Plant Disease • 2024 • 108:398-406 • https://doi.org/10.1094/PDIS-05-23-0930-RE

Spatiotemporal Patterns of Iris Yellow Spot Virus and Its Onion Thrips Vector, *Thrips tabaci*, in Transplanted and Seeded Onion Fields in New York

Lidia Komondy,[1,†] Christy Hoepting,[2] Marc Fuchs,[3] Sarah J. Pethybridge,[3] and Brian A. Nault[1]

[1] Department of Entomology, Cornell AgriTech, Cornell University, Geneva, NY 14456
[2] Cornell Regional Vegetable Program, Cornell Cooperative Extension, Albion, NY 14411
[3] Plant Pathology and Plant-Microbe Biology Section, School of Integrative Plant Science, Cornell AgriTech, Cornell University, Geneva, NY 14456

Abstract

Onion thrips, *Thrips tabaci* (Lindeman), transmits iris yellow spot virus (IYSV) and is one of the most important pests of Allium crops. IYSV is a member of the species *Tospovirus iridimaculaflavi* in the genus *Orthotospovirus* of the family *Tospoviridae*. This virus typically reduces overall onion bulb quality and weight but can also prematurely kill onion plants. IYSV is neither seed nor mechanically transmitted. Onion fields are typically established via seeds and transplants. A decade ago, onion thrips tended to colonize transplanted fields before seeded fields because plants in transplanted fields were larger and more attractive to thrips than smaller onions in seeded fields. Therefore, we hypothesized that the incidence of IYSV in transplanted fields would be detected early in the season and be spatially aggregated, whereas IYSV would be absent from seeded fields early in the season and initial epidemic patterns would be spatially random. In 2021 and 2022, IYSV incidence and onion thrips populations were quantified in 12 onion fields (four transplanted fields and eight seeded fields) in New York. Fields were scouted four times throughout the growing season (n = 96 samples), and a geospatial and temporal analysis of aggregation and incidence was conducted to determine spatiotemporal patterns in each field type. Results indicated that spatial patterns of IYSV incidence and onion thrips populations were similar early in the season, indicating that transplanted onion fields are no longer the dominant early-season source of IYSV in New York. These findings suggest the need to identify other important early-season sources of IYSV that impact New York onion fields.

Keywords: epidemiology, spatiotemporal analysis, *Thrips tabaci*, *Tospovirus iridimaculaflavi*

Onion thrips, *Thrips tabaci* (Lindeman), is one of the most important pests of dry bulb onion, *Allium cepa* L. (Gill et al. 2015). While leaf feeding by onion thrips larvae and adults can indirectly reduce bulb yield by 30 to 50% (Fournier et al. 1995; Pozzer et al. 1999), a greater concern to onion growers is the ability to transmit iris yellow spot virus (IYSV) (genus *Orthotospovirus*, family *Tospoviridae*), an invasive tospovirus that causes iris yellow spot disease (Cramer et al. 2017). Thrips are the only vectors of tospoviruses, and onion thrips is the principal vector of IYSV in onion with transmission efficiencies up to 76% (Birithia et al. 2013; Cortês et al. 1998; Kritzman et al. 2001; Leach et al. 2018; Nagata et al. 1999; Pozzer et al. 1999; Srinivasan et al. 2012). IYSV is neither transmitted through seed nor mechanically transmitted (Gent et al. 2006; Kritzman et al. 2001; Robène-Soustrade et al. 2006). Similar to other tospoviruses, IYSV can only be acquired by thrips larvae when feeding on an infected plant and can be transmitted by both larvae and adults for their lifespan (Chatzivassiliou et al. 2002; Nagata et al. 1999; Ullman et al. 2002; van de Wetering et al. 1999; Whitfield et al. 2005).

IYSV was first detected in onion in New York (NY) in 2006 (Hoepting et al. 2007) and has subsequently persisted as an annual constraint to production (Leach et al. 2018). Onions grown in NY are most commonly established either by seeds or transplanting "bare-root" (soilless) plants that are imported from the southwestern United States. Onions are seeded from late March to mid-May and transplanted from early April to early June. Onion bulbs are harvested from late July to late October. Multiple studies have reported that onion transplants introduced from the southwestern United States can be infected with IYSV with incidences between 0.5 and 50% and infested with onion thrips (Gent et al. 2006; Hsu et al. 2010; Leach et al. 2018). Only 0.5% of imported IYSV-infected onion transplants were estimated as sufficient to initiate a severe epidemic in NY (Leach et al. 2018).

Onion thrips adults preferentially colonize transplanted onion fields over seeded fields early in the season because plants in transplanted fields are larger at the time of thrips colonization (Hsu et al. 2011; Leach et al. 2018). Consequently, thrips populations tend to be higher in transplanted fields than in seeded fields early in summer. In addition to transplanted onion fields, other sources of IYSV in the landscape include several weed species and volunteer onions located in cull piles and fields where onions were grown the previous year (Hsu et al. 2010; Smith et al. 2011). Weed species in NY that serve as reservoirs for both onion thrips and IYSV include common burdock (*Arctium minus* Bernh.), dandelion (*Taraxacum officinale* G.H. Weber ex Wiggers), curly dock (*Rumex crispus* L.), and chicory (*Cichorium intybus* L.) (Smith et al. 2011). In western NY, Leach et al. (2018) identified significantly higher populations of viruliferous onion thrips adults along the edges of transplanted onion fields compared with those adjacent to other potential sources of IYSV (i.e., weedy areas next to onion fields and onion cull piles containing volunteer onions) and along edges of seeded onion fields. These results suggest an "edge effect" of onion thrips populations and IYSV-infected onion plants in transplanted onion fields but not in seeded fields early in the season. While results from the Leach et al. (2018) study identified transplanted onion fields as the most important early-season source for IYSV epidemics in this onion production system, information regarding the spatiotemporal patterns of IYSV incidence and thrips populations in IYSV-infected transplanted fields were not investigated. Such information could be valuable for improving existing approaches for managing both IYSV and its vector, which currently rely on insecticides that are

---

[†] Corresponding author: L. Komondy; lmk275@cornell.edu

Funding: This project was funded through several granting agencies including the New York Onion Research and Development Program.

e-Xtra: Supplementary material is available online.

The author(s) declare no conflict of interest.

Accepted for publication 19 August 2023.

timed following action thresholds (Leach et al. 2019; Nault and Shelton 2010; Regan and Nault 2022).

The purpose of this study was to compare the incidence of IYSV and populations of onion thrips in transplanted and seeded onion fields over time in western NY and identify factors that may contribute to IYSV epidemics in this region. Specific objectives were to quantify and compare spatiotemporal patterns of IYSV incidence and thrips populations in both transplanted and seeded onion fields and to depict and compare edge effects of IYSV and onion thrips between transplanted and seeded fields. We hypothesized that transplanted onion fields would have a higher initial incidence of IYSV and thrips populations as well as higher magnitudes of aggregation than those in seeded fields early in the season. We also hypothesized that there would be a more prominent edge effect of IYSV and thrips populations in transplanted onion fields compared with seeded onion fields early in the season because thrips prefer to colonize larger onion plants in transplanted fields.

Materials and Methods

Study location and production system

This study was conducted on the Elba Muck located northeast of Elba, NY (43.134°N; 78.099°W), in 2021 and 2022. The Elba Muck was chosen because it is one of the largest regions in the eastern United States where onions are intensively grown and where severe IYSV epidemics frequently cause significant economic losses (Hsu et al. 2010; Leach et al. 2018; Smith et al. 2015). The Elba Muck consists of ‘Carlisle’ and ‘Palms’ muck soils spanning nearly 2,200 ha, and onion is grown annually on approximately half this area (Soil Survey Staff 2023). Most onion fields are not rotated annually because muck is a premium soil type for onion production and growers cannot produce enough onions to meet buyer demand. Fields are typically 55 m, over 200 m long, and often bordered by dirt roads, drainage ditches, and willow hedgerows. Locations of all onion fields sampled are included in Supplementary Table S1.

In both years, the Elba Muck was separated into four regions in which one transplanted field and two seeded fields were sampled per region for a total of 12 fields (four transplanted fields and eight seeded fields) each year. All transplanted fields were grown with bareroot plants imported from the southwestern United States. None were examined for onion thrips or tested for IYSV before transplanting. Additionally, all onion cultivars grown commercially in NY lack resistance to onion thrips and IYSV (Cramer et al. 2017; Damon et al. 2014). Cultivars, planting, and harvest dates are included in Supplementary Table S1. Both transplanted and seeded onion fields were devoid of volunteer onion plants, which were either absent or removed manually before the experiment was initiated.

Sampling

IYSV-infected onion plants and onion thrips adults and larvae were sampled in fields using a grid-based sampling design. In each field, onion plants were sampled in an area that was 55 m wide and 55 m long. This area was overlaid with a 10 by 10 grid to create 100 squares such that each square was 5.5 m wide by 5.5 m long. Four onion plants were selected within each grid square, and the total number of onion thrips adults and larvae were counted, summed, and divided by four; this number was considered as the experimental unit (= mean number of thrips per plant per square). Immediately after thrips were counted, portions of these plants, which included the leaf axil and adjacent leaves, were removed and placed in plastic Ziploc bags (SC Johnson, Racine, WI) before being transported to Cornell AgriTech, Geneva, NY. The four-plant composite sample in each square was considered the sampling unit for IYSV testing.

All 12 fields were sampled multiple times throughout the growing season. In 2021, fields were sampled a total of four times. In 2022, fields were sampled a total of five times. Sampling periods when IYSV was initially detected in onion fields were considered “early.” In 2021, the first and second sample periods were designated as early, while the third and fourth sample periods were considered “late.” In 2022, the third and fourth sample periods were designated as “early,” while the fifth sample period was designated as “late.”

Serological assay for IYSV

Onion leaf tissue was removed from the inner leaves (including leaf axil) of each plant in the four-plant sampling unit to increase the likelihood of detecting IYSV (Boateng and Schwartz 2013; Hsu et al. 2011; Kritzman et al. 2001). The composite onion tissue sample weighed 1.5 g. A double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA; Agdia, Inc., Elkhart, IN) was used to detect IYSV following the procedure described in Voller et al. (1976). Absorbance or optical density at 405 nm was analyzed with a BioTek ELx 800 plate reader (BioTek, Winooski, VT). Samples from each sampling unit were duplicated in microtiter plates, and the mean optical density for each sampling unit was used to determine the sample absorbance. Mean absorbance values two times the negative control were deemed positive for IYSV (User Guide: DAS-ELISA Reagent Set, Agdia Inc.). The composite sample for each square was either positive or negative for IYSV and was used as the experimental unit in the analyses.

Statistical analyses

Data for each year were analyzed independently because weather, growing conditions, thrips populations, and IYSV incidence varied. Thrips populations and IYSV incidence were compared using repeated measures analysis of variance (ANOVA) followed by pairwise comparisons between field types ($P < 0.05$). The effect size was represented as (η^2_g), with the amount of variance explained by each of the model’s terms. An (η^2_g) value of 0.01 indicated a small effect, whereas values of $\eta^2_g = 0.06$ and $\eta^2_g = 0.14$ indicated a medium and large effect, respectively. Data were analyzed using R statistical software R 4.0.3 (R Core Team 2020) and packages ‘epiphy’ (Gigot 2023), ‘rstatix’, and ‘ggpubr’ (Kassambara et al. 2020).

Spatial analysis of IYSV epidemics and onion thrips populations

Spatial Analysis by Distance IndicEs (SADIE) was used to describe the spatial pattern of IYSV incidence and onion thrips populations in transplanted and seeded onion fields at four time points in 2021 and five points in 2022. The SADIE analysis used thrips counts per onion plant and x and y locations in grid number and distance (meters) to calculate the explanatory index of aggregation (I_a). In brief, SADIE uses the number of diseased units (e.g., composite sample of four onion plants) and the location of each sample to quantify the distance to regularity, D_r, which is defined as the minimum distance of shifts until all samples contain the same number of diseased units (Perry 1995, 1998; Perry et al. 1999). I_a is the ratio between the observed distance and the expected average distance to regularity based on randomizations, $I_a = D_r/E_r$ (Perry et al. 1999). $I_a = 1$ suggests a random pattern, while $I_a > 1$ implies an aggregated pattern, and $I_a < 1$ suggests a regular pattern. A two-sided hypothesis test was used to evaluate deviation of $I_a = 1$ from the null hypothesis of randomness (Perry 1998). Spatial arrangements were depicted within observed fields using red and green to identify significant local and gap clusters and different point sizes to denote magnitude based on the absolute local clustering index (Li et al. 2012; Xu and Madden 2005). The I_a was used to ascertain the spatial patterns for IYSV incidence, as well as onion thrips populations, because it quantifies the degree of clustering independent of the numeric values of the IYSV incidences or thrips populations (Winder et al. 2019). Here, we refer to the I_a values of IYSV incidence and thrips populations as the magnitude of aggregation for both IYSV incidence and thrips populations. The I_a values used in the analysis were computed using the *SADIE* function in the R package, ‘epiphy’. Aggregation values provided by the SADIE analysis were analyzed for differences in aggregation between fields using a Chi-square goodness of fit test computed using the *chisq* function in the R package, ‘epiphy’. The mean cumulative number of onion thrips was calculated by adding the mean number of thrips per plant for an entire year for both transplanted and seeded fields.

Edge effects were quantified in each field and compared using contour maps produced via SADIE. Each contour map in the study has a total of 100 points based on the 10 × 10 sampling regime and experimental design. To determine if an edge effect was present, IYSV incidence and thrips populations within the outer two rows or columns for each field (= edge) were compared with IYSV incidence and thrips populations of each field with all remaining samples. Our criteria for an "edge effect" was an edge that had at least eight of 20 sampling units categorized in the top half of the absolute index. All four edges of each field were compared using these criteria in the first sampling of 2021 and the third sampling of 2022.

Results

IYSV incidence and onion thrips populations in onion fields

In 2021, onion plants were sampled on the following four dates: 14 and 28 June, 12 July, and 2 August. In 2022, onion plants were sampled on the following five dates: 27 June, 11 July, and 1, 8, and 15 August. The seasonal mean incidence of IYSV-infected onion plant samples was three times greater in 2021 (46% incidence; Fig. 1A) than in 2022 (17% incidence; Fig. 1C). Seasonal mean populations of thrips per plant in 2021 (16 thrips per plant; Fig. 1B) was over twice as high as those in 2022 (seven thrips per plant; Fig. 1D). Higher populations of onion thrips in 2021 than in 2022 likely caused a disparity in IYSV incidence between the two growing seasons.

Mean incidence of IYSV-infected onion plants in transplanted fields did not differ significantly between seeded fields in both 2021 and 2022 ($P > 0.05$) (Fig. 1A and C). Early in the season, the mean incidence of IYSV in transplanted fields was 30 and 7% in 2021 (Fig. 1A) and 2022 (Fig. 1C), respectively, whereas the mean incidence in seeded fields was 23% in 2021 (Fig. 1A) and 13% in 2022 (Fig. 1C).

Late in the season each year, mean incidence of IYSV in seeded fields tended to be numerically greater than the incidence in transplanted fields (Fig. 1A and C). At this time, the mean incidence of IYSV in seeded fields was 75% in 2021 (Fig. 1A) and 50% in 2022 (Fig. 1C), whereas mean incidence in transplanted fields was 55% in 2021 (Fig. 1A) and 18% in 2022 (Fig. 1C).

Mean onion thrips populations did not differ significantly between transplanted and seeded fields in 2021 and 2022 ($P > 0.05$) (Fig. 1B and D). Early in the season (samplings 1 and 2 in 2021 and 3 and 4 in 2022), the mean number of onion thrips in transplanted fields was 17 thrips per plant in 2021 (Fig. 1B) and 14 thrips per plant in 2022 (Fig. 1D), while the mean number of onion thrips in seeded fields was eight and 10 thrips per plant in 2021 (Fig. 1B) and 2022 (Fig. 1D), respectively. The mean cumulative number of onion thrips in transplanted fields was 20 and 15 thrips per plant in 2021 (Fig. 1B) and 2022 (Fig. 1D), respectively. The mean cumulative number of thrips in seeded fields was nine and three thrips per plant in 2021 (Fig. 1B) and 2022 (Fig. 1D), respectively.

Spatial analyses of IYSV distribution in transplanted and seeded onion fields

Considering 48 sampling events in 2021, IYSV incidence was spatially aggregated in 34 of 48 samples (71%) (Supplementary Table S2; Fig. 2A) in 2021. In 2022, IYSV incidence was spatially

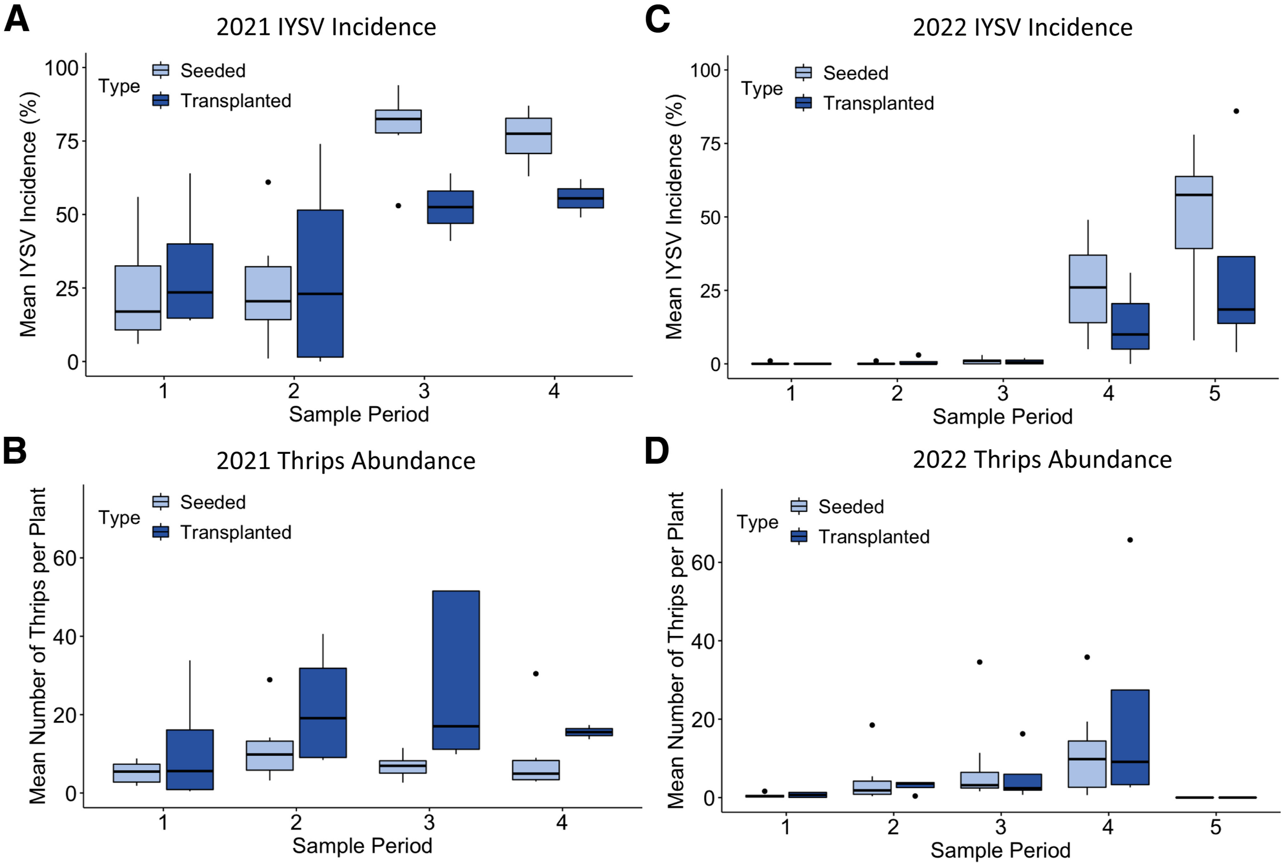


Fig. 1. Repeated measures analysis of **A and C,** mean iris yellow spot virus (IYSV) incidence and **B and D,** mean onion thrips populations in transplanted and seeded onion fields during the 2021 and 2022 seasons in New York. Samples were calculated using the mean IYSV incidence values (positive plant sample [+] per sampling square) and mean onion thrips populations (thrips per plant) in 2021 and 2022 ($P < 0.05$). Sample periods 1 to 4 in 2021 correspond with sampling dates beginning 14 June, 28 June, 12 July, and 2 August, 2021, for sample periods 1, 2, 3, and 4, respectively. Sample periods 1 to 5 in 2022 correspond with sampling dates beginning 27 June, 11 July, 1 August, 8 August, and 15 August, 2022, for sample periods 1, 2, 3, 4, and 5, respectively. Mean numbers of onion thrips per plant and IYSV per sampling unit were compared in each sample period. Composite fig. A: Analysis of variance (ANOVA), F (3, 36) = 2.5, $P = 0.075$, and $\eta^2_g = 0.17$; B: ANOVA, F (3, 36) = 1.55, $P = 0.22$, and $\eta^2_g = 0.12$; C: ANOVA, F (4, 48) = 1.03, $P = 0.4$, and $\eta^2_g = 0.08$; and D: ANOVA, F (4, 50) = 0.67, $P = 0.61$, and $\eta^2_g = 0.05$. Note: some data points are not contained within the box plots.

aggregated in 18 of 60 (30%) sampling events (Supplementary Table S3; Fig. 2C). SADIE characterized the heterogeneity of patches and gaps of IYSV-infected onion plants over time in transplanted and seeded onion fields (Fig. 3A, B, C, and D).

Magnitudes of aggregation of IYSV incidence in transplanted fields did not differ significantly from the magnitude of aggregation in seeded fields in 2021 and 2022 ($P > 0.05$) (Fig. 2A and C). Early in the season (sample periods 1 and 2 in 2021 and sample periods 3 and 4 in 2022), the mean I_a of IYSV incidence in transplanted fields was 1.34 with 100% of IYSV epidemics aggregated in 2021 (Fig. 2A) and 0.87 with 50% of transplanted fields exhibiting an aggregated IYSV pattern in 2022 (Fig. 2C), whereas the mean I_a of IYSV incidence in seeded fields was 1.28 with 100% of seeded fields exhibiting an aggregated IYSV pattern in 2021 (Fig. 2A) and 0.96 with 50% of fields exhibiting an aggregated pattern of IYSV in 2022 (Fig. 2C).

There were no IYSV edge effects observed in either transplanted or seeded fields in both years (Fig. 3A and C).

Spatial analyses of onion thrips in transplanted and seeded onion fields

SADIE characterized the heterogeneity of patches and gaps of onion thrips populations in all onion fields sampled (Fig. 3A, B, C, and D). Considering the 48 sampling events in 2021, onion thrips populations were spatially aggregated in 42 of 48 sampling events (87%) (Supplementary Table S4; Fig. 2B) in 2021. In 2022, onion thrips populations were spatially aggregated in 39 of 60 sampling events (65%) (Supplementary Table S5; Fig. 2D).

Aggregation of onion thrips populations in transplanted fields did not differ significantly from the populations in seeded fields in both 2021 and 2022 ($P > 0.05$) (Fig. 2B and D). At this time early in the season, the mean I_a of onion thrips populations in transplanted fields was 1.69, with 88% of fields exhibiting aggregated onion thrips populations in 2021 (Fig. 2B) and 2.05 with 100% of fields exhibiting aggregated onion thrips populations in 2022 (Fig. 2D). The mean magnitude of aggregation of onion thrips in seeded fields was 1.71 with 100% of fields exhibiting aggregated onion thrips populations in 2021 (Fig. 2B) and 1.58 with 88% of fields exhibiting aggregated thrips populations in 2022 (Fig. 2D).

There were significant edge effects in onion thrips populations in both transplanted fields and seeded fields in 2021 and 2022 (Fig. 3B and D). Early in the season (sample periods 1 in 2021 and 3 in 2022), the number of field edges (*n* = 16 field edges) with "edge effects" in transplanted fields was 6% (one of 16 fields) in 2021 (Fig. 3B; field 1A [east]). In 2022, the number of field edges with "edge effects" in transplanted fields was also 6% (one of 16 fields) (Fig. 3D; field 4A [south]).

Early in the season (sampling period 1) in 2021, the total number of field edges (*n* = 32 field edges) with "edge effects" in seeded fields was 13% (four of 32 fields; Fig. 3B; fields 1B [east], 2B [south], 3B [west], and 4C [west]). Early in the season (sampling period 3) in 2022, the total number of field edges with "edge effects" in seeded fields was 9% (three of 32 fields) (Fig. 3D; field 2B [south], 4B [south], and 4C [west]).

Magnitudes of aggregation in onion fields

Magnitudes of IYSV aggregation in transplanted fields did not differ significantly from the magnitudes of aggregation in seeded

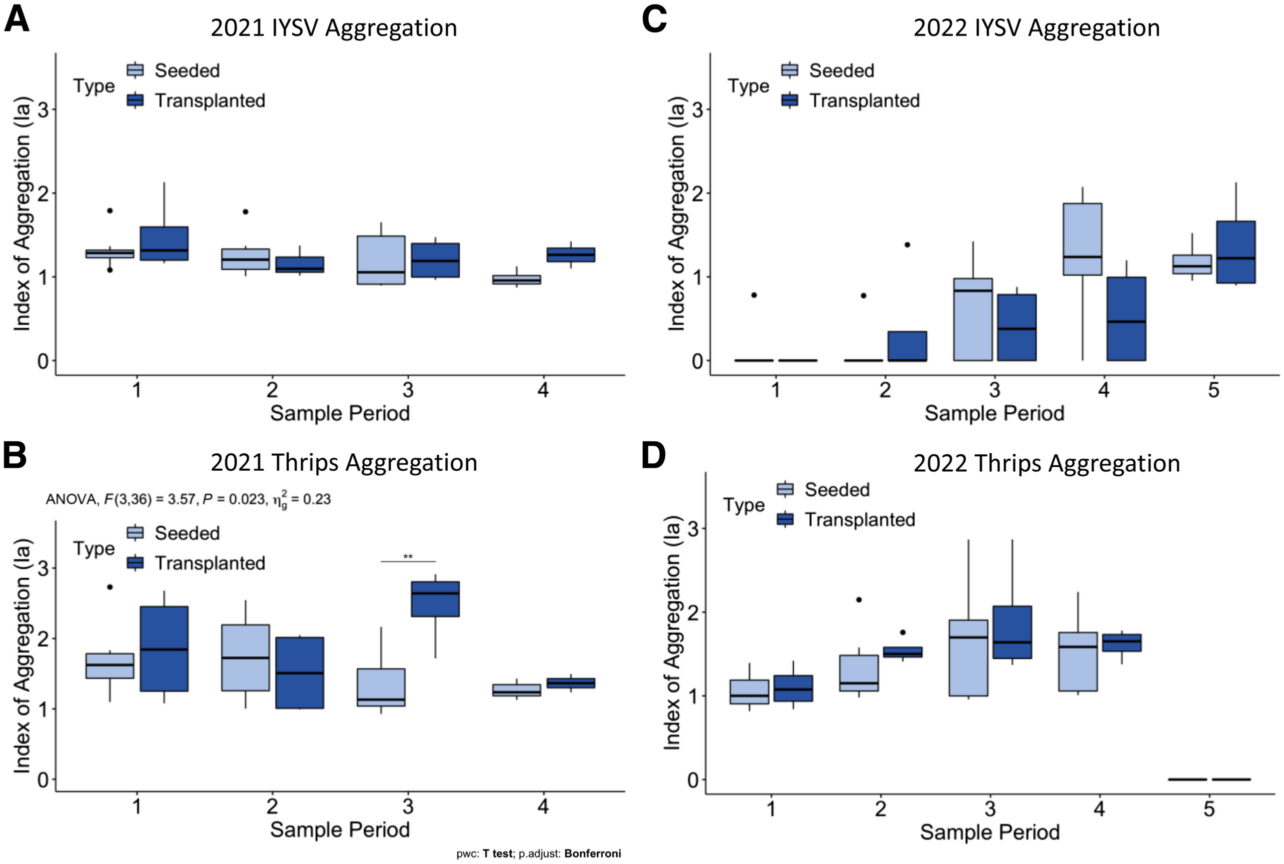


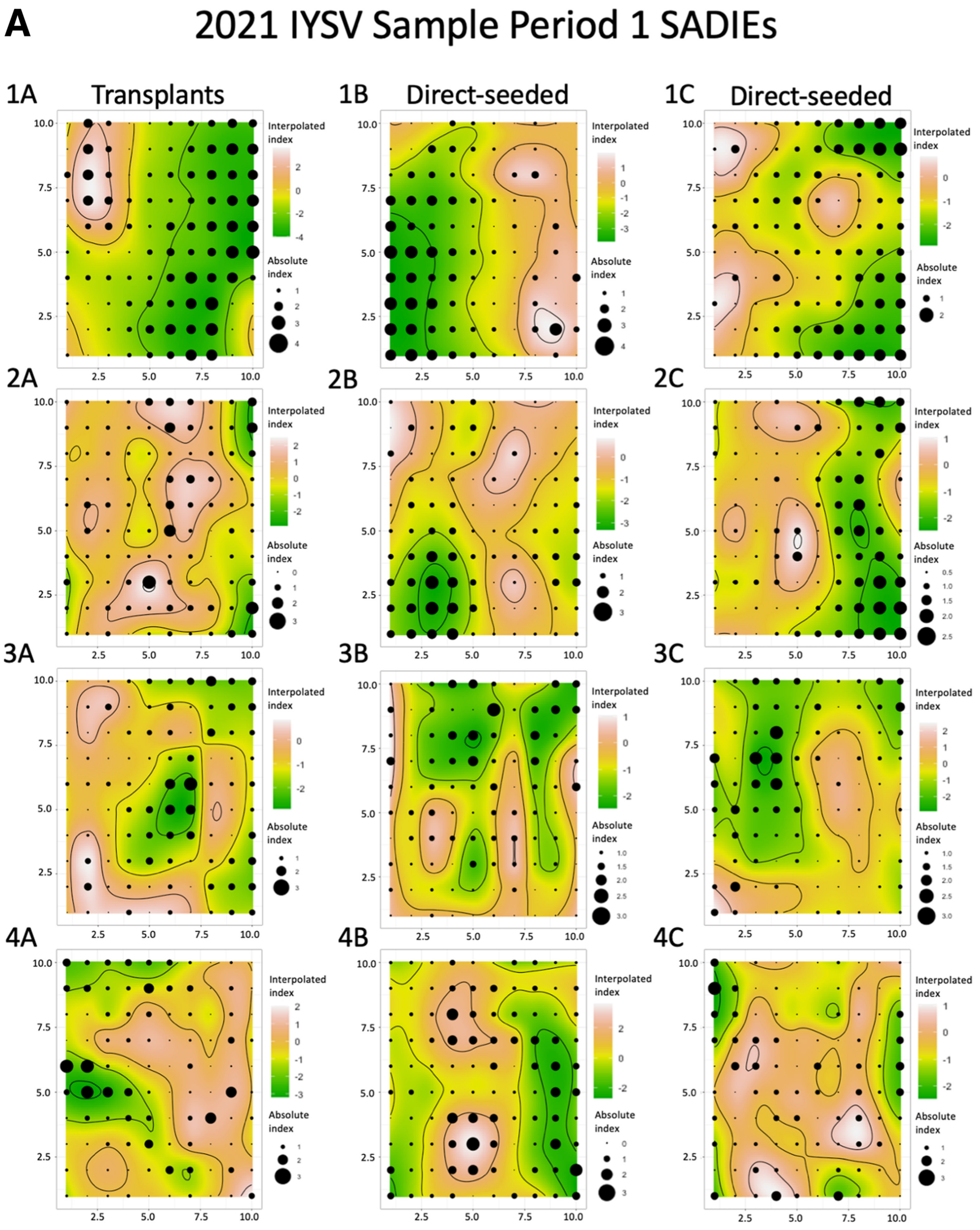
Fig. 2. Repeated measures analysis of iris yellow spot virus (IYSV) spatial analysis by distance indices (SADIE) of aggregation values and onion thrips populations in onion fields during the 2021 and 2022 seasons in New York where $P < 0.05$. Samples were calculated using the mean IYSV incidence values (positive plant sample [+] per sampling square) and mean number of onion thrips (thrips per plant). Sample periods 1 to 4 in 2021 correspond with sampling dates beginning 14 June, 28 June, 12 July, and 2 August, 2021, for sample periods 1, 2, 3, and 4, respectively. Sample periods 1 to 5 in 2022 correspond with sampling dates beginning 27 June, 11 July, 1 August, 8 August, and 15 August, 2022, for sample periods 1, 2, 3, 4, and 5, respectively. **A,** Analysis of variance (ANOVA), F (3, 35) = 0.79, $P = 0.51$, and $\eta^2_g = 0.06$; **B,** ANOVA, F (3, 36) = 3.57, $P = 0.023$, and $\eta^2_g = 0.23$ with significant differences between treatments in sample period 3 found using pairwise comparison and significance of $P < 0.005$ is denoted by a double asterisk (**); **C,** ANOVA, F (4, 50) = 1.99, $P = 0.11$, and $\eta^2_g = 0.14$; and **D,** ANOVA, F (4, 50) = 0.2, $P = 0.94$, and $\eta^2_g = 0.02$.

fields in 2021 and 2022 ($P > 0.05$; Fig. 2A and C). Magnitudes of IYSV aggregation in onion fields in 2021 and 2022 were similar throughout the growing seasons, but incidence increased in onion fields throughout the season in 2022.

Magnitudes of onion thrips aggregation in transplanted fields were significantly greater than those in seeded fields in 2021 ($F = 3.57$; $df = 3.36$; $P = 0.023$; Fig. 2B). For example, the magnitude of aggregation in transplanted fields was greater than the level in seeded fields during sampling 3 (Fig. 2B). Magnitudes of onion thrips aggregation did not differ significantly between field types in 2022 ($P > 0.05$; Fig. 2D).

Discussion

Fields transplanted with onion plants had similar early-season spatiotemporal patterns of IYSV incidence and onion thrips populations to those established by seed. Therefore, one of our initial hypotheses was refuted. We expected a higher incidence of IYSV in transplanted fields than in seeded fields early in the season because previous studies have shown that onion plants introduced from the southwestern United States often can be infected with IYSV (Boateng et al. 2014; Gent et al. 2006; Hsu et al. 2010; Leach et al. 2018). The absence of IYSV in onion transplants that were



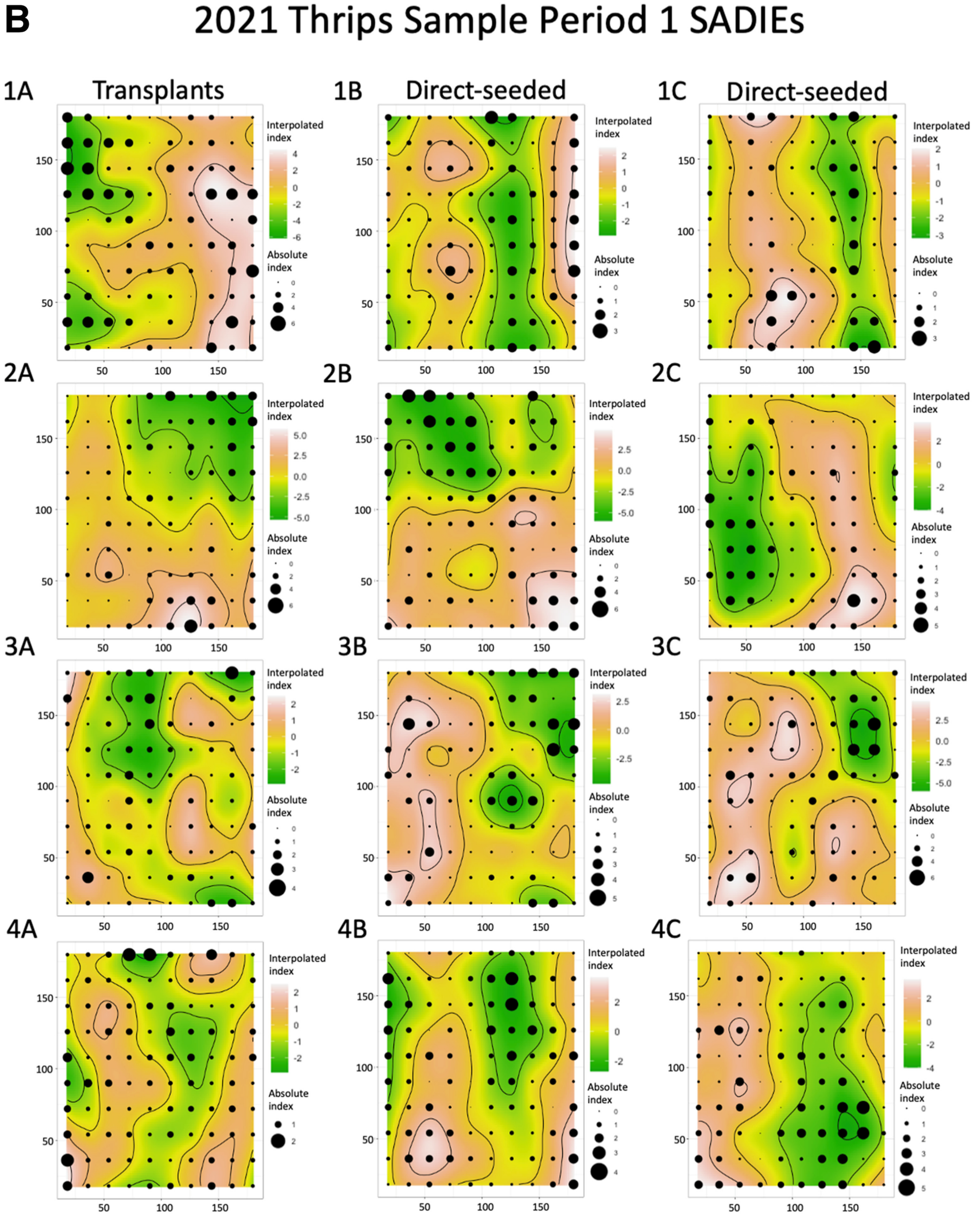
(*Continued*)

Fig. 3. A, B, C, and D, Spatial analysis by distance indices (SADIE) contour plots of mean iris yellow spot virus (IYSV) incidence and mean onion thrips populations in 2021 and 2022. The relative locations of the sampling units (10 × 10 square grid) and the number of diseased units per sampling unit (thrips and IYSV per square) were used to quantify the spatial arrangement of diseased units by calculating the distance to regularity. Data from each year represents the first sampling period that IYSV was detected, the first sampling period of 2021 (14 June), and the third sampling period of 2022 (11 July). Each field surveyed was made into a SADIE contour plot and given an index of aggregation (I_a) value and the significance value P_a that equates the degree of spatial pattern in a set of counts. Values equal to 1 indicate randomly arranged counts, while I_a values larger than 1 indicate aggregation of counts into clusters and I_a values less than 1 indicate regularity. Contour maps of local clustering were generated with statistically significant ($P < 0.05$) local clusters colored red, statistically significant gaps colored green, and point size assigned based on the absolute index value. All contour maps are arranged by cardinal direction, with the top of the maps oriented north.

introduced from the southwestern United States and used to establish fields in NY in 2021 and 2022 or its presence at an extremely low rate (less than 0.1%) might explain why the initial levels of IYSV in transplanted fields were not higher compared with seeded fields. We also expected higher early-season onion thrips populations in transplanted onion fields than in seeded fields. Onion thrips prefer to colonize transplanted onion fields rather than seeded ones early in the season because onion plants in transplanted fields are typically larger and more attractive than those in seeded fields (Hsu et al. 2010). Colonization of transplanted fields over those established by seed would likely lead to higher onion thrips populations and could eventually exacerbate IYSV spread (Gent et al. 2006; Hsu et al. 2010; Schwartz et al. 2014). The lack of early-season differences in IYSV incidence and onion thrips populations between field types in our study refuted our second hypothesis. This may be attributed to a significant change in the onion cropping system in western NY, which is now more balanced between transplanted and seeded onion acreage (B. Nault, personal observation). Onions are transplanted by hand, which is time consuming and now spans a longer period in spring than in previous years. Warmer and drier springs also have allowed onion growers to start transplanting earlier than in the past. Consequently, there is a considerable overlap in planting dates between transplanted and seeded onion fields (Supplementary Table S1). This change in production practices has resulted in a higher proportion of onion plants in transplanted fields being similar in size to those in seeded onion fields when onion thrips adults colonize fields in June. Therefore, the disparity in plant size between transplanted and seeded fields occurs much less frequently and may explain similar onion thrips colonization patterns between the two field establishment methods.

There are also perennial and biennial weed hosts and volunteer onion plants that are hosts for both IYSV and onion thrips in the NY onion cropping system (Hsu et al. 2010; Smith et al. 2011). While these weed hosts and volunteer plants can be early- to midseason sources for IYSV in the onion cropping system, transplanted onion fields have been shown to be the most dominant sources of virus inoculum (Leach et al. 2018). Another potential source of IYSV in this onion production region could be overwintered, viruliferous

Fig. 3. (*Continued from previous page*)



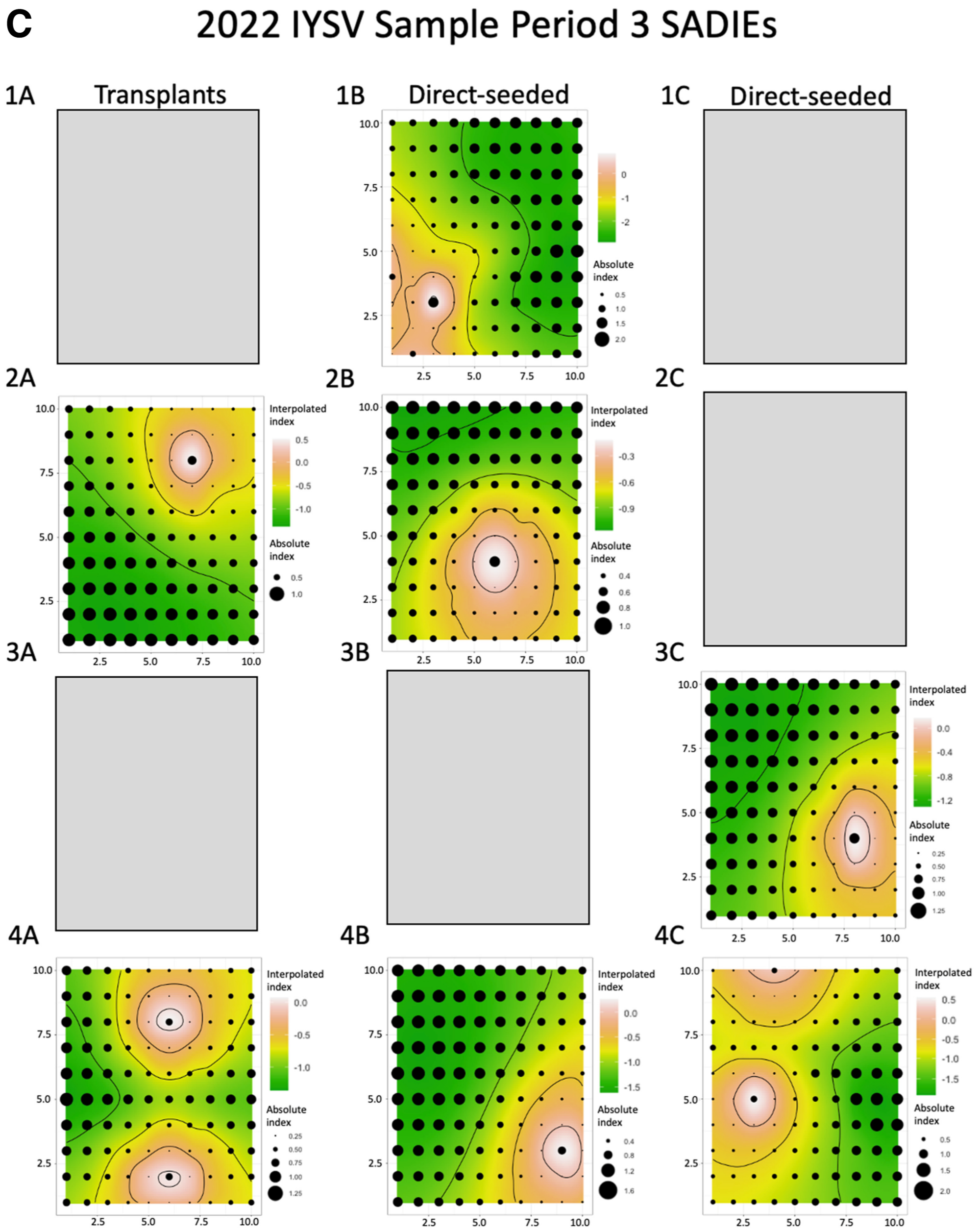
(*Continued*)

onion thrips adults that are likely distributed across the onion production region. While it is not known if IYSV can survive in *T. tabaci* between seasons, this scenario is likely and would explain why IYSV incidence was similar in transplanted and seeded onion fields. Overwintered, viruliferous thrips might directly colonize the largest onion plants, which currently could occur in either transplanted or seeded onion fields, depending on when they were planted in the spring.

No edge effects were observed for IYSV at the time of thrips colonization in 2021 (sampling 1) or 2022 (sampling 3) (Fig. 3A, B, C, and D). In contrast in two western Colorado onion fields, iris yellow spot disease gradients extending from the field edge into the field center were observed (Gent et al. 2004); however, this could have been accounted for by differences in field size and regional landscape. Disease gradients originating from field margins have also been reported in other thrips-tospovirus systems such as tomato spotted wilt virus in tomato and pepper (Gent et al. 2004; Gitaitis et al. 1998). The lack of IYSV edge effects early in the season in our study could be explained by a random assortment of IYSV-infected plants that were established in the field during transplanting. Another possibility is that viruliferous onion thrips adults randomly colonized onion fields rather than directionally from a field edge as we anticipated. Finally, we were surprised how early in the season IYSV was detected in seeded fields. These results suggest that viruliferous onion thrips adults may be overwintering within nonrotated fields, emerging early, and infecting the current onion crop.

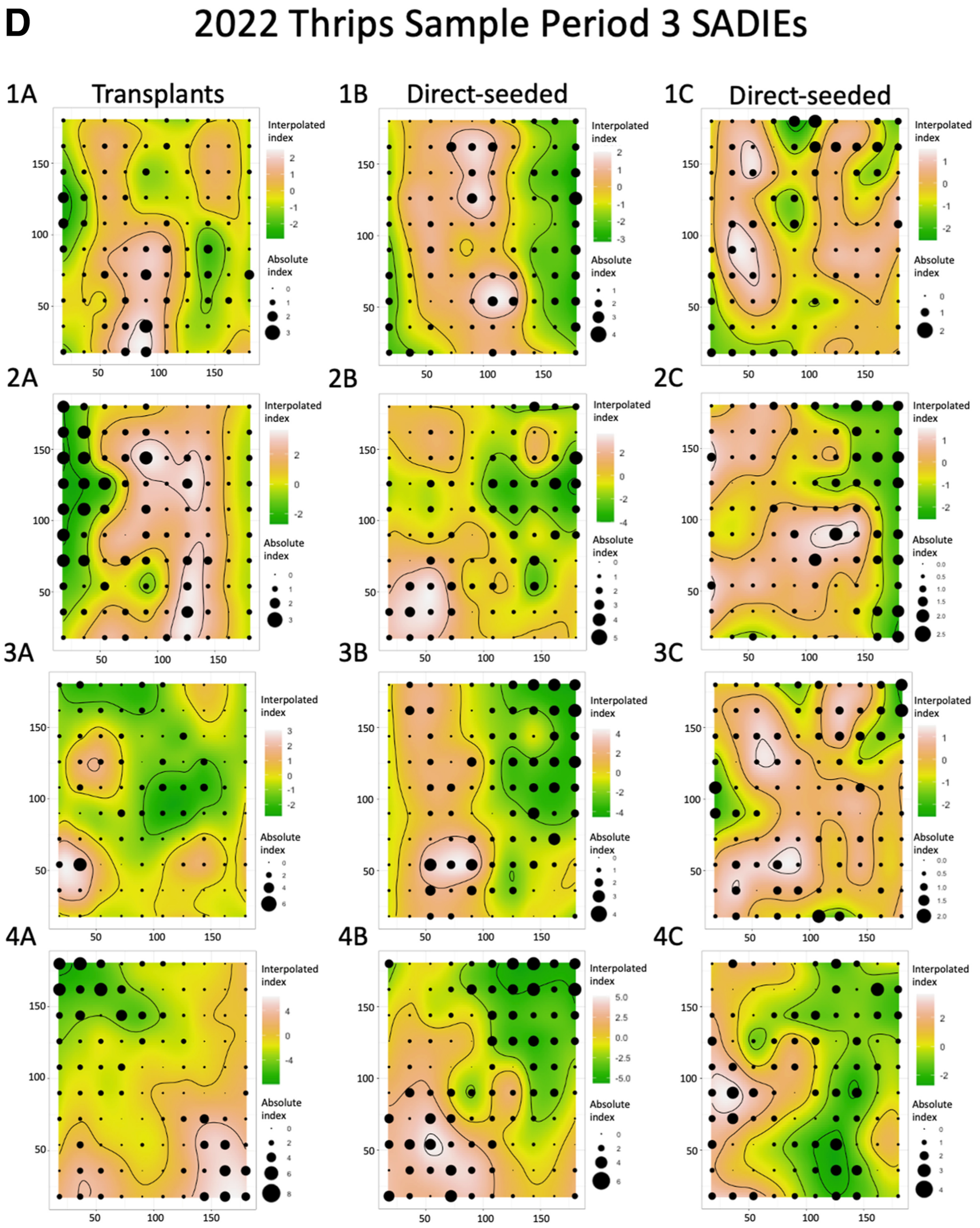
There were some examples of significant edge effects of onion thrips populations in both field types early in the season (Fig. 3A, B, C, and D). In these cases, adult onion thrips originating from outside onion fields likely dispersed into onion fields. The presence of onion thrips edge effects in both transplanted and seeded field types early in the season suggests that plants were similarly attractive to the colonizing adults. We hypothesized that all transplanted fields would be colonized before seeded ones because transplanted fields would have larger, more attractive plants than all seeded ones during adult colonization, but this was not the case.

Fig. 3. (*Continued from previous page*)



(*Continued*)

Fig. 3. (*Continued from previous page*)



Results from our study have changed our understanding about IYSV epidemiology and onion thrips population dynamics in the NY onion cropping system. Fields transplanted with onions imported into NY from the southwestern United States may no longer be the dominant early-season sources of IYSV and onion thrips. Therefore, recommendations to target onion thrips infestations in all transplanted onion fields before those in seeded fields to reduce IYSV incidence in the cropping system need revision. Rather than encouraging growers to focus on scouting only transplanted fields early in the season to assess onion thrips infestations, we will encourage them to scout all onion fields, regardless of whether they are transplanted or seeded. To further understand the risk of early-season IYSV epidemics in onion fields, future research is needed to investigate whether viruliferous onion thrips adults can overwinter successfully, when they are likely to colonize onion fields, and if targeting them with insecticides early in the season will reduce IYSV incidence.

Acknowledgments

We are grateful for help from our grower cooperators, technicians, and summer research assistants including M. Garlick, N. Hessler, L. Sellers, S. Mann, E. Shen, E. Equinozzi, M. Vetrovec, S. Wright, D. Doeblin, A. Marks, and L. Weber who patiently counted thrips and sampled onions for many summer months.

Literature Cited

Birithia, R., Subramanian, S., Pappu, H. R., Muthomi, J., and Narla, R. D. 2013. Analysis of *Iris yellow spot virus* replication in vector and non-vector thrips species. Plant Pathol. 62:1407-1414.

Boateng, C. O., and Schwartz, H. F. 2013. Temporal and localized distribution of *Iris yellow spot virus* within tissues of infected onion plants. Southwest. Entomol. 38:183-200.

Boateng, C. O., Schwartz, H. F., Havey, M. J., and Otto, K. 2014. Evaluation of onion germplasm for resistance to Iris yellow spot (*Iris yellow spot virus*) and onion thrips, *Thrips tabaci*. Southwest. Entomol. 39:237-260.

Chatzivassiliou, E. K., Peters, D., and Katis, N. I. 2002. The efficiency by which *Thrips tabaci* populations transmit *Tomato spotted wilt virus* depends on their host preference and reproductive strategy. Phytopathology 92:603-609.

Cortês, I., Livieratos, I. C., Derks, A., Peters, D., and Kormelink, R. 1998. Molecular and serological characterization of *Iris yellow spot virus*, a new and distinct tospovirus species. Phytopathology 88:1276-1282.

Cramer, C. S., Kamal, N., and Singh, N. 2017. Evaluating iris yellow spot disease incidence and severity in onion germplasm of varying leaf characteristics. HortScience 52:527-532.

Damon, S. J., Groves, R. L., and Havey, M. J. 2014. Variation for epicuticular waxes on onion foliage and impacts on numbers of onion thrips. J. Am. Soc. Hort. Sci. 139:495-501.

Fournier, F., Boivin, G., and Stewart, R. K. 1995. Effect of *Thrips tabaci* (Thysanoptera: Thripidae) on yellow onion yields and economic thresholds for its management. J. Econ. Entomol. 88:1401-1407.

Gent, D. H., du Toit, L. J., Fichtner, S. F., Mohan, S. K., Pappu, H. R., and Schwartz, H. F. 2006. *Iris yellow spot virus*: An emerging threat to onion bulb and seed production. Plant Dis. 90:1468-1480.

Gent, D. H., Schwartz, H. F., and Khosla, R. 2004. Distribution and incidence of *Iris yellow spot virus* in Colorado and its relation to onion plant population and yield. Plant Dis. 88:446-452.

Gigot, C. 2023. Analyzing plant disease epidemics with the R package epiphy. https://chgigot.github.io/epiphy/articles/epiphy.html

Gill, H. K., Garg, H., Gill, A. K., Gillett-Kaufman, J. L., and Nault, B. A. 2015. Onion thrips (Thysanoptera: Thripidae) biology, ecology, and management in onion production systems. J. Integr. Pest Manag. 6:6.

Gitaitis, R. D., Dowler, C. C., and Chalfant, R. B. 1998. Epidemiology of tomato spotted wilt in pepper and tomato in southern Georgia. Plant Dis. 82:752-756.

Hoepting, C. A., Schwartz, H. F., and Pappu, H. R. 2007. First report of *Iris yellow spot virus* on onion in New York. Plant Dis. 91:327.

Hsu, C. L., Hoepting, C. A., Fuchs, M., Shelton, A. M., and Nault, B. A. 2010. Temporal dynamics of *Iris yellow spot virus* and its vector, *Thrips tabaci* (Thysanoptera: Thripidae), in seeded and transplanted onion fields. Environ. Entomol. 39:266-277.

Hsu, C. L., Hoepting, C. A., Fuchs, M., Smith, E. A., and Nault, B. A. 2011. Sources of *Iris yellow spot virus* in New York. Plant Dis. 95:735-743.

Kassambara, A., Kosinski, M., and Biecek, P. 2020. Drawing Survival Curves Using 'ggplot2' (r package survminer.version 0.4.8).

Kritzman, A., Lampel, M., Raccah, B., and Gera, A. 2001. Distribution and transmission of *Iris yellow spot virus*. Plant Dis. 85:838-842.

Leach, A., Fuchs, M., Harding, R., Schmidt-Jeffris, R., and Nault, B. A. 2018. Importance of transplanted onions contributing to late-season *Iris yellow spot virus* epidemics in New York. Plant Dis. 102:1264-1272.

Leach, A. B., Hoepting, C. A., and Nault, B. A. 2019. Grower adoption of insecticide resistance management practices increase with extension-based program. Pest Manag. Sci. 75:515-526.

Li, B., Madden, L. V., and Xu, X. 2012. Spatial analysis by distance indices: An alternative local clustering index for studying spatial patterns. Methods Ecol. Evol. 3:368-377.

Nagata, T., Inoue-Nagata, A. K., Smid, H. M., Goldbach, R., and Peters, D. 1999. Tissue tropism related to vector competence of *Frankliniella occidentalis* for *Tomato spotted wilt tospovirus*. J. Gen. Virol. 80:507-515.

Nault, B. A., and Shelton, A. M. 2010. Impact of insecticide efficacy on developing action thresholds for pest management: A case study of onion thrips (Thysanoptera: Thripidae) on onion. J. Econ. Entomol. 103:1315-1326.

Perry, J. N. 1995. Spatial analysis by distance indices. J. Anim. Ecol. 64:303-314.

Perry, J. N. 1998. Measures of spatial pattern for counts. Ecology 79:1008-1017.

Perry, J. N., Winder, L., Holland, J. M., and Alston, R. D. 1999. Red-blue plots for detecting clusters in count data. Ecol. Lett. 2:106-113.

Pozzer, L., Bezerra, I. C., Kormelink, R., Prins, M., Peters, D., Resende, R. de O., and de Ávila, A. C. 1999. Characterization of a tospovirus isolate of *Iris yellow spot virus* associated with a disease in onion fields in Brazil. Plant Dis. 83:345-350.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Regan, K. H., and Nault, B. A. 2022. Impact of reducing synthetic chemical inputs on pest and disease management in commercial onion production systems. Agronomy 12:1292.

Robène-Soustrade, I., Hostachy, B., Roux-Cuvelier, M., Minatchy, J., Hédont, M., Pallas, R., Couteau, A., Cassam, N., and Wuster, G. 2006. First report of *Iris yellow spot virus* in onion bulb- and seed-production fields in Réunion Island. Plant Pathol. 55:288.

Schwartz, H. F., Gent, D. H., Fichtner, S. M., Otto, K., Boateng, C. O., Szostek, S., Cranshaw, W. S., and Mahaffey, L. A. 2014. *Thrips tabaci* (Thysanoptera: Thripidae) and *Iris yellow spot virus* associated with onion transplants, onion volunteers, and weeds in Colorado. Southwest. Entomol. 39:691-704.

Smith, E. A., Ditommaso, A., Fuchs, M., Shelton, A. M., and Nault, B. A. 2011. Weed hosts for onion thrips (Thysanoptera: Thripidae) and their potential role in the epidemiology of *Iris yellow spot virus* in an onion ecosystem. Environ. Entomol. 40:194-203.

Smith, E. A., Fuchs, M., Shields, E. J., and Nault, B. A. 2015. Long-distance dispersal potential for onion thrips (Thysanoptera: Thripidae) and *Iris yellow spot virus* (Bunyaviridae: Tospovirus) in an onion ecosystem. Environ. Entomol. 44:921-930.

Soil Survey Staff. 2023. Web soil survey, available at http://websoilsurvey.sc.egov.usda.gov/. United States Department of Agriculture, Natural Resources Conservation Service, Washington, DC. Accessed 9 February 2023.

Srinivasan, R., Sundaraj, S., Pappu, H. R., Diffie, S., Riley, D. G., and Gitaitis, R. D. 2012. Transmission of *Iris yellow spot virus* by *Frankliniella fusca* and *Thrips tabaci* (Thysanoptera: Thripidae). J. Econ. Entomol. 105:40-47.

Ullman, D. E., Meideros, R., Campbell, L. R., Whitfield, A. E., Sherwood, J. L., and German, T. L. 2002. Thrips as vectors of tospoviruses. Adv. Bot. Res. 36:113-140.

van de Wetering, F., van der Hoek, M., Goldbach, R., Mollema, C., and Peters, D. 1999. Variation in tospovirus transmission between populations of *Frankliniella occidentalis* (Thysanoptera: Thripidae). Bull. Entomol. Res. 89:579-588.

Voller, A., Bartlett, A., Bidwell, D. E., Clark, M. F., and Adams, A. N. 1976. The detection of viruses by enzyme-linked immunosorbent assay (ELISA). J. Gen. Virol. 33:165-167.

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

Winder, L., Alexander, C., Griffiths, G., Holland, J., Woolley, C., and Perry, J. 2019. Twenty years and counting with SADIE: Spatial analysis by distance indices software and review of its adoption and use. Rethink. Ecol. 4:1-16.

Xu, X., and Madden, L. V. 2005. Interrelationships among SADIE indices for characterizing spatial patterns of organisms. Phytopathology 95: 874-883.