Incidence of *Pandora neoaphidis* (Remaudière and Hennebert) Humber (Zygomycetes: Entomophthorales) in the *Myzus persicae* (Sulzer) Complex (Homoptera: Aphididae) on Three Species of *Brassica* in the Fall and Winter[1]

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Abstract The incidence of the aphid pathogen, *Pandora neoaphidis* (Remaudière & Hennebert) Humber, was monitored in populations of the *Myzus persicae* (Sulzer) complex (green peach aphid, *M. persicae,* and the tobacco aphid, *M. nicotianae* Blackman) on fall-planted cabbage, spinach-mustard, and turnip from 1993 to 1996. Each fall, the pathogen occurred at moderate levels in *M. persicae* complex on all three hosts. Average level of mycoses on the three host plants ranged from 10.0 to 14.3% in 1993, from 5.9 to 10.1% in 1994, and from 7.9 to 17.4% in 1995. Each year, the highest incidence of the pathogen in aphids on turnip and spinach-mustard was 20 to 25%, while the incidence on cabbage was 12 to 19%. In 1995 and over the 3 yrs combined, the levels of mycoses were significantly higher ($P \leq 0.05$) in aphids on turnip and spinach-mustard than on cabbage. Trends were similar in 1993 and 1994, but differences were not significant. Very low numbers of healthy aphids (<2 per 5 plants in 1994 to 5 aphids per 5 plants in late April 1996) and those infected with or killed by *P. neoaphidis* occurred on turnip, cabbage, and spinach-mustard from Jan to May. The *M. persicae* complex was significantly more abundant on cabbage than it was on spinach-mustard or turnip. The pathogen overwinters at very low levels in cadavers of *M. persicae* complex on *Brassica.*

Key Words *Pandora neoaphidis, Myzus nicotianae, Myzus persicae* complex, Brassicaceae, overwintering

A fungal pathogen, *Pandora neoaphidis* (Remaudière and Hennebert) Humber [=*Erynia neoaphidis* (Remaudière and Hennebert)], frequently causes epizootics in populations of the tobacco aphid, *Myzus nicotianae* Blackman, on tobacco in Virginia (Dara 1995), North Carolina and Kentucky (Yu et al. 1995, Brown et al. 1995). The pathogen also causes epizootics in *M. persicae* and various other species of aphids on several host plants throughout the year (Feng et al. 1990, Kish et al. 1994, McLeod et al. 1998, Sivcev 1992). It does not produce resting spores (Ben-Ze'ev and Kenneth 1982, Wilding and Brady 1984), but overwinters as condia in aphid cadavers, in the soil and on the foliage (Latteur 1977, Schofield et al. 1995, Nielsen et al. 1998).

The *M. persicae* complex includes two major insect pests, the green peach aphid, *M. persicae* (Sulzer), and the tobacco aphid, *M. nicotianae* Blackman (Blackman

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1987). Blackman (1987) described *M. nicotianae* as a tobacco-feeding form of *M. persicae* (Sulzer). The two species are very difficult to separate taxonomically (Blackman and Spence 1992), and they are now considered synonyms (Field et al. 1994, Margaritopoulos et al. 1998, Clements et al. 2000). The tobacco aphid causes serious reductions in tobacco yield and value (Reed and Semtner 1992). Various species of *Brassica* may serve as sources for the *M. persicae* complex that migrates into fields and colonizes tobacco in May and June. This study was undertaken to determine the incidence of *P. neoaphidis* in the *M. persicae* complex on three species of *Brassica* from Oct to May in the tobacco-producing region of Virginia.

Materials and Methods

Research was conducted at the Virginia Polytechnic Institute and State University Southern Piedmont Agricultural Research and Extension Center (SPAREC), Blackstone, VA from Oct to April or May 1993 to 1995 and in a home garden in Blackstone, VA about 6 km from the SPAREC from Oct 1995 through April 1996. Observations were made on three cool-season vegetable hosts (Brassicaceae) of the *M. persicae* complex: cabbage (*Brassica oleracea* var. *capitata* L. 'Bonnie Hybrid'), spinach-mustard (*B. perviridis* Bailey 'Tendergreen'), and turnip (*B. rapa* L. 'Purpletop White-Globe'). These hosts were interplanted with seven other species of Brassicaceae in 1993-1994 and ten other plant species (eight Brassicaceae, one Asteraceae, and one Chenopodiaceae) in 1994-1995. Only the three test hosts were planted in 1995-1996. Before planting, fertilizer (10-10-10) was broadcast at 1120 kg/ha and incorporated into each test site. Test plants were planted in single row plots (6 m long) arranged in a randomized complete block design with four replications. Cabbage was transplanted at 13 plants per row (46 cm within the row and 1.2 m between the rows). Turnip and spinach-mustard seeds were sown with a Precision Garden Seeder (Model 1001 B, Earthway Products, Bristol, IN). Plots were planted or sown on 15 Sept 1993, 22 Aug 1994, and 15 Sept 1995.

Counts were made about once a week from 22 Oct to 8 Dec 1993, from 13 Oct to 5 Dec 1994, and from 26 Oct to 17 Dec 1995. On each observation date, healthy aphids in the *M. persicae* complex and those infected with *P. neoaphidis* were counted on five randomly selected plants within each plot. Both living-infected (aphids showing symptoms of infection) and fungus-killed aphids were considered infected. Observations were discontinued in early- to mid-Dec of each year due to loss of plants associated with seasonally cold weather and resumed on plant regrowth and the few surviving plants in the late winter or early spring. Counts were made about once a week from 21 Feb to 18 May 1994. Plants were checked periodically for aphids and *P. neoaphidis* from 24 Feb to early April 1995, but counts were not made due to poor plant stands and very low numbers of aphids. In 1996, counts were made on 30 Jan and on four dates in late Mar and April.

Weather data were recorded at a weather station (Omnidata International Inc., Logan, UT) located about 1 km from the fields in 1993-94 and 1994-95 and about 6 km from the site in 1995-96. Temperature was measured with a PCRC-11 humidity transducer mounted in an ES-110 sensor (Omnidata International Inc., Logan, UT). Leaf wetness was measured with an ES-460 leaf wetness sensor (Omnidata International Inc., Logan, UT). Maximum and minimum temperatures, hours of leaf wetness >50%, and rainfall were recorded for each date.

Identification of *P. neoaphidis*. On each sampling date, conidia from a few cadavers were collected on coverslips and examined in lactophenol using a phase-contrast microscope. The identity of *P. neoaphidis* was confirmed based on the descriptions of Remaudière and Hennebert (1980), Wilding and Brady (1984), and Humber (1989).

Statistical analysis. The data were subjected to an analysis of variance for a randomized complete block design using PROC GLM (SAS Institute 1987). The incidence of the aphid complex and the percentage of aphids killed by or infected with *P. neoaphidis* were compared among hosts. Log (x + 1) transformed values for numbers of aphids and arcsine (x + 0.001) transformed values of percent infection were also tested with PROC GLM. Host effects were compared for each observation date, for each fall observation period (combined over all dates), and combined over the 3 yrs. Significantly different means were separated by Student-Newman-Kuhls (SNK) test ($P \leq 0.05$) (SAS Institute 1987). Means and standard errors for the aphid complex and the percentage infected with *P. neoaphidis* were calculated for entire fall observation periods for each year and combined over the 3 yrs. The abundance of the *M. persicae* complex and the incidence of *P. neoaphidis* on the three hosts were presented to show the trends for aphid populations and infection rates each fall.

Results and Discussion

Each fall, the *M. persicae* complex and its pathogen, *P. neoaphidis,* were found on all three vegetable crops (Fig. 1, Table 1). Cabbage supported higher numbers of aphids than turnip and spinach-mustard. Mycoses caused by *P. neoaphidis* in the *M. persicae* complex averaged 12% (10.0 to 14.3%) in 1993, 8.2% (5.9 to 10.1%) in 1994 and 13.2% (7.8 to 17.4%) in 1995 (Table 1). Infection levels in aphids on turnip and spinach-mustard attained highs of 21 to 24% each year, while those on cabbage peaked at 12 to 19% (Fig. 1). Aphids on turnip and spinach-mustard had significantly higher incidences ($P \leq 0.05$) of mycoses than those on cabbage in 1995 and over the 3 yrs combined, but not in 1993 or 1994. Low levels of the pathogen were also found in the *M. persicae* complex in Feb 1994 and 1995 and late April 1996.

1993-1994. The *M. persicae* complex was significantly more abundant ($P \leq 0.05$) on cabbage than on spinach-mustard and turnip from 22 Oct to 24 Nov, but not in Dec (Fig. 1A). Moderate levels of *P. neoaphidis* were observed in aphids on each host plant in Oct and Nov, but they declined to low levels in early Dec (Fig. 1D). When combined over observation dates, the percentage of aphids infected with *P. neoaphidis* was not significantly influenced by host plant ($P = 0.31$) (Table 1), but aphids had a significantly higher incidence of *P. neoaphidis* on turnip than on cabbage on 24 Nov (Fig. 1D). The *M. persicae* complex and *P. neoaphidis* were observed on turnip and spinach-mustard on 21 Feb. Aphids were not observed again until 3 April. The *M. persicae* complex averaged ≤ 2 aphids per 5 plants on turnip between 3 April and 18 May. No *P. neoaphidis* was observed after 21 Feb.

1994-1995. Once again, cabbage had significantly ($P \leq 0.05$) higher numbers of the *M. persicae* complex throughout the fall than turnip and spinach-mustard (Fig. 1B). The incidence of *P. neoaphidis* in aphids did not differ significantly ($P > 0.05$) among host plants on any of the observation dates or when combined for the fall (Fig. 1E, Table 1). However, turnip generally had higher percentages of infected aphids than cabbage (Fig. 1E). The pathogen was first observed on 21 Oct and reached its highest incidences on 16 Nov and 5 Dec (Fig. 1E). In the late winter and spring, low

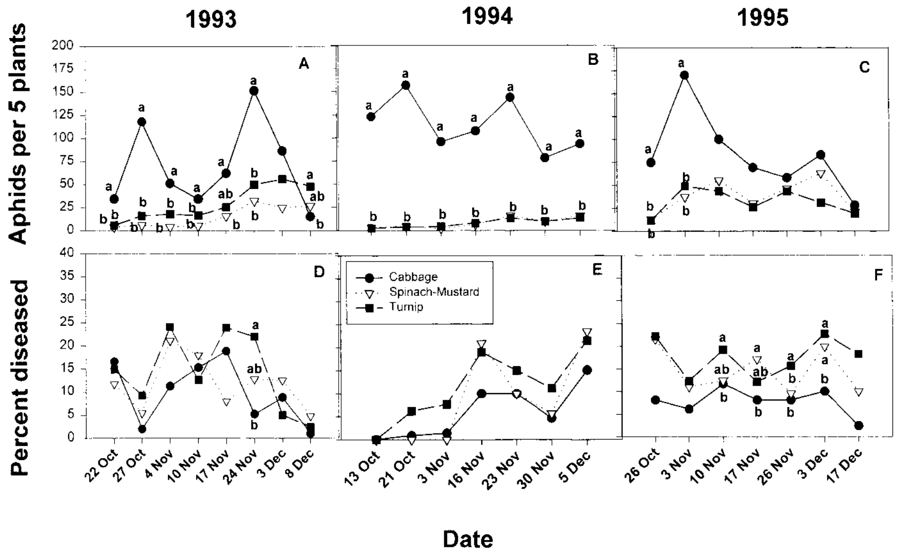

Fig. 1. Incidence of the *Myzus persicae* complex and the percent infected with *Pandora neoaphidis* on cabbage, spinach-mustard, and turnip in the falls of 1993 (A and D), 1994 (B and E) and 1995 (C and F). Data points surmounted by different letters are significantly different as indicated by Student-Newman-Kuhls (SNK) test ($P \leq 0.05$).

numbers of healthy aphids and aphids infected with *P. neoaphidis* were observed only on spinach-mustard on 24 Feb.

1995-1996. The *M. persicae* complex was more abundant ($P \leq 0.05$) on cabbage than on spinach-mustard and turnip during the fall and on 26 Oct and 3 Nov (Fig. 1C, Table 1). Turnip and spinach-mustard had higher ($P \leq 0.05$) percentages of aphids infected with *P. neoaphidis* than cabbage when combined over the fall (Table 1), and turnip had significantly higher percentages of aphids infected with the pathogen than cabbage from 10 Nov to 3 Dec (Fig. 1F). The incidence of *P. neoaphidis* remained relatively constant in the *M. persicae* complex on each host plant throughout the fall (Fig. 1F). Very few aphids and no *P. neoaphidis* were observed on 30 Jan 1996. After observations were resumed in the spring, the pathogen was found only at low levels (about 3%) in moderate populations of the aphid complex (5 aphids/plant) on cabbage on 29 April.

In Oct and Nov of each year, the environmental conditions favored the germination, development and sporulation of *P. neoaphidis*. However, changes in weather had little impact on the incidence of *P. neoaphidis* and major epizootics were not observed (Figs. 1 and 2). Except for frequent minimum temperatures below the threshold of 4°C (Milne and Bourne 1983), the temperatures were generally within the favorable range (4 to 25°C) for the germination, development and sporulation of *P. neoaphidis* (Yu et al. 1995, Milner and Bourne 1983) (Fig. 2). Cold temperatures in early Nov 1993 and mild temperatures in mid-Nov may have contributed to a decline

Table 1. Seasonal average populations of *Myzus persicae* complex and the incidence of infection with *Pandora neoaphidis*, Blackstone, VA, 1993 to 1996

Year and aphid host	Aphids/5 plants*	Percent diseased
1993		
Cabbage	69.2 ± 9.0 a	10.0 ± 1.5 NS
Spinach-mustard	14.1 ± 2.7 b	11.8 ± 2.3
Turnip	29.4 ± 4.9 b	14.3 ± 2.2
1994		
Cabbage	105.6 ± 11.3 a	5.9 ± 1.3 NS
Spinach-mustard	8.0 ± 1.6 b	8.7 ± 2.5
Turnip	7.6 ± 1.3 b	10.1 ± 2.5
1995		
Cabbage	83.4 ± 12.7 a	7.8 ± 1.0 b
Spinach-mustard	37.8 ± 4.6 b	14.5 ± 1.5 a
Turnip	31.6 ± 3.5 b	17.4 ± 1.8 a
3 year average		
Cabbage	86.2 ± 6.4 a	7.9 ± 0.8 b
Spinach-mustard	19.3 ± 2.2 b	11.5 ± 1.3 a
Turnip	22.5 ± 2.3 b	13.8 ± 1.2 a

* Means within a column and year not followed by the same letter are significantly different ($P \leq 0.05$) as indicated by Student-Newman-Kuhls test.

in aphid populations in the first half of Nov and an increase in aphid populations in mid- to late-Nov, respectively (Figs. 1A and 2). In general, the higher incidence of *P. neoaphidis* occurred during periods of mild weather in Nov and Dec (Figs. 1 and 2). High levels of *P. neoaphidis* occurred during warm periods in mid-Nov 1993, mid-Nov and early Dec, 1994, and early Dec 1995 (Figs. 1D, 1E, 1F, 2).

Each year, precipitation was well distributed throughout each observation period except for brief periods of dry weather in mid-Nov 1993, from late-Nov to mid-Dec 1994 and from mid-Nov to mid-Dec 1995. These dry periods did not appear to be related to the incidence of the pathogen (Figs. 1, 2). Rainfall exceeded 50 mm on 1 day each fall. There were slight to moderate declines in the incidence of *P. neoaphidis* after each event, but very cool weather that followed two of these events may have contributed to the declines (Figs. 1, 2).

The germination and sporulation of *P. neoaphidis* is highly dependent on free water or relative humidity ≥98% (Yu et al. 1995). The development and spread of *P. neoaphidis* was probably favored by relatively long periods of high leaf wetness (8 or more hours of leaf wetness per day) related to morning dews each year (Fig. 3). Milner and Bourne (1983) indicated that the duration of leaf wetness required for

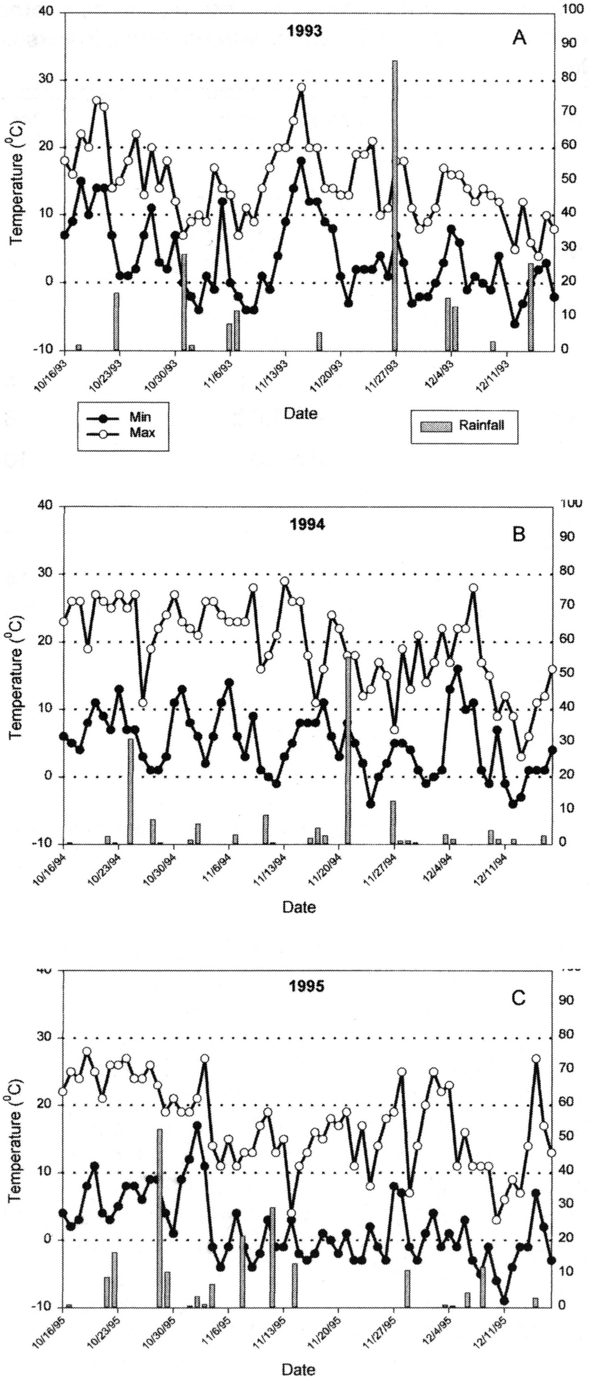

Fig. 2. Daily maximum and minimum temperatures and rainfall during 16 Oct to 15 Dec, 1993, 1994 and 1995.

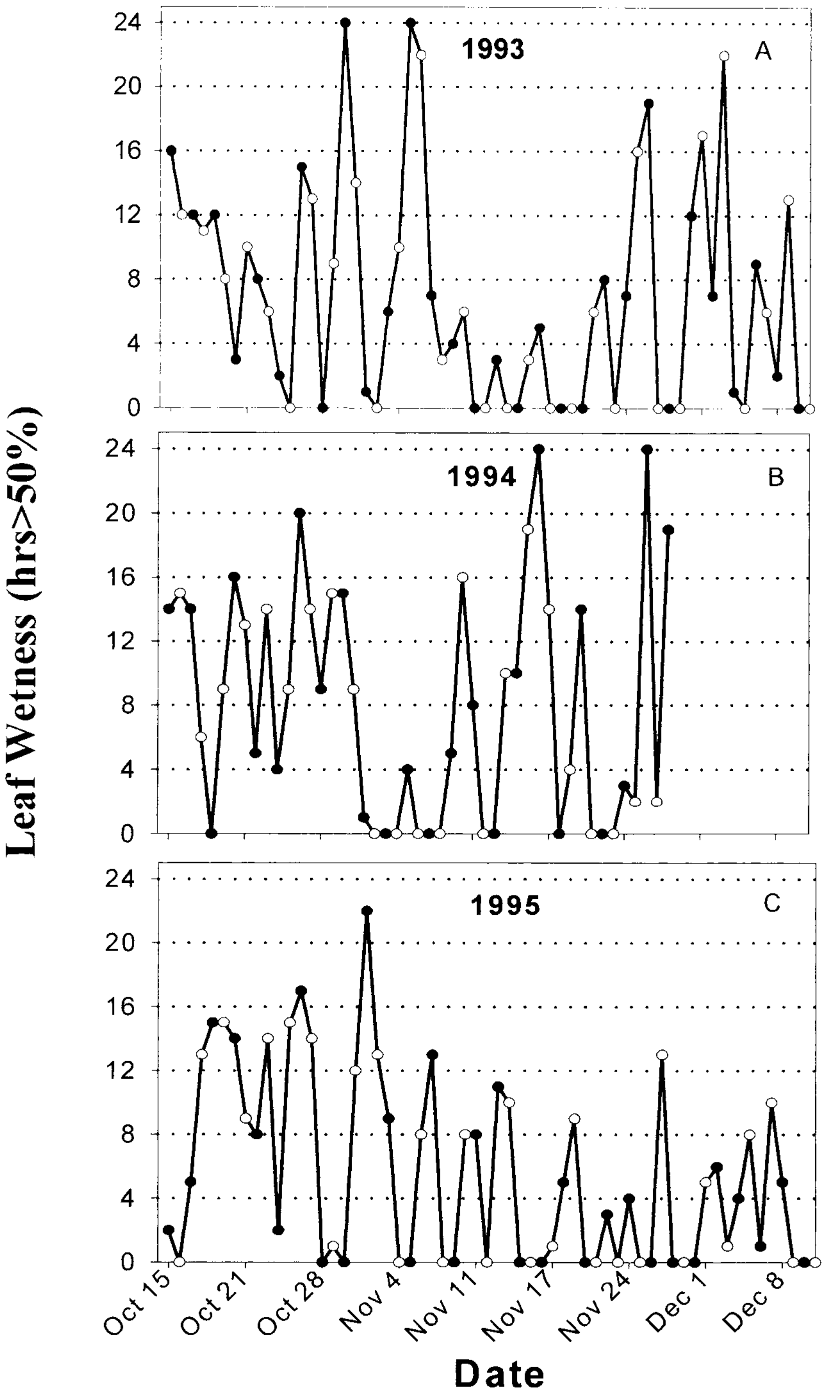

Fig. 3. Hours of leaf wetness of 50% or higher during 16 Oct to 15 Dec for 1993, 1994 and 1995.

spore germination was from 3 h at 20°C to 7 to 16 h at 10°C. These conditions must occur during germination and sporulation, but they are not needed when the pathogen is developing in the aphid. In addition to low temperatures, shorter photophases also lengthen the incubation time under fluctuating temperatures (Feng et al. 1998). The duration of leaf wetness did not appear to affect the incidence of *P. neoaphidis* in our study. In 1993, the highest incidence of *P. neoaphidis* occurred during the period of lowest leaf wetness from 12 to 22 Nov (Figs. 1B, 3). Duration of leaf wetness was moderate when the incidence of *P. neoaphidis* declined in Dec. In 1994, the incidence of *P. neoaphidis* increased most rapidly during periods of low leaf wetness in mid-Nov (Figs. 1D, 3). Relatively long periods of leaf wetness occurred in late Oct and early Nov when the incidence of *P. neoaphidis* was low. In 1995, leaf wetness appeared to have little impact on the level of *P. neoaphidis* (Figs. 1F, 3).

Pandora neoaphidis was a common pathogen of the *M. persicae* complex on the cabbage, turnip, and spinach-mustard in the falls (Oct-Dec) of 1993 to 1995. The higher incidence and earlier establishment of *M. persicae* complex on the vegetables in 1993 compared with 1994 may be related to a source of inoculum from tobacco regrowth in a nearby field (<500 m away) in 1993 (Dara 1995). In 1994 and 1995, the tobacco crops in the area were harvested and the residue was destroyed in early Oct. In Oct and early Nov 1993, alate aphids infected with *P. neoaphidis* were observed on the three plant species. Alate aphids are more susceptible to entomophtoraleans than apterae and are responsible for long-distance transmission of infection (Rockwood 1950).

Very low numbers of the *M. persicae* complex and low incidences of *P. neoaphidis* were observed in the test each spring. Although the numbers were low, these aphids could serve as sources for establishing the aphid and its pathogen on tobacco in April and early May. We have observed *P. neoaphidis* infecting *M. nicotianae* in tobacco plant beds in April, May and June, but *P. neoaphidis* rarely occurs in *M. nicotianae* on field tobacco before July in Virginia (Dara 1995).

The turnip aphid, *Lipaphis erysimi* (Kaltenbach), and the cabbage aphid, *Brevicoryne brassicae* (L.), on our test plants were also infected with *P. neoaphidis.* Populations of the turnip aphid were moderate in the fall and spring, while those for the cabbage aphid were low in the fall and moderate in the spring. These and many other species of aphids could also serve as hosts of *P. neoaphidis* in the spring (Wilding and Brady 1984). Sivcev (1992) also reported that *P. neoaphidis* was the primary species of entomopathogenic fungi infecting *B. brassicae.*

Unlike other entomophthoraleans, *P. neoaphidis* does not produce resting spores (Rockwood 1950, Waterhouse and Brady 1982, Wilding and Brady 1984) and its exact overwintering mechanism is unclear. Several studies indicate that *P. neoaphidis* survives and remains infective in the soil, in the host and on the foliage, and as cultures when exposed to winter temperatures (Remaudière and Michel 1971, Wilding 1973, Feng et al. 1992, Schofield et al. 1995, Nielsen et al. 1998). Structures thought to play a role in overwintering of the pathogen have been found in the cadavers of the pea aphid, *Acyrthosiphon pisum* (Harris), and the English grain aphid, *Sitobion avenae* F., killed by *P. neoaphidis* (Feng et al. 1992, Nielsen et al. 1998). Feng et al. (1990), MacLeod (1998), and Elkassabany et al. (1992) reported on epizootics of *P. neoaphidis* in various species of aphids on winter wheat and spinach during winter. These reports indicate that *P. neoaphidis* remains viable at low temperatures in the aphid hosts and the soil, or on foliage. Our observations also suggest that *P. neoaphidis* overwinters in the *M. persicae* complex infesting winter-annual cruciferous vegetable hosts from Oct to late April.

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