Heterothallism and Pathogenic Specialization in *Uncinula necator*

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ABSTRACT

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A collection of 35 isolates of *Uncinula necator* was established. Each isolate originated from a single chain of conidia. The collection included isolates from 10 species of *Vitis* and isolates from *Vitis* interspecific hybrids. Isolates were paired in all possible combinations on tissue culture plants of the *Vitis* interspecific hybrid cultivar Chancellor and were incubated for 60 days at 20 C. Initially, *U. necator* appeared to be composed of two mating types that comprised a bipolar heterothallic system. Ascocarps were produced abundantly within 14 days in approximately one-half of the pairings. However, three isolates consistently produced low numbers of fertile ascocarps 45–60 days after inoculation in pairings that initially appeared to be incompatible; one of these isolates produced sterile ascocarps after 45 days when grown alone. The time between inoculation and sporulation (latent period) of 35 isolates of *U. necator* from *Vitis* was 5–6 days at 20 C on in vitro Chancellor grapevines. Sixteen of the 35 isolates from *Vitis* spp. did not infect in vitro plants of *Parthenocissus quinquefolia*, and the latent period among the remaining 19 isolates ranged from 10 to 26 days. Three of 35 isolates from *Vitis* sporulated in 5–18 days on in vitro plants of *Parthenocissus tricuspidata*. None of five isolates from *P. quinquefolia* and only one of six isolates from *P. tricuspidata* sporulated on in vitro Chancellor grapevines. Isolates from *Vitis* did not differ significantly in the rate of colony expansion on seedlings of *V. vinifera* L. but differed in rate of colony expansion on seedlings of *V. labruscana*. The rate of colony expansion of isolates from *P. quinquefolia* and *P. tricuspidata* was greatly reduced on seedlings of *V. vinifera* and *V. labruscana* as compared to growth on seedlings of either *Parthenocissus* sp. Growth of isolates from *P. quinquefolia* was reduced on seedlings of *P. tricuspidata*. However, on seedlings of *P. tricuspidata*, one isolate from the *Vitis* interspecific hybrid cultivar Rosette grew more rapidly than it did on seedlings of *V. vinifera* or *V. labruscana*. Pathogenic specialization was not evident when *Vitis* isolates were grown on in vitro grapevines of a mildew-susceptible cultivar (Chancellor) or on seedlings of a mildew-susceptible *Vitis* sp. (*V. vinifera*) but could be identified on seedlings of a mildew-resistant *Vitis* sp. (*V. labruscana*). Isolates collected from *Vitis* spp., *P. tricuspidata*, and *P. quinquefolia* are likely to be best adapted to grow upon their respective hosts. However, certain isolates of *U. necator* can colonize and sporulate upon both *Vitis* and *Parthenocissus* spp.

Additional keywords: cleistothecia, pathogenicity, powdery mildew, virulence.

The ascigerous state of *Uncinula necator* (Schwein.) Burrill has been identified as the sole source of primary inoculum for epidemics of grape powdery mildew in New York (33) and as an important source of overwintering inoculum in California (45). The initiation, development, dispersal, survival, and dehiscence of cleistothecia, germination of ascospores, and infection of *Vitis* by ascospores have been described (19–21). Certain isolates of *U. necator* are heterothallic (1,18,43), and this has a profound influence upon when ascocarps form during an epidemic (19). Furthermore, the presence of compatible mating types may determine whether ascocarps form at all. For example, cleistothecia did not form for nearly 50 yr after the introduction of *U. necator* to Europe (3,58,59), and cleistothecia have only recently been reported in Australia (53) and Peru (14). After 1890, cleistothecia were reported successively from most viticultural regions of Europe (3,4,6–8,17,28–31,39,42,48,50,51,56). However, as recently as 1978, there were still areas within Europe where their formation was rare (11,27).

Among the powdery mildews, only nine species have been reported to be heterothallic (1,5,13,18,23,25,26,32,37,40,57). Three of these, *Erysiphe polygoni* DC. (43), *E. graminis* DC. (12), and *Sphaerotheca fuliginea* (Schlectend.:Fr.) Pollacci (24), have also been reported to be homothallic. Isolates of *U. necator* collected from *Parthenocissus quinquefolia* (L.) Planch. (43) were heterothallic, as were isolates collected from *Vitis* spp. (1,18). Although heterothallism in the powdery mildews has been assumed to be bipolar (9), convincing evidence of this is lacking for *U. necator*. Crosses of randomly collected isolates of *U. necator* by Al-Agealy in Iraq (1) indicate the presence of three or more mating types. Our first objective was to clarify the nature of heterothallism in *U. necator*.

Pathogenic specialization among isolates of *U. necator* collected from the various genera of the Vitaceae has not been reported, although several researchers have investigated resistance to *U.*

necator in *Vitis* spp. and cultivars. The most comprehensive study of host resistance to powdery mildew in the Vitaceae was that of Boubals (10). Plants were inoculated as detached leaf cultures and were also observed in the vineyard for mildew development from natural infection. Twenty-five *Vitis* spp. were examined, including 12 North American species, 12 Asian species, and 159 cultivars of *Vitis vinifera*. Although he attempted to identify sources of resistance to *U. necator*, the results were inconclusive, and poor correlations were often found between resistance in the laboratory and in the field. However, the mildew conidia for inoculations were collected from various greenhouse and vineyard plants, without regard to the possibility of pathogenic specialization. Thus, the results can only be discussed in the context of exposing plants to isolates of unknown pathogenicity and virulence. There have been many other reports of the relative susceptibility of grape species or cultivars to powdery mildew (3,11,15,16,22,35,36,44,47,49,55), but we are unaware of any study that has dealt with the possibility that pathogenic specialization could affect the results.

Pathogenic specialization is common in powdery mildews. Powers and Moseman (38) reported wide variation in pathogenicity from a collection of isolates derived from single ascospores of *Erysiphe graminis* DC and *E. g.* f. sp. *hordei* Em. Marchal. They recovered up to three pathogenic races from a single cleistothecium. Evidence on the importance of recombination in pathogenic variation in powdery mildews was provided by Welz and Kranz (52), who found higher frequencies of rare races, rare virulence factors, and greater diversity among progeny from ascospores of *E. g. hordei* as compared to conidial populations.

The evidence for pathogenic specialization in *U. necator* in previous studies is largely circumstantial and is based on inconsistencies in reports of the relative susceptibility of various grape species and cultivars. For example, Bulit and Lafon (11) reported that the North American species *V. labrusca* L. and *V. riparia* Michx. are "practically immune" to infection in Europe. However, in New York, 20–50% fruit infection is common on unsprayed vines of these species. The *Vitis* interspecific hybrid cultivar Vidal blanc is reported to be highly resistant to powdery mildew in Germany (46), and yet it is highly susceptible to powdery mildew in New York, USA (55). The inconsistency of relative susceptibility is temporal as well as spatial. In 1945, Suit (47) reported that fruit of the *Vitis* interspecific hybrid cultivars Dutchess and Missouri Riesling were uninfected and slightly infected, respectively, in New York vineyards, whereas *V. labruscana* L. H. Bailey 'Concord' was highly susceptible and was severely diseased. In New York in 1987, Missouri Riesling was rated as extremely susceptible to powdery mildew, whereas Dutchess and Concord were both rated as moderately susceptible (55).

In this paper, we report on an investigation of pathogenic specialization of *U. necator* on host genera within the Vitaceae and at the species level in *Vitis*. Our second objective was to determine the host range, virulence, and pathogenicity of isolates of *U. necator* collected from *Vitis* and *Parthenocissus* spp.

MATERIALS AND METHODS

Host plants. Methods for the production of in vitro grapevines have been described previously (19) and were used in this study to produce in vitro plants of *Vitis* and *Parthenocissus*. The in vitro plants were grown to a height of approximately 8 cm and bore three to five leaves before they were inoculated with *U. necator*. Seedlings were produced by harvesting ripe fruit of *V. vinifera* 'White Riesling,' *V. labruscana* 'Catawba,' wild *Parthenocissus quinquefolia*, and wild *P. tricuspidata* (Siebold & Zucc.) Planch. The fruit were crushed in barrels, and seeds were separated from the buoyant pulp and skins in water. The seeds were stratified in moist Perlite at 4 C for 8–12 wk. Seeds were germinated on moist filter paper at 20 C, and the germlings were planted in soil in 400-ml paper cups. Seedlings were grown in the greenhouse under natural light until they bore four true leaves.

Collection and maintenance of isolates of *U. necator*. The host plant and geographic location from which each isolate was collected is given in Table 1. Within a laminar-flow transfer hood, mildew colonies on leaves were viewed under a stereo microscope

TABLE 1. Origin of isolates of *Uncinula necator*

Isolate	Host	Location
268-1-CA	*V. vinifera* 'Chardonnay'	Bakersfield, CA
Vitis solonis GV21	*V. solonis*	Geneva, NY
V. rubra GV25	*V. rubra*	Geneva, NY
V. riparia F	*V. riparia*	Fredonia, NY
V. riparia D-HG	*V. riapria*	Dresden, NY
V. labrusca SRI	*V. labrusca*	Scituate, RI
V. champinii GV25	*V. champinii*	Geneva, NY
V. californica CA	*V. californica*	Davis, CA
V. berlandieri GV25	*V. berlandieri*	Geneva, NY
V. betulifolia GV42	*V. betulifolia*	Geneva, NY
V. argentifolia GV25	*V. argentifolia*	Geneva, NY
Steuben-VA	*Vitis* interspecific hybrid Steuben	Winchester, VA
Stover-LFL	*Vitis* interspecific hybrid Stover	Leesburg, FL
Rosette-N-11	*Vitis* interspecific hybrid Rosette	Naples, NY
Rosette-N-1	*Vitis* interspecific hybrid Rosette	Naples, NY
Riesling-G-HG	*V. vinifera* 'White Riesling'	Geneva, NY
Riesling-F	*V. vinifera* 'White Riesling'	Fredonia, NY
Pinot Noir-G-2	*V. vinifera* 'Pinot Noir'	Geneva, NY
Pinot Noir-G-1	*V. vinifera* 'Pinot Noir'	Geneva, NY
Niagara-F	*V. labruscana* 'Niagara'	Fredonia, NY
Ives-F	*V. labrusca* 'Ives'	Fredonia, NY
Elvira-F-HG	*Vitis* interspecific hybrid Elvira	Fredonia, NY
Elvira-F-2	*Vitis* interspecific hybrid Elvira	Fredonia, NY
Elivra-F-1	*Vitis* interspecific hybrid Elvira	Fredonia, NY
Delaware-F-HG	*Vitis* interspecific hybrid Delaware	Fredonia, NY
Delaware-F	*Vitis* interspecific hybrid Delaware	Fredonia, NY
Concord-F-DC	*V. labruscana* 'Concord'	Fredonia, NY
Concord-F	*V. labruscana* 'Concord'	Fredonia, NY
Chardonnay-LI-3	*V. vinifera* 'Chardonnay'	Riverhead, NY
Chardonnay-LI-2	*V. vinifera* 'Chardonnay'	South Hampton, NY
Chardonnay-LI-1	*V. vinifera* 'Chardonnay'	Riverhead, NY
Bunchgrape-NCSU-4	*Vitis* interspecific hybrid, unnamed	Raleigh, NC
Bunchgrape-NCSU-1	*Vitis* interspecifc hybrid, unnamed	Raleigh, NC
Aurore-D-HG	*Vitis* interspecific hybrid Aurore	Dresden, NY
Boston Ivy-1	*Parthenocissus tricuspidata*	Geneva, NY
Boston Ivy-2	*P. tricuspidata*	Amherst, MA
Boston Ivy-3	*P. tricuspidata*	Ithaca, NY
Boston Ivy-4	*P. tricuspidata*	Geneva, NY
Boston Ivy-5	*P. tricuspidata*	Geneva, NY
Boston Ivy-6	*P. tricuspidata*	Framingham, MA
Virginia Creeper-1	*P. quinquifolia*	Geneva, NY
Virginia Creeper-2	*P. quinquifolia*	Naples, NY
Virginia Creeper-3	*P. quinquifolia*	Naples, NY
Virginia Creeper-4	*P. quinquifolia*	Ithaca, NY
Virginia Creeper-5	*P. quinquifolia*	Seneca, NY

at ×70, and an individual chain of conidia was removed from the mildew colony with an eyelash fastened to a Pasteur pipette. The conidia were transferred to a detached healthy leaf in a double petri plate (33). The eyelash was sterilized in 70% ethanol and allowed to dry between transfers. After 7–14 days, colonies on leaves in double petri plates were subcultured again as above and then transferred to in vitro plants in 75-mm glass culture tubes. Mildew isolates were maintained at 20 C in a 12-h photoperiod and transferred aseptically to new in vitro plants every 4–8 weeks.

Mating of isolates from *Vitis* spp. Thirty-five isolates were paired in all 630 possible combinations on in vitro plants of the *Vitis* interspecific hybrid cultivar Chancellor (Fig. 1). The inoculated plants were incubated as described above for 60 days. At 3- to 7-day intervals, the plants were observed at ×30 for the production of cleistothecia. The number of days until the appearance of immature ascocarps was recorded, and at 60 days after inoculation the number of mature cleistothecia per cm^2 of leaf surface was recorded for each plant. Inoculations were replicated three times on separate plants, and the experiment was repeated twice. An additional four repetitions of this experiment were performed using only the isolate pairings presented in Figure 2.

Viability of ascospores in each mating was assessed 80 days after inoculation. Five groups of 10 cleistothecia were crushed on glass slides in water, stained as described by Widholm (54)

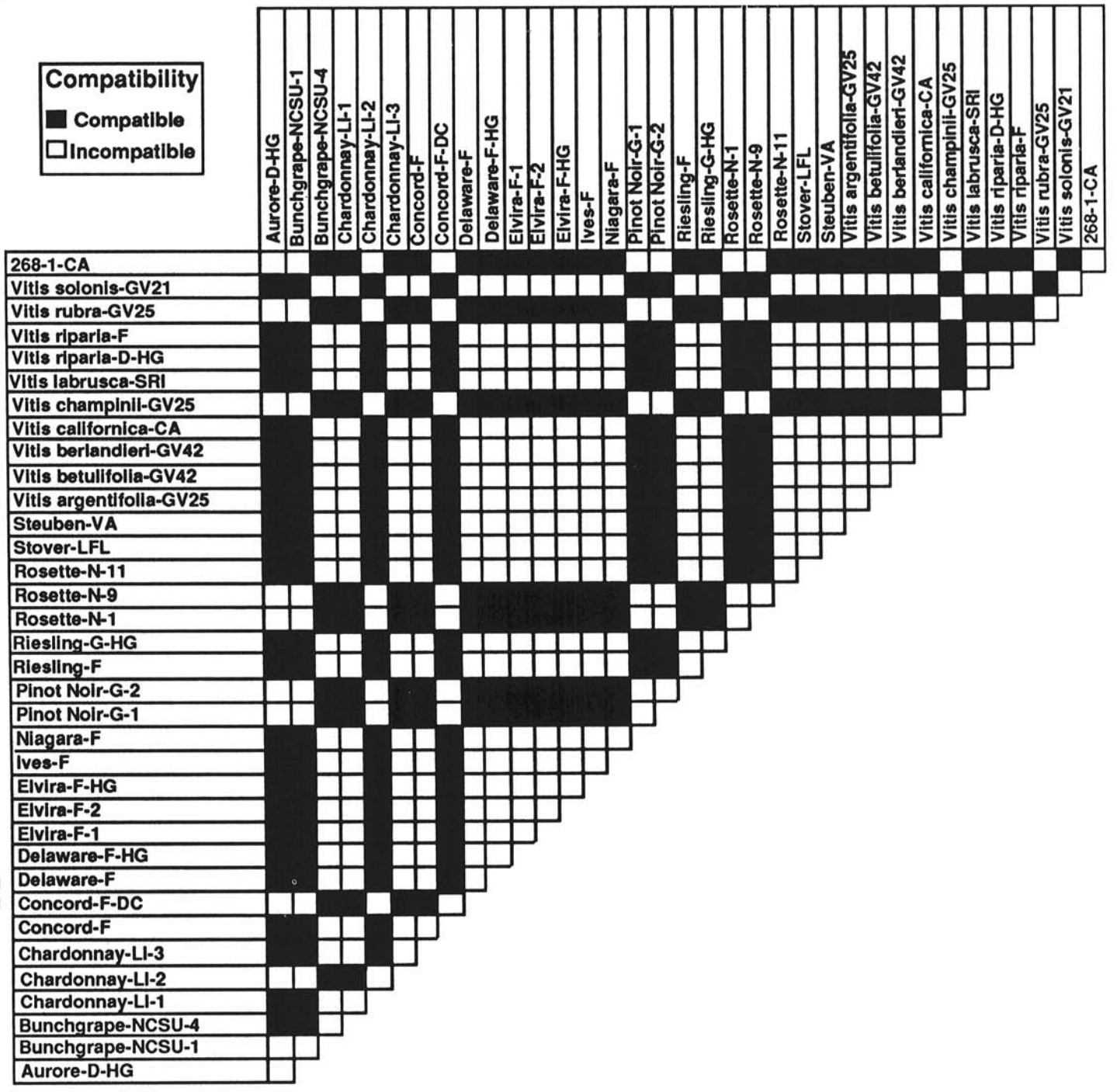

Fig. 1. Results of matings of 35 isolates of *Uncinula necator* from *Vitis* spp. 14 days after inoculation of in vitro Chancellor grapevines. A pairing was deemed to be compatible if one or more of the three replicate grapevines bore ascocarps in both repetitions of the experiment. Incompatible pairings produced no ascocarps within 14 days after inoculation.

with 1% fluorescein diacetate (Sigma Chemical Co., St. Louis, MO), and viewed under fluorescence microscopy. Viable ascospores displayed a bright green fluorescence. Cleistothecia from 25 matings in Figure 1 and all matings in Figure 2 were overwintered on the vineyard floor in mesh bags (33) until April, when viability of ascospores was assessed. Cleistothecia were also induced to discharge ascospores onto glass slides as described by Pearson and Gadoury (33). Ascospores from three groups of 10 cleistothecia were counted, and the percent ascospore germination in water after 24 h at 20 C was determined.

Pathogenicity and latent period of isolates on in vitro plants of *Vitis* and *Parthenocissus*. The ability to colonize leaf tissue and the length of time required for sporulation were determined for 35 isolates of *U. necator* from *Vitis* spp., six isolates from *P. tricuspidata*, and five isolates from *P. quinquefolia*. Three in vitro grapevines of the cultivar Chancellor and three in vitro plants of *P. quinquefolia* and *P. tricuspidata* were inoculated with each isolate, and the experiment was repeated.

Rate of colony expansion of isolates on seedlings of *Vitis* and *Parthenocissus*. Aqueous suspensions of conidia were prepared by vortex-mixing of an infected leaf from an in vitro plant in a 75-mm culture tube containing 5 ml of distilled water and 0.05% Tween-20 surfactant (Sigma, St. Louis, MO). The youngest expanded leaf of a four-leaved seedling was inoculated with a single 20-μl drop of the conidial suspension containing 10^4–10^5 conidia per milliliter. Thirty-five isolates from *Vitis*, six isolates from *P. tricuspidata*, and five isolates from *P. quinquefolia* were tested on seedlings of *V. vinifera, V. labruscana, P. quinquefolia*, and *P. tricuspidata*. Colony diameters on five seedlings were measured 7 and 14 days after inoculation and the growth rate computed as the mean daily increase of colony diameter. The experiment was repeated twice.

RESULTS

Mating of isolates from *Vitis* spp. Within 14 days after inoculation of in vitro plants, cleistothecia had been initiated in several isolate pairings (Fig. 1). An analysis of the data indicated that there were two mutually exclusive mating types. For example, isolate 268-1-CA formed ascocarps when paired with isolate *V. solonis* GV21, and the two were therefore compatible mating types. No isolate compatible with 268-1-CA was compatible with *V. solonis* GV21; that is, all isolates compatible with 268-1-CA were of the same mating type as *V. solonis* GV21 and were therefore incompatible with *V. solonis* GV21. This mutual exclusivity of two opposite mating types was consistent in all pairings 14 days after inoculation (Fig. 1) and is typical of bipolar heterothallic systems in other ascomycetes (2). However, between 45 and 60 days after inoculation, in certain pairings with the isolates *V. labrusca*-SRI, Ives-F, and Concord-F-DC, cleistothecia were initiated and matured (Fig. 2). Ives-F formed ascocarps when paired with itself after 45 days (Fig. 2), but tissues within the ascocarp did not differentiate.

In isolate pairings that were compatible within 14 days, cleistothecia were abundant on leaves 60 days after inoculation. The number of ascocarps per cm^2 of infected leaf tissue ranged from 239 to 526. In isolate pairings in which ascocarp formation was delayed until 45 days after inoculation, ascocarps were sparsely distributed and density ranged from 2 to 11 per cm^2 of infected leaf tissue. Although early formation of ascocarps resulted in significantly ($P = 0.001$) greater numbers of ascocarps, differences among matings in the number of ascocarps produced per cm^2 of infected leaf tissue within these two groups (early compatibility and delayed compatibility) were not significant ($P = 0.05$).

Viable ascospores were found in 95–100% of cleistothecia from each pairing 80 days after inoculation. This percentage decreased to 22–64% by April of the following spring. Germination of discharged ascospores ranged from 54 to 81%. Neither initial viability, survival during winter, nor germinability of ascospores was significantly affected ($P = 0.05$) by the choice of parental isolates.

Pathogenicity and latent period of isolates of *U. necator* on *Vitis* and *Parthenocissus* spp. There was little difference in the latent period among isolates obtained from *Vitis* spp. on in vitro grapevines of the cultivar Chancellor. Twenty-nine isolates sporulated 6 days after inoculation, and six isolates sporulated on day five (Table 2). Isolates from *Vitis* reproduced slowly or not at all on in vitro plants of *P. quinquefolia*, and the latent period ranged from 10 to 26 days (Table 2). None of five isolates from *P. quinquefolia* and only one of six isolates from *P. tricuspidata* sporulated on in vitro Chancellor plants. Isolates from *P. quinquefolia* sporulated in 9–11 days on *P. tricuspidata*, compared to 5–6 days on *P. quinquefolia*. Isolates from *P. tricuspidata* sporulated in 7–8 days on *P. tricuspidata* but did not sporulate on *P. quinquefolia*. Three isolates from *Vitis* sporulated in 5–18 days on *P. tricuspidata* (Table 2).

Rate of colony expansion of isolates of *U. necator* on *Vitis* and *Parthenocissus* spp. Isolates of *U. necator* from *Vitis* spp. did not differ significantly ($P = 0.05$) in the rate of colony expansion on seedlings of *V. vinifera*, but they differed in rate of colony expansion and sporulation on seedlings of *V. labruscana* (Table 3). The rate of colony expansion of isolates from *Parthenocissus* spp. was greatly reduced on seedlings of *V. vinifera* and *V. labruscana* as compared to growth rate on seedlings of either *Parthenocissus* spp. (Table 3). Growth of most but not all isolates from *P. quinquefolia* was reduced on seedlings of *P. tricuspidata* (Table 3). However, on seedlings of *P. tricuspidata*, growth of one isolate from the *Vitis* interspecific hybrid cultivar Rosette was greater than that obtained when the isolate was grown

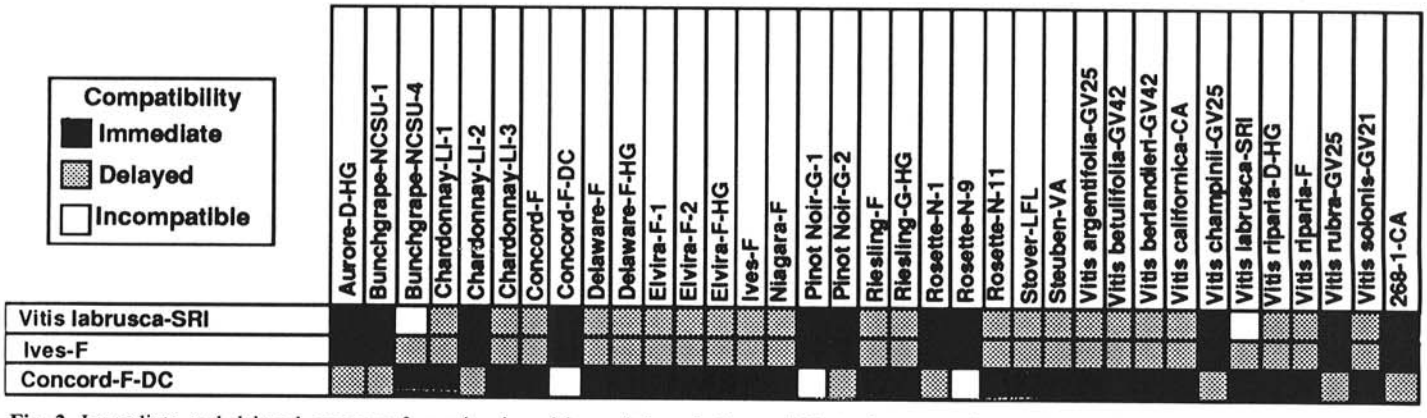

Fig. 2. Immediate and delayed ascocarp formation in pairings of three isolates of *Uncinula necator* from *Vitis* spp between 14 and 60 days after inoculation of in vitro Chancellor grapevines. A pairing was immediately compatible if ascocarps were borne within 14 days of inoculation on one or more of three replicate grapevines in four repetitions of the experiment. Delayed compatibility was indicated by appearance of ascocarps 45–60 days after inoculation on one or more of three replicate grapevines in four repetitions of the experiment. Incompatible pairings produced no ascocarps within 60 days after inoculation.

on seedlings of *V. vinifera* or *V. labruscana* (Table 3).

DISCUSSION

Heterothallism in *U. necator*. Results of crosses viewed 14 days after inoculation indicated the existence of two mutually exclusive mating types, and a possible bipolar heterothallic system (2). However, in protracted associations, three isolates (*V. labrusca*-SRI, Ives-F, and Concord-F-DC) had the capacity to initiate and mature cleistothecia when paired with isolates that initially appeared to be incompatible. This trait was not associated with a single mating type: Concord-F-DC formed cleistothecia readily with both *V. labrusca*-SRI and Ives-F. Furthermore, in 4 yr of growth as clonal isolates, no isolate produced ascocarps when grown alone, with the exception of Ives-F. Ives-F occasionally produced sterile ascocarps when two colonies of the isolate merged, indicating that merging of colonies might be a partial determinant of ascocarp initiation. Any possible pairing could therefore have four possible outcomes: 1) ascocarps form readily and abundantly, 2) ascocarp initiation is delayed and production is sparse, 3) sterile ascocarps devoid of ascogenous contents are produced, and 4) no ascocarps are initiated. Selection of parental isolates and whether ascocarp initiation was immediate or delayed did not appear to influence ascocarp survival or germination of ascospores.

Heterothallism in *U. necator* could explain several reports in the literature in which ascocarp formation was correlated with disease incidence and severity, host plant senescence, and host resistance (4,19,41). As pairing of compatible mating types is delayed by low disease incidence, or as disease development is delayed by high host resistance, ascocarp initiation would be delayed commensurately. The complex nature of this heterothallism may also explain the pattern of ascocarp

TABLE 2. Pathogenicity, mean latent period, and standard error of latent period (in parentheses), of isolates of *Uncinula necator* on in vitro vines of *Vitis* and *Parthenocissus*

Isolate	Latent period (days) on[z]		
	Vitis interspecific hybrid Chancellor	*P. quinquefolia*	*P. tricuspidata*
268-1-CA	6 (0)	19 (1.1)	F
V. solonis GV21	6 (0)	19 (1.2)	F
V. rubra GV25	6 (0)	F	F
V. riparia F	6 (0)	19 (1.5)	F
V. riparia D-HG	6 (0)	19 (1.7)	F
V. labrusca SRI	5 (0)	M	F
V. champinii GV25	6 (0)	15 (2.0)	F
V. californica CA	6 (0)	F	F
V. berlandieri GV25	6 (0)	10 (1.1)	F
V. betulifolia GV42	6 (0)	19 (1.8)	F
V. argentifolia GV25	6 (0)	F	F
Steuben-VA	5 (0)	16 (1.5)	F
Stover-LFL	6 (0)	F	F
Rosette-N-11	5 (0)	10 (0)	5 (0)
Rosette-N-9	6 (0)	M	9 (1.3)
Rosette-N-1	6 (0)	19 (0.8)	18 (1.3)
Riesling-G-HG	6 (0)	19 (1.6)	F
Riesling-F	6 (0)	F	F
Pinot Noir-G-2	6 (0)	F	F
Pinot Noir-G-1	6 (0)	F	F
Niagara-F	6 (0)	26 (2.2)	F
Ives-F	6 (0)	F	F
Elvira-F-HG	5 (0)	F	F
Elvira-F-2	6 (0)	F	F
Elvira-F-1	6 (0)	F	F
Delaware-F-HG	6 (0)	26 (2.5)	F
Delaware-F	6 (0)	F	F
Concord-F-DC	6 (0)	F	F
Concord-F	5 (0)	F	F
Chardonnay-LI-3	6 (0)	21 (1.9)	F
Chardonnay-LI-2	5 (0)	19 (1.0)	F
Chardonnay-LI-1	6 (0)	26 (2.9)	F
Bunchgrape-NCSU-4	6 (0)	F	F
Bunchgrape-NCSU-1	6 (0)	F	F
Aurore-D-HG	6 (0)	16 (0.6)	F
Boston Ivy-1	20 (1.5)	F	8 (0)
Boston Ivy-2	M	F	7 (1.4)
Boston Ivy-3	M	F	8 (0)
Boston Ivy-4	F	F	8 (0)
Boston Ivy-5	F	F	8 (0)
Boston Ivy-6	F	F	8 (0)
Virginia Creeper-1	F	5 (0)	10 (1.7)
Virginia Creeper-2	F	5 (0)	9 (0.8)
Virginia Creeper-3	F	6 (0)	11 (1.3)
Virginia Creeper-4	F	6 (0)	10 (1.0)
Virginia Creeper-5	F	6 (0)	10 (1.3)

[z] M indicates mycelial growth only when the experiment was terminated 30 days after inoculation. F indicates failure of the isolate to infect the plant.

TABLE 3. Rate of colony expansion of isolates of *Uncinula necator* on seedlings of *Vitis labruscana, V. vinifera, Parthenocissus quinquefolia*, and *P. tricuspidata*

Isolate	Rate of colony expansion (μm/day) on[z]			
	V. vinifera	*V. labruscana*	*V. quinquefolia*	*P. tricuspidata*
268-1-CA	96.5 a	28.3 a	16.1 a	F
V. solonis GV21	93.5 a	40.3 a	26.3 a	F
V. rubra GV25	96.2 a	38.5 a	F	F
V. riparia F	125.0 a	29.6 a	13.8 a	F
V. riparia D-HG	90.9 a	93.2 b	27.2 a	F
V. labrusca SRI	130.1 a	108.1 b	15.4 a	F
V. champinii GV25	91.2 a	22.7 a	18.9 a	F
V. californica CA	126.3 a	36.3 a	F	F
V. berlandieri GV25	93.3 a	68.2 c	38.1 b	F
V. betulifolia GV42	117.6 a	27.4 a	22.0 a	F
V. argentifolia GV25	91.8 a	56.1 b,c	F	F
Steuben-VA	98.8 a	25.9 a	13.7 a	F
Stover-LFL	137.1 a	33.5 a	F	F
Rosette-N-11	91.1 a	32.5 a	24.2 a	46.2 a
Rosette-N-9	102.9 a	101.6 b	14.3 a	178.5 b
Rosette-N-1	134.0 a	114.2 b	16.9 a	52,8 a
Riesling-G-HG	82.4 a	65.0 b,c	16.5 a	F
Riesling-F	86.3 a	36.2 a	F	F
Pinot Noir-G-2	92.9 a	89.8 b	F	F
Pinot Noir-G-1	109.4 a	78.0 b	F	F
Niagara-F	87.2 a	25.5 a	11.8 a	F
Ives-F	95.1 a	31.3 a	F	F
Elvira-F-HG	100.6 a	44.5 a	F	F
Elvira-F-2	106.3 a	21.7 a	F	F
Elvira-F-1	84.9 a	112.4 b	F	F
Delaware-F-HG	93.0 a	61.8 c	23.1 a	F
Delaware-F	98.9 a	45.2 a	F	F
Concord-F-DC	125.3 a	27.6 a	F	F
Concord-F	91.4 a	37.4 a	F	F
Chardonnay-LI-3	111.3 a	32.6 a	26.8 a	F
Chardonnay-LI-2	99.3 a	105.7 b	19.3 a	F
Chardonnay-LI-1	87.9 a	66.9 b,c	16.8 a	F
Bunchgrape-NCSU-4	129.2 a	34.2 a	F	F
Bunchgrape-NCSU-1	102.6 a	90.4 b	F	F
Aurore-D-HG	93.4 a	28.1 a	20.0 a	F
Boston Ivy-1	15.3 b	F	F	168.2 d
Boston Ivy-2	30.5 b	8.1 d	F	229.4 d
Boston Ivy-3	17.3 b	F	F	142.9 b
Boston Ivy-4	F	F	F	94.1 c
Boston Ivy-5	F	F	F	114.7 c
Boston Ivy-6	F	F	F	191.0 b,d
Virginia Creeper-1	F	F	205.5 c	92.9 c
Virginia Creeper-2	F	46.4 a	188.2 c	78.6 c
Virginia Creeper-3	F	F	165.0 c	85.7 c
Virginia Creeper-4	F	F	31.4 a	139.3 b
Virginia Creeper-5	F	F	179.8 c	84.1 c

[z] Growth rate was the mean daily diameter increase of mildew colonies between 7 and 14 days after inoculation. Numbers within columns followed by the same letter do not differ significantly at $P = 0.05$. F indicates failure of the isolate to infect the plant.

production seen when *U. necator* was introduced to Europe. For nearly 50 yr after its introduction to Europe in the mid-19th century, *U. necator* failed to produce cleistothecia (3,58,59). Thereafter, for a period of approximately 40 yr, there are reports from throughout Europe of the discovery of cleistothecia, but with the observation that they were formed sparsely, sporadically, and very late in the growing season (3,7,17,28,29). After 1939, cleistothecia were reported to be produced regularly and abundantly in several areas in Europe (4,6,31,42,48,51,56). Nonetheless, in 1978, there were areas in Europe where their occurrence was rare (11,27). This sequence of events could be explained by the initial introduction of a single mating type in the mid-19th century, as suggested in 1939 by Peyronel (34). This may have been followed by the introduction of an isolate that formed ascocarps only in protracted associations, resulting in sporadic and sparse production of cleistothecia. Isolates that were readily compatible and produced cleistothecia abundantly may have been introduced after 1939 or may have arisen naturally through recombination or mutation.

The phenomenon of delayed compatibility observed in certain isolates of *U. necator* may also explain how results of pairings performed by Al-Agealy (1) could indicate the existence of three or more mating types. Existence of this ability in other genera of powdery mildews could also explain the variability observed in thallism of *E. polygoni* (43), *E. graminis* (12,23,37), and *S. fuliginea* (24,25). Whether isolates appear to be homothallic or heterothallic may be related to the length of time that they are paired. Had we terminated our pairing experiments after 14 days, we would have concluded that *U. necator* was heterothallic and was composed of only two mating types. If a preponderance of isolates in a collection have the capacity to form ascocarps with most other isolates in protracted associations and only success or failure to form ascocarps is recorded, the isolate collection would appear to be homothallic.

Pathogenic specialization in *U. necator*. Pathogenic specialization among isolates from *Vitis* spp. could not be detected on Chancellor in vitro plants or on seedlings of *V. vinifera*. Both Chancellor and most cultivars of V. vinifera are highly susceptible to powdery mildew (15,55). On the more resistant *V. labruscana*, isolates differed greatly in the rate of colony expansion. Isolates from *Vitis* spp. also differed greatly in pathogenicity and latent period on in vitro plants and seedlings of *P. quinquefolia* and *P. tricuspidata*. The detection of variation in virulence among isolates required the involvement of substantial host resistance. Our results indicate that most isolates from *Vitis* have the capacity to be equally virulent on highly susceptible hosts, and that virulence on resistant hosts is not due to the inherent rapid growth of an isolate per se, but requires the specific ability to overcome host resistance.

In general, isolates collected from *Vitis* spp. were best adapted to grow upon *Vitis* spp. and grew slowly or not at all on seedlings of *Parthenocissus* spp. Within the genus *Parthenocissus*, growth of isolates from *P. quinquefolia* was reduced on *P. tricuspidata*. However, three *Vitis* isolates grew rapidly on *P. tricuspidata*. It is not surprising that isolates should be found growing upon those plants that proved to be the best host. Nonetheless, certain isolates of *U. necator* have a host range that spans genera within the Vitaceae.

The substantial variation observed in rate of colony expansion of *Vitis* isolates on *V. labruscana* illustrates one of the pitfalls of evaluating host resistance either with a small number of isolates or with isolates of unknown pathogenicity and virulence. Pathogenic specialization and variations in virulence among isolates may be one reason for the spatial and temporal inconsistencies in reports of host resistance in *Vitis* spp. and cultivars (11,46,47,55). Furthermore, collections of isolates from highly susceptible cultivars of *V. vinifera* may contain many isolates with relatively low virulence towards *V. labruscana* or other more resistant species. Thus, there are two factors to consider in evaluating the resistance of a *Vitis* clone to *U. necator*: 1) the proportion of isolates within the pathogen population to which the clone has a significant level of resistance, and 2) the degree of resistance in the clone to the most virulent isolates.

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