Transmission of *Mucor piriformis* to Fruit of *Prunus persica* by *Carpophilus* spp. and *Drosophila melanogaster*

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ABSTRACT

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Vinegar flies (*Drosophila melanogaster*) and nitidulid beetles (*Carpophilus hemipterus* and *C. freemani*) captured in peach and nectarine orchards in California were found to be contaminated with *Mucor piriformis, Rhizopus stolonifer, Monilinia fructicola, Cladosporium* spp., *Penicillium* spp., and other species of *Mucor*. *D. melanogaster* and *Carpophilus* spp. acquired propagules of *M. piriformis* and transferred them to 75–100% of injured peach fruit. In general, *C. hemipterus* transmitted *M. piriformis* to wounded fruit more efficiently than *C. freemani*. Propagules of *M. piriformis* persisted for at least 15 days on *D. melanogaster* and 11 days on *C. hemipterus*. Only the nitidulid beetles transmitted the fungus to uninjured peach fruit, causing fruit rot on 42–75% of uninjured fruit.

Each year, fruit rots caused by a complex of fungi result in significant losses of stone fruits in California. *Monilinia fructicola* (Wint.) Honey (cause of brown rot), *Rhizopus stolonifer* (Ehrenb.:Fr.) Vuill. (cause of Rhizopus rot), *Gilbertella persicaria* (Eddy) Hesseltine (cause of Gilbertella rot), and *Botrytis cinerea* Pers.:Fr. (cause of gray mold) can all cause serious damage on fruit held at ripening temperatures. Sporadic isolation over the past several years of *Mucor piriformis* Fischer from stone fruits held in cold storage (6) suggests that it too can cause serious postharvest rot of peach (*Prunus persica* (L.) Batsch) and nectarine (*P. persica* var. *nectarina* (Aiton) Maxim.).

In 1977, a significant amount of Mucor decay developed during cold-temperature transit of fresh-market peaches from California to the East Coast and of fresh-market nectarines from Chile to California (6). We observed abundant sporulation of *M. piriformis* on pear fruit found on the orchard floor in Oregon and suggested that insects might be involved in the spread of fungal propagules (8). Peach and nectarine decay in California caused by *R. stolonifer* and *Monilinia fructicola* and tomato decay caused by *M. hiemalis* Wehmer, *Geotrichum candidum* Link, and *Rhizopus* and *Alternaria* spp. have been associated with increased activity of nitidulid beetles (14) and vinegar flies (1,2), respectively. These same insect species, which are attracted to bark wounds on tree trunks, also vector the canker-causing pathogen *Ceratocystis fimbriata* Ellis & Halst. (11).

Insects influence the development of plant diseases in several ways, one being the dissemination of pathogens (5,15). Nitidulid beetles have been reported as vectors of brown rot and Rhizopus rot fungi in stone fruit orchards in California (14). This study was undertaken to determine whether nitidulid beetles and vinegar flies are responsible for the dissemination of *M. piriformis* in peach and nectarine fruit and to ascertain their role in the life cycle of the fungus.

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MATERIALS AND METHODS

Isolates. Two isolates of *M. piriformis* were used, one from a decayed peach in California (isolate CA [ATCC 52555]) and another from a decayed nectarine shipped from Chile to California (isolate CH [ATCC 52554]) (7).

Incidence of decayed fruits and use of healthy fruit to bait decay pathogens. We examined 100 decaying peaches of cultivar Carnival, 400 decaying peaches of cultivar Halloween, and 125 decaying nectarines of cultivar Autumn Grand on the floor of three orchards in Parlier in September 1982. Sporulating fungi were identified directly on decayed fruit. When field identifications could not be made, fruit tissues from the margins of decay lesions were placed on potato-dextrose agar (PDA) slants for subsequent isolation and identification of organisms.

Healthy peaches (cv. Halloween) were harvested from orchard trees at the University of California Kearney Agricultural Center (UCKAC) in Parlier and were placed directly in plastic cases. The stylar ends of fruits were rubbed with cheesecloth moistened with 70% ethanol to surface-sterilize them. Fifteen peaches in each case were wounded (4 mm deep) at five points with a cork borer (5-mm inner diameter), and five fruits per case were left unwounded to act as controls. Ten cases were distributed randomly in a commercial peach orchard in Parlier, and the fruits were left exposed from 4 p.m. until noon the next day. In addition to the uncovered cases, two cases (each with 15 wounded and five unwounded fruit) wrapped in insect-proof nylon mesh (0.25-mm^2 opening) were also placed in the orchard at the same time. All cases were collected and incubated at 0 C for 40 days. Four additional cases, each with 15 wounded and five unwounded fruit but with no field exposure, were incubated directly at 0 C for 40 days.

Pathogen acquisition and transmission: Field and laboratory trials. On 19 August 1982, 22 healthy peach fruit (cv. Fay Elberta) were wounded with a glass rod 2 mm in diameter, inoculated with 50 μl of a suspension containing 1.2×10^5 sporangiospores of *M. piriformis* per milliliter, and placed under two peach trees in an orchard in Davis where *M. piriformis* had not been detected in the soil in July 1982. In addition, 22 healthy and 22 wounded, uninoculated peaches were put into insect-proof cages or placed directly on the ground. After a 4- to 5-

day exposure, incidence of decay was recorded, and all fruits were returned to the laboratory and incubated at 0 C for 15 days.

When the fruits were gathered, 100 nitidulid beetles (*Carpophilus hemipterus* L. and *C. freemani* Dobson) and 100 vinegar flies (*Drosophila melanogaster* Meig.) were collected in plastic bags from each experimental area. All insects of each species were plated on dishes (10 insects per dish) of acidified PDA (APDA) and incubated at 4 C for 10 days. The entire experiment was repeated in September 1982 with Elberta peaches and again in October 1982 with Halloween peaches.

This experiment was also repeated in July, August, and September of 1983. For each treatment, 20 Elberta peaches were placed beneath each of three replicate trees on each date. Nitidulid beetles were collected from each experimental site, plated on APDA, and examined for development of *M. piriformis* as described above.

Pathogen-free (determined by plating insects on APDA) colonies of *D. melanogaster, C. hemipterus,* and *C. freemani* (obtained from the Stored-Product Insect Laboratory, Agricultural Research Service, U.S. Department of Agriculture, Fresno, CA) were used in laboratory experiments. Culture containers were 1,150-ml widemouthed glass jars with insect screen tops. To minimize fungus and mite contamination, a Whatman No. 40 filter paper was placed beneath the screen. Pathogen-free insects were fed autoclaved figs twice a week and were subcultured on fresh autoclaved figs. Beetles and flies were transferred to the fresh food source with an aspirator.

Ten insects of each species were placed in plastic bags for 24 hr with nectarines decayed by *M. piriformis.* They were then removed, plated on APDA, and incubated at 4 C for 10 days. Other groups of insects (five to 10 per species) were allowed to feed for the same 24-hr period on sterile dried figs, a culture of *M. piriformis* on PDA, or a nectarine fruit decayed by *M. piriformis.* These insects were then placed in plastic containers with four peaches and nectarines that had each been wounded five times on the stylar end with a glass rod 2 mm in diameter. The plastic containers were enclosed in plastic bags with a jar-lid screen with 0.25-mm^2 openings for air exchange. After 24–48 hr, the insects were removed and plated on dishes of APDA, which were then incubated at 4 C for 10 days. The plastic bags were discarded, and the containers were covered, incubated at 4 C for 10 days, and evaluated for decay of fruit. Excretions from *C. hemipterus* were also collected, plated on APDA dishes, and incubated at 4 C for 10 days. Each treatment was replicated three times, and the experiment was repeated twice. The experiment was again repeated the following year with the same insect species on peach (cv. Fay Elberta) and plum (*Prunus domestica* L. 'Casselman') fruit.

Assays of insects for contamination with *Mucor* spp. A total of 240 vinegar flies and 200 nitidulid beetles were randomly collected from nectarine fruits decaying from infection by *Monilinia fructicola* and/or *R. stolonifer* on the orchard floor at UCKAC. All insects were frozen overnight at −6 C, transferred to dishes of APDA, and incubated at 4 C for 4 days to permit germination of *M. piriformis* propagules while suppressing development of other common decay fungi. The dishes were then incubated at 0 C for 20 more days, and fungal colonies were identified and recorded. *M. piriformis* and other *Mucor* spp. were easily identified by their characteristic sporulation.

In two Fay Elberta peach orchards where fruit decaying from Rhizopus rot and brown rot were plentiful, *Carpophilus* spp., abundant on both types of decayed fruit, were collected and plated in one of the following ways: 1) on APDA dishes (five to eight insects per dish) incubated at room temperature (23 ± 1 C) for 3–4 days; 2) on APDA dishes incubated at 0–1 C for 30 days; 3) on PDA dishes amended with 5 μg of dicloran (Botran 75W) per millimeter of medium (to prevent development of *R. stolonifer*) and incubated at room temperature for 5 days. Fungal colonies were identified and recorded.

Persistence of *M. piriformis* in the insect species. Persistence of *M. piriformis* on vinegar flies and nitidulid beetles was studied in the field transmission experiments in October 1982 and September 1983. One hundred flies were collected 2 days before inoculation, on the day peaches were inoculated with *M. piriformis,* and 0, 1, 3, 5, 7, and 11 days after fruit was removed from the field. The flies were captured from the area surrounding the experimental fruit with a sweep net. One hundred nitidulid beetles (mixtures of *C. hemipterus* and *C. freemani*) were collected from the same area 2 days before inoculation, on the day of fruit inoculation, and 0, 3, 4, and 6 days after fruits were removed from the field. Collections of each species were discontinued when the insects could no longer be found in abundance in the experimental area. Collected insects were taken to the laboratory, plated on APDA, and incubated at 0–4 C for 10–15 days, and colonies of *M. piriformis* developing from the insects were recorded.

RESULTS

Isolates. Because the data pertaining to the CA and CH isolates of *M. piriformis* did not differ significantly ($P > 0.05$), the data were averaged.

Incidence of decayed fruits and use of healthy fruit to bait decay pathogens. Surveys in Parlier revealed that most (44–68%) of the decaying fruit on the orchard floor was infected by *Monilinia fructicola,* 16–28% was infected by *R. stolonifer,* and 8–20% was infected by both fungi (Table 1). *Mucor* spp. (identified as *M. piriformis, M. racemosus* Fresen., and *M. hiemalis* by culturing on APDA slants) were associated with only 3% of decaying fruit in a single orchard (Table 1). One fruit was covered with mycelia, sporangia, and zygospores of *M. piriformis.*

Among healthy fruits exposed in the orchard, all wounded peaches became infected by *Monilinia fructicola;* 32% also supported colonies of *B. cinerea,* and 1.5% were infected with *Penicillium* spp. Only three peaches (1.5%) were coinfected by *Mucor* spp. (two by *M. racemosus* and a third by *M. piriformis*). In contrast, only 8% of the wounded fruit covered with the insect-proof net developed decay from *Monilinia fructicola,* and none was decayed by *Mucor* spp. About 5% of unwounded fruit exposed in the field decayed from *Monilinia fructicola.* A total of 2% of fruits (wounded and unwounded) not exposed in the field and incubated at 0 C for 40 days developed decay.

Pathogen acquisition and transmission: Field and laboratory trials. All

Table 1. Percentage of decay of fruit on the floor of three peach and nectarine orchards in Parlier, CA

Type of rot	Orchard[x,y]		
	Nectarine (Autumn Grand)	Peach (Carnival)	Peach (Halloween)
Brown rot	44 a	48 a	68 a
Rhizopus rot	28 b	23 b	16 b
Brown rot and Rhizopus rot	8 c	20 b	12 b
Gilbertella rot	7 c	5 c	3 c
Aspergillus rot	6 c	0 c	0 c
Mucor rot	3 c[z]	0 c	0 c
Penicillium rot	1 c	2 c	1 c
Others (including yeasts)	4 c	2 c	0 c

[x] Survey was based on 125 nectarines, 100 Carnival peaches, and 400 Halloween peaches examined at five locations in each orchard in September 1982.

[y] Numbers in each column followed by the same letter do not differ significantly ($P < 0.05$) according to Duncan's multiple range test.

[z] One fruit decayed by *Mucor piriformis* had abundant zygospores on it.

fruits inoculated with *M. piriformis* on 19 August 1982 showed decay after a 3-day field exposure. Seventy-five percent of uninoculated but wounded peaches exposed on the ground also had decay from the fungus (Table 2). Assays of beetles and flies showed that 95 and 100%, respectively, were contaminated with the fungus. All wounded, uninoculated peaches kept in insect-proof cages and all unwounded, uninoculated fruit exposed on the orchard floor were free of Mucor decay (Table 2). In general, similar results were obtained in all repetitions of the experiments, although the incidence of *M. piriformis* on wounded, inoculated fruit was significantly lower on 16 October 1982 and 15 August 1983 than on the other dates (Table 2).

Nearly all (98%) of the cultured vinegar flies given access in the laboratory to nectarines infected by *M. piriformis* became contaminated with the pathogen. When these flies were given access to healthy, wounded fruits, 75 and 92% of the peaches and nectarines, respectively, developed decay from *M. piriformis*. All peaches to which flies were denied access remained healthy, but 17% of the insect-free nectarines developed Mucor decay.

Under laboratory conditions, *C. hemipterus* that had fed for 24 hr on a peach decayed by *M. piriformis* transmitted the fungus to 85.5% of the Fay Elberta peaches, causing 67.5% of the wounds to become infected. *C. freemani* transmitted the fungus to 30% of the peach fruit, with 18% of the wounds becoming infected. The percentage of contamination of beetles ranged from 96 to 100%. None of the controls (peaches enclosed with insects fed on sterile figs) decayed from *M. piriformis*. Excretions of the *C. hemipterus* that had previously fed on decayed fruit contained *M. piriformis* propagules, but excretions of insects fed on sterile dried figs were free of the pathogen. These experiments repeated in the following year produced similar results.

In another set of laboratory experiments, contaminated insects were given access to healthy fruits. In these trials, *C. freemani* and *C. hemipterus* transmitted *M. piriformis* to 42 and 75% of unwounded and 92 and 100% of wounded peach fruits, respectively. In contrast, 75% of wounded fruit exposed to contaminated vinegar flies decayed, whereas no decay occurred on unwounded fruit that was similarly exposed. Wounded and unwounded fruit exposed to insects fed on autoclaved figs remained free of decay.

Assays of insects for contamination with *Mucor* spp. Assays of vinegar flies and nitidulid beetles collected near decaying nectarines showed that about 75% were contaminated with *Cladosporium herbarum* (Pers.:Fr.) Link and other *Cladosporium* spp. (Table 3). *Mucor* spp. were obtained from 8% of the flies and 3% of the nitidulid beetles. Of five colonies developed from vinegar flies that produced zygospores, one was identified as *M. piriformis* and four as *M. hiemalis*. Zygospores were not produced on colonies developed from plated nitidulid beetles.

When *Carpophilus* spp. collected from *Rhizopus*-decayed peaches were plated and held at room temperature, all produced *R. stolonifer* colonies. However, 95% of the plates incubated at 0 C (to discourage growth of *R. stolonifer*) produced colonies of *Cladosporium herbarum*, 14% produced colonies of *Monilinia fructicola*, and 2% produced colonies of *Mucor* spp. and *Penicillium expansum* Link. In plates amended with 5 μg of dicloran per milliliter of medium, 5 and 1.5% of the insects obtained from peaches decaying from brown rot and Rhizopus rot, respectively, produced colonies of *Mucor* spp., including two isolates of *M. piriformis*.

Persistence of *M. piriformis* in the insect species. In the experiment conducted in October 1982, 84–95% of the vinegar flies collected 1–7 days after removal of decayed fruit developed colonies of *M. piriformis* when plated and incubated at 0 C for 10 days (Fig. 1). However, colonies of *M. piriformis* developed from only 23% of flies collected 11 days after fruit removal (Fig. 1).

Nitidulid beetles collected from peaches 0 and 2 days before fruit inoculation were free of *M. piriformis* propagules. However, 83, 90, 83, and 52% of beetles collected 0, 3, 4, and 6 days, respectively, after removal of fruit from the field were contaminated with *M. piriformis* (Fig. 2).

DISCUSSION

We have demonstrated that nitidulid beetles and vinegar flies from California stone fruit orchards were heavily contaminated with *Rhizopus* and *Monilinia* spp., confirming earlier observations (14). However, the presence of these fungal pathogens often reduces the chances for detecting slower-growing fungi. By

Table 2. Field acquisition and transmission of *Mucor piriformis* on peaches by nitidulid beetles (*Carpophilus hemipterus* and *C. freemani*) and vinegar flies (*Drosophila melanogaster*)

	Fruit decayed with *M. piriformis*[u] (%)				Insects with *M. piriformis* (%)[u,x]	
Date of test	Wounded, inoculated[v]	Wounded, uninoculated	Wounded, uninoculated, caged[w]	Unwounded, uninoculated	Nitidulid beetles	Vinegar flies
1982						
19 August	100 a	75 a	0	0	95 a	100 a
17 September	100 a	ND[y]	0	0	98 a	75 a
16 October	64 b	90 a	0	0	75 a	ND
1983						
26 July	99 a	100 a	0	0	80 a	ND
15 August	67 b	84 a	0	0	81 a	ND
3 September	100 a	97 a	7[z]	0	87 a	ND

[u] Values in each column followed by different letters are significantly ($P<0.05$) different according to Duncan's multiple range test.
[v] Fruit was wound-inoculated with 50 μl of a suspension of *M. piriformis* (1.2×10^5 spores/ml) and left in the field for 4–5 days. Decay was recorded after the fruit was gathered and incubated at 0 C for 15 days.
[w] Fruit was placed in insect-proof cages after wounding.
[x] Insects were collected 4–5 days after fruit inoculation, plated on APDA, and incubated at 4 C for 10 days.
[y] ND = not determined.
[z] A hole was detected in one of the cages.

Table 3. Isolation of fungi from bodies of adult vinegar flies (*Drosophila melanogaster*) and nitidulid beetles (*Carpophilus hemipterus* and *C. freemani*) collected near decaying nectarines in an orchard at Parlier, CA

Fungus isolated	*D. melanogaster*[a,b] (%)	*Carpophilus* spp.[a,c] (%)
Cladosporium spp.[d]	74.2	76.0
None	8.7	4.5
Mucor spp.	8.3[e]	3.0[f]
Penicillium spp.	3.3	4.5
Other zygomycetes	3.0	3.0
Various yeasts	1.3	6.0
Unidentified	1.2	3.0

[a] Insects were frozen overnight at −6 C, plated on acidified potato-dextrose agar, and incubated at 4 C for 4 days then at 0 C for 20 more days.
[b] A total of 240 flies were sampled in six locations.
[c] A total of 200 beetles were sampled in six locations.
[d] Primarily *Cladosporium herbarum*.
[e] 1% *M. piriformis*, 6% *M. hiemalis*, and 1.3% *M. racemosus*.
[f] 1% *M. hiemalis* and 2% *M. racemosus*.

incubating isolation dishes at 0 C or amending the medium with 5 μg of dicloran per milliliter, we were also able to detect *Mucor, Cladosporium,* and *Penicillium* spp. on these insects.

Fungi isolated from insects corresponded to species of fungi recorded on fruit decaying on the orchard floor. Fruit decay by *M. piriformis* and other *Mucor* spp. was found, and these fungi were isolated from insects collected in the same orchards. At least three species of insects—*C. hemipterus, C. freemani,* and *D. melanogaster*—acquired *M. piriformis* and transmitted it to healthy fruit, causing a high percentage of decay under both field and laboratory conditions.

The high efficiency of fungal transmission may be affected by the persistence of *M. piriformis* on these insects in part because of the characteristic adhesiveness of the surfaces of sporangiospores of certain *Mucor* spp., including *M. piriformis* (3,9). The virulence of these fungi may also contribute to the high percentage of transmission detected.

Wounded, uninoculated fruit placed in insect-proof cages remained free of Mucor decay, and only fruits, wounded or unwounded, that were visited by insects decayed from *M. piriformis*. Recovery of *M. piriformis* from insects exposed to decaying fruit indicated a high incidence of contamination (Table 2). Apparently, the legs and bodies of insects easily become contaminated when the insects visit sporulating decay lesions, and the insects then transfer some of the adhering sporangiospores when they visit new wounds. Similarly, vinegar flies transmit *G. candidum* (which causes Geotrichum rot of tomato) through contamination of their bodies (2).

The nitidulid beetles were able to transmit propagules to and cause decay on unwounded peaches. Because *M. piriformis* requires a wound for infection (T. J. Michailides, *unpublished*), decay development on unwounded peaches may be explained either by the presence of microwounds on the surface of the peach fruit that we did not detect or by the creation of wounds by the beetles.

Tate and Ogawa (14) reported that *C. freemani* was repelled by healthy nectarine slices but not by decaying slices. *C. freemani* is significantly ($P < 0.05$) less efficient in transmitting *M. piriformis* than is *C. hemipterus*, perhaps because they make fewer visits to healthy wounds than do *C. hemipterus,* since both species were equally contaminated with propagules of *M. piriformis*. Once decay started in some of the wounds, *C. freemani* was observed to be attracted to and to remain in those wounds. This difference may also explain the significantly ($P < 0.05$) lower percentage of infected wounds on fruits exposed to *C. freemani* than on those exposed to *C. hemipterus.*

In orchards with a high incidence of decayed fruit with abundant sporulation of *M. piriformis,* such as pear orchards in Hood River, OR, contamination of fruit flies can be expected to be very high (68–84%) (T. J. Michailides and R. A. Spotts, *unpublished*). In peach and nectarine orchards in California, fruit decay from *M. piriformis* is much less common (Table 1). Contamination of vinegar flies and nitidulid beetles with the fungus was very infrequent in our study (Table 3).

Many fungi, including *M. piriformis,* exist as two mating types that must be brought together for the production of sexual spores. Insects play a major role in this process with many fungi (5,15). Several observations support such a role with *M. piriformis*. First, zygospores developed from colonies originating from 3–38% of vinegar flies collected from pear orchards in Hood River and plated on APDA (T. J. Michailides and R. A. Spotts, *unpublished*), suggesting that the flies had been contaminated with both mating types of the fungus. Second, up to 15% of decayed pear fruit surveyed in a previous study (9) in the Hood River Valley harbored both mating types of the fungus at a time when vinegar flies were very abundant in the orchards, and 1.6% of these fruits had zygospores (10). Third, several vinegar flies collected from a nectarine orchard in Parlier and plated on APDA developed colonies bearing zygospores of *M. piriformis* and of *M.*

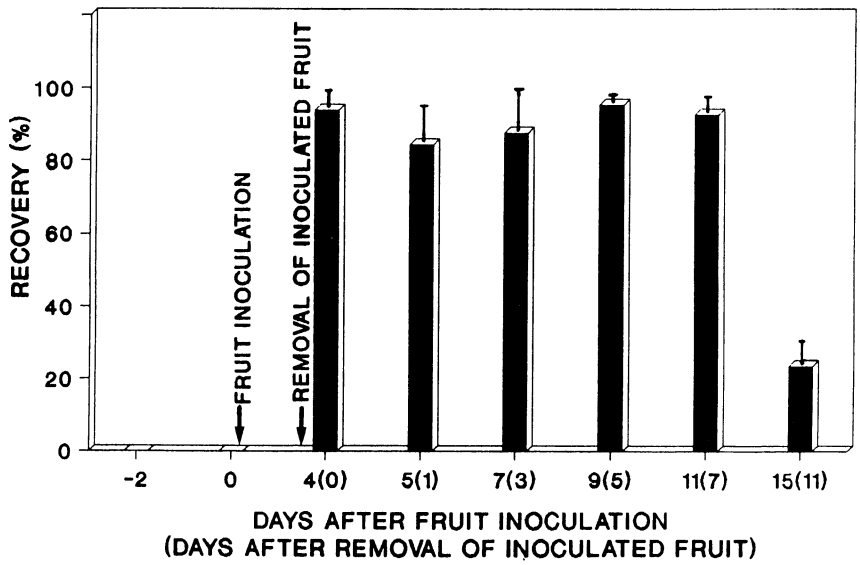

Fig. 1. Percentage recovery of *Mucor piriformis* from *Drosophila melanogaster* collected in a peach orchard in the vicinity of inoculated fruits 2 days before inoculation, on the day of inoculation, and up to 11 days after removal of the fruit. On each date, 100 insects were collected and plated on acidified potato-dextrose agar (five to 10 flies per dish). Vertical bars represent standard deviations.

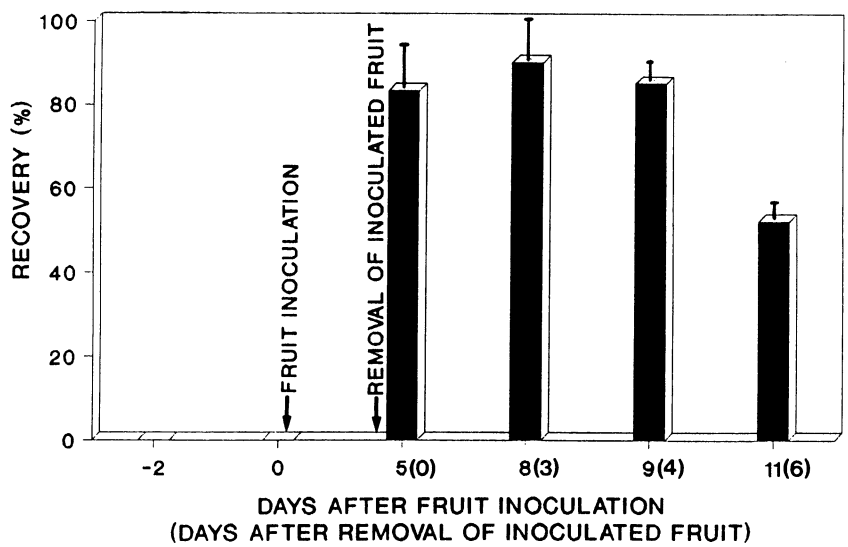

Fig. 2. Percentage recovery of *Mucor piriformis* from *Carpophilus hemipterus* and *C. freemani* collected in a peach orchard in the vicinity of inoculated fruits 2 days before inoculation, on the day of inoculation, and up to 6 days after removal of the fruit. On each date, 100 insects were collected and plated on acidified potato-dextrose agar (10 insects per dish). Vertical bars represent standard deviations.

hiemalis, which is also heterothallic (12).

Although nitidulid beetles contribute primarily to the dissemination of and inoculation of stone fruit with *Monilinia* and *Rhizopus* spp. (14), their role in disseminating other postharvest pathogens, such as *M. piriformis,* should not be ignored. Long-distance spread of sporangiospores of *M. piriformis* by nitidulid beetles is possible because of the beetles' foraging and migration habits.

Our findings suggest that nitidulid beetles and vinegar flies can vector *M. piriformis* from infected to healthy, wounded fruits. Both kinds of insects not only fed on the decaying fruits but also oviposited in them and thus completed their life cycle. As we suggested for pear orchards (8), sanitation practices, such as removing fruits from the ground, should reduce the inoculum potential of *M. piriformis* in peach and nectarine orchards and concomitantly eliminate an insect attractant. In Hawaii, for instance, removing fallen guava (*Psidium guajava* L.) fruit from the ground reduced the percentage of fruits infected by *M. hiemalis* transmitted by three species of fruit flies (4).

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