The Role of Aphid Abundance, Species Diversity, and Virus Titer in the Spread of Sweetpotato Potyviruses in Louisiana and Mississippi

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Abstract

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Sweet potato feathery mottle virus (SPFMV), *Sweet potato virus G* (SPVG), and *Sweet potato virus 2* (SPV2) are sweetpotato (*Ipomoea batatas*) potyviruses nonpersistently transmitted by aphids. Our objective was to determine how aphid abundance, aphid species diversity, and virus titers relate to the spread of SPFMV, SPVG, and SPV2 in Louisiana and Mississippi sweetpotato fields. The most abundant aphid species were *Aphis gossypii*, *Myzus persicae*, *Rhopalosiphum padi*, and *Therioaphis trifolii*. Aphids were captured during the entire crop cycle but virus infection of sentinel plants occurred mainly during the months of June to August. SPFMV was more commonly detected than

SPVG or SPV2 in sentinel plants. Virus titers for SPFMV were higher in samples beginning in late June. Because significant aphid populations were present during April to June when virus titers were low in sweetpotato and there was very little virus infection of sentinel plants, low virus titers may have limited aphid acquisition and transmission opportunities. This is the first study to comprehensively examine aphid transmission of potyviruses in sweetpotato crops in the United States and includes the first report of *R. maidis* and *R. padi* as vectors of SPFMV, though they were less efficient than *A. gossypii* or *M. persicae*.

Sweetpotato (*Ipomoea batatas* L.), a member of the Convolvulaceae family, is cultivated widely in tropical and subtropical areas and ranks among the top 10 most important food crops worldwide (27). In the United States, sweetpotato is increasingly regarded as a uniquely nutritious food and demand is increasing as more processed products becoming available (8). In Africa and parts of Asia, sweetpotato is an important food security crop, where it is relied upon during times of drought and famine when other crops fail (19).

Sweetpotato is vegetatively propagated and is prone to accumulate viruses which cause cultivar yield decline and reduce storage root quality (10,11). Of the sweetpotato viruses described thus far, the most common worldwide is *Sweet potato feathery mottle virus* (SPFMV; 8,28,31). In the United States, the most common viruses are the potyviruses SPFMV, *Sweet potato virus G* (SPVG), and *Sweet potato virus 2* (SPV2; synonym = *Ipomoea vein mosaic virus*) (8,31,41). SPVG and SPV2 are known to occur in China, Africa, and the United States and were recently reported in Australia and the Pacific region (37,43).

Effective implementation of disease management practices requires knowledge of numerous biological features that mediate pathogen transmission (13). In the case of vector-borne pathogens, virus epidemiology could depend on vector abundance, vector

species, host species, inoculum availability, pathogen strain, and local climate (13,14). Although SPFMV, SPVG, and SPV2 are prevalent in cultivated sweetpotato throughout the United States and frequently reinfect virus-tested planting material, there is little knowledge about what factors affect their spread.

Sweetpotato potyviruses commonly occur as mixed infections in the field (31,41). Mixed infections of SPFMV, SPVG, and SPV2 in 'Beauregard' sweetpotato usually show mild chlorotic spotting and veinal chlorosis or no symptoms, and cause yield losses of less than 15% (12,24). Although mechanical transmission of sweetpotato potyviruses can be accomplished using buffers and high-titer sources such as *I. nil*, transmission of these viruses in the field is mainly by several aphid species (28,29,42) in a nonpersistent manner (22,29). From past reports, aphids that transmit SPFMV include *Aphis gossypii* Glover, *A. craccivora* Koch, *Myzus persicae* (Sulzer), and *Lipaphis pseudobrassicae* (Davis) (28,29). Sweetpotato potyviruses can also infect other wild plants that are potential sources of inoculum (8); mainly, morning glory plants in the genus *Ipomoea* (28). In Louisiana, the morning glory *I. cordatotriloba* Dennst. (synonym *I. trichocarpa* Eill.) and *I. hederacea* Jacq. are common in and around sweetpotato fields, and *I. hederifolia* L., *I. lacunosa* L., and *I. wrightii* Wall. are also known wild hosts of SPFMV (9).

Aphids, particularly those in the family Aphididae, are of economic importance in temperate regions primarily due to their role as vectors of plant viruses, transmitting about 57% of known insect-vectored plant viruses (36). They possess biological characteristics that make them effective in acquiring and transmitting plant viruses such as specialized morphs adapted to different functions, host plant alternation, exceptionally short life cycles due to parthenogenetic reproduction, and a unique host-finding behavior that involves sap sampling (36). The sap-sampling behavior involves brief probes into the epidermal cells that may last for just a few seconds to determine acceptance or rejection of a plant for feeding. This behavior usually facilitates transmission of nonpersistent viruses whose titers are usually higher in epidermal and subepidermal plant cells (36). Aphids may take as little as 3 to 35 s

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to acquire and inoculate nonpersistent viruses but transmissibility of these viruses is lost within a period of 1 to 2 h (42,48). Therefore, the progress of virus spread in the field depends on the number of vectors alighting and probing plants (vector activity) as well as the natural ability of each aphid species to inoculate the virus (vector propensity) (14). Effective transmission of these viruses can easily be carried out by transient aphid species that do not necessarily colonize the host plant (14,35,36).

Aphid flight activity and species diversity have been monitored in other crop systems with the aim of understanding virus spread and timing of control strategies such as applications of insecticides, crop oils, or defoliant (36). In sweetpotato, the only recent study of aphid activity in relation to spread of sweet potato virus disease (SPVD) found that aphids were present throughout the study period in Uganda (7). SPVD is caused by synergism between the aphid-transmitted SPFMV and whitefly-transmitted *Sweet potato chlorotic stunt virus* (SPCSV). The authors did not report on aphid species diversity but emphasized more the relationship between whiteflies and spread of SPCSV rather than aphid spread of SPFMV. In Louisiana during the 1950s, Kantack et al. (20) trapped aphids using tangle-foot traps in sweetpotato fields in south Louisiana. The authors captured several aphid species, with the majority being *A. gossypii*, *M. persicae*, and *Macrosiphum euphorbiae*. Yellow and green pan traps and yellow sticky traps have been successfully used to monitor aphid flight activity and capture for species identification (14,16,36). Although most studies report a positive relationship between aphid abundance and virus spread, there are also cases where no relationship was found, depending on the season (44). Several studies have also reported fluctuation in virus spread incidences depending on prevailing aphid species diversity in terms of number of vector species and population density of individual species (16,36).

Aphid captures provide only an indirect measure of risk of virus spread. Therefore, other strategies such as exposure of sentinel plants at varying intervals at study sites or trapping live aphids and directly assaying for their ability to acquire and transmit viruses are commonly used to relate aphid flight activity to virus spread (36). Virus titer in host plants has been reported to vary depending on host species, infection status, growth stage, and season and this may impact virus acquisition and transmission by vectors (2,15,18,24,38,45,48). Higher virus titers in source leaves are related with increased transmission rates by aphids (2,15,48), indicating that titer levels may play an important role in spread of viruses apart from presence of vectors.

The aim of this study was to monitor aphid abundance, aphid species diversity and field virus titers in relation to the spread of potyviruses in Louisiana and Mississippi sweetpotato fields (plant beds and production fields). This knowledge is essential in designing proper management strategies to obtain the healthiest possible planting materials and minimize the impact of these potyviruses on sweetpotato yield and root quality.

Materials and Methods

Aphid trapping. Aphids were trapped using yellow sticky traps for total population counts for three consecutive years (2009 to 2011), and pan traps for use in species identification for four consecutive years (2008 to 2011) during the months of March to September at six sites in Louisiana. In Mississippi, aphids were trapped at three sites using both yellow sticky traps and pan traps for 2 years (2010 to 2011) during the months of April to September. Two of the sites in Louisiana, the Burden Research Center (BRC) in East Baton Rouge Parish and the Sweet Potato Research Station (SPRS) at Chase in Franklin Parish are research stations, and the other four were commercial sweetpotato farms located in St. Landry, West Carroll, Morehouse, and Franklin Parishes of Louisiana. Three sites (BRC, SPRS, and St. Landry) were sampled during the entire study period, while the other three sites (all located in north Louisiana) were each sampled for 1 year. Mississippi sites were commercial farms near Houlka in Chickasaw County, Bellefontaine in Webster County, and Vardaman in Cal-

houn County. The Chickasaw site was sampled for both years while the Webster and Calhoun sites were sampled in 2010 and 2011, respectively. Except for the SPRS site, which had some fields planted with virus-free plants and some fields planted with G1 plants that typically have 25 to 75% infection with SPFMV, all other sites were planted with later-generation plants that have 90 to 100, 10 to 70, and 5 to 40% infection with SPFMV, SPVG, and SPV2, respectively (12).

Yellow sticky traps (7.35 by 12.25 cm) with double-sided adhesive (Whitemire Micro-Gen Research Laboratories Inc., St. Louis) were attached to dark-green stakes (120 cm in height by 0.5 cm in diameter; Woodstream Corporation, Lititz, PA) using two small binder clips (Staples Inc., Framingham, MA) at 90 cm above the ground. The yellow sticky traps were exposed for weekly intervals at five different positions within each field, four at the corners and one at the center. Three sets of yellow and green pan traps were also exposed for weekly intervals in each field. One set was placed at the center, while the other two were placed at two diagonally opposed corners. The pan traps were small, rectangular, 1.4-liter plastic dishes (Servin Saver; Rubbermaid, Wooster, OH) containing yellow and green tiles (7.35 by 7.35 cm; Imola, Cooperativa Ceramica D' Imola S.C., Vittorio Veneto, Italia) and 50 ml of a 50:50 volume mixture of propylene glycol and water. They were supported in tomato wire cages just above the sweetpotato canopy. Sticky traps were wrapped in clear wrap films to prevent them from adhering together when collected from the field. Aphids on sticky traps were counted with the aid of a dissecting microscope (Bausch and Lomb, Rochester, NY) using $\times 7$ magnification. Pan trap contents were brought to the laboratory and insects extracted using a 7.5-cm-diameter Büchner funnel lined with filter paper, and inserted in a conical flask with a rubber pipe connected to a suction pump. Aphids collected from pan traps were preserved in 1.5-ml vials containing 95% ethanol for later identification. Aphids were identified to species or genus level with the aid of taxonomic keys based on assessment characteristics, including wing, abdomen, siphunculi, cauda, head, and antenna morphology, using magnification of $\times 35$ (dissecting microscope) or $\times 160$ (compound microscope) (6,33,40,47).

Sentinel plants. *I. setosa* Ker Gawl. (Brazilian morning glory) seedlings at the cotyledonary stage were used to monitor the spread of potyviruses. In Louisiana, plants were grown from seed (four plants/pot) in the greenhouse under wide temperature (10 to 32°C) and humidity (21 to 98%) ranges in 15-cm-diameter plastic pots (Belden Plastics, St. Paul, MN) containing an autoclaved soil mix consisting of one part river silt, one part sand, one part Jiffy-Mix Plus (Jiffy Products of America Inc., Norwalk, OH), and Osmocote 14-14-14 (Scotts-Sierra Horticultural Products Co., Marysville, OH) at 3.5 g/pot. Plants were not sprayed with insecticides. Single pots with up to two to four seedlings, depending on germination, were placed in the field next to sticky traps for a total of five pots in each field. Soil moisture was maintained by placing pots in water-filled nonperforated plastic seedling trays (Belden Plastics). In Mississippi, seed were germinated in 50 round-cell pro-trays (TLC Polyform, Inc., Phoenix, AZ) and 1-week-old seedlings were transplanted into pots (three per pot) filled with soilless media (Metro-Mix 366; Sun Gro Horticulture Canada Ltd., Seba Beach, Alberta, Canada) and kept in the greenhouse for another week before placing in the field (five pots per field). The plants were removed from the field on a weekly basis and placed in Bug Dorm cages (MegaView Science Co. Ltd, Taichung, Taiwan) in the greenhouse. They were monitored for expression of virus symptoms for an additional 2 weeks. Plants showing symptoms were recorded and leaves sampled for testing of SPFMV, SPVG, and SPV2 using nitrocellulose-membrane enzyme-linked immunosorbent assay (NCM-ELISA).

NCM-ELISA assays. The most widely used serological method (8) for detection of sweetpotato viruses is a membrane immunobinding assay known as NCM-ELISA. Because virus titers are often very low in sweetpotato, NCM-ELISA is generally used after grafting to indicator hosts such as *I. setosa*. Leaf tissue was

collected from symptomatic sentinel plants and assayed using antisera produced to the russet crack strain of SPFMV provided by J. W. Moyer (North Carolina State University, Raleigh), or antisera to isolates from Louisiana of SPVG and SPV2 provided by S. Fuentes (International Potato Center, Lima, Peru). A small piece (approximately 1 cm²) was collected from three different leaves with symptoms from each Brazilian morning glory plant and assayed as described previously (12).

Virus titer quantification. Real-time reverse-transcriptase polymerase chain reaction (real-time RT-PCR) assays are the most reliable assays for relative quantification of viruses from sweetpotato (8,24,25). These assays were used for virus titer quantification from sweetpotato Beauregard plants in plant beds and production fields at BRC on a weekly basis from May to September 2010 and 2011. Leaf portions (approximately 9 cm²) were collected arbitrarily from lower vine sections (preliminary experiments revealed greater SPFMV, SPVG, and SPV2 titers in lower leaves than middle or upper leaves of sweetpotato plants under field conditions) of five different plants and combined into a single composite sample in small envelopes. Five samples were collected each week and leaves were immediately placed in liquid nitrogen and transferred to the laboratory, where they were stored under refrigeration at -70°C until extraction of RNA. Assays were carried out according to procedures of Kokkinos and Clark using eukaryotic 18S rRNA for normalization (25). A fivefold standard curve of six dilutions was developed using a positive control of SPFMV-russet crack (RC), isolate 95-2, SPVG, and SPV2 RNA extracts from *I. nil* 'Scarlet O'Hara' (SOH) to test for any inhibition of optimal PCR conditions.

Morning glory weeds. Study sites in Louisiana were monitored for morning glory plants growing as weeds; their species diversity and time of first virus symptom appearance were recorded. Plant species were identified based on an identification key by Rogers and Oliver (39).

Virus vector testing. Two aphid species that had not previously been tested as vectors of sweetpotato potyviruses, *Rhopalosiphum maidis* and *R. padi*, were tested for their ability to transmit SPFMV. These two aphid species were selected because they were identified among those captured in pan traps, and it was possible to establish their colonies. *R. padi* was collected from winter wheat at the Louisiana State University Agricultural Center (LSU AgCenter) Sweet Potato Research Station (Chase) in Franklin Parish, LA in February 2012. *R. maidis* was collected from winter wheat at the LSU AgCenter Macon Ridge Research Station (Franklin Parish, LA) in March 2011. Aphid colonies were established on 'LA 841' wheat plants (*Triticum aestivum*) (not a host for sweetpotato viruses) from a group of apterae and maintained under laboratory conditions in screened cages at room temperature (20 to 22°C) and a photoperiod of 16 and 8 h (light and darkness, respectively). Plants were grown in a growth chamber with temperature set at 25°C, photoperiod of 14 and 10 h (light and darkness, respectively), and humidity at 80%. A cohort of 20 to 30 aphids was placed on fresh plants using a paint brush to establish new colonies every 2 to 3 weeks. In addition, *Myzus persicae*, maintained according to Wosula et al. (48), was used as a comparative standard because it is a known efficient vector of SPFMV.

Ipomoea cordatotriloba was used as the source plant of SPFMV because our previous study indicated *M. persicae* and *A. gossypii* transmit SPFMV more readily from this host than sweetpotato. SPFMV was established and maintained in *I. nil* SOH as described by Wosula et al. (48), from which it was mechanically inoculated to *I. cordatotriloba*. SOH plants were used as test plants at the cotyledonary stage, approximately 5 to 7 days after sowing. The transmission experiment treatments, replicates, and procedures were carried out as described by Wosula et al. (48) except, in this experiment, aphids were allowed to probe for 1 min instead of 30 s. A single aphid was placed on each test plant and, in each of five experiments, 20 test plants were used. Transmissions with *R. maidis* were done separately while transmissions with *R. padi* and *M. persicae* were done simultaneously.

Data analysis. Means and their respective standard errors for aphid counts on yellow sticky traps, aphid species counts in pan traps, percent infected sentinel plants, and virus titer were generated using SAS PROC MEANS procedures. Data for comparison of aphid numbers on yellow sticky traps at different locations within the field were log transformed and subjected to SAS PROC Generalized Linear Model procedures. PROC CORR procedure with Pearson's correlation coefficient was used to test for the relationship between aphid number and infection of sentinel plants. Transmission efficiency was estimated as number of infected test plants divided by total number of test plants, expressed as percentage. Maximum likelihood ratios were generated, and confidence intervals calculated using Microsoft Excel add-in PooledInfRate, version 3.0 (5).

Results

Aphid trapping. Although populations fluctuated with time, aphids were captured on yellow sticky traps throughout the monitoring period from March to September for the 3-year period at six sites in Louisiana and April to September for the 2-year period at three sites in Mississippi (Fig. 1A and B). When counts were averaged across all sites in Louisiana, aphid population peaks occurred in mid-April to late May and mid-August to mid-September (Fig. 1A). In Mississippi, a distinct peak occurred in late July to early August, with small fluctuations the remainder of the period (Fig. 1B). Aphid peaks were similar for different individual study sites within a state but, at three sites in Louisiana (Franklin, Morehouse, and BRC in 2009), major aphid peaks also occurred during the period of July to September (*data not shown*). Additional analysis of log-transformed aphid count data revealed no significant differences in aphid captures on sticky traps based on trap location within the field across all sites during the study period for Louisiana (F value = 2.04; P = 0.0863) and Mississippi (F value = 1.82; P = 0.1237).

Total aphids captured in yellow and green pan traps for the 4-year period at Louisiana sites and 2-year period at Mississippi sites

Fig. 1. Weekly average number of aphids captured on yellow sticky traps (number/trap) in sweetpotato fields in A, Louisiana (2009 to 2011) and B, Mississippi (2010 to 2011) (means $\pm$ standard error).

comprised 27 species (Tables 1 and 2). Louisiana sites had diverse aphid species and variable percentage compositions during the 4-year study period. In 2008, five aphid species (*A. gossypii*, *R. padi*, *Forda formicaria*, *R. maidis*, and *T. trifolii*) made up 93% of total aphids captured, with two (*A. gossypii* and *R. padi*) composing 75%. In 2009, six aphid species (*A. gossypii*, *F. formicaria*, *Macrosiphum euphorbiae*, *R. padi*, and *Sipha flava*) accounted for 92% of total aphids captured, with *A. gossypii* and *R. padi* making up 74%. In 2010, six aphid species (*A. gossypii*, *L. pseudobrassicae*, *Myzus persicae*, *R. padi*, and *T. trifolii*) accounted for 94% of total aphids captured, and *A. gossypii* and *R. padi* composed 51%. In 2011, seven aphid species (*A. gossypii*, *F. formicaria*, *L. pseudobrassicae*, *Uroleucon ambrosiae*, *M. persicae*, *R. padi*, and *T. trifolii*) accounted for 83% of total aphids captured, and *A. gossypii* and *R. padi* composed 47%. The known efficient vectors of sweetpotato potyviruses, *M. persicae* and *A. gossypii*, when combined, accounted for 56, 40, 26, and 18% in 2008, 2009, 2010, and 2011, respectively. Mississippi sites had aphid species diversity similar to Louisiana sites but percent composition differed during the 2-year study period. In 2010, three aphid species (*A. gossypii*, *M. persicae*, and *R. padi*) accounted for 90% of the total aphids captured, and *A. gossypii* and *M. persicae* alone composed 86%. In 2011, five aphid species (*A. gossypii*, *F. formicaria*, *L. pseudobrassicae*, *R. padi*, and *T. trifolii*) accounted for 93% of the total aphids captured, with *R. padi* and *T. trifolii* composing 58%. The known vectors *M. persicae* and *A. gossypii*, combined, accounted for 86 and 26% in 2010 and 2011, respectively.

The most dominant aphid species at all sites in both Louisiana and Mississippi were *A. gossypii*, *M. persicae*, *R. padi*, and *T. trifolii*. The general flight activity of these four species differed depending on state. In Louisiana, *A. gossypii* and *R. padi* were consistently present throughout the study period, with peaks occurring in April and mid-June to mid July, while *M. persicae* and *T. trifolii* were present during the period of March to mid-May, and absent or in very low numbers the rest of the season (Fig. 2A). In Mississippi, *A. gossypii* was the only species consistently present throughout the study period, with major peaks occurring in June

and July; whereas *M. persicae*, *R. padi*, and *T. trifolii* were present during the period of May to mid-June and in very low numbers or absent the rest of the season (Fig. 2B). Total aphids captured in pan traps at all sites during the entire study period were significantly higher in yellow pan traps ($n = 1,679$) than green pan traps ($n = 920$) ($\chi^2 = 5.4$, $P = 0.0196$). Among the most prevalent aphid species (having at least 10% of total population in any of the years), *R. padi* was the only species that had a significant difference in captures in different color pan traps, with more caught in yellow traps ($\chi^2 = 3.85$, $P = 0.0495$).

Sentinel plants. Although sentinel plants were placed in the fields throughout the study period, a majority of the infections

Table 2. Total number and percent composition of aphids captured in green and yellow pan traps in sweetpotato fields at sites in Mississippi, 2010 to 2011

Aphid species	Number (%)	
	2010	2011
<i>Acyrtosiphum pisum</i> (Harris)	11 (3.2)	6 (3.8)
<i>Anoecia</i> sp.	1 (0.3)	0 (0.0)
<i>Aphis craccivora</i> Koch	0 (0.0)	2 (1.3)
<i>Aphis gossypii</i> Glover	179 (52.6)	36 (23.1)
<i>Aphis</i> sp.	4 (1.2)	0 (0.0)
<i>Drepanaphis</i> sp.	3 (0.9)	0 (0.0)
<i>Forda formicaria</i> von Heyden	4 (1.2)	9 (5.7)
<i>Lipaphis pseudobrassicae</i> (Davis)	1 (0.3)	4 (2.6)
<i>Myzus persicae</i> (Sulzer)	115 (33.8)	3 (1.9)
<i>Rhopalosiphum maidis</i> (Fitch)	0 (0.0)	1 (0.6)
<i>Rhopalosiphum padi</i> (L.)	14 (4.1)	40 (25.6)
<i>Schizaphis graminum</i> (Rondani)	2 (0.6)	0 (0.0)
<i>Sipha flava</i> (Forbes)	0 (0.0)	1 (0.6)
<i>Therioaphis trifolii</i> (Monell)	3 (0.9)	50 (32.1)
<i>Uroleucon ambrosiae</i> (Thomas)	1 (0.3)	0 (0.0)
<i>Uroleucon</i> sp.	0 (0.0)	1 (0.6)
Unidentified/damaged	2 (0.6)	3 (1.9)
Aphids caught in yellow pan traps	216 (63.7)	81 (51.8)
Aphids caught in green pan traps	123 (36.3)	75 (48.2)
Total number of aphids caught	340	156

Table 1. Total number and percent composition of aphids captured in green and yellow pan traps in sweetpotato fields at sites in Louisiana, 2008 to 2011

Aphid species	Number (%)			
	2008	2009	2010	2011
<i>Acyrtosiphum pisum</i> (Harris)	0 (0.0)	0 (0.0)	0 (0.0)	4 (0.8)
<i>Amphorophora rubi</i> (Kalt.)	0 (0.0)	1 (0.1)	4 (0.5)	1 (0.2)
<i>Anoecia</i> sp.	0 (0.0)	1 (0.1)	0 (0.0)	3 (0.6)
<i>Aphis craccivora</i> Koch	0 (0.0)	0 (0.0)	0 (0.0)	25 (5.2)
<i>A. gossypii</i> Glover	117 (56.3)	235 (36.8)	138 (17.7)	68 (14.3)
<i>A. nasturtii</i> Kalt.	1 (0.5)	0 (0.0)	0 (0.0)	0 (0.0)
<i>Aphis</i> sp.	0 (0.0)	2 (0.2)	1 (0.1)	6 (1.2)
<i>Chaitophorus populicola</i> (Thomas)	0 (0.0)	1 (0.1)	3 (0.4)	0 (0.0)
<i>Colopha</i> sp.	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.2)
<i>Drepanaphis</i> sp.	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.2)
<i>Drepanosiphum</i> sp.	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.2)
<i>Eriosoma</i> sp.	0 (0.0)	0 (0.0)	0 (0.0)	2 (0.4)
<i>Forda formicaria</i> von Heyden	16 (7.7)	32 (4.9)	25 (3.2)	55 (11.4)
<i>Hylopterus</i> sp.	0 (0.0)	0 (0.0)	0 (0.0)	3 (0.6)
<i>Lipaphis pseudobrassicae</i> (Davis)	4 (1.9)	20 (3.1)	53 (6.8)	12 (2.5)
<i>Macrosiphum euphorbiae</i> (Thomas)	0 (0.0)	27 (4.2)	4 (0.5)	11 (2.3)
<i>Myzus persicae</i> (Sulzer)	0 (0.0)	18 (2.8)	121 (15.3)	27 (5.5)
<i>Rhopalosiphum maidis</i> (Fitch)	15 (7.2)	0 (0.0)	0 (0.0)	7 (1.2)
<i>R. padi</i> (L.)	39 (18.8)	238 (37.4)	262 (33.3)	157 (33.0)
<i>Rhopalomyzus</i> sp.	1 (0.5)	0 (0.0)	0 (0.0)	0 (0.0)
<i>Sarucallis kahawaluokalani</i> (Kirkaldy)	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.2)
<i>Schizaphis graminum</i> (Rondani)	0 (0.0)	0 (0.0)	0 (0.0)	4 (0.8)
<i>Sipha flava</i> (Forbes)	2 (0.9)	23 (3.6)	9 (1.1)	0 (0.0)
<i>Therioaphis trifolii</i> (Monell)	8 (3.4)	35 (5.5)	99 (12.6)	59 (12.2)
<i>Uroleucon ambrosiae</i> (Thomas)	2 (1.0)	4 (0.5)	65 (8.4)	19 (4.0)
<i>Utamphorophora</i> sp.	2 (0.9)	0 (0.0)	0 (0.0)	0.0
Unidentified/damaged	1 (0.5)	9 (1.4)	1 (0.1)	8 (1.6)
Aphids caught in yellow pan traps	138 (66.3)	459 (72.2)	482 (61.4)	303 (63.8)
Aphids caught in green pan traps	70 (33.7)	177 (27.8)	303 (38.6)	172 (36.2)
Total number of aphids caught	208	636	785	475

occurred during the months of June to August, with highest infections in July in both Louisiana and Mississippi sites (Fig. 3). In all, 78% of the total infections of sentinel plants occurred during July and August in Louisiana whereas, in Mississippi, 89% of total infections occurred during the same period. Very few sentinel plants were infected during the months of March to May (Fig. 3). The highest overall percent infection in total sentinel plants was 24% (120 infected plants) in 2011 at sites in Mississippi, while the lowest was 4% (39 infected plants) in 2011 at sites in Louisiana (Table 3). The greatest number of infected plants in a single week (27/30) occurred in the last week of July in 2011 at sites in Mississippi. Symptomatic plants tested positive for SPFMV (90 to 100%), SPVG (9 to 25%), and SPV2 (1 to 28%). Sixty-eight samples of symptomless plants were tested in 2011 and all were negative for all three viruses. Percent infection of sentinel plants at sites in Louisiana did not differ among the three years (4 to 5%) whereas, at sites in Mississippi, the infection incidence in 2011 (24%) was almost double that of 2010 (10%), despite the fact that much greater aphid populations (especially of *A. gossypii*)

Fig. 2. Weekly average number of the four most dominant aphid species (*Aphis gossypii*, *Myzus persicae*, *Rhopalosiphum padi*, and *Therioaphis trifolii*) captured in pan traps (total number for six pan traps) in sweetpotato fields in **A**, Louisiana (2009 to 2011) and **B**, Mississippi (2010 to 2011) (means $\pm$ standard error).

occurred in 2010 than 2011 during the period of virus transmission. Correlation analysis revealed a significant relationship between the total number of aphids captured on sticky traps and infection of sentinel plants at Mississippi sites ($r = 0.81$; $P < .0001$) whereas, for Louisiana sites, the relationship was not significant ($r = 0.13$; $P = 0.5575$). Correlation analysis with captures of the known efficient vector *A. gossypii* and infection of sentinel plants showed a significant relationship at Mississippi sites ($r = 0.57$; $P = 0.0083$) but not at Louisiana sites ($r = 0.35$; $P = 0.0656$).

Virus titer quantification. Titters of SPFMV in sweetpotato were generally higher during the period of late June to September, when plants were undergoing rapid vine growth in the field, compared with May to mid-June, when plants were in plant beds or just newly transplanted to the field (Fig. 4). SPVG titers varied greatly within and between seasons. They were greatest during late May and again in late August 2010 and in June 2011 (Fig. 5). SPV2 titers were greater during the period of early June and August 2010 and July 2011 (Fig. 6). Correlation analysis between SPFMV titers and infection of sentinel plants at sites in Louisiana revealed a significant positive relationship ($r = 0.45$; $P = 0.0337$). Correlation analysis with SPV2 showed a nonsignificant positive relationship ($r = 0.27$; $P = 0.2863$) whereas SPVG had a significant negative relationship ($r = -0.52$; $P = 0.0286$).

Morning glory weeds. A majority of the morning glory plants observed in sweetpotato plant beds and fields in Louisiana were annuals that germinated from seed, mainly between May and July. The most common species at all study fields were *I. hederacea* and *I. cordatotriloba* that occurred in the range of about one to 5 seedlings per 20 m². *I. lacunosa* was observed only at the Morehouse Parish, LA site. The St. Landry Parish, LA site had a high popula-

Fig. 3. Weekly average percent infection by sweetpotato potyviruses (means/field of *Ipomoea setosa* sentinel plants that showed potyvirus symptoms after 1 week exposure in sweetpotato fields and 2 weeks subsequent growth in a greenhouse) in Louisiana and Mississippi (means $\pm$ standard error).

Table 3. Number of *Ipomoea setosa* plants exposed in sweet potato fields, incidence of potyvirus symptoms and incidence of specific potyviruses as determined by NCM-ELISA in Louisiana 2009 to 2011 and Mississippi 2010 to 2011

Region, year	Number of plants		Total infected (%) ^a	SPFMV (%) ^b	SPVG (%) ^b	SPV2 (%) ^b
	Exposed	With symptoms				
Louisiana						
2009	1,394	66	5	97	9	6
2010	1,166	55	5	100	10	1
2011	1,129	39	4	100	15	3
Mississippi						
2010	405	40	10	95	25	28
2011	510	120	24	90	15	7

^a Percentage of all sentinel plants exposed that developed potyvirus symptoms.

^b Those plants that were symptomatic and tested positive for the respective virus species in either single or mixed infections. SPFMV = *Sweet potato feathery mottle virus*, SPVG = *Sweet potato virus G*, and SPV2 = *Sweet potato virus 2*.

tion of *J. tamnifolia* (up to about 10 seedlings per 1 m² in noncultivated plowed areas around the sweetpotato fields) throughout the 3-year period, while the other sites had very few plants of this species. Each year, virus symptoms were first observed on *I. hederacea* and *I. cordatotriloba* plants during the period of late June to mid-July at most sites whereas *J. tamnifolia* remained asymptomatic at these sites throughout the season.

Virus vector testing. *R. maidis* and *R. padi* successfully transmitted SPFMV from a singly infected *I. cordatotriloba*. This is believed to be the first report of transmission of SPFMV by *R. maidis* and *R. padi*, although they are less efficient vectors (1 and 2%, respectively) than *M. persicae* (22%) (Table 4).

Discussion

Despite the fact that aphids were present throughout the entire growing season, sweetpotato potyviruses were not transmitted to *I. setosa* sentinel plants to any significant extent in plant beds, where density and proximity of susceptible plants is greatest. Instead, transmission occurred primarily during a period after transplanting to production fields, when the sweetpotato vines were growing rapidly. Aphid numbers and species composition varied during the season and were not correlated with virus transmission to sentinel plants at sites in Louisiana. In fact, the period of greatest virus spread began in late June to early July, between the first and second peaks of aphid flight, which occurred in mid-April to early June and mid-August to early September, respectively. However, in

Mississippi, the major aphid flight coincided with the period of greatest virus transmission to sentinel plants.

Lack of significant differences in aphid captures based on trap location within each field suggests that their flight over sweetpotato fields is relatively uniform, indicating they are migratory transients that originate from other crops or plants and probably spread viruses uniformly within the field. The first peaks of aphid flight at sites in Louisiana could be attributed to migration of alates from their overwintering hosts, while the second could be related to redistribution of aphids due to deteriorating host quality in the landscape from crops such as wheat, corn, soybean, and cotton, and weedy species such as smell melon, nightshade, and Johnson-grass. In Mississippi, the midseason distinct peak could be attributed to redistribution of aphids among host plants; the first peak normally associated with migration from primary hosts that occurs in early season was not observed but aphids were present in low numbers.

Aphid species were diverse and varied in percent composition among years and within each season, although species captured in Louisiana and Mississippi were similar. Despite a large number of species captured, a few species (three to seven) accounted for over 83% of the population in any given year at sites in Louisiana or Mississippi. The most common species were *A. gossypii*, *M. persicae*, *R. padi*, and *T. trifolii*. Earlier studies by Kantack et al. (20) in south Louisiana sweetpotato fields, where aphids were trapped using tangle-foot traps, found mainly *A. gossypii*, *M. persicae*, and *Macrosiphum euphorbiae*. *A. gossypii* and *Myzus persicae* are the most efficient vectors of sweetpotato potyviruses of those species evaluated so far (48, this study). *A. gossypii* was captured in both states and was also present in the fields during most of the growing season. *M. persicae* was more abundant in Mississippi and was captured only during the months of April to May in both Louisiana and Mississippi, when little virus transmission was recorded. *R. padi* was present in both states, although it was more abundant in Louisiana where it occurred throughout the growing season, with peaks in April to May and in July. Whether *T. trifolii* can transmit sweetpotato viruses is unknown but it was present in both states, mainly during the months of April to May, and was more abundant in Mississippi. Although the number of aphids in yellow pan traps was higher compared with green pan traps, most of the species were captured in both traps. This indicates that, in our case, using yellow traps provided a better indication of aphid numbers but not necessarily species diversity.

Several authors have reported similar fluctuations of aphid population abundance and changes in species composition depending on season, year, and location (16,44). These fluctuations could be attributed to biotic factors such as aphid reproduction cycle; host plant quality and availability; predators, parasitoids, and ento-

Fig. 4. Average relative Sweet potato feathery mottle virus RNA titers in 'Beauregard' sweetpotato leaves sampled weekly at Burden Research Center in 2010 and 2011 (means $\pm$ standard error).

Fig. 5. Average relative Sweet potato virus G RNA titers in 'Beauregard' sweetpotato leaves sampled weekly at Burden Research Center in 2010 and 2011 (means $\pm$ standard error).

Fig. 6. Average relative Sweet potato virus 2 RNA titers in 'Beauregard' sweetpotato leaves sampled weekly at Burden Research Center in 2010 and 2011 (means $\pm$ standard error).

mophagous fungi; or abiotic factors such as rainfall, temperature, wind, and light intensity (17,30). Pest management practices such as the use of insecticides also affect development and survival of insects (21,23). Aphids, in rare cases, do colonize sweetpotato; *M. persicae* and *Macrosiphum euphorbiae* have been observed colonizing sweetpotato in Louisiana (C. A. Clark, *unpublished*). In 2009, *M. euphorbiae* heavily colonized sweetpotato plants in beds at the St. Landry site (up to 30 aphids/plant on Beauregard and 19 aphids/plant on 'Evangeline') prior to application of an aphicide but no aphids were observed colonizing at other sites. This could be the reason why this species was among the dominant species in 2009 but was very low or absent in other years. The St. Landry site in south Louisiana is under a mandatory spray program for controlling sweetpotato weevils. Certain insecticides are known to induce aphid outbreaks, and this probably contributed to colonization and rapid population increase by *M. euphorbiae* in these beds (23). Sweetpotato plant beds and production fields were scouted regularly for colonizing aphids, and none were observed. Therefore, most of the aphids were transient, noncolonizing migrants that originated from crops or vegetation surrounding sweetpotato fields, because only alates were captured on sticky traps or in pan traps. Noncolonizing species are typically more important in spreading nonpersistent viruses in a crop (35). This is because noncolonizing aphids are more likely to probe epidermal leaf cells and disperse rather than settle, hence increasing the likelihood of virus acquisition and transmission (32). Although both *A. gossypii* and *Myzus persicae* are known efficient vectors of sweetpotato potyviruses, the latter seems to play a lesser role in spread of these viruses in the field. *M. persicae* was found only during a short period when plants were still in plant beds, a trend also observed in a previous study (20), and a period when sentinel plants were not infected. Basky et al. (3) observed *M. persicae* early in the season and suggested that it could play a role in early transmission of *Zucchini yellow mosaic virus* in squash, and we cannot rule out the possibility that low levels of virus spread may occur in beds during this period. *A. gossypii* was consistently present during periods when potyviruses spread in the sweetpotato fields, a phenomenon that was also observed by Kantack et al. (20). Furthermore, laboratory studies of SPFMV transmission from sweetpotato and morning glory plants indicate that *A. gossypii* is a more efficient vector compared with *M. persicae* (48). Abundance and transmission efficiency are two major factors that determine vector propensity (14). Although *R. padi* was a less efficient vector of SPFMV under laboratory conditions in this study, it was present in large numbers and may also have contributed to the spread of SPFMV, as has been observed with *R. padi* and other potyviruses on other hosts (3,4,14). The other common species, *T. trifolii*, whose status as a vector of sweetpotato potyviruses is not known, is a vector of *Potato virus Y* (PVY), *Cucumber mosaic virus* (CMV), and *Bean yellow mosaic virus* (4,16). Most of the other aphid species captured in this study have not been assessed for their ability to transmit potyviruses and should be evaluated. Transmission by *R. maidis* and *R. padi* should also be evaluated under field conditions. These aphids were more restless during laboratory transmission experiments than *M. persicae*, which may have contributed to the less-efficient transmission of SPFMV. Ongoing research is further examining the behavior of aphids on different potential sweetpotato potyvirus source plants and its relationship to virus transmission.

Although sentinel plants were placed at sites throughout the study period, major infections occurred beginning in late June to August at sites in both Louisiana and Mississippi. The major sentinel plant infection period at sites in Mississippi coincided with total aphid peak and *A. gossypii* peak populations during the 2 years. During this period at sites in Louisiana, infection occurred during a period of relatively low total aphid populations based on individual species when *R. padi* population peaked. This difference could help explain the greater incidence of infection of sentinel plants (10% in 2010 and 24% in 2011) at sites in Mississippi compared with sites in Louisiana (5, 5, and 4% in 2009, 2010, and 2011, respectively). Although *A. gossypii* was present during virus

spread in Mississippi, the weak relationship between this species alone and infection of sentinel plants compared with the relationship between total aphids and infection of sentinel plants indicates that other species do play a role in spread of potyviruses.

Contrary to the Mississippi data and other studies which correlate aphid abundance and spread of nonpersistent viruses in crops (3,16), we found that virus spread in Louisiana was not correlated with aphid abundance. Other factors such as source and concentration of inoculum may also be involved in nonpersistent virus epidemics (35). In this study, as in a previous study (20), SPFMV transmission was greatest in the field a few weeks after the crop was transplanted, when vines were growing most vigorously. SPFMV titers were low during early season when plants were still in plant beds or had just been transplanted to the field. However, the titers increased in plants 3 to 4 weeks after transplanting to the field, when vines had begun to grow rapidly, and maximum titers occurred during the months of June to August. Symptoms followed a trend similar to that of virus titers: plants in the beds were asymptomatic most of the period and only developed mild symptoms of yellow vein chlorosis and yellow chlorotic spots from early June to the first week of July, when transplanting the crop was ending. During the second week of July to mid-August, plants displayed typical symptoms of purple and yellow chlorotic spots and yellow vein chlorosis. During mid-August to mid-September, only lower and middle leaves had diffuse purple discolorations, while the upper leaves were asymptomatic. The above-described symptoms are typical of naturally infected sweetpotato plants (i.e., grown in the field for several years) which test positive for these three potyviruses and negative for other known sweetpotato viruses (8,10), possibly indicating the presence of other unknown viruses. Several authors have reported fluctuation in virus titers with cropping season. These fluctuations are attributed to climatic changes, especially temperature and the physiological status of host plants (18,45).

The apparent association of higher SPFMV virus titers in late June to August with the period of peak transmission in the field in Louisiana relates well to laboratory transmission studies of SPFMV, in which higher transmission rates were obtained from sources with higher SPFMV (48). This suggests that virus titer levels can be a limiting factor to virus spread. Other authors have also observed increased transmission of virus from sources with higher titers compared with those with low titers; for example, *Watermelon mosaic virus* and CMV in muskmelon (2) and PVY in potato (15). Although morning glory seedlings were present in plant beds, none were observed to develop symptoms during the time transplants were being cut from the beds. Virus symptoms appeared on *I. hederacea* and *I. cordatotriloba* plants in fields during the period of late June to mid-July, about 6 to 8 weeks after sweetpotato plants were transplanted to the field or about 2 to 3 weeks after initial sentinel plant infections were observed. Because 1 to 2 weeks is required for these viruses to induce symptoms in these hosts, it suggests that morning glory plants were not the primary sources of inoculum but probably were also infected by the

Table 4. Sweet potato feathery mottle virus transmission from *Ipomoea cordatotriloba* to *I. nil* 'Scarlet O'Hara' by *Rhopalosiphum maidis*, *R. padi*, and *Myzus persicae* following 1-min acquisition probes

Aphid species	Transmission (%)	
	Mean ^a	95% CI ^b
<i>M. persicae</i>	22	14.7–30.9
<i>R. maidis</i>	1	0.0–4.7
<i>R. padi</i>	2	0.4–6.4
Control	0	NT

^a Number = 100 for each acquisition source (5 independent experiments with 20 plants each). Means within a column (aphid species) with an overlapping confidence interval (CI) range are not significantly different ($P > 0.05$).

^b NT = no transmission occurred therefore no confidence intervals can be calculated.

inoculum that infected the sentinel plants. However, the morning glory may serve as better sources of secondary inoculum that might extend the period of virus spread into later field stages because they develop higher titers of the virus and support greater levels of SPFMV transmission than sweetpotato in greenhouse conditions (48). This can be assessed further by quantifying virus titer in morning glory plants compared with sweetpotato under field conditions. The role of *J. tamnifolia* is not clear because symptoms were not observed on seedlings in this study, although infected plants have been found previously in sweetpotato fields (C. A. Clark, unpublished). Other weeds have also been reported to be better virus sources than the crops with which they coexist. For example, hairy nightshade is a better source of *Potato leafroll virus* compared with potato (1).

Previous studies indicated that, after one generation in the field, sweetpotato plants are commonly infected with SPFMV but, by the third to fourth generation, incidence of SPFMV was 100%, SPVG was 50 to 70%, and SPV2 was 25 to 30% (12). In this study, SPFMV was present in 90 to 100% of all symptomatic sentinel plants, followed by SPVG (9 to 25%) and SPV2 (1 to 28%). These results indicate that SPFMV is transmitted far more frequently under field conditions and is the dominant potyvirus spreading in Louisiana and Mississippi sweetpotato.

The increased frequency of transmission of SPFMV despite its occurrence in mixed infections with SPVG and SPV2 could be due, in part, to its preferential transmission in sweetpotato plants. *A. gossypii* transmits SPFMV preferentially compared with SPVG from mixed infected sources under laboratory conditions (48) but both were transmitted efficiently from singly infected source plants (41). Preferential transmission of SPFMV could also be due to competition for receptor sites in the aphid vectors, which may become saturated with SPFMV, giving higher transmission rates (34). SPFMV was originally differentiated into four strains: RC, common, ordinary, and East African (26). However, the C strain was separated in 2010 into a distinct species, *Sweet potato virus C* (SPVC), due to its nucleotide sequence divergence from the other three strains (46). Because the antiserum used for SPFMV detection in NCM-ELISA and the primer/probe set used in real-time RT-PCR for virus quantification do not differentiate SPFMV and SPVC, our use of SPFMV in this article reflects the original definition of this virus species (31) and includes both the SPFMV and SPVC sensu Untiveros et al. (46). When methods are available to differentially quantify SPFMV and SPVC, their roles in the sweetpotato potyvirus complex will need to be reevaluated.

In the United States, potyviruses have been managed through reducing virus inoculum by using limited-generation seed that is initially virus free and continually flushing out the diseased material (8). Despite this effort, sweetpotato plants in Louisiana and Mississippi fields are frequently reinfected at high rates with the predominant potyviruses. Results from this study can be used to help design additional management strategies to reduce reinfection of virus tested material. Little can be done to control the aphid vectors because most of them are transient migrants that originate from other crops and plants in the landscape and not sweetpotato. Furthermore, use of insecticides to control aphids has not reduced spread of nonpersistent viruses because of the very short period required for their acquisition and inoculation (14). Morning glory plants in sweetpotato fields were mostly annuals that showed virus symptoms concurrently with the sentinel plants, suggesting that sweetpotato itself is the major source of primary inoculum in commercial production fields. Earlier studies by Clark et al. (12) reveal that most of the sweetpotato plants grown out in growers' fields in Louisiana are already infected with potyviruses. Although morning glory plants may not be sources of primary inoculum, they could act as sources of secondary inoculum once infected, potentially providing a high-titer source of virus after titers have declined in the sweetpotato. Future research should evaluate the potential role of such morning glory populations in potyvirus epidemiology to determine if using fields with minimal morning glory populations can help reduce reinfection of sweetpotato "seed" root crops.

Based on our results, growers could establish their field plantings beginning with the furthest fields from plant beds, especially if they intend to have multiple cuttings taken from the beds. This will minimize rapid infection of plants still in beds with abundant inoculum in field plants whose virus titer levels increase rapidly 3 to 4 weeks after transplanting. Seed production fields should also be located away from any other sweetpotato plants, especially of previous generations, that could act as sources of inoculum. Davis et al. (14) suggest isolation from sources of inoculum as one of the cultural practices to minimize spread and infection of viruses.

Several strategies have been used in other crop systems to minimize spread of nonpersistent viruses. Although resistance has been used to manage several sweetpotato diseases, resistance to potyviruses or their vectors has not been evaluated and could present a long-term strategy to minimizing losses (14). Other strategies include use of mineral oil sprays, reflective mulches, and barrier or protector plants (14). Further studies should be carried out to determine whether these and other strategies can be used to minimize virus spread in the sweetpotato system. This study has identified the critical period of the sweetpotato crop when such management strategies could best be deployed to reduce infection with SPFMV. In Mississippi, infection of sentinel plants was greater in 2011 than 2010 even though *A. gossypii* and total aphid populations were greater in 2010, suggesting that aphid numbers were not the limiting factor to virus spread. However, the fact that peak aphid flights coincided with maximum incidence of virus infection suggests that the aphid flights may also have coincided with maximum virus titers in the sweetpotato. To effectively reduce virus spread in the field, any new strategies need to take virus titers in source plants into account and be accompanied by strategies to reduce available inoculum such as through use of virus-tested or clean propagation material.

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