Host Range Expansion of the Alfalfa Rust Pathogen

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ABSTRACT

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A systematic investigation of the host range of a monouredinial isolate (KR1-1) of *Uromyces striatus* from alfalfa (*Medicago sativa*) was undertaken. The extent of susceptibility to this pathogen within plant tribes closely related to alfalfa was determined. A total of 844 plant introductions, representing 345 species or subspecies from 27 genera, was tested. The plants tested included representative species from the tribe Trifolieae (which includes alfalfa) and seven additional tribes closely related according to current phylogenetic descriptions of the Leguminosae. Six of the eight tribes contained genera with susceptible species that supported urediniospore production. A total of 141 species or subspecies from 11 genera was susceptible to KR1-1. Susceptible plants from the tribes Trifolieae, Cicereae, and Vicieae generally supported profuse urediniospore production, whereas susceptible species in the tribes Genisteae, Galegeae, and Hedysareae supported sparse urediniospore production. No susceptible species were found in the tribes Coronilleae or Loteae. The distribution of degree of susceptibility followed the current proposed phylogenetic relationships of these tribes. These results indicated that an isolate of *U. striatus*, found as a parasite of alfalfa, is capable of surviving and reproducing on a broad range of plant species. Parasitic efficiency was decreased with increased phylogenetic distance of the host species from alfalfa. The extent of the host range probably is a significant factor in the epidemiology of this alfalfa pathogen.

The host range of an obligate plant-parasitic species is of interest from two standpoints: epidemiology and taxonomy. The epidemiological competence of a particular isolate of a pathogen is influenced greatly by the plant species on which the fungus can reproduce. Historically, eradication of alternate and alternative hosts of phytopathogenic fungi was advocated as a means of diminishing disease impact and dispersion. A thorough knowledge of the plant species capable of supporting reproduction of the fungus is vital to the success of this approach. Also, as pointed out elsewhere (6), an understanding of the host and distribution ranges of plant pathogens is vital for making informed decisions regarding disease diagnosis and quarantine.

As first shown by Flor (4) and reviewed by Loegering (5), the genic systems of obligate plant parasites and their hosts must interact in a very specialized way before parasite reproduction (compatible interaction) can occur. Flor's work, and the work of many others, clearly indicates that this interaction represents a highly evolved condition. From this observation, it follows that plant species capable of functioning as a host of the same stage of an obligate parasite likely share a common evolutionary history. This concept was applied to the Leguminosae (Fabaceae) by El-Gazzar (3), who demonstrated that susceptibility to *Uromyces* rusts follows a characteristic distribution within the plant family, suggesting a common evolutionary history of the genera involved. El-Gazzar's treatise represented a synthesis of more than 50 published works dating from the late nineteenth century. His review included 235 species of *Uromyces*; 105 were reported to have a host range of a single species. An additional 74 *Uromyces* species had host ranges that included more than one species but were limited to a single genus. Host ranges of other *Uromyces* species ranged from several species of a few genera to 20 genera from nine tribes susceptible to *Uromyces anthyllidis*. *Uromyces striatus* J. Schröt was reported as a parasite of 29 species from the genera *Medicago*, *Trigonella*, or *Trifolium*, all within the tribe Trifolieae.

Although the work of El-Gazzar firmly established that some rust fungus species are capable of reproducing on numerous plant host species from several genera, it did not address directly the question of specificity of a single isolate of the pathogen. It is possible, for example, that an isolate of *U. striatus* from alfalfa (*Medicago sativa* L.) would not cause disease on clover, while the reverse could be true for an isolate of the same species found infecting clover. The objective of this study was to determine the range of plant species capable of supporting reproduction of a single isolate of *U. striatus* initially found causing rust of alfalfa.

MATERIALS AND METHODS

Seeds from all accessions were obtained through the Germplasm Resources Information Network (GRIN) maintained by the U.S. Department of Agriculture, Beltsville, Maryland. Seeds were scarified with sandpaper and planted 1 to 2 cm deep in pasteurized mason's sand. Plants were grown at 25°C under continuous cool-white fluorescent lighting (108 E m^{-2} s^{-1}) in growth chambers. Plants were grown to a minimum of two true leaves before inoculation.

The taxonomic classification of plants was provided by the GRIN system. To guard against misclassification and/or errors in planting, numerous accessions of the same species were compared morphologically, whenever possible. All accessions were grown to full flower for these comparisons. In the few instances where one accession did not appear to match the other accessions of the same designation, the plants were compared to descriptions in taxonomic keys. All accessions that appeared to be misclassified were omitted from this study; no attempt was made to reclassify them.

Isolate KR1-1 was isolated from a field-grown alfalfa plant near Manhattan, Kansas. The isolate was subcultured from a single, well-isolated pustule and was increased and maintained on Kanza alfalfa plants grown in a growth chamber at 25°C and a 16-h photoperiod. Isolate KR1-1 was determined to be *U. striatus* by the characteristic striations on teliospores (2). Urediniospores were collected using a cyclone spore collector (1). Inoculations were made as described previously (8). Briefly, this method consists of dispersing urediniospores (1 mg/ml) in a dilute solution of surfactant (2 drops of Tween 20 per 100 ml of distilled water), spraying it onto the plants to runoff, incubating the plants in darkness in closed containers at 25°C and 100% relative humidity for 24 h, and returning them to 25°C and a 16-h photoperiod. Several susceptible control alfalfa

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plants were included with each inoculation. Control plants were Kanza or an experimental line known to be highly susceptible to alfalfa rust.

Development of rust symptoms was assessed 14 days after inoculation. Initial assessments were made with a hand lens. Questionable plants were examined carefully under a binocular dissecting microscope with 50× magnification. In the case of very small pustules, active sporulation was confirmed by hand-sectioning infected leaves and examining under 100× magnification. Plants were scored as susceptible only if erumpent pustules were observed. This criterion was adopted because it has explicit applicability to epidemiological concerns, indicating which species can serve as source populations of the alfalfa rust pathogen. A subjective estimate of level of susceptibility also was made for each entry. Estimated numbers of pustules per leaf and the presence of necrotic tissue at the infection sites were recorded. All plants scored resistant 14 days postinoculation were examined again 21 to 24 days postinoculation. Although all susceptible controls behaved as expected, all plants again classified as resistant were inoculated a second time, and the cycle was repeated. As a further test of reliability, 233 accessions were planted a second time, the plants were inoculated, and the results of the second test were compared to the results of the first.

RESULTS AND DISCUSSION

A total of 844 plant accessions was tested; 837 had been identified to species. No accessions classified as resistant in the first test were classified subsequently as susceptible in a second test.

Susceptibility to KR1-1 was broadly based, encompassing 141 species or subspecies from 11 genera in six tribes (Table

Table 1. Plant tribes and species of *Fabaceae* susceptible[a] to a monouredinial isolate of *Uromyces striatus*

Tribe	Species[b]	Tribe	Species[b]	Tribe	Species[b]
Cicereae	*Cicer anatolicum* Alef.		*M. truncatula* Gaertner		*T. obscurum* Savi-238365
	C. arietinum L.		*M. turbinata* (L.) Allioni		*T. ochroleucum* Huds.
	C. bijugum Rech.	Trifolieae	*Melilotus altissimus* Thuill		*T. ornithopodioides* (L.) Sm.
Galegeae	*Galega orientalis* Lam.		*M. elegans* Salzm. ex Ser.		*T. palaestinum* Boiss.-369060,
Vicieae	*Lathyrus aphaca* L.-219924		*M. indica* (L.) All.		-369062, -292476
	L. inconspicuus L.-358858		*M. infestus* Guss.		*T. pallidum* Bory & Chaub.
	L. ochrus (L.) DC.-206373		*M. italicus* (L.) Lam.		*T. patens* Schreb.
	L. szowitsii Boiss		*M. neapolitanus* Ten.		*T. pauciflorum* Lojac.-353425,
Genisteae	*Lupinus argenteus* var. *tenellus*		*M. officinalis* Lam.		-353729, -369072, -369076,
	Pursh.		*M. suaveolens* Ledeb.		-369083
	L. sericeus Pursh.		*M. speciosus* Durieu		*T. phleoides* Pourr. ex Willd.-
Trifolieae	*Medicago arabica* (L.) Huds.		*M. tauricus* (M.B) Ser.		120201, -208727
	M. blancheana Boiss.	Hedysareae	*Onobrychis hypargyrea* (L.)		*T. pilulare* Boiss.-292479
	M. brachycarpa Fischer ex M.B.		Schinz & Thell		*T. retusum* L.
	M. cancellata M.B.	Vicieae	*Pisum sativum* subsp. *abyssinicum*		*T. rueppellianum* Fresen.
	M. constricta Durieu		(A. Brown) Govorov.		*T. scabrum* L.-419338
	M. coronata (L.) Bartalina		*Pisum sativum* subsp. *elatius* L.		*T. scutatum* Boiss.
	M. disciformis de Candolle		*Pisum sativum* subsp. *sativum* L.		*T. spumosum* L.-117404
	M. doliata Carmignani	Trifolieae	*Trifolium affine* C. Presl.		*T. squarrosum* L.
	M. fischeriana (Ser.) Trautv.		*T. africanum* Ser.		*T. striatum* L.-3029, -75
	M. glomerata Balbis		*T. alpestre* L.		*T. strictum* L.-369134
	M. granadensis Willdenow		*T. aureum* Thuill		*T. subterraneum* L.
	M. hybrid Traut.		*T. batmanicum* Katzn.		*T. s.* subsp. *brachycalycinum*
	M. intertexta (L.) Miller		*T. berytheum* Boiss. & Bl.		Katzn. & Morley
	M. italica (Miller) Fiori		*T. bocconei* Savi-287976		*T. sylvaticum* Gerard ex Loisel.-
	M. laciniata (L.) Miller		*T. campestre* Schreb.		287978, -369119, -369120
	M. littoralis Rohde		*T. canescens* Willd.		*T. tomentosum* L.-226532,
	M. lupulina L.		*T. caucasicum* Tausch		-233722, -287962
	M. medicaginoides (Retz) Small		*T. cherlerie* L.-292470, -535683		*T. trichocephalum* M.B.-251210
	M. minima Bartalini		*T. chilense* Hook. & Arn.		*T. variegatum* Nutt.
	M. monantha (Meyer) Trautv.		*T. clusii* Godr. & Gren.		*T. vesiculosum* Savi-233782
	M. monspeliaca (L.) Trautv.		*T. clypeatum* L.-202804, -292472		*Trigonella anguina* L.
	M. murex Willdenow		*T. dasyurum* C. Presl.		*T. arabica* Del.
	M. noeana Boissier		*T. diffusum* Ehrh.		*T. balansae* Boiss. & Reuter
	M. orbicularis (L.) Bart.		*T. dubium* Sibth.		*T. coelesyriaca* Boiss.
	M. platycarpos (L.) Trautv.		*T. echinatum* M.B.-419371		*T. coerulescens* (M. Breb.)
	M. polyceratia (L.) Trautv.		*T. gemellum* Savi		Halacsy
	M. polymorpha L.		*T. glanduliferum* Boiss.		*T. corniculata* (L.) L.
	M. popovii (Korovin) Sirj.		*T. globosum* L.		*T. cretica* (L.) Boiss.
	M. praecox de Candolle		*T. glomeratum* L.		*T. foenum-graecum* L.
	M. radiata L.		*T. hirtum* All.-120146, -227256,		*T. glabra* Thunb.
	M. rigidula (L.) Allioni		-249846, -279847, -302969,		*T. g.* subsp. *uncata* (Boiss
	M. rugosa Desrousseaux		-348886		.& Noe) Lassen
	M. ruthenica (L.) Ledebour		*T. incarnatum* L.		*T. gladiata* Steven ex M.B.-
	M. sativa L.		*T. isthmocarpum* Brot.-535692		253474
	M. sativa subsp. *falcata* (L.)		*T. lappaceum* L.		*T. kotschyi* Boiss.
	Arcang.		*T. meduseum* Bl. ex Boiss.		*T. macrorrhyncha* Boiss.
	M. sativa subsp. *caerulea*		*T. micranthum* Viv.-240756		*T. schlumbergeri* Boiss.
	Schmalh.		*T. microdon* Hook & Arn.		*T. spicata* Sibth. & Smith
	M. sativa subsp. *varia* L.		*T. miegeanum* Maire		*T. spruneriana* (Boiss) Huber.
	M. sativa subsp. *viscosa* L.		*T. montanum* L.		Mor. var. *sibthorpii*
	M. sauvageii Negre		*T. nigrescens* subsp. *petrisavii*	Vicieae	*Vicia faba* L.
	M. scutellata (L.) Miller		(Clem.) Holmboe-238368		*V. f.* var. *minuta* L.
	M. tenoreana Seringe				

[a] Supported urediniospore production.
[b] Plant introduction numbers of susceptible accessions are listed for those species that also were represented by resistance accessions (not listed).

Table 2. Plant tribes and species resistant[a] to a monouredinial isolate of *Uromyces striatus*

Tribe	Species[b]	Tribe	Species[b]	Tribe	Species[b]
Loteae	*Anthyllis cornicina* L.	Hedysareae	*Hedysarum alpinum* L.		*O. natrix* L.
	A. lotoides L.		*H. carnosum* Dest.		*O. pubescens* L.
	A. tetraphylla L.		*H. coronarium* L.	Coronilleae	*Ornithopus perpusillus* L.
	A. vulneraria L.		*H. gmelinii* Ledeb.		*O. pinnatus* (Miller) Druce
	A. v. subsp. *polyphylla* DC.		*H. glomeratum* Dietr.		*O. compressus* L.
Galegeae	*Astragalus adsurgens* Pallas		*H. spinosissimum* L.		*O. perpusillus* L.
	A. alpinus L.		*H. sulphurescens* Rydb.		*O. sativus* Brot.
	A. asper Jacq.	Loteae	*Hymenocarpos circinnatus* (L.) Savi	Galegeae	*Oxytropis campestris* var. *varians* (Rydb.) Barnely
	A. asterias Steven ex Ledeb.		*H. c.* var. *nummularius* (DC.) Bomm.		*O. lambertii* var. *bigelovii* A-Gray
	A. atropilosulus var. *venosus* (Hochst.) J.B. Gillett	Vicieae	*Lathyrus annuus* L.		*O. pilosa* (L.) DC.
	A. bourgaeanus Cosson		*L. chloranthus* Boiss.		*O. sericea* var. *spicata* (Hook.) Barneby
	A. cicer L.		*L. cicera* L.		
	A. commixtus Bunge		*L. clymenum* L.	Vicieae	*Pisum fulvum* Sibth. & Smith
	A. corrugatus Bertol.		*L. hirsutus* L.	Coronilleae	*Scorpiurus muricatus* L.
	A. edulis Durieu ex Bunge		*L. latifolius* L.		*S. vermiculatus* L.
	A. filicaulis Fischer & C. Meyer ex Kavelin & Kir.		*L. nigrivalvis* Burkart	Galegeae	*Sutherlandia microphylla* Burchell ex DC.
	A. galegiformis L.		*L. nissolia* L.	Trifolieae	*Trifolium alexandrinum* L.
	A. globiceps Bunge		*L. sativus* L.		*T. amabile* Humb., Bonpl., & Kunth
	A. hamosus L.		*L. tingitanus* L.		*T. ambiguum* M.B.
	A. incanus L.		*L. tuberosus* L.		*T. angustifolium* L.
	A. inflexus Douglas ex Hook.	Vicieae	*Lens culinaris* Medikus		*T. argutum* Sol.
	A. lasioglottis Steven ex M.B.	Galegeae	*Lessertia herbacea* (L.) Druce		*T. arvense* L.
	A. lindheimeri Engelm. ex A. Gray	Loteae	*Lotus angustissimus* L.		*T. badium* Ledeb.
	A. lurorum Bornm.		*L. arabicus* L.		*T. burchellianum* Ser.
	A. membranaceus (Fischer ex Link) Bunge		*L. arenarius* Brot.		*T. caudatum* Boiss.
	A. monspessulanus L.		*L. chihuahuanus* (S. Watson) E. Greene		*T. cernuum* Brot.
	A. nuttallianus DC.		*L. collinus* (Boiss.) Heldr.		*T. cheranganiense* J.B. Gillett
	A. odoratus Lam.		*L. conimbricensis* Brot.		*T. constantinopolitanum* Ser.
	A. onobrychis L.		*L. corniculatus* L.		*T. dichroanthum* Boiss.
	A. ovinus Boiss.		*L. creticus* L.		*T. echinatum* var. *carmeli* M.B.
	A. pallescens M.B.		*L. cytisoides* L.		*T. fragiferum* L.
	A. podocarpus C. Meyer		*L. denticulatus* (E. Drew) E. Greene		*T. hausskнechtii* Boiss.
	A. polybotrys Boiss.		*L. edulis* L.		*T. heldreichianum* (Gib & Belli) Hausskin.
	A. ponticus Pallas		*L. glinoides* Del.		*T. ligusticum* Balb. ex Loisel.
	A. pulchellus Boiss.		*L. halophilus* Boiss. & Spruner		*T. lupinaster L.*
	A. racemosus Pursh		*L. mearnsii* (Britton) E. Greene		*T. medium* L.
	A. rytilobus Bunge		*L. oblongifolius* (Benth.) E. Greene		*T. michelianum* Savi
	A. scorpiurus Bunge		*L. ornithopodioides* L.		*T. michelianum* var. *balansae* (Boiss.) Azn
	A. sesameus L.		*L. palustris* Willd.		*T. mutabile* Portenschl.
	A. siliquosus Boiss.		*L. parviflorus* Desf.		*T. nigrescens* Viv.
	A. sinicus L.		*L. peregrinus* L.		*T. pannonicum* Jacq.
	A. stevenianus DC.		*L. purshianus* Clements&S.E. Clements		*T. physodes* Stev. ex M.B.
	A. stipulatus D. Don ex Sims		*L. subpinnatus* Lagasca		*T. pratense* L.
	A. sulcatus L.	Genisteae	*Lupinus albicaulis* Douglas		*T. pratense* var. *sativum* Schreb.
	A. tephrosioides Boiss.		*L. albus* L.		*T. purpureum* Loisel.
	A. tibetanus Benth. ex Bunge		*Lupinus angustifolius* L.		*T. reflexum* L.
	A. tribuloides Del.		*L. arbustus* Douglas ex Lindley		*T. repens* L.
	A. trimestris L.		*L. argenteus* Pursh		*T. resupinatum* L.
	A. uliginosus L.		*L. atlanticus* Gladst.		*T. rubens* L.
	A. utriger Pallas		*L. burkei* S. Watson		*T. semipilosum* Fresen.
	A. vaginatus Pallas		*L. hispanicus* Boiss. & Reuter		*T. spadiceum* L.
	A. vegetus Bunge		*L. leucophyllus* Douglas ex Lindley		*T. stellatum* L.
	A. verus Olivier		*L. littoralis* Douglas		*T. suffocatum* L.
	A. vesicarius L.		*L. luteus* L.		*T. thalii* Vill.
	A. vulpinus Willd.		*L. polyphyllus* Lindley		*T. tomentosum* var *lanatum* Zoh.
Cicereae	*Cicer chorassanicum* (Bunge) Popov		*L. sulphureus* Douglas ex Hook.		*T. vernum* Phil.
	C. cuneatum Hochst.	Trifolieae	*Melilotus albus* Medikus	Trifolieae	*Trigonella caerulea* (L.) Ser.
	C. echinospermum P. Davis		*M. dentatus* (Waldst. & Kit.) Pers.		*T. calliceras* Fischer ex in. Bieb.
	C. judaicum Boiss.		*M. hirsutus* Lipsky	Vicieae	*Vicia hirsuta* (L.) Gray
	C. pinnatifidum Jaub. & Spach		*M. polonicus* (L.) Desr.		*V. sativa* L.
	C. reticulatum Ladiz.		*M. segetalis* (Brot.) Ser		*V. s.* subsp. *amphicarpa* (Boiss.) Asch. & Graebner
Coronilleae	*Coronilla coronata* L.		*M. siculus* (Turra) Vitman ex B.D. Jackson		*V. s.* subsp. *cordata* (Wulfen ex Hoppe) Arcang.
	C. orientalis Miller		*M. sulcatus* Desf.		*V. s.* subsp. *nigra* (L.) Ehrh.
	C. rostrata Boiss. & Spruner		*M. wolgicus* Poiret		*V. sicula* (Raf.) Guss.
	C. scorpioides (L.) Koch	Hedysareae	*Onobrychis caput-galli* (L.) Lam.		
	C. varia L.		*O. pedunculares* (Cav.) DC.		
Genisteae	*Genista tinctoria* L.	Trifolieae	*Ononis adenotricha* Boiss.		
Galegeae	*Glycyrrhiza echinata* L.		*O. arvensis* L.		
	Gueldenstaedti atia verna (Georgi) Boriss		*O. mitissima* L.		

[a] Did not support urediniospore production.

[b] Species listed are those that were represented only by resistant accessions.

1). Six of the eight tribes tested included some species that supported reproduction of the fungus; all tribes also included resistant species (Table 2). Examples of sporulation on diverse host species are shown in Figure 1. Susceptibility was not always uniform in terms of levels of sporulation among species, among accessions within a species, or among plants within an accession. For example, sporulation ranged from rare, small, open pustules accompanied by extensive necrosis on a few plants of *Lupinus sericeus* Pursh. to hundreds of large erumpent pustules per leaf of all plants of all accessions of *M. sativa*. Differences among accessions within a species were common. For example, all of the plants of three accessions (PI226532, 233722, 287962) of *Trifolium tomentosum* L. supported extensive urediniospore production, whereas none of the plants of 10 other accessions of this species supported sporulation. Susceptibility within an accession also was not necessarily uniform. One accession of *Trifolium cherleri* L. (PI292470) was represented in the first trial by 18 plants; three were reasonably good hosts, supporting about 15 to 50 erumpent pustules per leaf. All other plants were free of symptoms. All plants were grown to full flower and carefully compared to each other and to the taxonomic description of *T. cherleri* (10). All plants were determined to have been identified correctly. A second test of this accession supported the results of the first, suggesting that this line is heterogeneous for susceptibility to *U. striatus* isolate KR1-1.

There were many cases of uniformity of reaction within a species. For example, 42 accessions of *Trifolium alexandrinum* L. were tested; no evidence of susceptibility was seen. Seven accessions of *Pisum sativum* L. were all uniformly susceptible (Fig. 1B). Symptomless plants were extremely rare in accessions of *M. sativa* tested with isolate KR1-1.

A subjective classification of the levels of spore production on the various species clearly showed a pattern of sporulation intensity. This pattern is represented in Figure 2, superimposed on a portion of the divergence pattern of the Leguminosae suggested by Polhill (7). An interpretation of these patterns is that the suitability as a host of KR1-1 is greatest in alfalfa and the tribe Trifolieae, somewhat less in the Cicereae and Vicieae, poor in the Hedysareae and Galegeae, and nonexistent in the Loteae and Coronilleae. This interpretation is in concordance with the relationships suggested by Polhill (7) (Fig. 2).

Our results differed slightly from those reported by El-Gazzar (3). The host range of *U. striatus* as determined by historical records of the pathogen included five species, *Trigonella caerulea* (L.) Ser., *Trifolium arvense* L., *T. badium* Ledeb., *T. lupinaster* L., and *T. repens* L., that we found to be resistant to *U. striatus* isolate KR1-1 (Table 2). This result suggests that host ranges of specific isolates of the fungus may differ.

The only other systematic investigation of the host range of an obligate parasite causing diseases in the Leguminosae that we are aware of dealt with powdery mildew caused by *Erysiphe polygoni* DC. (9). Stavely and Hanson (9) reported that a

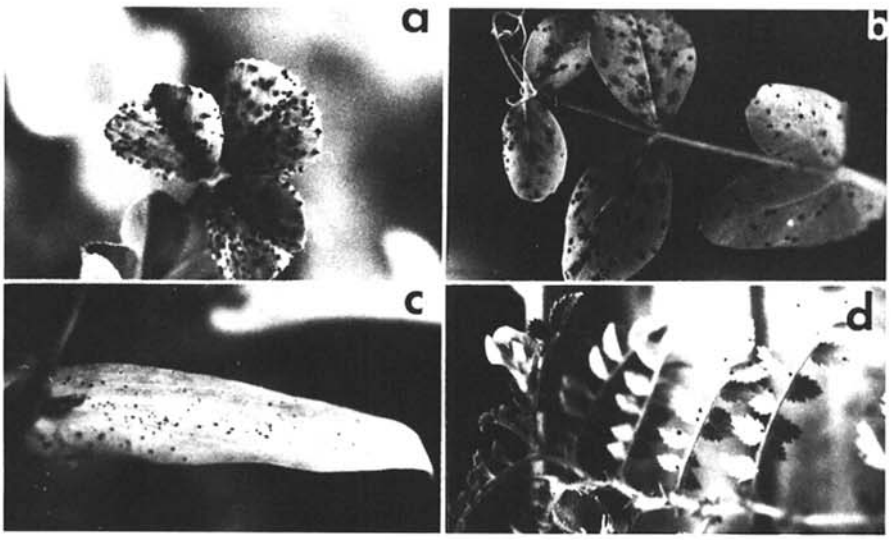

Fig. 1. Minus-sense probes generated from pBS51IIIX4-6, which contained cDNA from the 3' half of cucumber mosaic cucumovirus subgroup II (CMV-S) RNA 3. Three minus-sense transcripts of different lengths (P1, P2, and P3), represented as the lower three horizontal lines, were obtained using the restriction sites shown. In these transcripts the CMV 3' sequences are close to the T7 promoter of the pBS M13- vector.

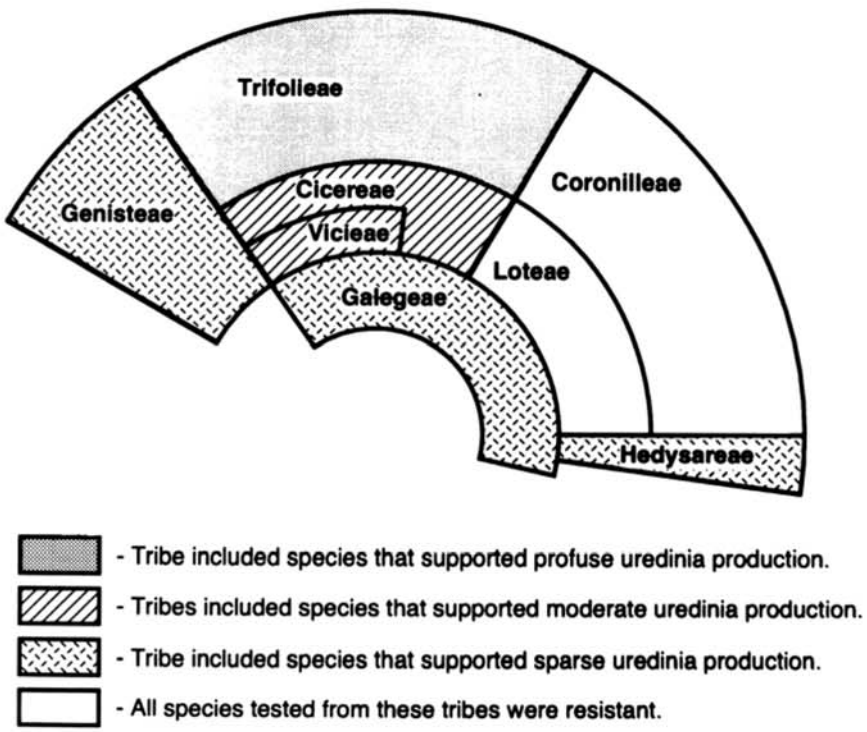

Fig. 2. Characterization of virions and subgrouping of cucumber mosaic cucumovirus (CMV) pepper isolates. **(A)** Comparison of virions of CMV pepper isolates obtained from tobacco plants. Analysis was made in 1% agarose gels electrophoresed for 1 h and stained with ethidium bromide. CMV-S (subgroup II, "fast") and CMV-P (subgroup I, "slow") were used as standards. Lanes labeled 35, SD1, Gi, Ke, Or, and SD2 contain virions from representative CMV isolates from each of the six collection sites. Isolate 35 is a representative of the 19 isolates found in one field in Ventura County. **(B)** Autoradiograph of a dot blot hybridization of RNA from CMV pepper isolates with two different subgroup-specific probes. Probes were generated from plasmids pFNY3 (subgroup I) and pLS-87 (subgroup II). CMV-P and CMV-S were used as standards representing subgroup I and II, respectively, and CMV isolates are labeled as in A.

single isolate of *E. polygoni* from red clover (*Trifolium pratense* L.) was capable of infecting and reproducing on 48 species from eight genera. As with the *Uromyces* rusts, early work with the powdery mildews of the Leguminosae reported the fungi as being extremely host species-specific (9). Our results reported here and the results of Stavely and Hanson (9) indicate that the range of plant species capable of supporting reproduction of particular isolates of obligate parasites of the Leguminosae may be considerably more extensive than commonly believed.

The one isolate of *U. striatus* we used may not fully represent the potential host range of other isolates with the same taxonomic designation. El-Gazzar (3) reported that the host range of *U. striatus* includes five species that we found to be resistant to isolate KR1-1. Whether the isolates included in the studies summarized by El-Gazzar were capable of infecting alfalfa is unknown. Therefore, our results should be considered as representing the minimum host range that a fungus causing alfalfa rust may have.

An understanding of the host range of an isolate from a crop species provides insight into the potential risks of disease on that crop originating from other crop or weed species and into the evolutionary relationships of the host species. From an epidemiological standpoint, the results we have presented suggest that an outbreak of alfalfa rust may originate on or disperse by means of numerous other species. Some alternative species, such as garden pea, are grown commonly in alfalfa-producing regions. Although the relative importance of these species in the epidemiology of alfalfa rust is unknown, it is now clear that they are capable of playing a significant role.

From a taxonomic standpoint, we agree with El-Gazzar (3) that much can be learned of the relationships of host species based on the shared characteristic of susceptibility to an obligate parasite. The results presented here are in concordance with the current phylogeny of the Leguminosae. If we assume that the compatible interaction of *U. striatus* and leguminous plants developed once in evolutionary history, the broadness of the host range suggests that the compatibility is quite strongly conserved, even though considerable morphological and reproductive divergence occurred among the plant species.

LITERATURE CITED

1. Cherry, E., and Peet, C. E. 1966. An efficient device for the rapid collection of fungal spores from infected plants. Phytopathology 56:1102-1103.
2. Cummins, G. B. 1978. Rust Fungi on Legumes and Composites in North America. University of Arizona Press, Tucson.
3. El-Gazzar, A. 1981. Systematic implication of susceptibility to *Uromyces* rusts in Leguminosae. Pages 979-994 in: Advances in Legume Systematics. R. M. Polhill and P. H. Raven, eds. Ministry of Agriculture, Fisheries and Food, Royal Botanic Gardens, London.
4. Flor, H. H. 1956. The complementary genic systems in flax and flax rust. Adv. Genet. 8:29-54.
5. Loegering, W. Q. 1978. Current concepts in interorganismal genetics. Annu. Rev. Phytopathol. 16:309-320.
6. McCain, J. W., Hennen, J. F., and Ono, Y. 1990. New host species and state distribution records for North American rust fungi (Uredinales). Mycotaxon 39:281-300.
7. Polhill, R. M. 1981. Papilionoidae. Pages 191-204 in: Advances in Legume Systematics. R. M. Polhill and P. H. Raven, eds. Ministry of Agriculture, Fisheries and Food, Royal Botanic Gardens, London.
8. Skinner, D. Z., and Stuteville, D. L. 1989. Influence of temperature on expression of resistance to rust in diploid alfalfa. Crop Sci. 29:675-677.
9. Stavely, J. R., and Hanson, E. W. 1966. Pathogenicity and morphology of isolates of *Erysiphe polygoni*. Phytopathology 56:309-318.
10. Zohary, M., and Heller, D. 1984. The genus *Trifolium*. The Israel Academy of Science and Humanities, Jerusalem, Israel.