

Aphid (Hemiptera: Aphididae) Species Composition and Potential Aphid Vectors of Plum Pox Virus in Pennsylvania Peach Orchards

C. M. WALLIS,¹ S. J. FLEISCHER,² D. LUSTER,³ AND F. E. GILDOW¹

J. Econ. Entomol. 98(5): 1441–1450 (2005)

ABSTRACT Plum pox, an invasive disease recently identified in Pennsylvania stone fruit orchards, is caused by the aphid-transmitted *Plum pox virus* (genus *Potyvirus*, family *Potyviridae*, PPV). To identify potential vectors, we described the aphid species communities and the seasonal dynamics of the dominant aphid species within Pennsylvania peach orchards. Aphids were trapped weekly in 2002 and 2003 from mid-April through mid-November within two central Pennsylvania orchards by using yellow and green water pan traps. In total, 42 aphid species were identified from both orchards over 2 yr. Within orchards, actual species richness ranged from 24 to 30 species. The Abundance Based Coverage Estimator predicted species richness to range from 30 to 36 species, indicating that trap catches were identifying most aphid species expected to occur in the orchard. Three species, *Rhopalosiphum maidis* (Fitch), *Aphis spiraeicola* Patch, and *Myzus persicae* (Sulzer), were consistently dominant across locations and years. Orchard-trapped populations of these three species peaked in a similar chronological sequence each year. As expected, trap color influenced the total number and distribution of the predominate species collected. However, the same dominant species occurred in both yellow and green traps. Based on the seasonal population dynamics reported here and on published vector efficacy studies, the most probable significant PPV vector was identified as *A. spiraeicola*. If the PPV pathogen escapes current quarantine or if subsequent reintroductions of PPV occur, these data will be useful for developing plum pox management strategies.

KEY WORDS population dynamics, *Prunus*, Potyvirus, aphid-trapping

PLUM POX OR SHARKA DISEASE, which is caused by the potyvirus *Plum pox virus* (genus *Potyvirus*, family *Potyviridae*, PPV), can affect a variety of commercial *Prunus* species, including nectarine, peach, plum, apricot, and cherry (Levy et al. 2000b). At least four genetically distinct strains (PPV-D, -M, -C, and -EA) differ in geographic distribution, host range, symptom severity, and transmission efficiency. Various PPV strains are distributed throughout Europe and along the eastern end of the Mediterranean basin (Roy and Smith 1994), in Chile (Rosales et al. 1998), and recently in North America (Levy et al. 2000a). In the United States, plum pox was first detected in Pennsylvania in fall 1999 and in Ontario, Canada, in 2000. All PPV isolates currently characterized in North and South America are related to the PPV-D type isolates (Damsteegt et al. 2001).

In areas where plum pox is endemic, such as eastern Europe, the disease can be severe with a possibility of 80–100% yield losses (Kolber et al. 2001). Symptoms vary with virus strain, host species, and cultivar. In susceptible plum cultivars, typical symptoms of leaf

chlorosis and necrosis lead to tattered leaves and fruit showing chlorotic rings. Infected apricot cultivars produce misshapen and necrotic fruit. In peach, symptoms are less obvious for many cultivars but chronic infection leads to premature yield reductions and death of trees. Because high concentrations of the virus are not produced and the virus is unevenly distributed in trees, it is difficult to detect and verify in disease surveys. In addition, diseased trees often remain symptomless for several years after infection and function as reservoirs for PPV survival and spread to neighboring trees and orchards. When PPV was first detected in Adams County, Pennsylvania, in September 1999, a preliminary survey by the Pennsylvania Department of Agriculture and USDA Animal and Plant Health Inspection Service (APHIS) determined that the outbreak was localized. For this reason, a quarantine and eradication effort was immediately initiated in an effort to prevent survival and spread of the virus. To date, ≈23% of the noncherry stone fruit orchards in Pennsylvania have been destroyed (Ruth Welliver, Pennsylvania Department of Agriculture, Harrisburg, PA, personal communication).

Because plum pox is difficult to detect, PPV can be accidentally spread long distances and past natural barriers by shipments of infected budwood, rootstocks, or grafted seedlings. Once PPV-infected tissue is established, natural spread within and between or-

¹ Department of Plant Pathology, The Pennsylvania State University, University Park, PA 16802.

² Department of Entomology, The Pennsylvania State University, University Park, PA 16802.

³ USDA-ARS Foreign Disease-Weed Research Unit, Ft. Detrick, MD 21702.

chards occurs by aphids in a nonpersistent manner (Shukla et al. 1994). Nonpersistently transmitted viruses can be acquired and transmitted by aphids within seconds during quick test probes into epidermal cells, used to sample host suitability for feeding. This also has been referred to as "probing-mediated" transmission by Zeyen and Berger (1990). Effective transmission can be carried out by transient aphid species that do not necessarily feed on or colonize the host plant. It is generally accepted that potyviruses such as PPV are typically not carried long distances before infectivity is lost by the aphid vector; however, there is evidence suggesting that under specific environmental conditions some potyviruses may be transported long distances by migrating aphids (Zeyen and Berger 1990). How far PPV-infective vectors travel and retain the ability to transmit PPV from an infected source tree is unknown. In Europe, the primary aphid vectors of PPV have been determined from Romania (Isac et al. 1998), Spain (Llacer and Cambra 1998), Hungary (Gaborjanyi and Basky 1995), and France (Labonne et al. 1995). These studies determined the species composition of aphid populations in orchards and identified the dominant species vectoring PPV. Approximately 20 different species of aphids were reported to transmit PPV with varying degrees of efficiency. Species composition of the aphid vector populations in orchards varied depending on geography, resulting in different primary vectors. In eastern Europe, *Hyalopterous pruni* (Geoffroy) and *Phorodon humuli* (Schrank) are thought to be important PPV vectors, based on the timing of species abundance corresponding to maximum PPV spread in orchards. In western Europe, *Aphis spiraeicola* (Patch) and *Myzus persicae* (Sulzer) are more prevalent vector species known to be associated with efficient PPV transmission in orchards.

In addition, genetic differences among populations of an aphid species can vary in their ability to transmit potyviruses (Sohi and Swenson 1964, Singh et al. 1983, Lupoli et al. 1992). For PPV, a population of *Aphis gossypii* (Glover) in southern France efficiently vectored PPV, yet other populations from France and Spain failed to efficiently transmit the virus (Avinent et al. 1991, Labonne et al. 1995). Therefore, it is necessary to test local populations when attempting to identify important virus vectors within a geographical area. In an earlier work (Gildow et al. 2004), different aphid species were collected live while feeding on peach trees or herbaceous plants from an orchard environment in Adams County, Pennsylvania. Virus-free colonies were initiated from these aphids, and the progeny were tested in greenhouse trials for their ability to transmit Pennsylvania isolates of PPV. Four aphid species [*Myzus persicae*, *Aphis spiraeicola*, *Aphis fabae* (Scopoli), and *Brachycaudus persicae* (Passerini)] were efficient vectors, and eight [*Rhopalosiphum padi* (L.), *Metopolophium dirhodum* (Walker), *Acyrtosiphon pisum* (Harris), *Aphis glycines* (Matsamura), *Aulacorthum solani* (Kaltenbach), *Macrosiphum euphorbiae* (Thomas), *Rhopalosiphum maidis*

(Fitch), and *Sitobion avenae* (F.)] were inefficient or nonvectors.

Currently, the species composition and population dynamics of aphids in Pennsylvania *Prunus* orchards are poorly documented. Thus, it is imperative that the aphid species composition of Pennsylvania peach orchards, and their vectoring efficiencies, be determined to understand how plum pox could spread if the eradication effort is unsuccessful, or if PPV is reintroduced into the United States in the future. Several trapping methods, including suction traps, water pan traps, and sticky string traps, have been compared for studies of aphid species diversity and population dynamics (Halbert et al. 1986; Labonne et al. 1989; Avinent et al. 1991, 1993; Boiteau 1990). When trapping aphids for identification, sampling methods may influence estimates of aphid population size and species richness. For example, suction traps are very efficient at indiscriminately collecting aerial alates from specific volumes of air at specific heights over time. However, not all species in the aerial population land and probe on the crop of interest (Boiteau 1990). Water pan traps located within a crop more accurately indicate those species landing in the crop. Differential attraction of aphid species to yellow versus green traps, however, may bias the species composition of the collection (Halbert et al. 1986, Seif 1988, Avinent et al. 1991). Although there is conflicting evidence, in general, yellow pan traps tended to be more attractive than green traps to specific species, such as, *A. spiraeicola*, *M. persicae*, and *R. maidis*. Other species, such as *A. gossypii*, *Lipaphis erysimi*, *M. euphorbiae*, and *R. padi*, have been reported in some studies to be more attracted to green pan traps (Boiteau 1990, DiFonzo et al. 1997). Comparisons among these studies are biased by the different trap compositions used resulting in variations of reflected light quality. However, regardless of the exact reflectance spectra, yellow pan traps tend to collect greater numbers of aphids compared with green traps. The green pan traps collect fewer aphids, but they are thought to better represent ratios of aphid species similar to those landing on the crop foliage (Irwin 1980). Sticky string traps used extensively in France (Labonne et al. 1989) produced species richness data similar to suction traps. In apricot orchards in Spain (Avinent et al. 1993), aphids trapped by nonselective sticky line traps were similar in species composition and abundance to aphids trapped on sticky leaves on trees and green pan traps mirrored those species landing predominately on tree stems. Therefore, species composition and richness are strongly influenced by trap characteristics, and more than one trap type might be necessary for a complete understanding of aphid populations entering a crop.

Our study focused on identifying the aphid species occurring in central Pennsylvania peach orchards. Our primary objectives were to identify predominate aphid species occurring in central Pennsylvania orchards, to verify the presence of probable PPV vector species, and to describe the temporal dynamics of

some of the dominant species that would most likely be involved with vectoring PPV.

Materials and Methods

Aphid Trapping. Aphid trapping was conducted in two peach, *Prunus persicae* (L.) Batsch, orchards during the 2002 and 2003 growing seasons from mid-May, beginning at blossom break (week 16), to early November, after leaf fall (week 42). Orchards of ≈ 15 ha each were located near Stormstown, PA (Centre County) and Milroy, PA (Mifflin County). The orchards consisted of mixed cultivars with trees 3 to 4 m in height. Five sampling sites were positioned in each orchard: one sample site within the first row of trees midway along each of the four borders of the orchard and one in the center of the orchard. Surrounding vegetation around each orchard was recorded. The trap types were yellow and green water pan traps. The water traps were prepared according to Avinent et al. (1991) by spray painting square 25 by 25 by 8-cm plastic storage containers with emerald green or sunshine yellow paint (Krylon, Cleveland, OH). The water traps were placed on wooden platforms held 1.5 m above the ground on steel fence posts, with the different colored traps on separate platforms separated by one tree but within 5 m of each other at each sample site.

Aphid Species Identification. We collected aphids once or twice every week, depending on environmental conditions and the amount of rain received. The aphids collected from traps were stored in 70% alcohol for future identification. Aphids were mounted for species identification by using a method modified from standard protocols (Pike et al. 1990). Briefly, aphid were removed from the 70% ethanol and placed into 10% (wt:vol) KOH in labeled wells of a ceramic plate and heated at medium setting on a hot-plate until the aphids become translucent (≈ 30 min). A small hole was then punctured through the exoskeleton laterally into the abdomen by using a small dissecting probe made from a size two mounting pin (Hamilton Bell Co., Montvale, NJ), and aphids were incubated in the KOH for an additional 10 min. The aphid abdomen was then gently pressed with the bent elbow of a dissecting pin until nymphs were flushed from the body cavity. Aphids were then sequentially transferred to 70% ethanol for 5 min and then to two changes of absolute ethanol for 5 min each. A drop of Polymount mounting medium (Polysciences, Inc., Warrington, PA) was placed directly onto the center of a labeled glass microscope slide, and a specimen was mounted directly into the drop. A slide cover was then placed over the aphid, taking care to maintain aphid appendages in a proper orientation for clear viewing. Species were identified using Smith et al. (1992). Additional verification of species identification used Blackman and Eastop (2000). Initial aphid identifications were made under the direction of Dr. Randi Eckel (R.V.W.E. Consulting, Frenchtown, NJ). Dr. Eckel confirmed species identities of all selected voucher specimens and all difficult-to-

identify specimens. Voucher specimens were selected on the basis of shared morphological characteristics used to identify similar aphids to species. Voucher specimens of all species identified are stored at the Frost Entomological Museum (Department of Entomology, Pennsylvania State University, University Park, PA). Additional voucher specimens of the known PPV vector species were identified and cataloged by S. E. Halbert (Florida Department of Agriculture, Gainesville, FL) and M. Stoetzel (Systematic Entomology Laboratory, USDA, Beltsville, MD).

Analysis. Species richness estimates for aphid communities from Milroy, Stormstown, or both orchards over both years were made using EstimateS (version 6, R. K. Colwell, <http://viceroy.eeb.uconn.edu/estimates/>), by using the Abundance-based Coverage Estimator (ACE) as described by Colwell et al. (1994) and Chazdon et al. (1998) (see Tringe et al. 2005 for a recent example of these tools for estimating biodiversity metrics). A G-statistic from a categorical analysis, using PROC FREQ in SAS 9.1.3 (SAS Institute, Cary, NC), was conducted to determine whether yellow or green had an influence on species composition. Populations of selected species were graphed to examine their relative seasonal dynamics.

Results

Aphid Species Richness and Composition. In total, 928 aphids in 2002 and 1,624 aphids in 2003 were caught in the water pan traps and were subsequently identified. We identified a total of 42 aphid species (Table 1) within both orchards, with 33 species identified in 2002 and 34 species identified in 2003. The Stormstown orchard had 27 and 30 species identified in 2002 and 2003, respectively, whereas the Milroy orchard had 24 and 30 species identified in 2002 and 2003, respectively. This measured species richness from orchard trap counts near the end of the collecting season asymptotically approached estimates of species richness modeled using the Abundance-based Coverage Estimator described by Colwell et al. (1994). The abundance-based coverage model predicted that total species richness (Fig. 1) for the Stormstown orchard in 2002 and 2003 was 32 and 34 species, respectively; and for the Milroy orchard, 29 and 36 species, respectively. Species richness estimates predicted that four to six additional species of aphids might have been present for either year compared with the actual number of species identified. The similarity of our actual counts to the estimated species richness values, and their consistency across years and locations in central Pennsylvania, suggest that these biodiversity metrics are realistic, reasonably stable with current taxonomy, and approach the maximum expected values for this ecologically relevant sampling method.

Nine species were considered dominant (Table 2) because they exceeded $>2\%$ relative abundance for either year. The other 33 species listed in Table 1, which we considered rare species, occurred at $<2\%$ relative abundance. Two percent was chosen as the

Table 1. Aphid species trapped in water pans traps in two Pennsylvania peach orchards, 2002–2003

Aphid species		
<i>Acyrtosiphon pisum</i> (Harris)	<i>Drepanaphis nigricans</i> Smith*	<i>Pemphigus populitransversus</i> Riley**
<i>Anoecia corni</i> (F.)	<i>Drepanaphis sabrinae</i> Miller	<i>Pemphigus populivinae</i> Fitch
<i>Anoecia oenotherae</i> Wilson*	<i>Dysaphis tulipae</i> (Boyer de Fonscolombe)**	<i>Periphyllus americanus</i> (Baker)**
<i>Aphis fabae</i> Scopoli*	<i>Eriosoma lanigerum</i> (Hausmann)	<i>Prociphilus fraxinifolii</i> (Riley)*
<i>Aphis gossypii</i> Glover	<i>Eulachnus rileyi</i> (Williams)	<i>Pterocomma bicolor</i> (Oestlund)**
<i>Aphis lugentis</i> Williams*	<i>Hyperomyzus lactucae</i> (Passerini)**	<i>Pterocomma smithiae</i> (Monell)**
<i>Aphis nasturtii</i> Kaltenbach**	<i>Lipaphis erysimi</i> (Kaltenbach)	<i>Rhopalomyzus poae</i> (Gill)
<i>Aphis pulchella</i> Hottes & Frison**	<i>Macrosiphum euphorbiae</i> (Thomas)	<i>Rhopalosiphum maidis</i> (Fitch)
<i>Aphis spiraecola</i> Patch	<i>Monellia caryella</i> (Fitch)	<i>Rhopalosiphum nymphaeae</i> (L.)*
<i>Brachycaudus persicae</i> (Passerini)	<i>Myzus persicae</i> (Sulzer)	<i>Rhopalosiphum padi</i> (L.)
<i>Brevicoryne brassicae</i> (L.)	<i>Nearctaphis bakeri</i> (Cowen)**	<i>Sipha flava</i> (Forbes)*
<i>Capitophorus elaeagni</i> (del Guercio)	<i>Nearctaphis clydesmithi</i> Hille Ris Lambers	<i>Sipha glyceriae</i> (Kaltenbach)*
<i>Carolinaia rhois</i> (Monell)	<i>Nearctaphis crataegifoliae</i> (Fitch)	<i>Tetraneura nigriabdominalis</i> (Sasaki)
<i>Chaitophorus neglectus</i> Hottes & Frison	<i>Pemphigus populicaulis</i> Fitch	<i>Therioaphis trifolii</i> (Monell)

All species listed captured in both 2002 and 2003, except *species trapped only in 2002, and **species trapped only in 2003.

level to display individual species because species with a lower percentage occurred at a very incidental rate (1% or less of total catch, equivalent to fewer than a total of 25 specimens captured over both seasons). Of the nine most commonly occurring species, six met the 2% dominant criteria in both years. These consistently dominant species were *R. maidis*, *A. spiraecola* (= *A. citricola* van der Goot), *M. persicae*, *Tetraneura nigriabdominalis* (Sasaki), and *Therioaphis trifolii* (Monell) for the Milroy orchard in both years;

and *R. maidis*, *A. spiraecola*, *M. persicae*, and *M. euphorbiae* for the Stormstown orchard in both years.

Only three species were consistently dominant across all locations in both years, *R. maidis*, *A. spiraecola*, and *M. persicae*, with *R. maidis* and *A. spiraecola* consistently being the most numerous aphids observed and trapped. These three species had a temporal sequence of population peaks (Figs. 2 and 3) beginning with *A. spiraecola* in early July. Populations of *A. spiraecola* peaked each year in both or-

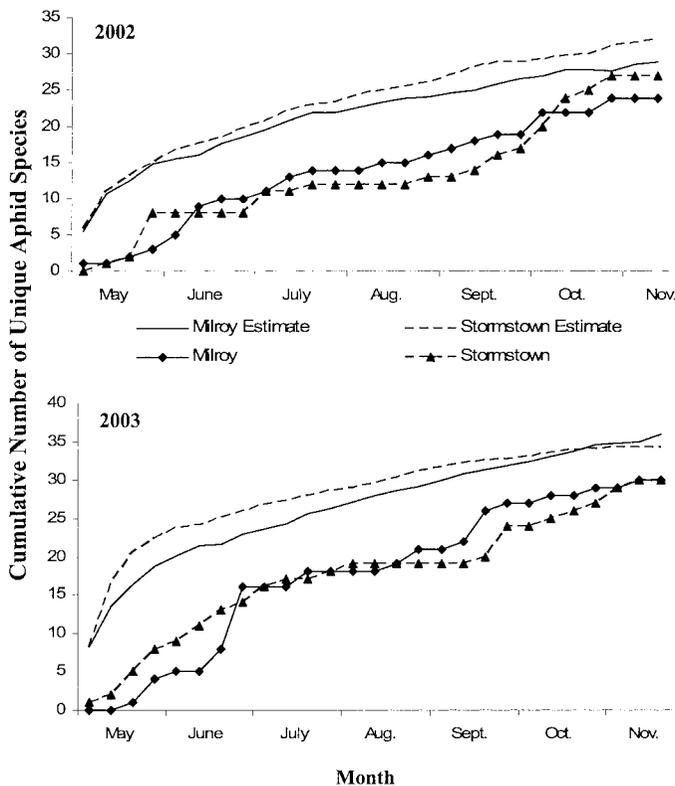


Fig. 1. Estimate of the species richness (S) by using ACE (Colwell and Coddington 1994), and the actual cumulative unique species per week collected in two central Pennsylvania peach orchards (Milroy and Stormstown, PA) in 2002 and 2003. It should be noted that 2003 went 1 wk longer than 2002.

Table 2. Number of aphids trapped in two Pennsylvania peach orchards in each of 2 yr and the percentage composition of each of the nine most dominant aphid species identified

Aphid species	2002		2003		Total	
	No.	%	No.	%	No.	%
<i>Rhopalosiphum maidis</i>	400	43	388	23	788	31
<i>Aphis spiraeicola</i>	124	13	191	12	315	12
<i>Tetraneura nigriabdominalis</i>	36	4	156	10	192	8
<i>Myzus persicae</i>	98	11	82	5	180	7
<i>Aphis gossypii</i>	12	1	132	8	145	6
<i>Lipaphis erysimi</i>	8	1	102	6	110	4
<i>Macrosiphum euphorbiae</i>	23	2	86	5	109	4
<i>Therioaphis trifolii</i>	21	2	59	4	80	3
<i>Brachycaudus persicae</i>	33	4	24	1	57	2
Other species ^a	173	19	404	25	577	23
Total	928	100	1,624	100	2,552	100

Orchards were located near Stormstown and Milroy, PA.

^a Thirty-three aphid species each making up <2% relative abundance were grouped as other species.

chards from early July to early August. Populations of *R. maidis* peaked beginning in late July through mid-August and *M. persicae* populations peaked from mid-September to mid-October.

Although other species, such as *T. nigriabdominalis* and *A. gossypii*, were equivalent to *M. persicae* in the percentage of the total populations trapped over 2 yr, these other species did not occur consistently in all

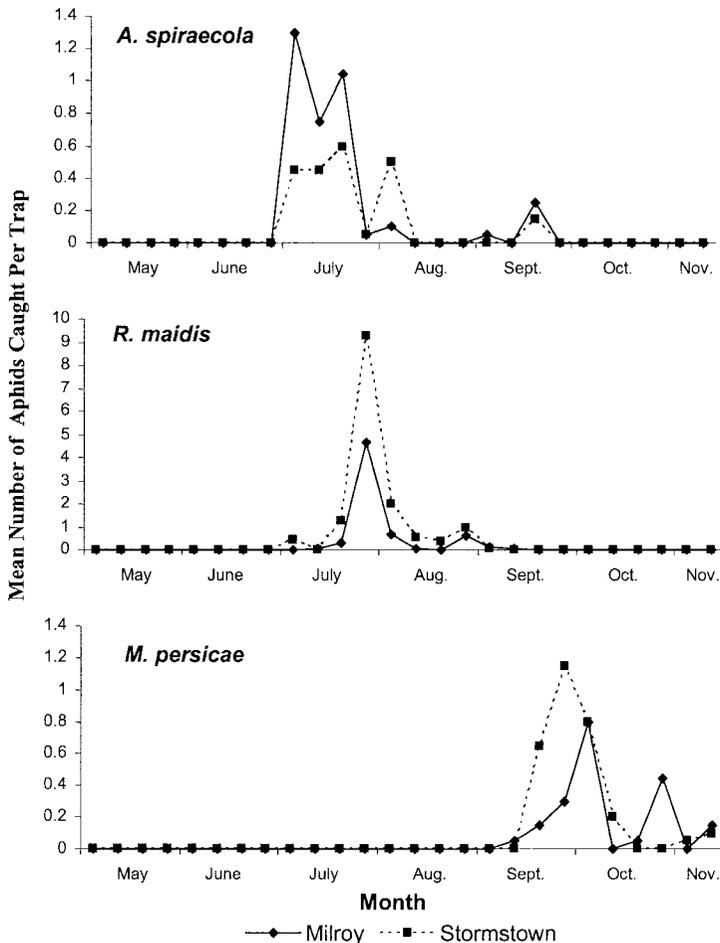


Fig. 2. Seasonal dynamics of three dominant species of aphids collected in two central Pennsylvania peach orchards in 2002 showing the temporal succession of seasonal peaks in combined green and yellow water pan trap catches.

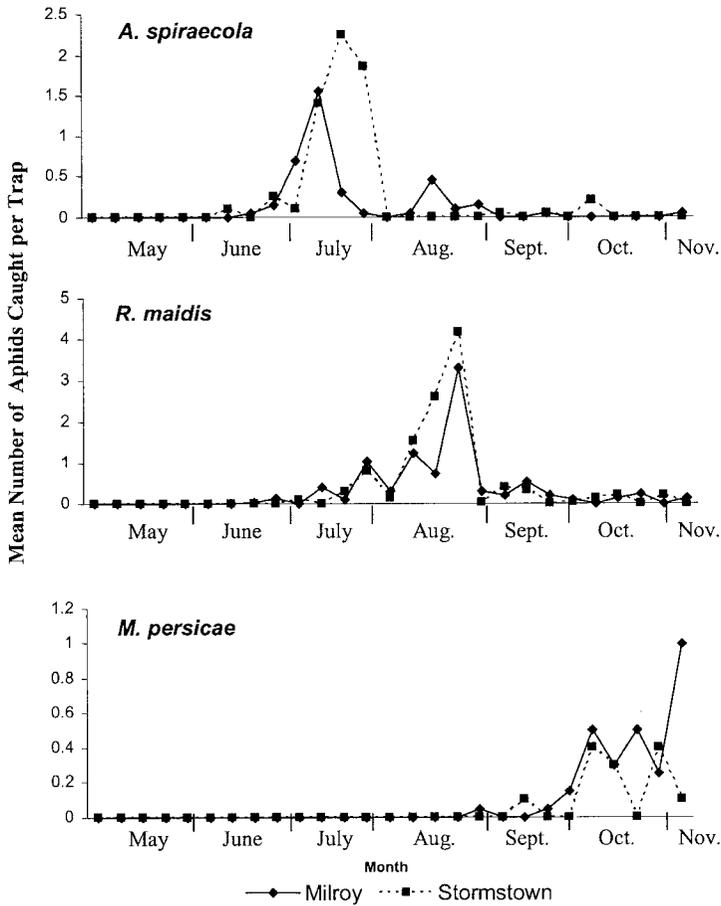


Fig. 3. Seasonal dynamics of three dominant species of aphids collected in two central Pennsylvania peach orchards in 2003 showing the temporal succession of seasonal peaks in combined green and yellow water pan trap catches.

locations or in large numbers in both years, and the data for these species were influenced by rare migrations into the peach orchard over a short time period. In previous tests, *A. spiraecola* and *M. persicae* were demonstrated to be competent vectors of PPV, however, the most common species, *R. maidis*, did not transmit Pennsylvania isolates of PPV (Gildow et al. 2004). *A. gossypii* is a known inefficient vector of PPV in some parts of Europe; however, American populations of this species have not been tested for their ability to transmit PPV.

Trap Comparisons. We compared the distribution of aphids captured in yellow and green traps to determine how trap color might influence the ratio of potential PPV vector species captured. The percentage of total aphids of each of the nine dominant species collected in either yellow or green pan traps are shown in Table 3. Color did have an effect on the distribution of species trapped ($G = 118.20$, $df = 18$, $P < 0.001$). Although the same nine dominant species were represented in both treatments, the ranking of species from most to least numerous varied depending on trap color. Differences were most notable with *R. maidis*, *A. spiraecola*, *M. persicae*, *A. gossypii*, and

T. trifolii. With both colors, *R. maidis* remained the most dominant species, however, the degree of dominance decreased in the green traps. Also, with green traps the dominance of *A. spiraecola* and *M. persicae* decreased, whereas that of *A. gossypii* and *T. trifolii* increased compared with yellow traps. When data for the obviously color-influenced dominant population

Table 3. Influence of trap color on species composition of aphid populations collected in two central Pennsylvania peach orchards in 2002 and 2003

Aphid species	No. collected	% total no. (n)	
		Yellow trap (n = 1827)	Green trap (n = 149)
<i>Rhopalosiphum maidis</i>	788	41	24
<i>Aphis spiraecola</i>	315	16	13
<i>Tetraneura nigriabdominalis</i>	192	10	13
<i>Myzus persicae</i>	180	10	5
<i>Aphis gossypii</i>	145	7	14
<i>Lipaphis erysimi</i>	110	5	8
<i>Macrosiphum euphorbiae</i>	109	5	7
<i>Therioaphis trifolii</i>	80	3	15
<i>Brachycaudus persicae</i>	57	3	1

Orchards were located near Stormstown and Milroy, PA.

Table 4. Percentage of each of the nine dominant aphid species trapped in yellow or green water pan traps in two central Pennsylvania peach orchards in 2002 and 2003

Aphid species	No. collected	% no. collected for each species	
		Yellow trap	Green trap
<i>Rhopalosiphum maidis</i>	788	95	5
<i>Aphis spiraecola</i>	315	94	6
<i>Tetraneura nigriabdominalis</i>	192	90	10
<i>Myzus persicae</i>	180	96	4
<i>Aphis gossypii</i>	145	86	14
<i>Lipaphis erysimi</i>	110	89	11
<i>Macrosiphum euphorbiae</i>	109	91	9
<i>Therioaphis trifolii</i>	80	73	27
<i>Brachycaudus persicae</i>	57	98	2

Orchards were located near Stormstown and Milroy, PA.

of *R. maidis* was excluded and analyzed for the eight less frequent species, there was still a significant effect of color on the aphids species distribution ($G = 61.69$, $df = 16$, $P < 0.001$). The preferential attraction of the nine dominate aphid species to yellow becomes obvious when the percentages of each species captured in yellow and green traps was observed (Table 4). However, *A. gossypii* and *T. trifolii* showed an increased attraction to green compared with the other species, supporting the observation of increased dominance of these species in populations captured in green traps.

Discussion

In total, 42 aphid species were detected in central Pennsylvania peach orchards, with 33 and 34 species identified in 2002 and 2003, respectively. Based on the number of aphid species captured in each orchard, this biodiversity metric ranged from 24 to 34 species each year. Because our sampling technique might not capture all aphid species within a community, a species richness model (Colwell et al. 1994, Chazdon et al. 1998) was used to provide a statistical estimate of the number of species that might be expected to occur within the orchard ecosystem studied. Estimated species richness varied from 30 to 36 based on asymptotic estimators, among years and orchards. The model estimate data suggest that species richness detected by trapping was close to the asymptotic maximum values that might be expected, thus only a few, and probably rare, additional species might be detected with more extensive trapping. Although techniques such as suction traps may estimate a higher species richness for aerobiota, our pan-trapping data and modeled estimates, which consistently converged among locations and years, show a good approximation of species richness for aphids associated with peach canopies and thus potentially vectoring PPV. In addition, species richness values of 24–34 species are similar to those obtained using yellow or green pan traps in other temperate cropping systems (Halbert et al. 1986, DiFonzo et al. 1997, Nault et al. 2004). Boiteau (1990) reported that only ≈50% of the aphid species that were trapped in suction traps over potato fields actually entered the crop and were collected by pan traps.

The five most dominant aphid species trapped in peach orchards in Pennsylvania were *R. maidis* (31%), *A. spiraecola* (12%), *T. nigriabdominalis* (8%), *M. persicae* (7%), and *A. gossypii* (6%) (Table 2). Of these, only *R. maidis*, *A. spiraecola*, and *M. persicae* were consistently identified in all locations in both sampling years. The species composition of the orchards reflected the adjacent landscape. One peach orchard (Milroy) was located adjacent to small grain, maize, and alfalfa field crops and apple orchards. The other orchard (Stormstown) was located immediately adjacent to an apple orchard and a forest of mixed hardwoods. Both orchards were geographically located in a ridge and valley topography surrounded by large stands of hardwood forests. Twenty-four species identified have forest trees as their primary hosts, and many of these species use herbaceous secondary hosts that may occur within and around orchards. Because these species were generally trapped in low numbers (<1%) or infrequently, we hypothesize that these 24 species were trapped within the orchards during their migrations between hosts. The high ranking of *Tetraneura nigriabdominalis* and *A. gossypii* were due primarily to a single large immigration of aphids into orchards during a 1-wk period in only some trap locations in 2003. Ability of *T. nigriabdominalis* to transmit PPV has not been tested. Common species of *Tetraneura* are heteroecious and holocyclic between elm (*Ulmus* sp.) and roots of grasses (Poaceae) (Blackman and Eastop 2000). However, this species is only a rare transient into orchards, suggesting that it would probably not be responsible for large-scale PPV spread. In Europe, populations of *A. gossypii* are reported as either relatively inefficient vectors of PPV or as nonvectors (Labonne et al. 1995, Llacer et al. 1998). Current tests of two North American clones of *A. gossypii* in our laboratory suggest that these clones are either very inefficient or nonvectors (unpublished data). At least four species we trapped colonize *Prunus* spp. as their overwintering host: *B. persicae*, *Rhopalosiphum nymphaeae* (L.), *R. padi*, and *M. persicae* (Stoetzel and Miller 1998). Only *B. persicae* and *M. persicae* must overwinter on peach, and *R. nymphaeae* and *R. padi* do not colonize peach readily. In addition, *R. nymphaeae* and *R. padi* were not captured in large numbers (at most eight individuals in a year) and are unlikely to be the major vectors of PPV. In a recent study (Gildow et al. 2004), the most numerous aphid captured, *R. maidis*, did not transmit Pennsylvania isolates of PPV, whereas *A. spiraecola* and *M. persicae* were very competent vectors. Although *B. persicae* was shown to be a moderate vector of PPV and colonizes peach, it is not commonly observed in Pennsylvania orchards. Based on these observations, we suspect that *A. spiraecola* and *M. persicae* are the most likely key potential vectors of plum pox in Pennsylvania.

Our results are similar to those reported by Avinent et al. (1991) comparing different trap designs in apricot orchards in Spain. In their work using flight-intercepting sticky nylon string traps within the plant canopy, *A. gossypii* was by far the most numerous

species followed by *A. spiraeicola* and then *M. persicae*. Increasing acreage of adjacent citrus crops resulted in large migrating populations of *A. gossypii* entering stone fruit orchards, and these aphids were captured from the air on string traps at a much higher rate than *A. spiraeicola*. However, in both yellow and green pan traps, *A. spiraeicola* dominated. Because *A. gossypii* was unable to transmit PPV in transmission tests, Avinent et al. (1991) concluded that *A. spiraeicola* was probably the most significant vector of PPV. Labonne et al. (1995) working in apricot orchards in France identified a total of 34 aphid species over a 6-yr period with a predominance of *A. spiraeicola* making up 15% of the population, followed by *A. gossypii* (4%), *M. persicae* (3%), and *Rhopalosiphum maidis* (0.8%). In transmission tests *M. persicae* and *A. spiraeicola* transmitted to 10 and 18% of inoculated trees and *A. gossypii* failed to transmit. In subsequent tests, some clones of *A. gossypii* were shown to be inefficient vectors of PPV and other populations were nonvectors.

In warmer climates of peach production, PPV symptoms and virus titer are adversely affected by high ambient temperatures. Symptom remission and virus concentration in infected tissues often decreases with high summer temperatures and under these conditions it is thought that infected trees may not serve as effective PPV sources for secondary spread. In addition, young newly developing foliar tissues in early summer generally have higher virus titers that decrease as the leaf ages and symptoms become less detectable. For effective PPV spread, therefore, timing of optimal host susceptibility, optimal virus titer and optimal vector population should coincide. Whether the relatively mild climates of Pennsylvania summers would adversely influence PPV transmission is not known. Very little is known about PPV transmission efficiency and mechanisms of spread under field conditions. The relationship between the timing of inoculation, systemic spread in the tree, and virus survival over winter is also unknown. All of these concerns need further investigation. However, it seems unlikely that trees inoculated late in summer or early fall would maintain a systemic infection once leaf senescence is initiated.

To better understand how potential vector populations corresponded to seasonal dynamics in the peach orchard, we examined the population dynamics of the three most consistently detected aphid species and related this to when plum pox might be spread during the growing season (Figs. 2 and 3). The most dominant species in our survey, *R. maidis*, peaked from mid-July to mid-August, but it failed to transmit Pennsylvania isolates of PPV when tested (Gildow et al. 2004). The two potential major vectors of plum pox, *A. spiraeicola* and *M. persicae*, had distinct population peaks in June–July and in September–October, respectively. Because *M. persicae* had its population peak very late in the growing season, when trees were rapidly losing leaves from senescence, we hypothesized that there was a very low probability that plum pox would be able to sustain a systemic infection of the tree and survive the winter. Although *M. persicae* was

detected moving into the peach orchards for overwintering in September and October, no *M. persicae* were captured in the late spring and early summer. It seems few individuals of *M. persicae* moved around within the peach orchard canopy during the growing season. In comparison, *A. spiraeicola* populations began to increase in early June and peaked in mid- to late July. This coincides with the time peach trees show optimal symptoms and have good virus titer in infected leaves. Because *A. spiraeicola* was an effective vector of Pennsylvania isolates of PPV and is by far the most numerous vector species detected during the growing season, *A. spiraeicola* becomes implicated as a primary vector for plum pox in Pennsylvania.

It has been known for some time that yellow can greatly increase the number of migrating aphids captured in a water pan trap (Kring 1972). For maximum aphid detection sensitivity by using pan traps, yellow would be a preferred color. However, results do not necessarily mirror aphid landing behavior in the crop canopy (Irwin 1980). Avinent et al. (1991) reported that yellow traps affected the ratio of aphid species being trapped from the total population in apricot orchards. We also confirmed that water pan trap color did influence the relative abundance of species collected in peach orchards (Table 3). All species were differentially attracted to the yellow traps compared with green traps, some more than others (Table 4). Yellow traps did not increase the number of different species or the definition of the most dominant species detected in the population, but they did alter the ratio of species to one another; as predicted by Halbert et al. (1986). Behavioral studies are needed to determine which trap design most accurately reflects the aphid species composition that typically land, probe, and feed on peach vegetation in an orchard.

Due to its effective vectoring of PPV and its consistent dominant presence as transients in peach orchards during the early to midsummer, *A. spiraeicola* is the most likely dominant species responsible for much of the spread of plum pox in Pennsylvania. It remains to be seen whether successful management of this aphid would adequately control the spread of PPV should it become endemic. Nonpersistently spread viruses can be acquired and transmitted rapidly; therefore, transient aphids moving rapidly through orchards can be relevant to our understanding of how PPV might spread. Controlled PPV transmission tests in our laboratory (Gildow et al. 2004) and others (Labonne et al. 1995) have shown that many aphid species are capable of transmitting PPV at very low levels, especially if large numbers of aphids are used per plant. It has been shown that at least 50,000 aphids may land and probe on an apricot tree in one season and that at least one in a thousand aphids trapped in PPV-infected orchards can transmit PPV (Labonne et al. 1994). That means that each tree could be subjected to ≈ 50 potential inoculation probes per year. Therefore, the contribution to PPV spread by inefficient vector species occurring in high densities at the right time in the orchard during infrequent immigrations should not be discounted. There remain many unan-

swered questions concerning PPV survival and spread. However, if PPV becomes established in the United States due to failure of the eradication program, or if even more efficiently transmitted strains of PPV are introduced in the future, it is exactly this type of information that will be needed for developing integrated pest management strategies.

Acknowledgments

We acknowledge the valuable assistance of Bill Sackett and Mary Beth Wiseman for assisting in trap maintenance and aphid identification; and Brooks Way of Way's Orchards, Stormstown, PA, and David Esh of Esh's Orchard, Milroy, PA, whose orchards allowed this study to be possible. This research was supported in part by USDA Cooperative Agreement 58-1920-1-131 and a grant from the Pennsylvania Department of Agriculture, contract no. 442317.

References Cited

- Avinent, L., A. Hermoso de Mendoza, and G. Llacer. 1991. Comparison of traps for capture of alate aphids (Homoptera, Aphidinea) in apricot tree orchards. *Agronomie* 11: 613-618.
- Avinent, L., A. Hermoso de Mendoza, and G. Llacer. 1993. Comparison of sampling methods to evaluate aphid populations (Homoptera, Aphididae) alighting on apricot trees. *Agronomie* 13: 609-613.
- Blackman, R. L., and V. F. Eastop. 2000. *Aphids on the world's crops*, 2nd ed. Wiley, New York.
- Boiteau, G. 1990. Effect of trap color and size on relative efficiency of water-pan traps for sampling alate aphids (Homoptera: Aphididae) on potato. *J. Econ. Entomol.* 83: 937-942.
- Chazdon, R. L., R. K. Colwell, J. S. Denslow, and M. R. Guariguata. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica, pp. 285-309. *In* F. Dallmeier and J. A. Comiskey [eds.], *Forest biodiversity research, monitoring and modeling: conceptual background and Old World case studies*. Parthenon Publishing, Paris, France.
- Colwell, R. K., and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. Ser. B* 345: 101-118.
- Damsteegt, V., A. L. Stone, D. G. Luster, F. E. Gildow, L. Levy, and R. Welliver. 2001. Preliminary characterization of a North American isolate of plum pox virus from naturally infected peach and plum orchards in Pennsylvania, USA. *Acta Hort.* 550: 145-152.
- DiFonzo, C. D., D. W. Ragsdale, E. B. Radcliffe, N. C. Gudmestad, and G. A. Secor. 1997. Seasonal abundance of aphid vectors of potato virus Y in the Red River Valley of Minnesota and North Dakota. *J. Econ. Entomol.* 90: 824-831.
- Gaborjanyi, R., and S. Basky. 1995. Correlation between migration of aphid vector and natural spread of plum pox virus. *Acta Hort.* 386: 201-206.
- Gildow, F., V. Damsteegt, A. Stone, W. Schneider, D. Luster, and L. Levy. 2004. Plum pox in North America: identification of aphid vectors and a potential role for fruit in virus spread. *Phytopathology* 94: 868-874.
- Halbert, S. E., G. Zhang, and Z. Pu. 1986. Comparison of sampling methods for alate aphids and observations on epidemiology of soybean mosaic virus in Nanjing, China. *Ann. Appl. Biol.* 109: 473-483.
- Irwin, M. E. 1980. Sampling aphids in soybean fields, pp. 239-259. *In* M. Kogan and D. Herzog [eds.], *Sampling methods in soybean entomology*. Springer, New York.
- Isac, M., S. Preda, and M. Marcu. 1998. Aphid species—vectors of plum pox virus. *Acta Virol.* 42: 233-234.
- Kolber, M., M. Nemeth, I. Dulic-Markovic, M. Isac, T. Malinowski, B. Zawadzka, A. Myrta, Y. Prichodko, M. Topchiiska, A. Chernets, et al. 2001. Current situation of plum pox disease on stone fruit species in middle and eastern Europe. *Acta Hort.* 550: 73-78.
- Kring, J. B. 1972. Fight behavior of aphids. *Annu. Rev. Entomol.* 17: 461-492.
- Labonne, G., F. Lauriaut, and J. Quiot. 1989. Comparison de trois types de pieges pour l'échantillonnage des populations de pucerons ailes. *Agronomie* 9: 547-557.
- Labonne, G., F. Lauriaut, M. Yvon, et J. B. Quiot. 1994. Dissemination du plum pox par les pucerons: analyse des vecteurs potentiels du virus dans un verger d'abricotiers. *Eur. Plant Prot. Organ. (EPPO) Bull.* 24: 681-690.
- Labonne, G., M. Yvon, J. B. Quiot, L. Avinent, and G. Llacer. 1995. Aphids as potential vectors of plum pox virus: comparison of methods of testing and epidemiological consequences. *Acta Hort.* 386: 207-218.
- Levy, L., V. Damsteegt, and R. Welliver. 2000a. First report of Plum pox virus (sharka disease) in *Prunus persica* in the United States. *Plant Dis.* 84: 202.
- Levy, L., V. Damsteegt, R. Scorza, and M. Kolber. 2000b. Plum pox potyvirus disease of stone fruits. <http://www.apsnet.org/online/feature/plumpox>.
- Llacer, G., and M. Cambra. 1998. Thirteen years of sharka disease in Valencia, Spain. *Acta Hort.* 472: 379-384.
- Lupoli, R., G. Labonne, and M. Yvon. 1992. Variability in the transmission efficiency of potyviruses by different clones of *Aphis gossypii*. *Entomol. Exp. Appl.* 65: 291-300.
- Nault, B. A., D. A. Shah, H. R. Dillard, and A. C. McFaul. 2004. Seasonal and spatial dynamics of alate aphid dispersal in snap bean fields in proximity to alfalfa and implications for virus management. *Environ. Entomol.* 33: 1593-1601.
- Pike, K. S., L. Boydston, and D. Allison. 1990. Alate aphid viviparae associated with small grains in North America: a key and morphometric characterization. *J. Kans. Entomol. Soc.* 63: 559-602.
- Rosales, M., Hinrichsen, P., and Herrera, G. 1998. Molecular characterization of Plum pox virus isolated from apricots, plums, and peaches in Chile. *Acta Hort.* 472: 401-405.
- Roy, S., and I. M. Smith. 1994. Plum pox situation in Europe. *Eur. Plant Prot. Organ. (EPPO) Bull.* 24: 515-523.
- Shukla, D. D., Ward, C. W., Brunt, A. A. 1994. Plum pox virus, pp. 382-385. *In* *The Potyviridae*. CAB International, Wallingford, Oxon, United Kingdom.
- Seif, A. A. 1988. Comparison of green and yellow water traps for sampling citrus aphids at the Kenya coast. *E. Afr. Agric. For. J.* 53: 159-161.
- Singh, M. N., S.M.P. Khurana, and B. B. Nagaich. 1983. Evidence on heredity variations in the virus transmission efficiency of aphid clones. *Z. Pflanz* 90: 345-351.
- Smith, C. F., R. W. Eckel, and E. Lampert. 1992. A key to many of the common alate aphids of North Carolina. *Tech. Bull. No. 299*. North Carolina Agric. Res. Service, North Carolina State University, Raleigh, NC.
- Sohi, S. S., and K. G. Swenson. 1964. Pea aphid biotypes differing in bean yellow mosaic virus transmission efficiency of aphid clones. *Entomol. Exp. Appl.* 7: 9-14.
- Stoetzel, M., and Miller, G. L. 1998. Aphids (Homoptera: Aphididae) colonizing peach in the United States or with potential for introduction. *Fla. Entomol.* 81: 325-345.

- Tringe, S. G., C. von Mering, A. Kobayashi, A. A. Salamov, K. Chen, H. W. Chang, M. Podar, J. M. Short, E. J. Mathur, J. C. Detter, et al. 2005. Comparative metagenomics of microbial communities. *Science (Wash. DC)* 308: 554–557.
- Zeyen, R. L., and Berger, P. H. 1990. Is the concept of short retention time for aphid-borne nonpersistent plant viruses sound? *Phytopathology* 80: 769–771.

Received 26 October 2004; accepted 22 June 2005.
