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Monitoring Seasonal Distribution of Thrips Vectors of Soybean Vein Necrosis Virus in Alabama Soybeans

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Abstract

Soybean vein necrosis virus (SVNV), a new virus in the genus *Orthotospovirus*, has been found in all soybean-growing regions in the United States and Ontario, Canada. Soybean thrips, *Neohydatothrips variabilis* (Beach) (Thysanoptera: Thripidae), tobacco thrips, *Frankliniella fusca* (Hinds) (Thysanoptera: Thripidae), and eastern flower thrips, *Frankliniella tritici* (Fitch) (Thysanoptera: Thripidae) are reported vectors of this virus, but there are no reports on their distribution in Alabama. A monitoring study was conducted in 2015 and 2016 to determine thrips species composition and abundance in Alabama soybean agroecosystems. Thrips were monitored weekly by collecting them on yellow sticky traps and soybean plant parts including foliage and reproductive structures. All three reported vectors of SVNV were identified in Alabama, with *N. variabilis* and *F. tritici* as the predominant species, while *F. fusca* was not consistently collected from soybean plants. Four additional thrips species were collected, of which *Echinothrips americanus* (Morgan) (Thysanoptera: Thripidae) was commonly found on soybean at all three locations. Results presented in this study provide new information about seasonal thrips species abundance in soybean agroecosystems in Alabama, and is an important first step to understanding thrips vector species of epidemiological importance in the Southern United States.

Key words: thrips, population dynamics, *Glycine max*, *Orthotospovirus*, *Soybean vein necrosis virus*

Soybean (*Glycine max* (L.) Merr.) is one of the dominant oil seed crops in the United States grown primarily for animal feed, human consumption, and other industrial uses. In 2016, the United States produced 4.2 billion bushels of soybean valued at \$40 billion (USDA 2016a). In Alabama, soybeans are one of the five leading commodities in the state with a value of \$129.2 million in 2016 (USDA 2016b). In 2008, a thrips-transmitted *Orthotospovirus* (Bunyavirales: Tospoviridae), *Soybean vein necrosis virus* (SVNV), was identified in the southeastern United States (Tzanetakis et al. 2009), and since has been reported in all soybean growing areas in the United States and Canada (Tenuta 2012). SVNV disease symptoms are characterized by localized brown necrotic blotches along the major veins of the upper and lower leaf surface, resulting in a scorched appearance of the damaged leaves (Zhou and Tzanetakis 2013). In Alabama, SVNV was first detected in soybean fields from Limestone County in 2012 and has been recorded in 27 counties to date (Conner et al. 2013, Sikora et al. 2017).

Orthotospoviruses are transmitted by thrips in a persistent and propagative manner (Ullman et al. 1997, Whitfield et al. 2005, Rotenberg et al. 2015). SVNV was the first *Orthotospovirus* reported to be seed transmitted (Groves et al. 2016), although the

frequency of seed transmission remains unknown. SVNV is transmitted most efficiently by soybean thrips, *Neohydatothrips variabilis* (Beach) (Thysanoptera: Thripidae) (Zhou and Tzanetakis 2013), but is also transmitted by tobacco thrips, *Frankliniella fusca* (Hinds) (Thysanoptera: Thripidae), and eastern flower thrips, *Frankliniella tritici* (Fitch) (Thysanoptera: Thripidae) (Keough et al. 2016). Although thrips are commonly found on soybean, injury has only been reported when chemical injury or drought exacerbate feeding injury (Huckaba et al. 1988, Reisig et al. 2012). Few studies have been conducted to document thrips species infesting soybean season-long. The predominant thrips species collected from soybean foliage and terminals throughout the growing season in Indiana, Kentucky and Missouri were *F. fusca*, *F. tritici*, and *N. variabilis* (Irwin et al. 1979). In North Carolina and Virginia *F. fusca* and *N. variabilis* were the predominant species collected from seedlings and upper trifoliates during the first 5 wk after planting, but *F. occidentalis* and *F. tritici* were also collected (Reisig et al. 2012). In Wisconsin and Iowa thrips flying in soybean fields were monitored with yellow sticky traps, and *F. tritici* was the most abundant species captured. Other orthotospovirus vectors including *N. variabilis*, *Thrips tabaci* (Lindeman) (Thysanoptera: Thripidae), *F. fusca*, and *Frankliniella*

occidentalis (Pergande) (Thysanoptera: Thripidae) each comprised 1–4.4% of the total thrips captured (Bloomingdale et al. 2017). The thrips species infesting soybeans season-long in Alabama are unknown. In addition, there are few studies that monitor both thrips dispersal events and thrips found on plants. This limits inferences about the potential vectors responsible for virus spread, timing of primary spread, and the importance of secondary spread within the crop.

SVNV is the only known *Orthotospovirus* to infect soybeans in the United States, with the exception of *Tomato spotted wilt virus* (TSWV), which was detected in Alabama in 2008, but was asymptomatic in soybean (Sikora et al. 2012). Timing of SVNV spread to soybeans is not currently understood. Timing of TSWV spread is related to dispersal behavior of thrips vectors, including *F. fusca*, and has been well characterized for other crops grown in the southeast including peanut, tobacco, and vegetables. Primary spread of TSWV from sources outside of the crop system are responsible for the majority of virus incidence in these crops, and occurs when thrips disperse from senescing weed hosts of both the virus and thrips vectors to new hosts in the spring (Groves et al. 2001, Groves et al. 2003, Nault et al. 2003, Morsello et al. 2008, Morsello and Kennedy 2009, Chappell et al. 2013, Srinivasan et al. 2014). Young crops are more susceptible to TSWV infection than mature plants (Culbreath et al. 1996, Todd et al. 1997, Shrestha et al. 2015), and symptoms of infection are generally apparent 4 to 6 wk after emergence (Eckel et al. 1996, Culbreath and Srinivasan 2011). Reported hosts of SVNV include *Ipomoea hederacea* (Jacq.), *Cucurbita pepo* (L.), *Vigna unguiculata* (L.), *Pueraria montana* (Lour.), *V. radiata* (L.), *Dendranthema grandiflorum* (Ramat.), *Nicotiana benthamiana* (L.), *N. tabacum* (L.), and *N. glutinosa* (L.) (Zhou and Tzanetakis 2013, Zhou et al. 2018). Common hosts of the virus and vector remain poorly understood because detection of the virus in weed surveys has been very low, and to our knowledge comprehensive host surveys have only been conducted for *F. fusca* early-season before spring dispersal events. Secondary spread of TSWV within the cropping system has limited importance in vegetable and peanut crops (Garcia et al. 2000, Culbreath et al. 2003, Coutts et al. 2004), may be caused by vector species different than those responsible for primary spread (Beaudoin 2011), and feeding on foliar versus reproductive plant tissue may have different transmission outcomes (Houle and Kennedy 2017). In contrast to other orthotospoviruses, SVNV disease symptoms are observed during late-reproductive growth stages (August–October), but whether or not this is due to early-season infections that do not become symptomatic until late-season, or late-season infections is not currently understood. The objectives of this study were to identify thrips species present in Alabama soybean fields throughout the growing season, and to identify dispersal and colonization events that may lead to primary and secondary spread of SVNV to and within soybean fields. Dispersing thrips were monitored weekly on yellow sticky traps, and in collections from soybean plant foliage and reproductive structures. The results of this study present a first step toward identifying the abundance and distribution of SVNV vectors to gain a better understanding of the epidemiology of SVNV in Alabama.

Materials and Methods

One-acre soybean sentinel plots, free of foliar insecticide or fungicides, were established in 2015 and 2016 at the Plant Science Research Center (Auburn, AL), E.V. Smith Agricultural Research Station - Plant Breeding Unit (Tallassee, AL), and Wiregrass Research and Extension Center (Headland, AL). In 2015, soybean

variety Pioneer 93Y92R was planted in Tallassee on May second, Auburn on April sixth, and Headland on May twenty-first. In 2016, variety Pioneer 46T54R was planted on May 2 at Tallassee, April 7 in Auburn, and June 10 in Headland. Fields were maintained throughout the season with herbicide and fertility production practices recommended by the Alabama Cooperative Extension System (Alabama Cooperative Extension System 2018). Thrips dispersal events were monitored with 12.7 × 7.6 cm yellow sticky card traps (Great Lakes IPM, Inc., Vestaburg, MI). One sticky trap was placed on each field border, for a total of four traps per location. Sticky traps were attached to a 1.2-m pole using binder clips to hold the sticky card, and clothespins to adjust the height on the pole. Traps were suspended just above the soybean canopy, and were adjusted throughout the growing season to maintain this level above the crop. Traps were collected and replaced weekly from 1 to 2 wk after planting until crop senescence. Collected traps were sandwiched in clear plastic sheet protectors 11" × 8.5" inserts (Avery Products Corporation, Brea, CA), and refrigerated at 4°C until thrips were counted and slide mounted for identification. The total number of thrips per sticky card was recorded. When thrips numbers were equal to or less than 25 per trap, all thrips were identified to species. When the number of thrips per trap exceeded 25, a subsample of 25 randomly selected thrips were identified, and then the total number of each species per trap was estimated based on the proportion of each species in the subsample (Morsello et al. 2008). Individual thrips were removed from sticky traps by soaking the traps in Histo-Clear-II solvent (National Diagnostics, Atlanta, GA) for 30–60 min to dissolve the glue. Individual thrips were removed from this solution with a fine paintbrush and placed into a vial of 90% EtOH until slide mounting. Adult thrips were slide mounted using CMC-10 (Masters Chemical Co. Elk Grove, IL) and identified to the species level under 100× magnification using taxonomic keys for Terebrantia suborder (Palmer et al. 1992). Identification of adults from sticky traps was only made in 2016 due to limited resources in 2015.

To determine thrips species composition in soybean fields, plant samples were collected throughout the growing season at each location in 2015 and 2016. Each sample was comprised of 40 plant parts collected across the field, and different age leaves and types of plant tissue were collected separately because thrips species may exhibit differences in feeding behavior or occupy different niches. Samples were collected for the following plant parts: 1) terminal trifoliate, 2) trifoliates from upper one-third of the canopy, 3) trifoliates from middle one-third of the canopy, 4) trifoliates from lower one-third of the canopy, 5) flowers, and 6) pods. Samples were collected down the entire length of four rows at evenly spaced distances across the field, and included two edges, a row located in the middle one-third, and a row located in the middle two-thirds of the field. Samples were placed directly into a jar of soapy water before they were picked from randomly selected plants to prevent dislodging thrips from the plant before collection. Each plant part was collected separately during different trips through the field, and therefore, were independent of each other. Thrips were collected from the foliage and soapy water by filtration using a Buchner Funnel lined with 9-cm fast filter papers, 1,000-ml filtering flask and a vacuum pump. After filtration, the filter papers were immediately sandwiched in a sheet of plastic wrap and frozen at –20°C until thrips were counted and slide mounted for identification. The total number of adult and immature thrips collected on the filter papers were counted under 20× magnification and saved in 1.5-ml tubes with 70% EtOH. All adult thrips extracted were slide mounted and identified as described above.

Data Analysis

Average thrips counts from yellow sticky traps were analyzed as the total number of thrips and the total number of each species, separately. Data were analyzed as repeated measures (PROC GLIMMIX, SAS 9.4, SAS Institute 2013) using a negative binomial distribution, trap number as a random variable, and specifying the NLOPTIONS statement and TECH=NRRIDG option to achieve normality and optimize model fit. Thrips species composition data from the 2016 sticky traps were transformed using $\log(x+1)$ to normalize the distribution, and analyzed using PROC MIXED (SAS Institute 2013). Due to a high number of zeros across sampling dates, the total numbers of immatures and adults from plant samples were pooled for analyses. The average number of thrips recovered from plant samples were subject to analysis using SAS PROC GLIMMIX. Data were normalized using a negative binomial distribution or $\log(x+1)$ transformation, where appropriate. Separate analyses were conducted using the number of immatures, adults, and adults of each species as the dependent variables, and collection location, year, life stage and/or plant part as independent variables. Species were excluded from analysis if the number of individuals collected were too low for model convergence. Mean comparisons tests for all analyses were conducted using Tukey's procedure.

Results

A total of 17,594 adults and 2,251 immature thrips were collected from sticky card and plant samples during the course of this study, in which 4,046 adults were identified to species. Seven different thrips species were identified, including *F. tritici* (68.4%), *N. variabilis* (23.9%), *Echinothrips americanus* (Morgan) (Thysanoptera: Thripidae) (3.4%), *F. fusca* (2.7%), *F. williamsi* (Hood) (Thysanoptera: Thripidae) (0.7%), *F. schultzei* (Trybom) (Thysanoptera: Thripidae) (0.04%), and *Microcephalothrips abdominalis* (Crawford DL) (Thysanoptera: Thripidae) (0.02%). A small number of *Frankliniella* spp. (0.7%) were not present in the taxonomic key used, and therefore, were not identified to species. Only one *M. abdominalis* and *F. schultzei* were collected from yellow sticky card traps during one and two collection periods, respectively. *Frankliniella williamsi* and *E. americanus* had not been reported in previous thrips surveys in soybean (Irwin et al. 1979, Reisig et al. 2012, Bloomington et al. 2017). *E. americanus* was consistently collected and comprised a large number of individuals from plants but not sticky card traps, and, therefore, was included in statistical analyses. Of the seven species identified, only *F. schultzei*, *F. tritici*, *F. fusca*, and *N. variabilis* are known vectors of orthotospoviruses (Riley et al. 2011, Rotenberg et al. 2015), and only the last three are reported as vectors of SVN (Keough et al. 2016).

Total Numbers and Species of Dispersing Thrips Captured on Sticky Traps

The number of dispersing thrips was analyzed separately for each location using repeated measures with date as the independent variable, number of thrips as the dependent variable, and sticky card trap as a random variable. In 2015, there were significant differences among the number of dispersing thrips captured on yellow sticky traps across sampling dates in Tallassee ($F = 16.25$; $df = 18, 40.97$; $P < 0.0001$) and Auburn ($F = 20.48$; $df = 18, 40.97$; $P < 0.0001$), but not Headland ($F = 1.04$; $df = 9, 15.53$; $P = 0.454$). Up to four dispersal peaks were observed across locations, but because adults

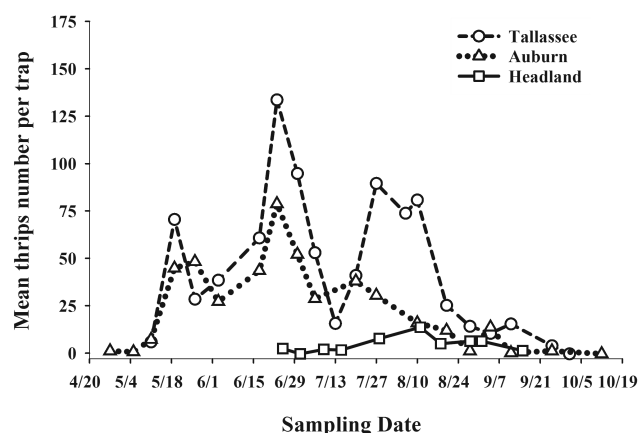


Fig. 1. Mean total number of dispersing thrips captured on yellow sticky card traps by sampling dates at all locations in 2015.

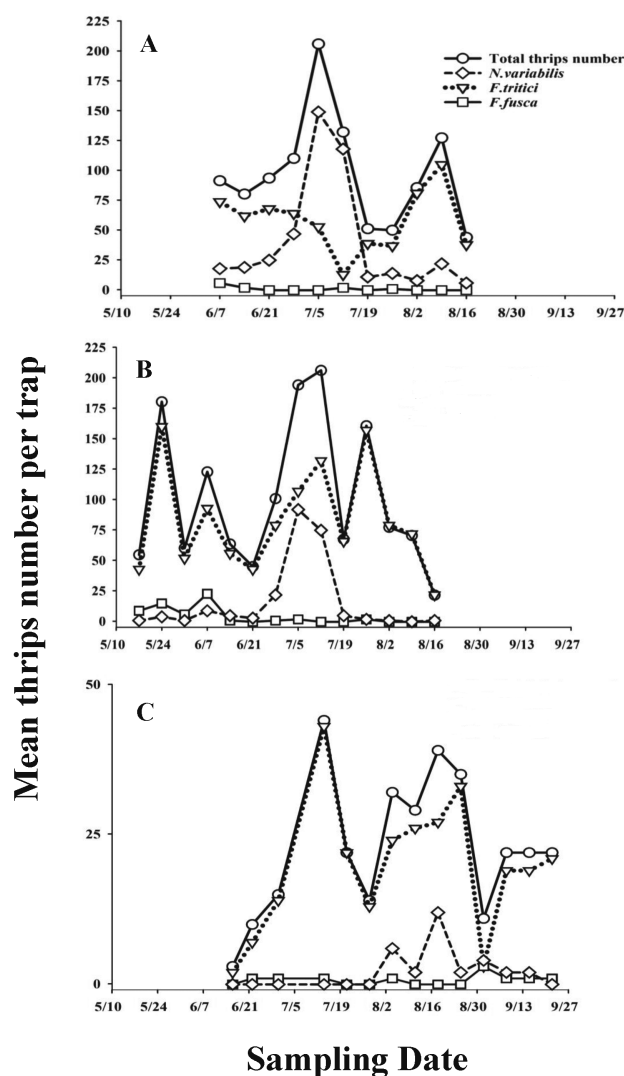


Fig. 2. Mean total number of thrips and mean number of each species captured on yellow sticky traps by sampling dates in 2016 in (A) Tallassee, (B) Auburn, and (C) Headland.

were not identified in 2015 relative species composition could not be determined (Fig. 1). In 2016, more thrips were captured on sticky traps than in 2015, and there were significant differences in adult

captures among sampling periods observed at all three locations: Tallassee ($F = 5.43$; $df = 10, 28.06$; $P = 0.0002$), Auburn ($F = 13.77$; $df = 13, 11.92$; $P < 0.0001$) and Headland ($F = 5.33$; $df = 14, 33.81$; $P < 0.0001$). In 2016, seven thrips species were identified across all locations and sampling weeks. *F. tritici* (77.3%) was the most dominant species identified followed by *N. variabilis* (17.8%), *F. fusca* (3%), *F. williamsi* (0.8%), *E. americanus* (0.06%), *F. schultzei* (0.06%), and *M. abdominalis* (0.03%); 0.9% were unidentified *Frankliniella* species. *F. tritici* comprised the majority of thrips captured across dates at all locations, and exhibited two to four major dispersal events throughout the growing season (Fig. 2A–C). *N. variabilis* was the second most abundant species captured at all locations, but only exhibited one to two dispersal events, with the largest occurring in July or August, depending on the location. Captures of other species were low at all locations.

Distribution of Adults, Immatures, and Species on Soybean Plants

An analysis was conducted on the entire dataset of thrips adult and immature counts in 2015–2016 to identify whether or not there were differences in the main effects of thrips life stage, where they were collected on the plant, where they were collected in the state,

and between years. In this analysis life stage ($F = 29.94$, $df = 1, 691$, $P \leq 0.0001$), plant part ($F = 12.57$, $df = 5, 691$, $P \leq 0.0001$), collection location ($F = 61.35$, $df = 2, 691$, $P \leq 0.0001$), and year ($F = 32.85$, $df = 1, 691$, $P \leq 0.0001$) were highly significant. There were significantly more thrips collected in 2015 than 2016 from plant tissue, but the effect of year could be confounded with soybean variety if the varieties used in this study differed in host plant quality for thrips. The number of immatures collected from plants was significantly higher (4.47 ± 0.45) than the number of adults (1.96 ± 0.21), and significantly fewer thrips were collected from Headland than the other two locations. Most thrips were collected from upper, middle, terminal, and lower leaves, flowers, and pods, respectively. Across years, the total number of thrips on upper, middle, and terminal leaf samples was not significantly different, nor was the number of thrips on middle, terminal, lower leaves, and flowers, although the numbers were generally lower on these parts. Significantly fewer thrips were collected on pods than all other plant samples.

Next, data were analyzed by year, collection location, and life stage to examine differences in thrips counts among plant parts. There were significant differences in the number of adults among plant parts in Tallassee in 2015 ($F = 3.19$, $df = 5, 42$, $P = 0.0156$) and 2016 ($F = 6.48$, $df = 5, 57$, $P < 0.0001$); Auburn in 2015 ($F = 3.18$, $df = 5, 40$, $P = 0.0165$) and 2016 ($F = 3.81$, $df = 5, 56$, $P = 0.0048$);

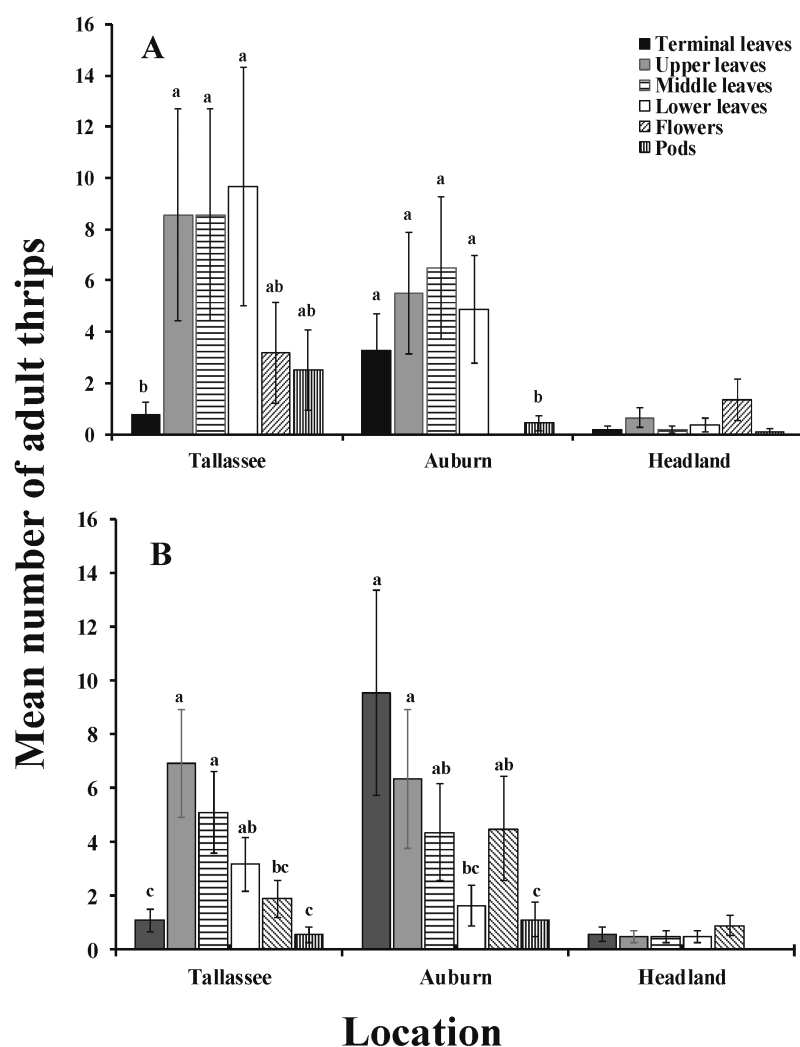


Fig. 3. Mean (\pm SE) number of adult thrips collected from plant samples at each collection location in (A) 2015 and (B) 2016. Bars with the same letter are not significantly different than other samples collected from the same location.

but not Headland either year where the number of thrips sampled was generally low (2015: $F = 1.63$, $df = 5, 56$, $P = 0.1662$ and 2016: $F = 0.28$, $df = 5, 57$, $P = 0.9220$) (Fig. 3). The number of immatures was significantly different among plant parts in Tallassee in 2015 ($F = 4.57$, $df = 5, 43$, $P = 0.0020$) and 2016 ($F = 2.76$, $df = 5, 57$, $P = 0.0266$); Auburn in 2015 ($F = 5.77$, $df = 5, 40$, $P = 0.0004$) and 2016 ($F = 4.55$, $df = 5, 58$, $P = 0.0014$); and Headland in 2015 ($F = 3.01$, $df = 5, 56$, $P = 0.0179$) but not 2016 ($F = 1.45$, $df = 5, 67$, $P = 0.2170$) (Fig. 4).

Last, analyses were conducted to examine the main effects of species, plant part, geographic location, year, and the interaction of species and plant location on the number of adults collected during this study. There were only sufficient observations of *E. fusca*, *N. variabilis*, and *E. americanus* to include in the analyses of species. An analysis with all data showed that the effects of species ($F = 0.36$, $df = 2, 860$, $P = 0.6998$) and year ($F = 0.00$, $df = 1, 860$, $P = 0.9627$) were not significant factors, but the effects of plant part ($F = 6.94$, $df = 5, 860$, $P < 0.0001$), geographic location ($F = 31.36$, $df = 2, 860$, $P < 0.0001$), and the interaction of species and plant part ($F = 7.06$, $df = 10, 860$, $P < 0.0001$) were highly significant. Based on these results, an analysis using data from both years was conducted by location and species with the number of thrips as the dependent variable and plant part as the independent variable. There were no significant differences in the number of individuals collected from

different plant parts in Tallassee for *E. tritici* ($F = 0.90$, $df = 5, 108$, $P = 0.4819$) or *E. americanus* ($F = 0.63$, $df = 5, 108$, $P = 0.6742$); Auburn for *E. americanus* ($F = 0.75$, $df = 5, 96$, $P = 0.5877$); or Headland for *N. variabilis* ($F = 0.30$, $df = 5, 83$, $P = 0.9124$), *E. tritici* ($F = 1.59$, or $df = 5, 83$, $P = 0.1727$), or *E. americanus* ($F = 0.85$, $df = 5, 48$, $P = 0.5201$) (Fig. 5). There were significant differences in the numbers of *N. variabilis* among plant locations in Tallassee ($F = 9.14$, $df = 5, 108$, $P < 0.0001$) and in Auburn ($F = 4.72$, $df = 5, 96$, $P = 0.0007$), and for *E. tritici* ($F = 2.63$, $df = 5, 96$, $P = 0.0284$) in Auburn (Fig. 5). Numbers of *E. tritici* and *N. variabilis* on plants generally increased concurrent with or 1 wk after a peak in the numbers collected on yellow sticky cards occurred. Trends cannot be compared for *E. americanus* because it was only identified from yellow sticky card samples during two collection periods in Headland.

Discussion

This is the first study to examine composition and abundance of both dispersing and colonizing thrips in Alabama soybean agroecosystems. All three reported vectors of SVNV were found at each study location. *N. variabilis* and *E. tritici* were the predominant species identified, but the relative abundance of both was different between the central (Tallassee and Auburn) and southern (Headland) collection locations, with *E. tritici* more abundant in Headland relative to

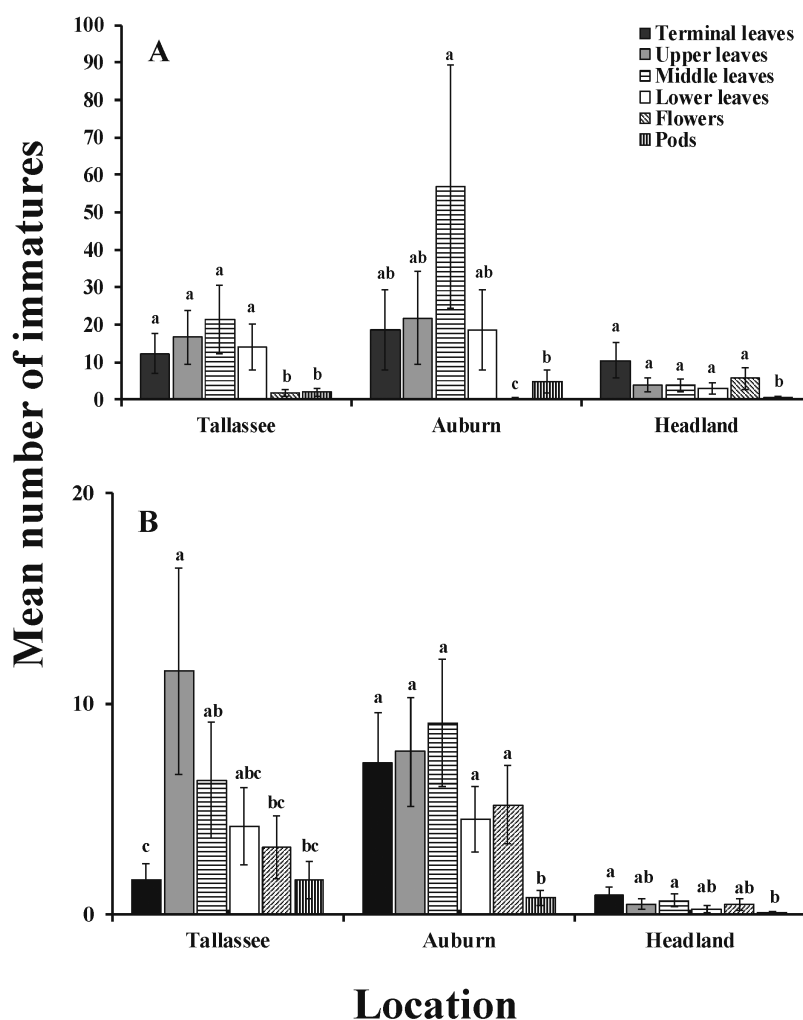


Fig. 4. Mean (\pm SE) number of immature thrips collected from plant samples at each collection location in (A) 2015 and (B) 2016. Bars with the same letter are not significantly different than other samples collected from the same location.

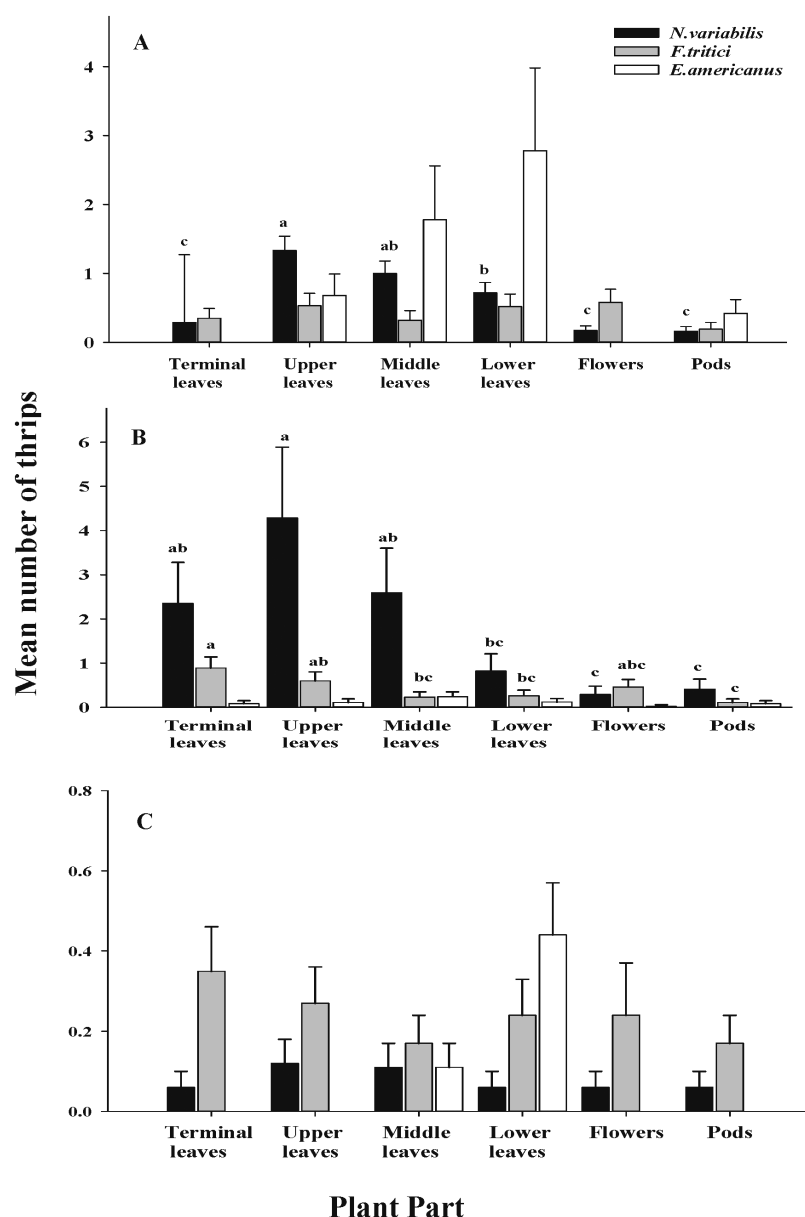


Fig. 5. Mean (\pm SE) number of thrips species collected from plant samples in (A) Tallassee, (B) Auburn, and (C) Headland, averaged across 2015 and 2016. Bars with the same letter are not significantly different among observations for the same species.

N. variabilis. Few *F. fusca* were found at any location. The findings of this study corroborate previous research from other states reporting *N. variabilis* and *F. tritici* as the predominant species (Irwin et al. 1979, Reisig et al. 2012, Bloomingdale et al. 2017), and these results were observed in both plant and sticky trap samples. Four additional thrips species were identified, of which *E. americanus* also comprised a large number of individuals collected. *E. americanus* is a pest of greenhouse and ornamental plants, and has been collected from over 100 cultivated and native plants in the southeastern United States (Oetting et al. 1993, Childers and Nakahara 2006), but has not been reported to transmit orthotospoviruses. A higher number of thrips were generally collected from younger leaves, with *F. tritici* usually more common in terminals and flowers (Supp. Figs. S1 and S2), which was also observed by Irwin et al. (1979). However, there is not consistent statistical support for plant-part associations among species, adults, immatures, locations or years. This could be due to the low sample size across collection dates and ecological factors

associated with thrips phenology, host phenology, variety/host quality, thrips population size, and thrips species composition at each location (Supp. Figs. S1–S6).

Infection and symptom development in relation to timing of primary and/or secondary disease spread is not currently understood. A 3-yr study across six Midwestern states documented that viral infection can influence quality of harvested soybean seed, but has little effect on yield loss (Anderson et al. 2017). A low effect of SVN infection on yield may suggest that SVN has low virulence to soybean, that disease spread to the crop occurs late enough in the cropping season that yield impacts are minimized due to mature plant resistance, or that pod set has advanced enough that yield impacts are minimized. Based on trapping data from this study, primary spread by *F. tritici* could occur because large flights of this species were observed multiple times during the growing season beginning in May. Primary spread by *N. variabilis* may also occur, but only one or two flights of *N. variabilis* were observed. The

largest and most consistent flight of *N. variabilis* across locations occurred between early-July and early-August, which is roughly 1 to 2 mo before SVNV symptoms are observed in the crop (Conner et al. 2013, E. J. Sikora, personal communication). Immatures were found on all plant parts, but were primarily recovered from foliage samples. Identification of immatures would clarify which species are reproducing on soybean to understand the potential for secondary spread within the crop by *N. variabilis* and *F. tritici*, which were the predominant adult vector species collected from plants. Immatures were not identified in this study because the resources needed to make additional collections and rear field-collected immatures to adult for identification were not available. In the future, molecular methods such as the recently developed qPCR assay for identifying species of adult and immature thrips in cotton (Wang et al. 2018), could be further developed for identification of soybean-inhabiting thrips species.

This study is an important first step to understanding thrips vector species of epidemiological importance in the Southern United States, and seasonal dispersal and colonization events that may be related to primary and secondary spread by thrips vectors. It also documents other thrips species that are present in Alabama soybean producing areas, including vectors of other orthospoviruses, although the results are not directly comparable to commercial settings because they come from fields that were not treated with insecticides. Future studies are needed to improve knowledge about thrips-virus-plant interactions underlying symptomology of SVNV in soybeans to better understand the timing of virus spread contributing to the final virus incidence in soybean crops. A better understanding of soybean varieties exhibiting resistance or tolerance to thrips vectors or SVNV may also be important in understanding incidence of SVNV in soybean production regions, and impacts of SVNV on soybean quality and yield. This information will be especially valuable should the status of this virus continue to change.

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

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