Environmental Entomology, XX(X), 2018, 1–7
doi: 10.1093/ee/nvy021
Research

Physiological Ecology

Factors Affecting Population Dynamics of Thrips Vectors of *Soybean vein necrosis virus*

Stacy Keough,[1] Jonathan Danielson,[1] Jordan M. Marshall,[1] Doris Lagos-Kutz,[2] David J. Voegtlin,[3] Rajagopalbabu Srinivasan,[4] and Punya Nachappa[1,5]

[1]2101 E. Coliseum Blvd, Indiana University-Purdue University Fort Wayne, Fort Wayne, IN 46805, [2]United States Department of Agriculture-Agricultural Research Service, Urbana, IL 61801, [3]Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, Champaign, IL 61820, [4]University of Georgia, Griffin, GA 30223, and [5]Corresponding author, e-mail: nachappa@ipfw.edu

Subject Editor: Melody Keena

Received 23 October 2017; Editorial decision 29 January 2018

Abstract

Thrips-infesting soybeans were considered of minor economic importance, but recent evidence of their ability to transmit a newly identified soybean virus, *Soybean vein necrosis virus* (SVNV), has raised their profile as pests. Season-long surveys were conducted using suction traps to determine the effects of temperature and precipitation on the spatiotemporal patterns of three vector species of SVNV, *Neohydatothrips variabilis* (Beach) (Thysanoptera: Thripidae) (soybean thrips), *Frankliniella tritici* (Fitch) (Thysanoptera: Thripidae) (eastern flower thrips), and *Frankliniella fusca* (Hinds) (Thysanoptera:Thripidae) (tobacco thrips) in soybean fields in Indiana in 2013 and 2014. In addition, soybean fields were surveyed for presence of SVNV in both years. We found that the magnitude and timing of thrips activity varied greatly for the three species. *N. variabilis* activity peaked in mid-August each year.The peak activity for *F. tritici* occurred between late-June, and a second peak in activity was observed in early-August, while *F. fusca* activity remained more or less the same with no peak. There was no gradient in thrips populations from southern to northern locations.This suggests that these insects are not migratory and may overwinter in soil or perennial noncrop host plants and other weed hosts in Indiana.The capture rates of *N. variabilis* and *F. tritici* were only related to temperature, and capture rates of *F. fusca* were not related to either variable. SVNV was first detected in mid-late August, which coincided with the peak of the primary vector, *N. variabilis*. The virus was not detected earlier in the season despite peaks in *F. tritici* activity. Our results may be used in weather-based models to predict both thrips dynamics as well as SVNV outbreaks.

Key words: Thrips, *Soybean vein necrosis virus*, Degree-day, Precipitation, Population dynamics

Phytophagous thrips comprise one of the most abundant arthropods found in soybean fields (Blickenstaff and Huggans 1963, Irwin et al. 1979, Reisig et al. 2012). A handful of studies have surveyed thrips species composition in soybean. In the United States, thrips species recorded on soybean include, *Neohydatothrips variabilis* (Beach) (Thysanoptera: Thripidae) (soybean thrips), *Frankliniella tritici* (Fitch) (Thysanoptera: Thripidae) (eastern flower thrips), *Frankliniella fusca* (Hinds) (Thysanoptera: Thripidae) (tobacco thrips), and *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (western flower thrips) (Irwin et al. 1979). More recently, Bloomingdale et al. (2017) reported as many as 13 different species captured on yellow sticky traps in Wisconsin. Thrips are an early-season pest colonizing the crop from early-May until late-August (Irwin et al. 1979). In Illinois, Kentucky, and Missouri, populations of *F. tritici* peak earlier than *N. variabilis* (Irwin et al. 1979). Thrips are cell-content feeders and damage leaves by piercing cell walls with their stylet and sucking up cell contents (Chisholm and Lewis 1984). The yield loss due to thrips feeding has been reported as minimal, hence, thrips-infesting soybeans are considered of minor economic importance (Reisig et al. 2012). But recent evidence of their ability to transmit a newly identified soybean virus, *Soybean vein necrosis virus* (SVNV) has raised their profile as pests (Zhou and Tzanetakis 2013, Keough et al. 2016). Until recently, *N. variabilis* was the only known vector of SVNV (Zhou and Tzanetakis 2013). However, *F. tritici* and *F. fusca* have also been confirmed as vectors of SVNV but are less efficient in transmission than the primary vector, *N. variabilis* (Keough et al. 2016). The identification of new vector species and their ability to survive and reproduce on soybean can have serious consequences for SVNV epidemics in soybean-growing areas.

SVNV, an emerging *Tospovirus*, was first discovered in 2008 in Arkansas and Tennessee (Tzanetakis et al. 2009). In the field, symptoms typically appear in mid to late summer and can be

randomly distributed in the canopy (Tzanetakis et al. 2009). Currently, SVNV has been confirmed in 19 mid-western states and has also been detected in Ontario, Canada (Bloomingdale et al. 2015). Little is known about the virus and the losses associated with the disease. In a recent multistate study, it was reported that SVNV did not affect yield, however, seed quality was affected. Oil concentration decreased by 0.11% as disease incidence increased by 1%. There was also decrease in fatty acid profiles including linolenic, linoleic, and stearic acids between 0.5 and 0.15%. These results suggest that SVNV negatively affects soybean seed quality, which may affect the marketability of soybeans for premium markets (Anderson et al. 2017).

Tospovirsues including SVNV are exclusively transmitted from plant-to-plant via adult thrips. Transmission dynamics is dependent on vector populations, species diversity, and weather factors affecting population dynamics (Madden et al. 2000, Groves et al. 2003, Morsello and Kennedy 2009, Morsello et al. 2010, Chappell et al. 2013). The major factors affecting thrips population dynamics are temperature and precipitation. For both *F. fusca* and *Thrips tabaci* (Thysanoptera: Thripidae), degree-day which takes into account average daily temperatures above the developmental threshold was found to be the most important factor that influenced thrips population dynamics and timing of spring dispersal (Morsello et al. 2008, 2010). Precipitation has both positive and negative effects on thrips in the field. Rainfall can kill juvenile stages of thrips and suppress flight activity of adults, thus decreasing thrips dispersal (Morsello and Kennedy 2009, Chappell et al. 2013). In some cases, dispersal was affected up to 5–6 wk after precipitation occurred (Morsello et al. 2010). However, precipitation also benefits the growth of host plants, which would increase thrips population growth.

There is no published information on the factors influencing population dynamics of thrips-infesting soybean or spread of SVNV by thrips vectors. The present study was undertaken to better understand weather effects on population dynamics of the primary vector, *N. variabilis* and secondary vectors, *F. tritici* and *F. fusca*. Specifically, we evaluated the influence of temperature (growing degree-days [GDD]) and rainfall index (RI) (factor of the amount of precipitation and the number of days in which precipitation occurred) on seasonal abundance of the above-mentioned thrips species caught using suction traps located in soybean fields throughout five Purdue Agricultural Centers (PACs) in the state of Indiana. In addition, we conducted season-long surveys of SVNV incidence in soybean fields in the same locations.

Materials and Methods

Suction Trap Collection and Thrips Identification

Seasonal patterns of adult thrips were determined by analyzing suction trap samples from the North Central Regional Soybean Aphid Suction Trap Network. The suction trap provided an accurate estimation of winged aphid adults captured in suction traps to aphid densities on soybean plants (Rhainds et al. 2010). Hence, we expect a positive correlation between thrips captured in suction traps and those that are colonizing the crop. In Indiana, suction traps are set up in five PACs. We analyzed samples from five PACs including, Davis Purdue Agriculture Center (DPAC: 40.2545° N, −85.1503° W), North East Purdue Agriculture Center (NEPAC: 41.1024° N, −85.3991° W), Pinney-Purdue Agriculture Center (PPAC: 41.4442° N, −86.9303° W), South East Purdue Agriculture Center (SEPAC: 39.0350° N, −85.5291° W), and Throckmorton Purdue Agriculture Center (TPAC: 40.1747° N, −86.5409° W) (Fig. 1). In all locations,

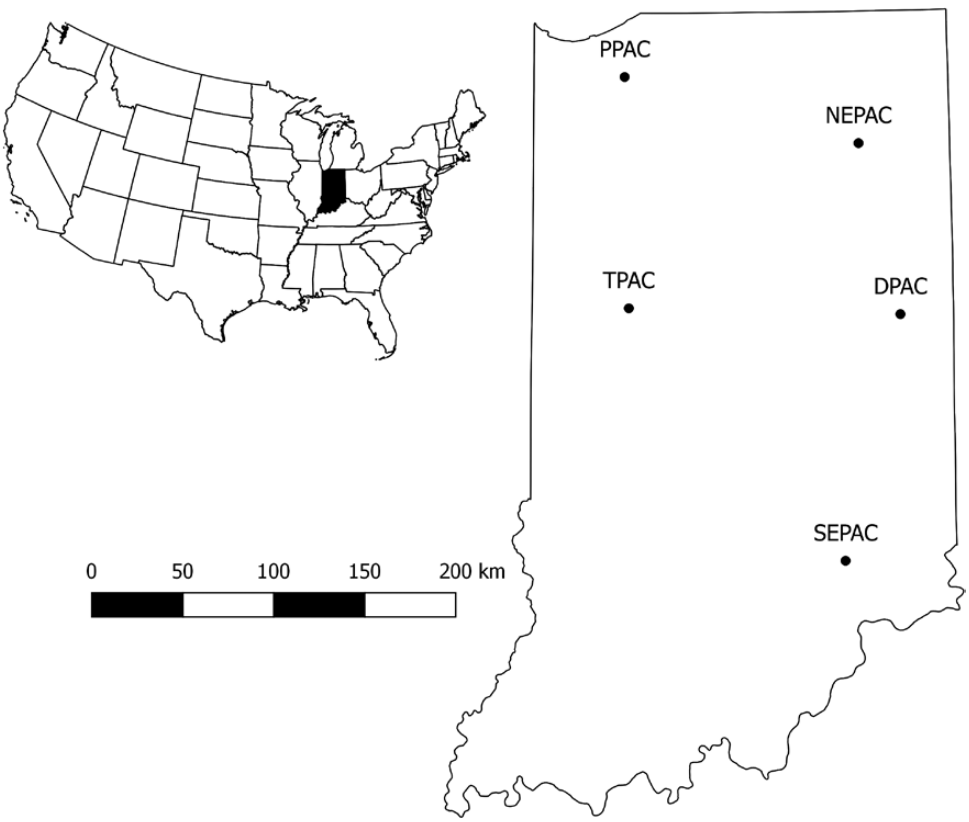

Fig. 1. Purdue Agricultural Center (PAC) locations where thrips were sampled in Indiana in 2013 and 2014.

Becks NR or Pioneer cultivars in maturity group 3 were planted between 15 and 30 May in 2013 and 2014. The suction traps sampled the air column at 6.7 m above the ground from 7:00 a.m. to 8:00 p.m. between May and October. Insects were trapped in a bottle filled 1/3 full with 50% propylene glycol and 50% water. The collection bottle was removed and replaced weekly from all traps. The suction trap samples were shipped from the University of Illinois, Urbana-Champaign to our laboratory. The thrips counts were performed starting from 21–28 June to 12–29 October in 2013 and 23–30 May to 24–31 October in 2014. Suction trap contents were filtered, and adult thrips were sorted under a dissection microscope. Identification of thrips species was performed using published keys based on morphological characteristics (Mound and Kibby 1998, Moritz et al. 2001, Hoddle et al. 2008, Mound 2010) for thrips captured in 2013. We only performed counts for the three most abundant species, *F. tritici*, *N. variabilis*, and *F. fusca* in 2014 but not for the other thrips species. However, preliminary sorting and identification showed similar thrips diversity in both years.

Weather Data

Weather data for each location were downloaded from two databases. The first database, Indiana State Climate Office (iclimate.org) was used to obtain average high and low temperatures for each specific PAC location. GDD was calculated using the following equation:

$$\text{GDD} = \left(\text{Daily high T } [°\text{C}] + \text{Daily low T } [°\text{C}]\right) / 2 - \text{Developmental Threshold}\,(°\text{C})$$

Since the specific lower developmental threshold is not known for all species of thrips, 10°C was used as the lower developmental threshold, which is generally accepted as an appropriate approximation for many insect species (Herms 2004). GDD was summed from 1 January through 1 d before the start of the trapping interval.

Precipitation data, including total precipitation and number of days of precipitation, were downloaded from the Midwest Regional Climate Center, using the cli-MATE database. Because total precipitation and the number of precipitation days were correlated ($P < 0.0001$), these variables were combined into a single variable called RI as per Morsello et al. (2010), which was calculated by multiplying centimeters of precipitation by the number of precipitation days for each time interval, for each year, and each location. When available, the precipitation data used were collected directly at the PAC locations. For the locations in which precipitation data were not collected directly at the PACs, the nearest possible location to the PAC was used. The RI was summed similar to GDD_{10}, from 1 January through 1 d before the start of the capture interval.

Monitoring SVNV Occurrence

In 2013 and 2014, SVNV occurrence was monitored at the five PAC locations, DPAC, NEPAC, PPAC, SEPAC, and TPAC, where the thrips survey was conducted (Fig. 1). In addition, we also surveyed South West Purdue Agriculture Center (SWPAC). Monitoring was initiated when plants were in V4–V5 stage (mid-June) and continued every 2 wk until first appearance of the virus in all locations. Around 10–15 symptomatic leaves from different plants were harvested per visit in each location. Leaves were chosen based on the presence of SVNV symptoms such as chlorosis or yellowing and red-brown, irregular-shaped lesions along the vein. Asymptomatic or healthy leaves were also collected from the same fields in each location. Approximately 100 mg of leaf tissues was excised from each leaf and placed in 1.7-ml microcentrifuge tubes. The samples were flash frozen in liquid nitrogen and transported back to the lab for analysis of SVNV.

Detection of SVNV using Reverse-Transcriptase PCR

Asymptomatic and symptomatic leaf tissues were tested for the presence of SVNV using reverse transcriptase (RT)-PCR using SVNV-NP-specific primer pairs as per the study by Keough et al. (2016). Total RNA was extracted using the Trizol (Invitrogen, Grand Island, NY) method, checked for purity and quantity using a Nanodrop ND 100 (Thermo Scientific, Pittsburgh, PA). RNA was then treated with Turbo DNase (Invitrogen) to remove DNA contamination. Complete removal of DNA was verified by PCR using DNase-treated RNA as template for amplification with the internal control ELF-1B. Two micrograms of RNA were used as a template for cDNA synthesis using the Verso cDNA synthesis kit (Thermo Scientific). The cDNA was used for RT-PCR and the cycling conditions were as follows: 2-min incubation at 94°C followed by 40 cycles of 30-s denaturation at 94°C, 10-s extension at 55°C, and 1-min extension at 72°C and a final 10-min incubation at 72°C. The amplicons from a subset of plants were cloned as described in the study by Keough et al. (2016), sequenced, and compared to SVNV-NP sequences deposited in GenBank.

Statistical Analysis

The total number of *N. variabilis*, *F. tritici*, and *F. fusca* in each trap interval were converted to captures per day by dividing the total value by seven (for the 7-d capture interval). Mean number of thrips captured per day or capture rate was compared across locations and years with a two-way repeated-measures analysis of variance (ANOVA). We used the earliest interval capturing thrips as our start interval for analysis. The mean numbers of thrips captured per day for each species were log-transformed to stabilize variance before regression analysis. Generalized additive models (GAMs) were estimated for the three thrips species captured using GDD_{10} and RI as independent variables within mgcv package (version 1.8-22; (Wood 2011) in R (version 3.4.3; R Core Team 2017). The default thin plate regression splines were used as the smoothing term and a Gaussian model family. A reverse stepwise variable selection was used for model selection, removing variables with a *P*-value above alpha, and selecting models with the least generalized cross-validation (GCV) score. *P*-values presented for GAM are estimates based on the likelihood of an independent variable being predictive of the dependent variable and can vary up to two times an actual *P*-value (Wood 2006). Because of this variability, alpha was set to 0.025 for GAM model variable selection. GCV score is an information criterion indicating better fit models with lower scores (Wood 2006). GDD_{10} and RI values for GAM analysis were summed from 1 January to 1 d before the start of the trapping interval. All statistical analyses were performed using R (version 3.4.3). Gaussian curves were fit to mean thrips capture rates at the five sites pooled across years to identify peak capture weeks using SigmaPlot (version 13.0).

Results

In 2013, there were 20 wk of continuous trapping starting from 21 June to 29 October, which coincided with the soybean-growing season in Indiana. In 2014, there were 24 weeks of trapping starting from 23 May to 31 October. Eight different species of thrips were captured in soybean fields in Indiana in 2013 with *F. tritici* comprising the majority of captures (Table 1). Among the thrips species

Table 1. Thrips species captured in suction traps in Indiana during the 2013 sampling season

Species	Percentage capture
Frankliniella tritici	64.61
Frankliniella spp.	21.74
Neohydatothrips variabilis	7.18
Frankliniella fusca	4.72
Anaphothrips sp.	0.24
Thrips tabaci	0.14
Echinothrips sp.	0.10
Phlaeothrips sp.	0.05
Thrips spp.	0.05
Unknown	1.16

captured, four are known to transmit tospoviruses including, *F. tritici*, *N. variabilis*, *F. fusca*, and *T. tabaci*. Of special interest to us were the vectors of SVNV, *N. variabilis*, *F. tritici*, and *F. fusca*, hence, the analysis was focused on these three species.

In 2013, suction trap samples were only obtained from 21 June, hence (week 24), there is no record of thrips activity before this date. In 2014, the suction traps were not operated until early May, hence captures showed no thrips activity until early May (week 20; Fig. 2A and B). For dates with available thrips data, we found that the magnitude and timing of activity varied greatly for the three species. The peak activity for *F. tritici* occurred in mid-late June (weeks 24 and 26), and a second peak in activity was observed in early August (week 32). *N. variabilis* activity peaked between mid-late August each year (weeks 34–36). While *F. fusca* activity remained more or less the same with no peak. Similar observations were made in both years (Fig. 2A and B).

There was no main effect of either location or year for either of the three thrips species (Table 2). Additionally, we found no interaction between location and year for these species. Since main effects and interactions did not exist in our analysis, we pooled the data for subsequent multiple regression analyses across locations and years for each species. For *N. varabilis*, RI did not significantly add to the GAM ($F = 0.05$, $P = 0.820$). However, the subsequent models with only GDD_{10} resulted in a significant model ($F = 6.71$, $P < 0.001$, $R^2 = 0.22$; Fig. 3A). Without RI included resulted in a slightly lower GCV compared to the GAM with it included (0.192 vs 0.194, respectively). Similarly, RI did not significantly add to the GAM for *F. tritici* ($F = 1.15$, $P = 0.460$). Again, GDD_{10} significantly predicted *F. tritici* in the subsequent GAM ($F = 13.78$, $P < 0.001$, $R^2 = 0.34$; Fig. 3A). Since RI had no influence on the model, GCV scores were not different between the models (GCV = 0.293). No significant models were produced from GAM analysis of *F. fusca* captures. While *F. tritici* peaked at approximately 500 GDD_{10}, both *F. tritici* and *N. variabilis* declined in captures similarly after approximately 1,400 GDD_{10} (Fig. 3A). Pooling data across years and locations, Gaussian curves provided clearer evidence of peak activity in relation to time (Fig. 3B). Both *F. fusca* and *N. variabilis* had curve peaks in weeks 34–35 (mid-late August; Fig. 3B). Because of the variable capture rates of *F. tritici* (Fig. 2), the Gaussian curve for this species fit poorer than the other two (*F. fusca*: $F_{2,24} = 54.91$, $P < 0.001$, $R^2 = 0.82$; *F. tritici*: $F_{2,24} = 8.70$, $P = 0.002$, $R^2 = 0.44$; *N. variabilis*: $F_{2,24} = 61.91$, $P < 0.001$, $R^2 = 0.84$). However, *F. tritici* curve peaked in weeks 24–26 (mid-late June; Fig. 3B).

The SVNV-NP amplicons obtained from testing potentially infected plants were sequenced, and the partial NP sequence was 99% similar to SVNV-NP gene sequences in GenBank. There was no difference in sequences of SVNV-NP obtained from the different PAC

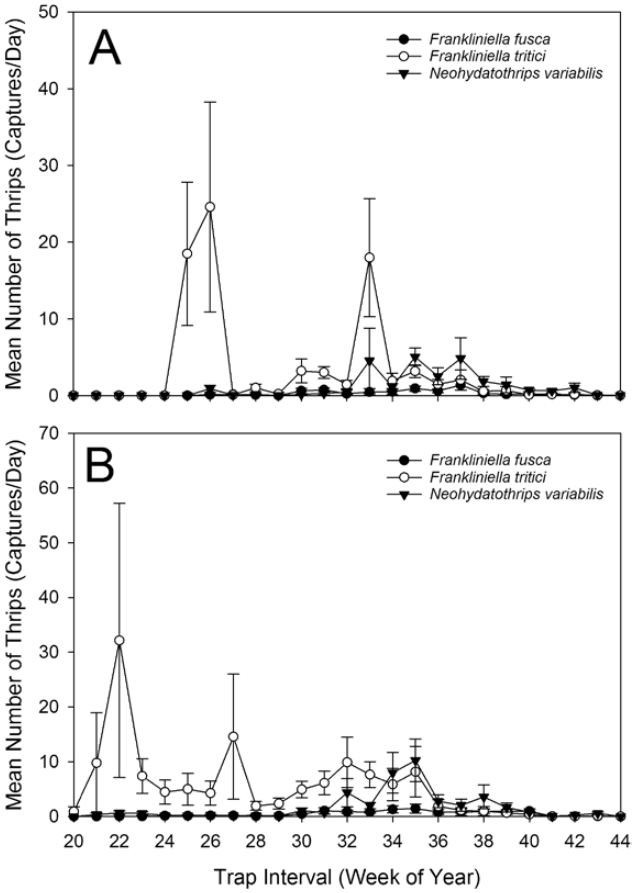

Fig. 2. Mean number of *Neohydatothrips variabilis, Frankliniella tritici,* and *Frankliniella fusca* captured per day during the 1-wk trapping intervals at five sites in Indiana during (A) 2013 and (B) 2014, with standard error.

locations. The SVNV-NP sequence is deposited in NCBI GenBank under accession number MG190869. In 2013 and 2014, SVNV was first detected between 15 and 30 August when soybeans were in R5-R6 (reproductive stage). In 2013, total of 57 leaves were tested using RT-PCR out of which 79% were positive for SVNV. The virus was detected in all locations with the highest incidence (100%) observed in DPAC and TPAC (Table 3). In 2014, 54 leaves were tested out of which 59% showed presence of SVNV. The virus presence was confirmed in all locations except in NEPAC. The virus was not detected in any of the asymptomatic leaf tissues (Table 3).

Discussion

The present study was undertaken to evaluate the relative effects of temperature and rainfall on seasonal population dynamics of thrips vectors of SVNV in soybean fields in Indiana. In addition, we conducted surveys of SVNV in the same locations with the goal of relating thrips population dynamics and SVNV occurrence. Our study found a rich diversity of phytophagous thrips inhabiting soybean fields in Indiana. Eight different species of thrips were captured including, *F. tritici*, *F. fusca*, *Frankliniella* spp., *Echinothrips* sp., *N. variabilis*, *Phlaeothrips* sp., *T. tabaci*, and *Thrips* spp. This is consistent with previous reports that documented a variety of thrips in soybean fields (Blickenstaff and Huggans 1963, Irwin et al. 1979, Bloomingdale et al. 2017). Little is known about phytophagous thrips and their association with soybean. Recently, it was reported

Table 2. Two-way repeated measures analysis of variance results over 1-wk trapping intervals comparing location ($n = 5$) and years (2013 and 2014) for *Neohydatothrips variabilis, Frankliniella tritici,* and *Frankliniella fusca* (log captures per day)

	Location		Year		Location × year interaction	
Species	$F_{4,200}$	P	$F_{1,200}$	P	$F_{4,200}$	P
N. variabilis	1.18	0.319	0.34	0.561	0.05	0.995
F. tritici	0.28	0.889	1.19	0.277	1.89	0.113
F. fusca	0.66	0.624	0.20	0.887	0.61	0.658

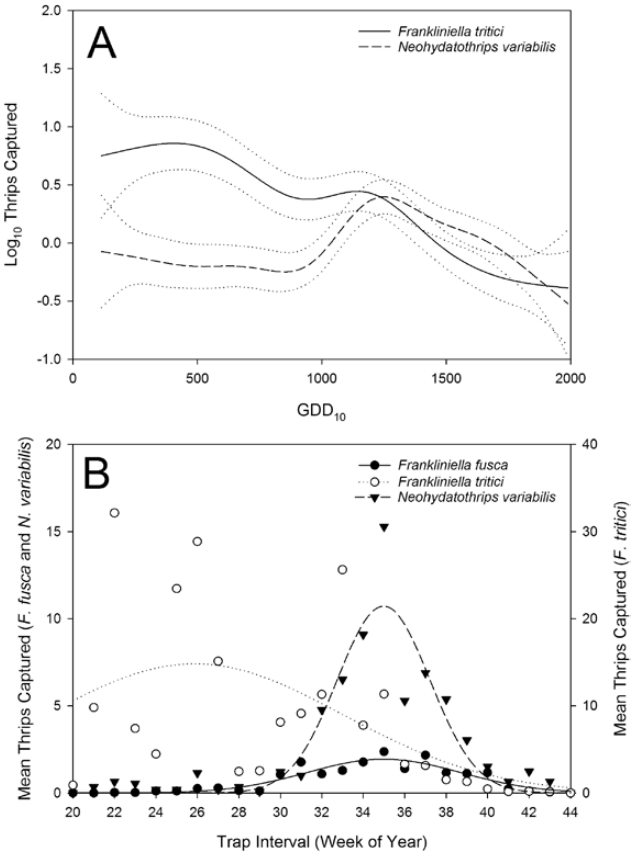

Fig. 3. (A) Generalized additive models for *Neohydatothrips variabilis* and *Frankliniella tritici* estimated based on smoothing via accumulated growing degree days (GDD_{10}) (±2 × standard error [dotted lines]). (B) Mean number of *Neohydatothrips variabilis, Frankliniella tritici,* and *Frankliniella fusca* captured per day during each trapping interval at five sites in Indiana pooled between 2013 and 2014, with Gaussian curves fit to species data.

that *N. variabilis, F. tritici,* and *F. fusca* transmit an emerging soybean virus, SVNV (Zhou and Tzanetakis 2013, Keough et al. 2016). These three species accounted for more than half of the thrips species caught in our study. Similar results were reported in Wisconsin where *F. tritici* comprised over three-quarters of the total captures followed by *N. variabilis* and *T. tabaci* (Bloomingdale et al. 2017).

All three thrips species occurred in soybean fields throughout the growing season, but the magnitude and timing of population peaks varied. Populations of *F. tritici* peaked earlier and declined sooner than *N. variabilis* and *F. fusca*. These findings are consistent with previous surveys that described earlier peaks of *F. tritici* compared to *N. variabilis* (Irwin et al. 1979). *F. tritici* colonizes flowering parts of broad-leaved host plant, grasses, and maize during silking but before and after silking it colonizes soybean. In Indiana,

Table 3. Percentage of leaf samples that tested positive for *Soybean vein necrosis virus* (SVNV) using RT-PCR in August of 2013 and 2014

Location	2013 (%)	2014 (%)
PPAC	75 (12/16)	100 (8/8)
TPAC	100 (12/12)	100 (8/8)
NEPAC	–	0 (0/8)
DPAC	100 (10/10)	50 (4/8)
SEPAC	80 (8/10)	100 (10/10)
SWPAC	33 (3/9)	17 (2/12)

silk emergence occurs sometime between late June to late July, this may in part, explain the two peaks of *F. tritici* activity before and post silking. In addition, early-season peaks of *F. tritici* were higher with greater population density compared to the other two species. *N. variabilis* colonize alfalfa and other broad-leaved plant species early in the season and then move to and reproduce on soybean throughout the growing season (Irwin et al. 1979). The third species, *F. fusca* was present at a low level on soybean. Interestingly, *F. fusca* was the most abundant thrips species on soybean in eastern United States, which suggests that soybean is a suitable host for *F. fusca* (Reisig et al. 2012).

Previous research suggested that *F. tritici* and *N. variabilis* migrate from the southern states possibly even Mexico (Irwin et al. 1979). However, a recent survey of *N. variabilis* in Iowa and Wisconsin showed that there was no south to north gradient in terms of thrips captures and that *N. variabilis* activity was not due to migratory population but depended on local landscape and flora (Bloomingdale et al. 2017). The current study also found no main effect of either location for any of the thrips species (Table 2). This suggests that these insects may use perennial noncrop host plants, weed hosts, and even soil to overwinter during winter months.

Weather variables such as temperature and rainfall are critical for development and dispersal of thrips populations (Lewis 1997, Morsello et al. 2008, Morsello and Kennedy 2009, Morsello et al. 2010, Chappell et al. 2013). Hence, we hypothesized that the temperature measured as GDD and rainfall measured as a factor of amount and frequency of precipitation would be important determinants of thrips species colonizing soybean. Our models suggested that temperature has variable impact on different thrips species. Both *F. tritici* and *N. variabilis* declined in capture rates after approximately 1,400 GDD. Temperature can have both positive and negative effects on thrips population growth and dispersal (Lewis 1997; Groves et al. 2001, 2003; Morsello et al. 2008; Morsello and Kennedy 2009; Morsello et al. 2010; Chappell et al. 2013). Insects cannot develop below the threshold temperature, and they need to accumulate enough degree-days to complete their life cycle. Alternatively, warm temperatures may favor thrips development but also accelerate senescence of host plants, which causes thrips to disperse and

ultimately results in decline in the population (Morsello et al. 2008). We found that *N. variabilis* and *F. tritici* populations begin to decline during September (Fig. 2A and B; Fig. 3A) at which time soybeans begin maturity (R7) stage, which is characterized by shedding of leaves and appearance of mature pods. Hence, we believe rising temperature had a strong effect on host plant senescence, which resulted in declining thrips population. Previous research showed that precipitation during specific periods before trapping interval can negatively impact thrips population (Morsello et al. 2010). However, we did not find significant GAMs that included rainfall. Our regression model that included GDD_{10} only explained a small percentage of the total variation in the number of *N. variabilis* and *F. tritici* captured (22 and 34%, respectively). We hypothesize that the variation in soybean crop distribution, abundance, maturation, and senescence likely has larger impact on thrips populations compared to weather variables. Others factors including, agricultural practices, initial thrips population size, thrips behavior, presence of predators and parasites, and even type of trap used can affect the number of thrips captured. Hence, future studies should include additional parameters beyond temperature and precipitation.

We expect to find a strong relationship between SVNV incidence and number of adult thrips captured in each location because adults are the mobile stage that are primarily responsible for transmission of the virus. Transmission of tospoviruses to healthy plants occurs only if adult thrips acquired the virus while feeding as first instars on an infected plant (Whitfield et al. 2005). Recently, it was reported that SVNV was seed transmitted in up to 6% of soybean seed collected from a commercial soybean field in Iowa (Groves et al. 2016). This is the first report of a *Tospovirus* being seed transmitted. Seed transmission may be a way the virus proliferates, which can influence disease development. Our study found that population of adult *N. variabilis*, peaked between mid-late August, which coincided with SVNV occurrence in all locations in Indiana. This may, in part, suggest that *N. variabilis* is primarily responsible for transmitting SVNV to soybean in Indiana and is expected based on previous findings (Zhou and Tzanetakis 2013, Keough et al. 2016). In contrast, SVNV was not detected earlier in the season despite peaks in *F. tritici* activity. Previous research showed that *F. tritici* (6.36%) is a poor transmitter of the virus compared to *N. variabilis* and *F. fusca* (71.51 and 36.40%, respectively) (Keough et al. 2016). At the time of the survey, vector status of *F. tritici* and *F. fusca* was not known. With the current knowledge about the low transmission efficiency of *F. tritici*, possibly greater number of plants needed to be sampled to detect the virus earlier in the season. Future studies should focus on testing other factors such as virus isolate, host plant cultivar, inoculum pressure, and plant age that can also affect virus transmission (Stumpf and Kennedy 2005, 2007). It was recently reported that SVNV does not affect yield but does impact seed quality (Anderson et al. 2017). We believe that impact of SVNV on soybean yield may be related to the timing of thrips activity and timing of SVNV infection. For instance, the interaction between timing of infection and incidence levels of *Soybean mosaic virus* was correlated with a reduction in soybean yield occurring at or before soybean flowering (R1) (Ren et al. 1997). The peak activity for the primary vector and SVNV infection was in mid-late August, by which time the crop is in advanced growth stage (R5–R6: beginning seed-full seed set) and hence, the disease may not threaten yield.

In conclusion, our study recorded eight thrips species in Indiana soybean including three vector species of SVNV, *N. variabilis*, *F. tritici*, and *F. fusca*. *F. tritici* was the predominant SVNV vector followed by *N. variabilis* and *F. fusca* in our captures. The timing and magnitude of population peaks for the three species varied with *F. tritici* having peaked earlier than *N. variabilis* and *F. fusca*. Finally, our data revealed co-occurrence of SVNV and primary vector, *N. variabilis* populations in soybean fields in Indiana. Neonicotinoid seed treatments have been found to be effective in controlling thrips populations in soybean in the eastern United States (Reisig et al. 2012); however, the effectiveness of insecticide treatments on SVNV incidence is yet to be investigated. One alternative strategy that has been discussed is changing the planting date to try to limit disease incidence and weather data could be useful in determining the new planting date.

Acknowledgments

Support was provided by funds from the Indiana Soybean Alliance and North Central Soybean Research Program. We are grateful to our collaborators Jeff Boyer (DPAC), Phil Walker (NEPAC), Jon Leuck (PPAC); Don Biehle (SEPAC), Peter Illingworth and Christian Krupke (TPAC), and Dennis Nowaskie (SWPAC). We would like to acknowledge Dr. James R. Nechols and Vamsi J. Nalam for helpful comments on an earlier version of the manuscript. We also thank three anonymous reviewers for their helpful suggestions that improved the manuscript.

References Cited

Anderson, N. R., M. D. Irizarry, C. A. Bloomingdale, D. L. Smith, C. A. Bradley, D. P. Delaney, N. M. Kleczewski, E. J. Sikora, D. S. Mueller, and K. A. Wise. 2017. Effect of Soybean vein necrosis on yield and seed quality of soybean. Can. J. Plant Pathol. 39: 334–341.

Blickenstaff, C. C., and J. L. Huggans. 1963. Soybean insects and related arthropods in Missouri. Missouri Agric. Exp. Stat. Res. Bullet. 803: 1–51.

Bloomingdale, C., C. Bradley, M. Chilvers, L. Giesler, R. Groves, D. Mueller, D. Smith, A. Tentuta, and K. Wise. 2015. Soybean Vein Necrosis Virus. Crop Protection Network Bulletin. CPN-1003.

Bloomingdale, C., M. D. Irizarry, R. L. Groves, D. S. Mueller, and D. L. Smith. 2017. Seasonal population dynamics of Thrips (Thysanoptera) in Wisconsin and Iowa soybean fields. J. Econ. Entomol. 110: 133–141.

Chappell, T. M., A. L. Beaudoin, and G. G. Kennedy. 2013. Interacting virus abundance and transmission intensity underlie *Tomato spotted wilt virus* incidence: An example weather-based model for cultivated tobacco. PLoS One. 8: e73321.

Chisholm, I., and T. Lewis. 1984. A new look at thrips (Thysanoptera) mouthparts, their action and effects of feeding on plant tissue. Bull. Entomol. Res. 74: 663–675.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2001. Overwintering of *Frankliniella fusca* (Thysanoptera: Thripidae) on winter annual weeds infected with *Tomato spotted wilt virus* and patterns of virus movement between susceptible weed hosts. Phytopathology. 91: 891–899.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2003. Seasonal dispersal patterns of *Frankliniella fusca* (Thysanoptera: Thripidae) and *Tomato spotted wilt virus* occurrence in central and eastern North Carolina. J. Econ. Entomol. 96: 1–11.

Groves, C., T. German, R. Dasgupta, D. Mueller, and D. L. Smith. 2016. Seed transmission of *Soybean vein necrosis virus*: the first tospovirus implicated in seed transmission. PLoS One. 11: e0147342.

Herms, D. A. 2004. Using degree-days and plant phenology to predict pest activity, pp. 49–59. In: V. Krischik, and J. Davidson (eds.), IPM (Integrated Pest Management) of Midwest Landscapes. Regents of the University of Minnesota. Minnesota Agricultural Experiment Station Publication SB-07645.

Hoddle, M. S., L. A. Mound, and D. L. Paris. 2008. Thrips of California, CBIT Publishing, Queensland, Australia.

Irwin, M. E., K. V. Yeargan, and N. L. Marston. 1979. Spatial and seasonal patterns of phytophagous thrips in soybean fields with comments on sampling techniques. Environ. Entomol. 8: 131–140.

Keough, S., J. Han, T. Shuman, K. Wise, and P. Nachappa. 2016. Effects of Soybean vein necrosis virus on life history and host preference of its vector,

Neohydatothrips variabilis, and evaluation of vector status of *Frankliniella tritici* and *Frankliniella fusca*. J. Econ. Entomol. 109: 1979–1987.

Lewis, T. 1997. Thrips as crop pests, CABI International, Institute of Arable Crops Research, Rothamsted, Harpenden, Hertfordshire, United Kingdom.

Madden, L. V., M. J. Jeger, and F. Van den Bosch. 2000. A theoretical assessment of the effects of vector-virus transmission mechanism on plant virus disease epidemics. Phytopathology. 90: 576–594.

Moritz, G., D. Morris, and L. Mound. 2001. ThripsID: pest thrips of the world. An interactive identification and information system. ACIAR, Australia, CSIRO Publishing, Melbourne, Australia.

Morsello, S. C., and G. G. Kennedy. 2009. Spring temperature and precipitation affect tobacco thrips, *Frankliniella fusca*, population growth and tomato spotted wilt virus spread within patches of the winter annual weed *Stellaria media*. Entomol. Exp. Appl. 130: 138–148.

Morsello, S. C., R. L. Groves, B. A. Nault, and G. G. Kennedy. 2008. Temperature and precipitation affect seasonal patterns of dispersing tobacco thrips, *Frankliniella fusca*, and onion thrips, *Thrips tabaci* (Thysanoptera: Thripidae) caught on sticky traps. Environ. Entomol. 37: 79–86.

Morsello, S. C., A. L. Beaudoin, R. L. Groves, B. A. Nault, and G. G. Kennedy. 2010. The influence of temperature and precipitation on spring dispersal of *Frankliniella fusca* changes as the season progresses. Entomol. Exp. Appl. 134: 260–271.

Mound, L. 2010. Thysanoptera (Thrips) of the World – a checklist, http://www.ces.csiro.au/thysanoptera/worldthrips.html. Accessed 1 June 2014.

Mound, L., and G. Kibby. 1998. Thysanoptera: an identification guide, 2nd ed., CAB International, New York, NY.

Reisig, D. D., D. A. Herbert, and S. Malone. 2012. Impact of neonicotinoid seed treatments on thrips (Thysanoptera: Thripidae) and soybean yield in Virginia and North Carolina. J. Econ. Entomol. 105: 884–889.

Ren, Q., T. Pfeiffer, and S. Ghabrial. 1997. *Soybean mosaic virus* incidence level and infection time: interaction effects on soybean. Crop Sci. 37: 1706–1711.

Rhainds, M., H. J. Yoo, K. L. Steffey, D. J. Voegtlin, C. S. Sadof, S. Yaninek, and R. J. O'Neil. 2010. Potential of suction traps as a monitoring tool for *Aphis glycines* (Hemiptera: Aphididae) in soybean fields. J. Econ. Entomol. 103: 186–189.

Stumpf, C. F., and G. G. Kennedy. 2005. Effects of tomato spotted wilt virus (TSWV) isolates, host plants, and temperature on survival, size, and development time of *Frankliniella fusca*. Entomol. Exp. Appl. 114: 215–225.

Stumpf, C. F., and G. G. Kennedy. 2007. Effects of tomato spotted wilt virus isolates, host plants, and temperature on survival, size, and development time of *Frankliniella occidentalis*. Entomol. Exp. Appl. 123: 139–147.

Tzanetakis, I., R. Wen, M. Newman, and M. Hajimorad. 2009. Soybean vein necrosis virus: A new threat to soybean production in Southeastern United States. Phytopathology. 99: S131.

Whitfield, A. E., D. E. Ullman, and T. L. German. 2005. Tospovirus–thrips interactions. Annu. Rev. Phytopathol. 43: 459–489.

Wood, S. N. 2006. Generalized additive models: an introduction. Chapman and Hall, Boca Raton, FL.

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. Royal Stat. Soc B 73: 3–36.

Zhou, J., and I. E. Tzanetakis. 2013. Epidemiology of soybean vein necrosis-associated virus. Phytopathology. 103: 966–971.