous Crops

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ABSTRACT

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A study was made of the morphology of urediniospores and primary infection structures of 12 isolates of six legume-infecting species of *Uromyces*. Infection structures were sufficient to distinguish among species. Isolates of *Uromyces viciae-fabae* proved to be specialized with respect to host, because each isolate infected only cultivars of the species from which it was collected. Host-specialized isolates of *U. viciae-fabae* also were morphologically distinct, differing in both spore dimensions and infection structure morphology. In particular, the shape and dimensions of the substomatal vesicle were distinctive. These results support the view that *U. viciae-fabae sensu lato* is a species complex.

Additional keywords: rust, teliospore

Many species of *Uromyces* can cause important diseases of grain legume and forage legume crops: *Uromyces appendiculatus* (Pers.:Pers.) Unger on common bean (*Phaseolus vulgaris* L.), *U. ciceris-arietini* Jacz. in Boyer & Jacz. on chickpea (*Cicer arietinum* L.), *U. lupinicolus* Bub. on lupine (*Lupinus albus* L.), *U. pisi* ((Pers.) D.C.) Wint. on pea (*Pisum sativum* L.) and grasspea (*Lathyrus* sp.), *U. striatus* J. Schröt. on alfalfa (*Medicago sativa* L.), *U. viciae-fabae* (Pers.) J. Schröt. on faba bean (*Vicia faba* L.), and *U. vignae* Barclay on cowpea (*Vigna unguiculata* (L.) Walp.) (13).

Identification of species of *Uromyces* on legumes currently is based on the morphology of telia, teliospores, uredinia, and urediniospores. In many cases, however, telia are not available because their formation depends on rust species, host properties, and environmental conditions. Additionally, rust species often are difficult to identify on the basis of urediniospore morphology alone; two common features, germ pore number and arrangement, may not be easy to determine and often are not diagnostic in any case. The host species also is used in identification, but several rust species may infect the same host plant species. It also is possible that a rust fun-

gus may infect a plant species that previously was thought to be resistant.

The morphology of infection structures of rust fungi may be helpful in the diagnosis of rust species and subspecific taxa (11,12,21). The infection structures of rust fungi form in sequence: germ tube, appressorium, substomatal vesicle (SSV), primary infection hyphae (PIH), haustorial mother cells (HMCs), secondary hyphae (SIH), and haustoria. In previous studies, the morphology, dimensions, and orientation of SSV, PIH, HMC, and SIH differed among rust species and subspecific taxa (11,12,21).

U. viciae-fabae sensu lato has been reported all over the world on dozens of species of *Lathyrus*, *Lens*, *Phaseolus*, *Pisum*, and *Vicia* (6), although it is most commonly reported as the rust of faba bean (*Vicia faba*) (4-7,15,17,22). Its broad, compiled host range is in conflict with a few preliminary demonstrations of host specialization (7,15). Species complexes are a common phenomenon among rust fungi (3,10). Such complexes are characterized by cryptic species that are reproductively isolated from one another due to the absence of a common host. Closer examination can reveal subtly distinctive morphology among host-specialized species that previously were thought to be impossible to distinguish. Thus, further consideration of both morphological variation and host specialization within *U. viciae-fabae sensu lato* would appear justified.

The first objective of this work was to observe the morphology of infection structures of a number of species of *Uromyces*

that infect legume crops. Second, we sought to determine whether isolates of *U. viciae-fabae sensu lato* are host specialized and, if so, whether infection structures of such isolates would prove distinctive.

MATERIALS AND METHODS

Rust isolates. Twelve isolates of six rust species on eight legumes were collected in Spain, Morocco, Egypt, Italy, and Canada (Table 1). Single pustule isolates were obtained from each rust sample and increased in isolation on seedlings of the respective host species (Table 1) in separate growth chambers with filtered ventilation.

Spore morphology. Freshly collected urediniospores and teliospores from inoculated susceptible host plants were mounted in lactophenol-ethanol and observed with bright-field microscopy. Thirty spores from each isolate were measured and the color and spore surface morphology were determined. The number and location of the germ pores also were recorded after mounting the urediniospores in lactophenol/ethanol 0.05% trypan blue and gentle heating.

Plant inoculation. Four plants of each host (Table 1) with their third to fourth leaves fully expanded were inoculated by dusting freshly collected urediniospores (0.5 mg/plant) mixed with pure talcum powder (1:10, vol/vol). Isolates VICLCII and VICVSI were inoculated on *P. sativum* cv. Messire because we found that the infection structures could be more clearly observed on that host than on their respective hosts. Morphology of infection structures has been reported to be independent of the plant species on which they are grown (11,21). This was verified by also observing infection structures developed on their respective hosts, confirming that the host did not influence infection structure morphology. Inoculated plants were incubated at 100% relative humidity at 20°C in darkness for 24 h. *Lupinus albus* developed necrotic lesions after 24 h of incubation; therefore, it was incubated for only 8 h.

Sample preparation and observation. At least four leaf segments (2 to 3 cm² each) per inoculated plant were harvested 47 h after inoculation (hai). They were fixed in acetic acid-ethanol (1:3, vol/vol) for 30 min, boiled in 0.05% trypan blue in lactophenol-ethanol (1:2, vol/vol) for 10

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min, and cleared in a nearly saturated aqueous solution of chloral hydrate (5:2, wt/vol) for at least 24 h (16). Segments then were mounted in glycerol on object slides for microscopy.

At least 30 germplings per leaf segment were studied using white light, phase contrast microscopy at $\times 1,000$ magnification. Occasionally, germplings were found that had developed malformed infection struc-

tures. These germplings were ignored. For each germpling, the morphology of infection structures, especially SSV and PIH, was determined. This included dimension and shape of the SSV, presence or absence of septa, and number, diameter, and orientation of PIH. Typical germplings per species were photographed.

Host range of *U. viciae-fabae*. Seedlings of two cultivars each of *V. faba*, *V.*

sativa L., and *Lens culinaris* Medik. were inoculated in the growth chamber as indicated above with isolates VICI1, VICVS, and VICLC, collected on *V. faba*, *V. sativa*, and *L. culinaris*, respectively. Twelve days after inoculation, infection type (IT) and disease severity (DS) were assessed. IT was recorded following the scale of Stakman et al. (19), where 0 = no symptoms, ; = necrotic flecks, 1 = minute pustules

Table 1. Host and origin of rust isolates

Isolate	Species	Collected on	Geographic origin	Multiplied on
CICE1	<i>Uromyces ciceris-arietini</i>	Chickpea (<i>Cicer arietinum</i>)	Córdoba, Spain	Chickpea cv. Fardón
LUPI1	<i>U. lupinicolus</i>	Lupine (<i>Lupinus albus</i>)	Huelva, Spain	Lupin cv. Arthur
PISI1	<i>U. pisi</i>	Pea (<i>Pisum sativum</i>)	Córdoba, Spain	Pea cv. Messire
PISI2	<i>U. pisi</i>	Pea (<i>Pisum sativum</i>)	Winnipeg, Canada	Pea cv. Messire
PISI3	<i>U. pisi</i>	Pea (<i>Pisum sativum</i>)	Kafr El-Sheikh, Egypt	Pea cv. Messire
STR11	<i>U. striatus</i>	Alfalfa (<i>Medicago sativa</i>)	Jerez, Spain	Alfalfa cv. Baraka
VICI1	<i>U. viciae-fabae</i> ex <i>V. faba</i>	Faba bean (<i>Vicia faba</i>)	Córdoba, Spain	Faba bean cv. Baraca
VICI2	<i>U. viciae-fabae</i> ex <i>V. faba</i>	Faba bean (<i>Vicia faba</i>)	Kafr El-Sheikh, Egypt	Faba bean cv. Baraca
VICI3	<i>U. viciae-fabae</i> ex <i>V. faba</i>	Faba bean (<i>Vicia faba</i>)	Sicily, Italy	Faba bean cv. Baraca
VICVS11	<i>U. viciae-fabae</i> ex <i>V. sativa</i>	Common vetch (<i>Vicia sativa</i>)	Córdoba, Spain	Common vetch line A-01
VICLC11	<i>U. viciae-fabae</i> ex <i>L. culinaris</i>	Lentil (<i>Lens culinaris</i>)	Morocco	Lentil cv. Eston
VIGN1	<i>U. vignae</i>	Cowpea (<i>Vigna unguiculata</i>)	Kafr El-Sheikh, Egypt	Cowpea local cultivar

Table 2. Features of urediniospores and teliospores of different *Uromyces* spp. infecting legume crops^x

Rust sample	Urediniospore				Teliospore dimensions (μm)				
	Avg. dimensions (μm)		Germ pores		Length	Width	Pedicel		
	Length	Width	Avg. no.	Position ^y			Length	Width ^z	Apex length
<i>Uromyces ciceris-arietini</i> (CICE1)	20.7 d	19.8 ab	6.8 a	Scattered	20.3 e	18.3 c	5.8 d	7.3 b	nd
<i>U. lupinicolus</i> (LUPI1)	20.5 d	19.7 b	3.0 c	Scattered	20 e	17.6 cd	nd	nd	nd
<i>U. pisi</i> (PISI1)	20.8 d	19.8 ab	3.9 b	Near. eq.	22 d	17 d	25.3 c	5.2 c	nd
<i>U. striatus</i> (STR11)	19.7 e	18.2 c	6.0 c	Eq.	20.3 e	16.1 e	5.5 d	3.6 d	nd
<i>U. viciae-fabae</i> ex <i>Vicia faba</i> (VICI1)	24.2 a	20.5 a	3.5 b	Eq. to near. eq.	31 a	22.7 a	66.9 a	7.3 b	7 a
<i>U. viciae-fabae</i> ex <i>V. sativa</i> (VICVS11)	21.7 c	18.3 c	3.6 b	Eq. to near. eq.	27.2 c	20.7 b	51.6 b	7.4 b	6.3 b
<i>U. viciae-fabae</i> ex <i>Lens culinaris</i> (VICLC11)	21.4 cd	19.9 ab	3.4 bc	Eq. to near. eq.	29.3 b	21.0 b	52.0 b	9.0 a	5.1 c
<i>U. vignae</i> (VIGN1)	23.4 b	20.1 ab	1.9 d	Supraeq.	31 a	20.8 b	23.2 c	7.3 b	3.5 d

^x Means within a column followed by the same letter are not significantly different according to Duncan's multiple-range test ($P < 0.05$).

^y Near. = nearly, eq. = equatorial, avg. = average, nd = not determined.

^z Pedicel width at union with spore.

Fig. 1. Teliospores of **A**, *Uromyces ciceris-arietini*, **B**, *U. lupinicolus*, **C**, *U. pisi*, **D**, *U. striatus*, **E**, *U. viciae-fabae* ex *Vicia fabae*, and **F**, *U. vignae*. The bar represents 10 μm.

barely sporulating, 2 = necrotic halo surrounding small pustules, 3 = chlorotic halo, and 4 = well-formed pustules with no associated chlorosis or necrosis. DS was recorded as a visual estimation of the percentage of leaf area covered by rust pustules.

RESULTS

Urediniospore and teliospore morphology of rust species differed in quantitative traits, such as number and position of germ pores of the urediniospores and length and width of the teliospores, and in qualitative traits, such as presence or ab-

sence of a thick apex on the teliospores (Table 2; Fig. 1).

Infection structures of the rust species studied were distinct. SSVs of *U. ciceris-arietini* were globose, normally with one protrusion but occasionally two. Two PIH or, rarely, one of semivertical orientation

Fig. 2. Micrographs of germlings of leguminous rust fungi in whole mount preparations of seedling leaves. The bars represent 10 μ m. **A**, *Uromyces ciceris-arietini*. Note the protrusion (arrow) and two primary infection hyphae (PIH) that formed from the substomatal vesicle (SSV). **B**, Germling of *U. lupinicolus*. The SSV is narrowly oblong with three PIH (arrows). **C**, SSV of *U. pisi*. **D**, Germling of *U. striatus*. The SSV has three protrusions (arrows) and three PIH. **E**, Germling of *U. viciae-fabae* ex *Vicia fabae*. Note the septa (arrows). **F**, Germling of *U. viciae-fabae* ex *Lens culinaris*. The SSV is globose and has two PIH. **G**, Germling of *U. viciae-fabae* ex *V. sativa*. The SSV has a croissant-like shape with four PIH (arrows). **H**, Clear globose SSV of *U. vignae*.

grew from the SSV (Figs. 2A and 3A). SSVs of *U. lupinicolus* were irregular and more or less narrowly oblong to globoid, from which two to many PIH grew with semivertical orientation (Figs. 2B and 3B). SSVs of *U. pisi* were oblong to oval, with both ends curved deeply into the mesophyll to form one PIH each. Because of this vertical orientation of PIH, germlings were difficult to photograph (Figs. 2C and 3C). The two additional samples of *U. pisi* sampled from Canada and Egypt also showed this morphology. SSVs of *U. striatus* were more or less globoid, with one to four protrusions and one to three PIH. The protrusions may be initials of PIH, and

could have delimited an HMC. PIH started horizontally but then grew semivertically (Figs. 2D and 3D). SSVs of *U. vignae* were globoid with one PIH, which grew vertically but then horizontally, and branched to form a network of hyphae (Figs. 2H and 3H).

The host-specialized isolates of *U. viciae-fabae* were similar in general shape and color of spores, but differed in spore dimensions (Table 2) and in infection structure morphology (Table 3). Urediniospores of the three samples were globoid or ovoid, yellowish brown, and echinulate, with three to four equatorial to nearly equatorial germ pores. Teliospores were

ovoid to subgloboid, dark amber brown, and smooth, with long, golden-yellow pedicels. The isolate of *U. viciae-fabae* ex *V. faba* differed significantly from the other two in urediniospore and teliospore dimensions, length of the teliospore pedicels, and apex length. There were significant differences between the isolates from *V. sativa* and *L. culinaris* in teliospore length, pedicel width, and apex length (Table 2).

SSVs of *U. viciae-fabae* ex *V. faba* were fusiform to cylindrical tubes, growing as a continuum from the appressorium directly into the mesophyll; therefore, at one pole there was the appressorium and at the other pole two PIH were formed that grew horizontally. Occasionally a septum was present in the PIH (Figs. 2E and 3E). The two additional samples of *U. viciae-fabae* ex *V. faba* collected in Egypt and Italy also showed this morphology.

SSVs of *U. viciae-fabae* ex *L. culinaris* had no consistent shape. They varied from oval to globoid, normally with two PIH. Most of the PIH had a vertical orientation (Figs. 2F and 3F). The SSV of *U. viciae-fabae* ex *V. sativa* also were variable, ranging from oval to croissant-like, sausage-like, or triangular. The SSVs had three to four PIH, arising from various positions. They often showed a swelling where side branches arose. The orientation of the PIH was semivertical (Figs. 2G and 3G).

The three isolates of *U. viciae-fabae*, each collected from a different host species, only caused substantial infection on cultivars of the species from which they were collected (Table 4). This suggests that *U. viciae-fabae sensu lato* consists of host-specialized populations.

DISCUSSION

The morphology of infection structures was found to provide additional characteristics to identify rust taxa independently from the host, as reported for rusts of grasses (11,21) and onions and leeks (12). In the present work, the morphology of infection structures was similar for three *U. pisi* isolates and also for three isolates of *U. viciae-fabae* ex *V. faba* from three provenances. These results provide preliminary support for the conclusion that the morphology of infection structures hardly varies within taxa, as has been demonstrated in grass rusts (11,21). The germling morphology of the VICLCI1 isolate of *U. viciae-fabae* ex *L. culinaris* was very similar irrespective of whether they developed on pea or on lentil. Although the structures were more easily observed on pea, their morphology was not affected by the host. The same applies for isolate VICVSI1 of *U. viciae-fabae* ex *V. sativa*, for which infection structures were the same on pea and common vetch. The independence of infection structure morphology from plant species in which the infection takes place also has been reported for grass rusts (11,21).

Fig. 3. Drawing of typical germlings of leguminous rust isolates. **A**, *Uromyces ciceris-arietini*. Note the protrusion and two primary infection hyphae (PIH) that formed from the substromatal vesicle (SSV). **B**, Germling of *U. lupinicolus*. The SSV is narrowly oblong with three PIH. **C**, SSV of *U. pisi*. **D**, Germling of *U. striatus*. The SSV has three protrusions and three PIH. **E**, Germling of *U. viciae-fabae* ex *Vicia faba*. Note the septa. **F**, Germling of *U. viciae-fabae* ex *Lens culinaris*. The SSV is globoid and has two PIH. **G**, Germling of *U. viciae-fabae* ex *V. sativae*. The SSV has a croissant-like shape with four PIH. **H**, Clear globoid SSV of *U. vignae*.

The procedure followed here is simple and does not require microtomy. However, a drawback of infection-structure morphology as a character for identification is the requirement of viable inoculum. Thus, herbarium specimens cannot be included in such studies. The method also is not as sensitive as identification on the basis of molecular markers (23). On the other hand, even when teliospores are available, *U. lupinicolus* and *U. ciceris-arietini* are difficult to distinguish (Fig 1; Table 2), but their infection structures are distinctive (Fig 2; Table 3). *U. vignae* could be separated from all other rusts used in this study on the basis of teliospore morphology (Table 2; Fig 1), but teliospores of *U. vignae* are similar to those of *U. appendiculatus* (4); therefore, it would be useful to see if the morphology of germings can separate these two species.

The differences in infection structures among species may be exploited in certain phytopathological studies, where a host is inoculated with two rust species to investigate induced resistance and induced susceptibility. Infection structures also could be useful in epidemiological studies involving several rust taxa where it is necessary to identify individual sporelings for which the host is unknown (e.g., trapped airborne spores). These differences also could be useful to quantify contamination of inoculum by a second species or to carry out competition studies involving several species; for example, in studies of *C. arietinum* infected with both *U. ciceris-arietini* and *U. striatus* (8,18) or pea infected with both *U. pisi* and *U. viciae-fabae* (13). The differences between germings of each taxon were substantial and should enable differentiation of the two species at the level of individual sporelings.

The present study confirmed that *U. viciae-fabae sensu lato* is a species complex. Cummins (4) stated that *U. viciae-fabae* is circumglobal on *Lathyrus*, *Pisum*, and *Vicia* spp., with *V. faba* the host of the neotype. However, we demonstrated here the existence of host-specialized isolates that cannot infect *V. faba*. A degree of host

specialization within *U. viciae-fabae* was already acknowledged by Gümman (7), but all the *formae speciales* suggested by Gümman were able to infect *V. faba*. Seymour (15) also reported that the rust of *V. sativa* did not infect *V. faba*, but did not study the morphology of that rust and simply considered it to be a race of *U. viciae-fabae*. Our data indicate that *U. viciae-fabae* may be subdivided into populations with differential pathogenicity to *V. faba*, *V. sativa*, or *L. culinaris* (Tables 2 and 4). More research is needed to further clarify the ultimate classification of the *U. viciae-fabae* complex.

The rust of pea has been ascribed to either *U. viciae-fabae* (1,4,7) or *U. pisi* (7,14,20,22). Our three pea isolates, collected in Spain, Canada, and Egypt, belong to *U. pisi* based on infection structures and host range. We cannot exclude the possibility of *U. viciae-fabae* isolates infecting pea. In fact, we have observed high levels of infection on pea in the growth chamber after inoculation with *U. viciae-fabae* isolates from faba bean, but we were unable to get *U. viciae-fabae* established in the field in any of 200 pea accessions, even after repeated artificial inoculations (*unpublished results*). It would be interesting to attempt to confirm reports of infections of pea by *U. viciae-fabae* under field conditions (2,9,17).

This is the first report of *U. lupinicolus* on *Lupinus albus*, *U. striatus* on *Medicago sativa*, *U. viciae-fabae* on *Vicia sativa*, and *U. pisi* on *P. sativum* occurring in Spain.

All were collected in the south of the country. *U. lupinicolus* and *U. striatus* were observed late in the crop season and caused little damage. *U. viciae-fabae* on vetch and *U. pisi*, observed early in the crop season in small experimental plots, appeared to be quite aggressive pathogens in those plots, and could become serious agricultural problems.

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Table 4. Host range of *Uromyces viciae-fabae* isolates^z

Host (entrada)	<i>U. viciae-fabae</i> ex <i>V. faba</i> (VICI1)		<i>U. viciae-fabae</i> ex <i>V. sativa</i> (VICVSI1)		<i>U. viciae-fabae</i> ex <i>L. culinaris</i> (VICLCI1)	
	IT	DS (%)	IT	DS (%)	IT	DS (%)
<i>V. faba</i> cv. Amcor	4	25	0	0	0	0
<i>V. faba</i> cv. Baraca	4	30	0	0	0	0
<i>L. culinaris</i> cv. Indian Head	0	0	0	0	4	30
<i>L. culinaris</i> cv. Eston	;	0	1	1	4	30
<i>V. sativa</i> line V01	0	0	4	15	0	0
<i>V. sativa</i> line V08	0	0	4	20	0	0

^z IT = infection type, on a 0-to-4 scale according to Stakman et al. (19) and DS = disease severity expressed as percentage of leaf area covered by rust symptoms.

Table 3. Features of primary infection structures of different *Uromyces* spp. infecting legume crops^x

Rust sample	Primary infection hyphae				Substomatal vesicle			
	Number	Growth ^y	Avg. width (µm)	Shape ^z	Avg. dimension (µm)		Avg. number	
					Length	Width	Protrusions	Septa
<i>Uromyces ciceris-arietini</i> (CICE1)	2	SV	4.7 ef	Glob	13.1 f	11.9 bc	1.1	0
<i>U. lupinicolus</i> (LUP11)	>2	SV	5.2 bc	Ob to glo	13 f	10.9 cd	0	0
<i>U. pisi</i> (PISI1)	2	V	4.2 g	Ob to oval	16.5 cd	9.7 e	0	0
<i>U. striatus</i> (STRI1)	1-3	SV	4.8 e	Glo	15.2 de	12 bc	2.3	0
<i>U. viciae-fabae</i> ex <i>V. faba</i> (VICI1)	2	H	4.9 de	Fus to cyn	29.9 a	9.8 de	0	0.4
<i>U. viciae-fabae</i> ex <i>V. sativa</i> (VICVSI1)	3-4	SV	5.6 a	Oval to cro	17.7 c	13.7 a	0	0
<i>U. viciae-fabae</i> ex <i>L. culinaris</i> (VICLCI1)	2	V	5.3 ab	Oval to glo	20.1 b	11.8 c	0	0
<i>U. vignae</i> (VIGN1)	1	V then H	4.4 fg	Glo	14 ef	12.5 b	0	0

^x Means within a column followed by the same letter are not significantly different according to Duncan's multiple-range test ($P < 0.05$).

^y Direction of growth: SV = semivertical, V = vertical, H = horizontal.

^z Glo = globoid, Ob = oblong, Fus = fusiform, cyn = cylindrical, cro = croissant-like.

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