Long-Distance Dispersal Potential for Onion Thrips (Thysanoptera: Thripidae) and *Iris yellow spot virus* (*Bunyaviridae: Tospovirus*) in an Onion Ecosystem

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ABSTRACT Onion thrips, *Thrips tabaci* Lindeman, is a worldwide pest of onion whose feeding damage and transmission of *Iris yellow spot virus* (IYSV) may reduce onion yields. Little is known about the seasonal dynamics of *T. tabaci* dispersal, the distance of dispersal, or the movement of thrips infected with IYSV during the onion-growing season. To address these questions, *T. tabaci* adults were collected using transparent sticky card traps in commercial onion fields three times during the onion-growing season (June, July, and late August) at varying heights above the canopy (0.5–6 m above soil surface) and with trap-equipped unmanned aircraft (UAVs) flying 50–60 m above onion fields during August sampling periods in 2012 and 2013. Randomly selected subsamples of captured *T. tabaci* were tested for IYSV using RT-PCR. Most *T. tabaci* adults were captured in late August and near the onion canopy (<2 m) throughout the season. However, 4% of *T. tabaci* adults captured on sticky cards were at altitudes ≥2 m, and *T. tabaci* were also captured on UAV-mounted traps. These data strongly suggest that long-distance dispersal occurs. More *T. tabaci* captured on sticky cards tested positive for IYSV in August (53.6%) than earlier in the season (2.3 to 21.5% in June and July, respectively), and 20 and 15% of *T. tabaci* captured on UAV-mounted traps tested positive for IYSV in 2012 and 2013, respectively. Our results indicate that *T. tabaci* adults, including viruliferous individuals, engage in long-distance dispersal late in the season and likely contribute to the spread of IYSV.

KEY WORDS *Thrips tabaci*, population ecology, *Tospovirus*, *Allium cepa*

Worldwide, onion thrips, *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), is a major pest of *Allium* crops such as onion, *Allium cepa* L., and many other crops (Lewis 1997). *T. tabaci* cause reductions in onion bulb yields by feeding on leaf tissue (Fournier et al. 1995, Childers 1997), and by transmitting onion pathogens, including *Iris yellow spot virus* (IYSV) (*Bunyaviridae: Tospovirus*) (Gent et al. 2006).

T. tabaci is the principal insect pest of onion in New York where it may complete up to five generations per year (Andaloro and Shelton 1983, Fekrat et al. 2009). Adult *T. tabaci* emerge from overwintering habitats from late March through May (Larentzaki et al. 2007). These adults may colonize volunteer onions growing from bulbs remaining in the field from the previous season (Larentzaki et al. 2007, Hsu et al. 2011), while others may colonize weeds adjacent to onion fields from the previous season (Smith et al. 2011). Onion fields in upstate New York are typically seeded or transplanted in April and early May, but *T. tabaci* does not begin colonizing these crops until mid-June when onions have at least three to four leaves. Multiple generations will develop on onion crops until fields are harvested, starting in late July and ending in September. Typically, *T. tabaci* population levels in onion fields increase as the season progresses, despite the repeated use of insecticides (Hsu et al. 2010). During the season, *T. tabaci* adults may engage in short-distance (trivial) dispersal, long-distance dispersal, or both, but these movements have not been documented.

Trivial dispersal is the short, day-to-day movement of insects within the immediate habitat, and is driven by food, shelter, or mating cues (Southwood 1962, Dingle and Drake 2007). Long-distance dispersal may be considered either migratory or nonmigratory. Migratory insect dispersal involves a temporary suspension of trivial dispersal behaviors based on environmental or developmental cues (Dingle and Drake 2007). This is followed by an intentional, persistent movement away from the original habitat and into a new one, where trivial behaviors may resume (Kennedy 1985, Dingle 1996). Long-distance dispersal may also occur involuntarily via weather systems, in the absence of migratory behavioral changes (Johnson 1967). For the purposes of this paper, we do not attempt to differentiate between types of long-distance dispersal and will refer to the dispersal behaviors of *T. tabaci* in terms of either "long-distance" or "trivial." The altitude at which winged insects fly can provide insight into whether

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they engage in either long-distance or trivial dispersal. The upper limit of the surface boundary layer of the atmosphere (SBL threshold) and lower limit of the planetary boundary layer is considered an altitude threshold for such a designation and is defined as 2.5 times the altitude of the surrounding topography (Oke 1987, Isard and Gage 2001). Above this threshold, small insects such as thrips are under less influence of surface turbulence caused by air currents interacting with earth's surface in the SBL and under more direct influence of the laminar flow and higher wind speeds of the greater airmass and weather systems moving through the area. At such altitudes, insects may be transported longer distances under favorable wind conditions.

IYSV is a yield-reducing pathogen of onion and other *Allium* crops. Symptomatic onions exhibit necrotic leaf lesions that coalesce and reduce the plant's ability to photosynthesize, reducing bulb yield (Gent et al. 2004). Thysanopterans are the sole insect vectors of viruses in the genus *Tospovirus*. While tobacco thrips, *Frankliniella fusca* (Hinds), has successfully transmitted IYSV in laboratory studies using lisianthus, *Eustoma russellianum* (Salisbury) (Srinivasan et al. 2012), *T. tabaci* is the only known vector of IYSV in onion (Gent et al. 2006). *T. tabaci* acquires IYSV as a first instar and the virus becomes circulative and propagative (Ullman et al. 1992, Whitfield et al. 2005). Second instars and adults are capable of transmitting the virus (Ullman et al. 1992, Wijkamp et al. 1993, Moritz et al. 2004). IYSV is not seed transmitted, nor is it easily mechanically transmitted (Kritzman et al. 2001, Gent et al. 2004, Bulajić et al. 2009).

In New York, the incidence of IYSV in onion fields is typically low to undetectable in June and July, but increases substantially in August (Hsu et al. 2010). The source of IYSV may be variable, including imported onion plants from the southwestern United States that are transplanted in fields in April and May (Hsu et al. 2011); it may overwinter locally in volunteer onions and weed hosts (Hsu et al. 2011; Smith et al. 2011, 2012), overwinter in the vector, or be introduced each spring by thrips immigrating from other regions. It is not known if viruliferous *T. tabaci* engage in long-distance dispersal and whether their dispersal increases as the season progresses.

The goal of this study was to improve our understanding about dispersal of *T. tabaci* and IYSV in an onion ecosystem. Specific objectives were as follows: 1) describe and compare dispersal activity of *T. tabaci* adults at different periods during the onion-growing season, 2) determine whether *T. tabaci* engages in long-distance dispersal, 3) compare dispersal activity of viruliferous *T. tabaci* at different periods during the season, and 4) determine if IYSV has the potential to be moved long distances by its vector. We hypothesize that more dispersing *T. tabaci* adults will be captured later than earlier in the season, they will engage in both trivial and long-distance dispersal, and are more likely to carry IYSV late than early in the season in thrips that engage in both trivial and long-distance movement.

Materials and Methods

Studies were conducted in the Elba Muck region in western New York in 2012 and 2013. The Elba Muck is the second-largest contiguous muck soil region in New York, and onion production in this region ranks second in the state. The region covers ~2,400 ha, 1,200 of which are onion crops. The remaining hectares are predominantly potato crops, with a few hectares of soybean, turf, and field corn located at the southern and western margins of the region. Some fields are planted with winter cover crops before onions are planted in the spring. A majority of the onion crop fields are never rotated. Fields are bordered by drainage ditches, gravel roads, and occasional *Salix* sp. windbreaks (height ~0.5–2 m), which represent the only permanent vegetation in the center of this region (Supp Fig. 1 [online only]).

Sampling *T. tabaci* Adult Dispersal. To identify *T. tabaci* dispersal patterns during the onion-growing season, the study was conducted in commercial onion fields during three sampling periods, which will be referred to as "early season" (16–21 June 2012; 10–15 July 2013), "mid-season" (26–31 July 2012; 31 July–5 August 2013), and "late season" (21–26 August 2012; 26–31 August 2013). Sampling periods were chosen by scouting for the presence of *T. tabaci* in onion crops in the early-season period, and by identifying similar onion plant maturity in the mid- and late-season periods. Onion plants sampled during early season, mid-season, and late-season periods were in the 4 to 6 leaf stage, 7 to 9 leaf stage, and the 10 + leaf stage, respectively. Late-season sampling occurred when onion plants were fully grown, and when <5% of plants were beginning to lodge (a sign that the crop is nearing harvest maturity). In each sampling period, thrips were continuously sampled over five consecutive days (120 h). During each of these sampling periods, *T. tabaci* adults were collected at varying heights (see below) because altitude may be considered an indicator for relative potential dispersal distance (Oke 1987, Isard and Gage 2001). Thrips were sampled passively by trapping adults on aerial sticky card traps, and trapping adults using unmanned aerial vehicles (UAVs). UAV collections were conducted using techniques based on those described by Aylor et al. (2011). *T. tabaci* collected from all traps were identified using the key published by Moritz et al. (2001). Voucher specimens are held at Cornell University's New York State Agricultural Experiment Station in Geneva, NY.

Sampling T. tabaci *With Pole-Mounted Sticky Cards.* Aluminum poles (6 m tall; Fig. 1) were placed in four commercial onion fields (one pole at each field, >0.5 km apart) within the Elba Muck (Supp Fig. 1 [online only]). The same locations were used in each of the sampling seasons (early, mid-, and late 2012 and 2013). Colorless, translucent sticky cards (Catchmaster model #904, AP&G Co., Inc, Brooklyn, NY) were mounted on poles at five heights (one trap at each height on each pole): onion leaf height (~0.5 m), and at 1, 2, 4, and 6 m in altitude above the soil surface. Colorless sticky cards were selected to avoid confounds

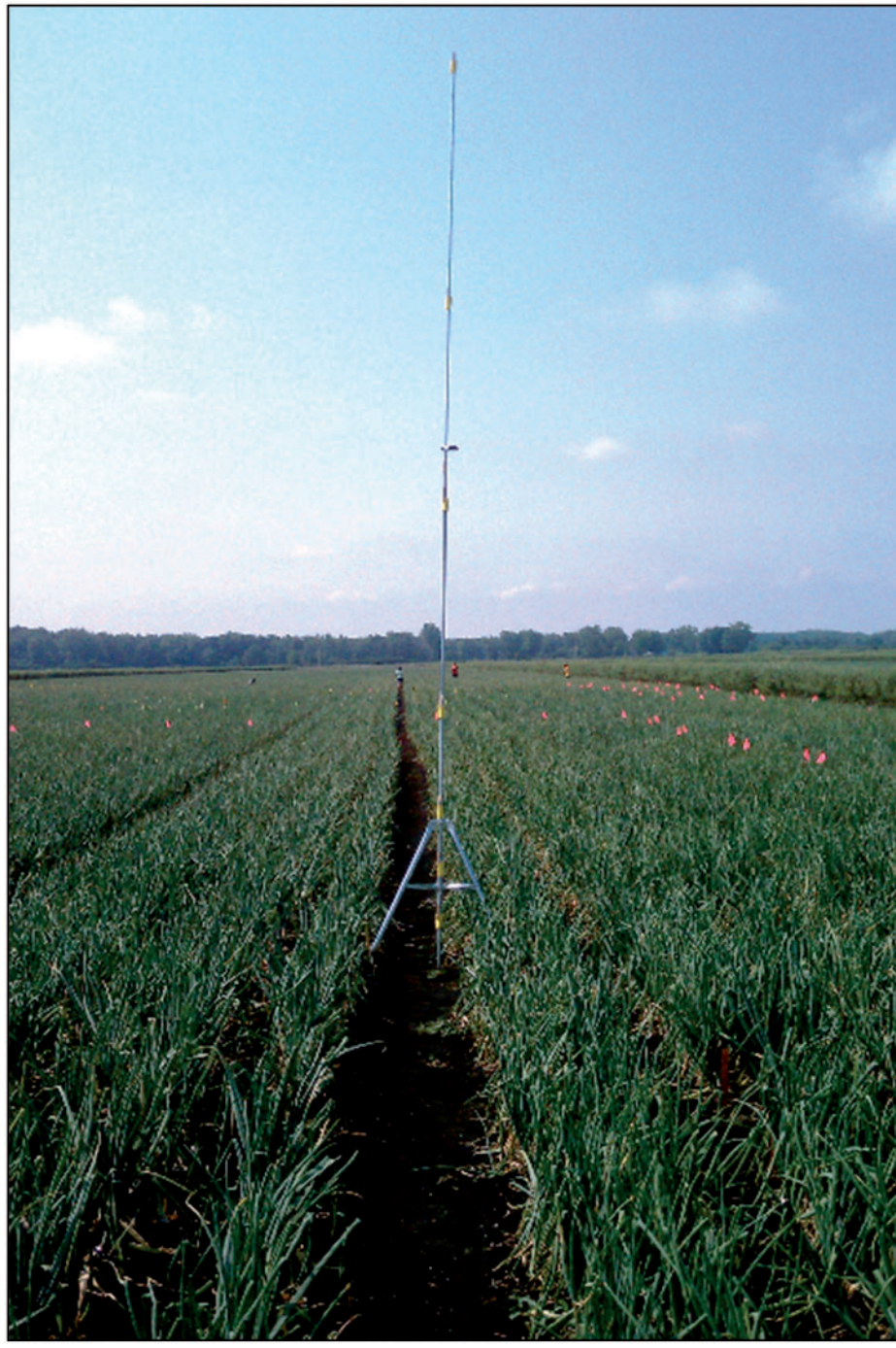

Fig. 1. Pole-mounted trapping system. Onion canopy is at maximum height (~0.75 m). Note the *Salix* sp. hedgerow to the right of the image (~1.25 m high, ~15 m from trapping pole) and the tree line in the background (1–1.4 km away from the trapping pole from left to right of image). This image was taken during preliminary studies when yellow traps were utilized. Colorless, translucent traps were used during the current study.

due to the known attraction of *T. tabaci* to traps of certain colors (Demirel and Cranshaw 2005). Mounting the sticky cards at different heights allowed separation of thrips behavior below and above the SBL threshold. Onion fields in the Elba Muck region are located on flat terrain with onion plants roughly 0.5–0.75 m in height. Given that the SBL threshold is 2.5 times the height of the surrounding topography, this would result

in an average SBL threshold altitude of 1.25–1.875 m, meaning that thrips caught at the 2 m height would be very close to the SBL threshold. For this reason, *T. tabaci* observed dispersing at altitudes ≤2 m were conservatively considered to be dispersing at or below the SBL threshold (=trivial flight), and those dispersing >2 m above the soil surface were considered to be above the SBL threshold, and presumed to be engaged in long-distance dispersal.

Sticky cards were wrapped around the poles, adhesive facing outward, and then fixed in place by pole-mounted clothespins (trap circumference = 17 cm; area = 98.6 cm^2). Clothespins were mounted on the poles using zip-ties or Velcro strips. Cards were collected and immediately replaced at least three times daily. Collected cards were kept in ice-filled coolers until they could be transferred to a refrigerator (3°C), and ultimately a freezer (−18°C) until thrips could be identified to species and sex. All *T. tabaci* adults on pole-mounted traps were recorded in 2013. However, in 2012, extremely high densities of thrips on some cards precluded counting all thrips, so densities on ~4% of these cards (62/1460) were estimated by extrapolating from the number of *T. tabaci* counted in the surface area of a subsample (20% of the card surface).

T. tabaci populations in onion fields were documented by visually recording densities of adult *T. tabaci* on 15 randomly selected onion plants (45–75 plants per day) at one of the four trapping locations during the time sticky cards were sampled. The location of these recordings remained constant for the duration of each sampling period (season) each year. For example, all counts were recorded at one trapping location during the "early" season sampling period of 2012, but were recorded in a different trapping location for the duration of the "mid-" season sampling period, and so on.

Sampling T. tabaci *Using UAVs.* UAVs were utilized to sample *T. tabaci* adults in the atmosphere above onion fields in the Elba Muck region. Thrips collections were made 50–60 m above onion fields, between 6–10 p.m. (2–3 flights per evening). This period was chosen due to the relative prevalence of afternoon- and evening-dispersing thrips observed during preliminary studies. The duration of each flight was 30 min. Fourteen flights were made in 2012, and 18 flights were made in 2013, all of which coincided with the late-season sampling period each year to take advantage of expected higher densities of dispersing thrips. On each UAV, 10 modified petri plates served as traps. Four petri plates (100 by 15 mm) were modified by replacing the base with thrips-proof screen (150 by 150 μm) and spraying the mesh with nonstick cooking spray as an adhesive to capture thrips aloft. Six smaller petri plates (50 by 9 mm) were used intact, but the bottom surfaces were coated with adhesive (nonstick cooking spray or petroleum jelly) after grinding off the 1-mm lip on the bottom. Traps were placed in cold storage (−10°C) until thrips could be identified to species and sex, and the numbers recorded. All *T. tabaci* were counted on UAV traps in 2012 and 2013.

IYSV Detection in *T. tabaci* Adults. *T. tabaci* adults were tested individually for the presence of IYSV using reverse-transcriptase polymerase chain reaction (RT-PCR) assays. A subsample of *T. tabaci* was collected from aerial sticky cards for testing. A total of 339 (of 58,157 trapped) *T. tabaci* were tested in 2012 (83 from early, 115 from mid-, and 145 from late season, respectively), and 438 (of 7,981 trapped) were tested in 2013 (206 from early, 109 from mid-, and 123 from late season, respectively). *T. tabaci* collected from pole-mounted traps for IYSV testing were taken only from the lowest and highest cards on each pole (0.5 and 6 m, respectively) in order to estimate the proportion of viruliferous individuals dispersing below and above the SBL threshold. Individuals were subsampled from a single sampling day during mid- and late 2012 and late 2013, but due to low numbers, subsamples were taken from all sampling days in the early season of both 2012 and 2013, and the mid-season of 2013. *T. tabaci* collected with UAV-mounted traps were subsampled for IYSV testing in 2012 ($n = 220$ randomly selected *T. tabaci* of 303 collected), and due to low numbers, all *T. tabaci* collected from UAVs were tested in 2013 ($n = 22$). *T. tabaci* were removed from cards and traps by placing a single drop of solvent (De-Solv-It, Orange-Sol Household Products, Inc., Gilbert, AZ) on randomly selected individuals for 10–30 s, then removing the thrips with a fine-tipped paintbrush. *T. tabaci* were then placed individually in 0.5-ml centrifuge tubes (USA Scientific, Ocala FL) and immediately stored at −80°C.

Total Ribonucleic Acid (RNA) Isolation for IYSV Detection in T. tabaci. Individual thrips were processed by adding TRK lysis buffer supplemented with β-mercaptoethanol (β-me; 200 μl TRK buffer and 4.0 μl β-me per sample) as an antioxidant and homogenized at 30 Hz for 2 min using a Qiagen TissueLyser in the presence of RNase free acid washed glass beads (Sigma-Aldrich, Glass Beads, Acid-Washed 425-600 mm, cat # G8772-10G). The Omega MicroElute RNA Kit (Omega Bio-Tek, Norcross, GA) was used for total RNA isolation from sampled *T. tabaci* following the manufacturer protocols. Total *T. tabaci* RNA was eluted in 15 μl of 10 mM Tris-HCl pH 8.0 and used as template to amplify IYSV genetic elements by RT-PCR

RT-PCR Protocol for IYSV Detection in T. tabaci *and Molecular Confirmation of* T. tabaci *Identity.* The Qiagen one-step RT-PCR kit was used for IYSV detection using primer pairs IYSV-N402F 5′-ACTCAC-CAATGTCTTCAAC-3′ and IYSV-N402R 5′-GGCTT CCTCTGGTAAGTGC-3′ designed in the N gene of several IYSV isolates from New York that were characterized in 2007–2008. To confirm the identity of *T. tabaci*, primers ThMCOI-F 5′-CGGGAACGGGAT-GAACAG-3′ and ThMCOI-R 5′-GGTCCCCTCCCC CTCTA-3′ designed in the mitochondrial cytochrome oxidase subunit I (COI) gene sequence (GenBank accession no. DQ228494) were used. RT-PCR reactions contained total thrips RNA (1 μl), IYSV primers (1 μM each), *T. tabaci* MCOI primers (0.1 μM each), dNTP (5 mM), RNasin (0.1 μl), 5 × buffer (2.5 μl), enzyme mix (0.5 μl), and sterile RNAse free water for a

final volume of 12.5 µl. Cycling conditions were 50°C for 30 min (1 cycle), 95°C for 15 min followed by 30 cycles of 94°C for 30 s, 50°C for 1 min, 72°C for 1 min, and a final extension at 72°C for 10 min. RT-PCR products (402 bp for IYSV and 325 bp for *T. tabaci*) were resolved by electrophoresis on 1.5% agarose gels and staining with ethidium bromide prior to visualization under ultra-violet illumination.

IYSV Sequence Determination and Analysis. The 402-bp IYSV N gene amplicons obtained by RT-PCR from randomly selected *T. tabaci* samples were extracted from agarose gels with the QIAquick purification kit (Qiagen) and sequenced bidirectionally at the DNA Sequencing facility at Cornell University in Ithaca, NY. Sequences were analyzed and compared using the DNASTAR Lasergene software (version 7.2). The program CLUSTAL W was used for alignment of nucleotide sequences (Thompson et al. 1994).

Statistical Analyses. Unless otherwise noted, all statistical analyses were performed using a mixed model (JMP Pro 11.0.0, SAS Institute, 2013), and considering trap location as a random variable.

Pole-Mounted Sticky Cards. Densities of *T. tabaci* trapped on pole-mounted sticky cards were analyzed for the effects of year (2012 and 2013), season (early, mid-, and late), altitude (0.5, 1, 2, 4, and 6 m), and their interactions. The dependent variable in this model was the mean total number of adults captured at each altitude over one sampling period (= 120 h; $n = 4$ locations). To calculate this dependent variable, all *T. tabaci* were summed for each altitude at each location over the duration of the 5-d, 120-h sampling period. These data were log transformed (Log_{10} (1 + *T. tabaci*)) before analysis.

IYSV Analyses. Percent IYSV-positive *T. tabaci* was calculated for both pole-mounted and UAV-collected *T. tabaci*. Only specimens that yielded RT-PCR product with the *T. tabaci*-specific primers ThMCOI-F/R were taken into account in these analyses. Pole-mounted IYSV-positive thrips samples were analyzed for the effects of year, season, altitude, and the interaction of year and season. Limited degrees of freedom prevented an effective modeling of the full 3-way factorial of the main effects, so the model ($Proportion_{IYSV\text{-}positive\ T.\ tabaci\ per\ trap\ card} \sim year + season + altitude + [year*season]$) was selected using the Bayesian information criterion (Schwartz 1978). Thrips were collected from only the highest and lowest cards for IYSV analysis (none from 2 m), and the *altitude* parameter was created via binary pooling of altitudes either below or above our identified SBL threshold (below: 0.5 and 1 m; above: 4 and 6 m). This precluded analyzing IYSV proportion using the same model or method as *T. tabaci* densities.

Results

***T. tabaci* Dispersal.** All *T. tabaci* adults captured on sticky cards in 2012 and 2013 were females. Numbers of *T. tabaci* adults captured on sticky cards were significantly affected by the main effects of year, season, and altitude, and the interaction of year and season (Table 1). The log-transformed mean number (± SE) of *T. tabaci* adults captured per sticky card over 120 h in 2012 (1.82 ± 0.15) was significantly higher than the number captured in 2013 (1.42 ± 0.1). There also were significantly greater densities of *T. tabaci* on sticky cards sampled during late season compared with mid-season and early season; significantly more thrips were captured during mid-season than early season (Fig. 2).

Table 1. Summary statistics for the main effects and their interactions of a three-way mixed model analysis (α = 0.05) for *T. tabaci* dispersal factors in commercial onion fields in western New York

Effects	df	*F* ratio	Prob > *F*
Year[a]	1, 87	25.8	<.00001
Season[b]	2, 87	105.8	<.00001
Altitude[c]	4, 87	36.2	<.00001
Year × Season	2, 87	66.9	<.00001
Year × Altitude	4, 87	0.2	0.9117
Season × Altitude	8, 87	0.4	0.9380
Year × Season × Altitude	8, 87	0.5	0.8515

[a]2012–2013.
[b]Early (June), middle (late-July), and late (late-August) periods of the onion-growing season of each year in Elba, NY.
[c]Altitude above the onion field surface as an indicator for potential dispersal distance.

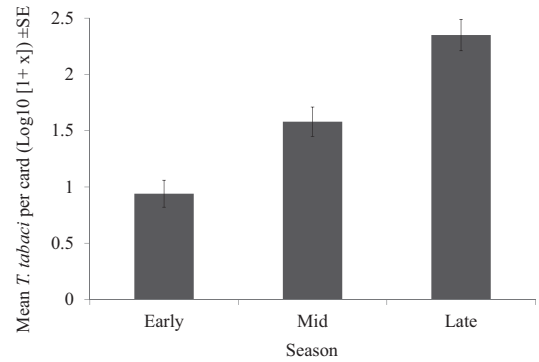

Fig. 2. Seasonal dispersal of *T. tabaci* collected 0.5–6 m above onion fields in the Elba Muck onion-growing region near Elba, NY (2012–2013).

T. tabaci densities on sticky cards at altitudes of 0.5, 1, and 2 m were significantly greater than densities at 4 and 6 m (Fig. 3). Thus, significantly more thrips were captured below the SBL threshold (96%) than above the SBL threshold. These results suggest that most thrips were engaged in short-distance, trivial flight. While thrips trapped on cards may have been either ascending or descending in flight, perhaps not all thrips captured below the SBL threshold were engaged in trivial flight and not all thrips captured above the SBL threshold were engaged in long-distance dispersal. In other words, some thrips captured below the SBL threshold may have eventually breached the SBL threshold had they not been trapped. Similarly, some thrips captured below the SBL threshold may have been arriving from a long distance away.

Densities of *T. tabaci* on sticky cards were significantly affected by an interaction between year and

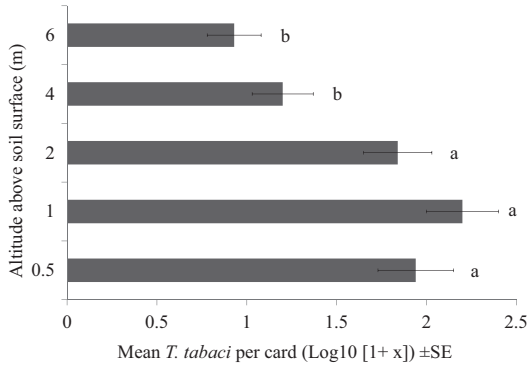

Fig. 3. *T. tabaci* densities at various altitudes above the soil surface in onion crops in the Elba Muck onion-growing region near Elba, NY (2012–2013).

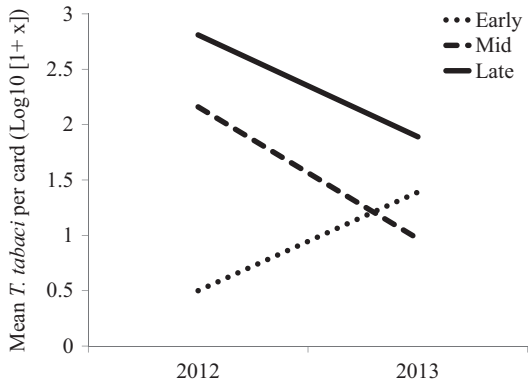

Fig. 4. Interaction of Year and Seasonality on *T. tabaci* dispersal in the Elba Muck onion-growing region near Elba, NY.

season (Fig. 4). Mean densities of *T. tabaci* on sticky cards in early season 2012 were lower than those in early season 2013, whereas mean densities of *T. tabaci* on sticky cards in mid- and late season in 2012 were greater than those in 2013. Differences in temperature during the growing seasons in 2012 and 2013 were likely responsible for these trends. Weather data were obtained from the Northeast Regional Climate Center (2014) and degree-days ($DD_{11.5°C}$) for *T. tabaci* were identified (Edelson and Magaro 1988). There was a higher accumulation of $DD_{11.5°C}$ at the time of "early"-season sampling in 2013 compared with "early" 2012, but $DD_{11.5°C}$ accumulations for "mid-" and "late" season sampling periods were higher in 2012 compared with the same seasons in 2013 (Fig. 5).

Patterns of dispersing *T. tabaci* adults caught on sticky cards and nondispersing *T. tabaci* adults observed on onion plants were similar each year (Fig. 6). These results, coupled with high numbers of thrips engaging in trivial flight, suggest that at the time of sampling, dispersing adult *T. tabaci* likely originated within onion fields, rather than from external sources. The ratio of mean numbers of adult *T. tabaci* captured

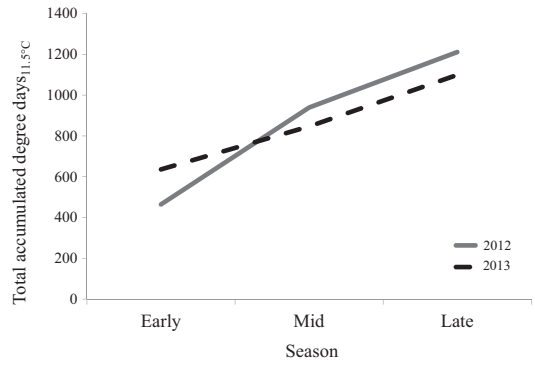

Fig. 5. Cumulative degree $days_{50°C}$ in Elba, NY.

on all pole-mounted traps per day to mean numbers of adult *T. tabaci* per plant per day (i.e., dispersing: non-dispersing) increased from season to season in both 2012 (0.30:1, 1.39:1, and 4.33:1 in early, mid-, and late seasons, respectively) and 2013 (1.55:1, 2.34:1, and 3.61:1 in early, mid-, and late seasons, respectively). These results suggest that there are more *T. tabaci* dispersing as the onion-growing season progresses and that *T. tabaci* are more inclined to disperse later in the season.

Over the course of fourteen 30-min UAV flights in 2012, 303 *T. tabaci* adults were captured (301 females and 2 males), while 22 *T. tabaci* adults (all female) were captured over eighteen 30-min flights in 2013. These results strongly suggest that *T. tabaci* adults engage in long-distance dispersal, and that both sexes engage in this behavior.

***T. tabaci* Carrying IYSV.** The proportion of *T. tabaci* testing positive for IYSV was significantly impacted by the main effect of season, while the main effects of year and altitude, and the interaction year* season were not statistically significant (Table 2). Percentages of IYSV-positive *T. tabaci* increased from early to mid- to late season (Fig. 7). Twenty percent and 15% of *T. tabaci* adults collected from UAV-mounted traps tested positive for IYSV in 2012 and 2013, respectively.

IYSV Confirmation in Thrips by Sequencing. To confirm the nature of the IYSV N-gene elements in *T. tabaci* captured on sticky cards and UAV-mounted traps, 20 randomly selected amplicons obtained by RT-PCR were sequenced. Sequence analysis of a 377-bp fragment of the N-gene from 10 *T. tabaci* captured on sticky cards and 10 *T. tabaci* captured on UAV-mounted traps indicated 99.2–100% identity at the nucleotide level. The IYSV N-gene also showed 100% identity at the nucleotide level with an isolate from onion in New York (GenBank JQ973065.1), and 99% with isolates from onion in Washington State (GenBank JQ973066.1), Idaho (GenBank KF263487.1), Colorado (GenBank KF263484.1), New Mexico (GenBank KF263485.1), and Pennsylvania (GenBank JQ952568). These sequencing efforts confirmed the presence of IYSV N-gene elements in *T. tabaci* captured on sticky cards and UAV-mounted traps.

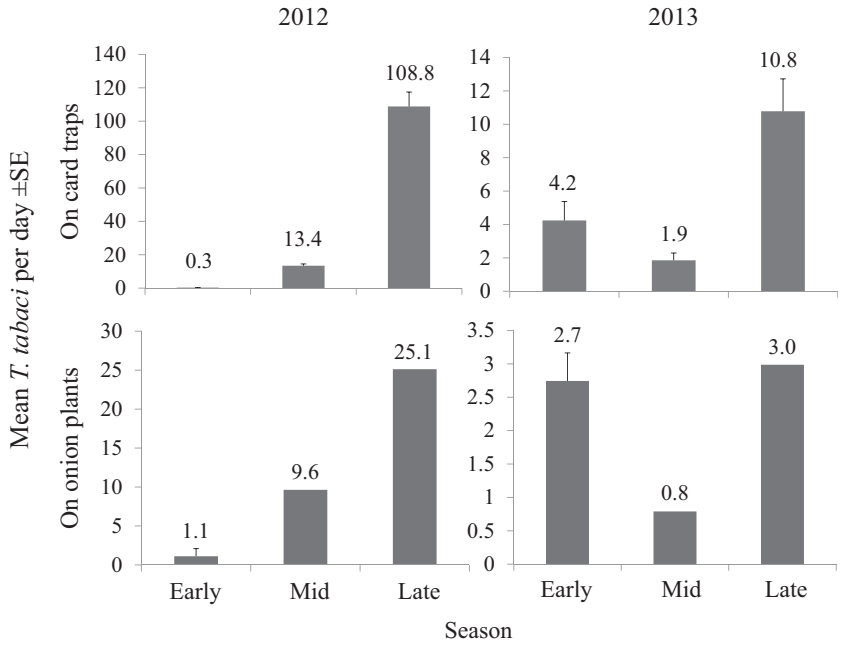

Fig. 6. Mean *T. tabaci* adults per day on sticky card traps (per card) and onion plants (per plant) in commercial onion fields in the Elba Muck onion-growing region near Elba, NY. Note: *y*-axis scales differ.

Table 2. Main effects and interactions of a mixed model analysis ($\alpha = 0.05$) for IYSV incidence in dispersing *T. tabaci* captured on pole-mounted traps (0.5–6 m above soil surface).

Effects	df	*F* ratio	Prob > *F*
Year[a]	1, 148.9	0.02	0.8744
Season[b]	2, 142.3	37.08	<.00001
Altitude[c]	1, 148.3	2.6	0.1116
Year*Season	2, 149	2.2	0.1107

[a]2012–2013.
[b]Early (June), middle (late-July), and late (late-August) periods of the onion-growing season of each year in Elba, NY.
[c]Altitude above the onion field surface as an indicator for potential dispersal distance. Samples were categorized as being either above (4–6 m) or below (0.5–1 m) the SBL threshold (~2 m above soil surface).

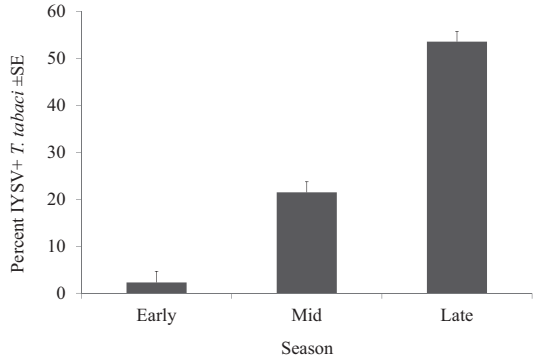

Fig. 7. Seasonal incidence of IYSV in dispersing *T. tabaci* in Elba, NY (≤6 m aloft).

Discussion. *T. tabaci* dispersed in greatest numbers late in the onion-growing season (late August), when adult densities were also highest in onion fields. This phenomenon is likely elicited by a combination of ideal weather conditions, crop maturity, and harvest activities. Onion crops begin to senesce ~2–3 wk prior to harvest. Reductions in host-plant quality have been shown to elicit dispersal in thrips populations (Rhainds and Shipp 2003). Additionally, onion growers often cease using insecticides to manage thrips near harvest because thrips feeding on the senescing foliage is not likely to reduce bulb yield (EAS, personal observation). Rapid thrips population increases combined with an insecticide-free period of up to several weeks may allow *T. tabaci* densities to increase dramatically in an onion field prior to harvest. Exodus flight from dense populations is common among insect pests, and has been recorded in other Thysanopterans (Lewis 1997). All of these factors create ideal conditions for mass *T. tabaci* dispersal events late in the growing season in onion fields, and can explain why we observed an increased propensity for dispersal.

Higher densities of dispersing *T. tabaci* were observed below the SBL threshold, suggesting short-distance (trivial) dispersal. Studies by Shelton et al. (2003, 2006) indirectly support the occurrence of trivial dispersal in *T. tabaci* populations that resulted in localized populations. In their studies, insecticide resistance patterns in *T. tabaci* populations between fields located in proximity and managed in a similar manner by the same onion grower were often very different. Temporal and spatial patterns of IYSV incidence in onion fields also suggest

that *T. tabaci* populations tend to remain relatively localized (du Toit 2004, Gent et al. 2004, Hsu et al. 2010).

T. tabaci adults were observed at altitudes of at least 50–60 m above the soil surface, indicating long-distance dispersal movement. Other thrips species have been recorded at much greater altitudes (Hardy and Milne 1938, Glick 1939, Lewis 1965), and have even been recorded hundreds of kilometers offshore above the Atlantic, Pacific, Indian, and Southern Oceans (Gressit et al. 1960, Holzaptel and Harrel 1968, Yoshimoto et al. 1962), and traversing the Tasman sea from Australia to New Zealand (McLaren et al. 2010). A study by Laughlin (1977) suggests that under hot, dry conditions, *Thrips australis* (Bagnall) individuals could survive in the air for less than a day, while cooler, more humid conditions likely would allow individuals to survive for more than 24 h. If high enough in the atmosphere and with the proper weather conditions, this would allow populations to disperse hundreds of kilometers. Felland et al. (1994) attributed heavy infestations of *Frankliniella tritici* (Fitch) in strawberry crops in Illinois, a state where *F. tritici* does not overwinter (Stannard 1968), to springtime weather systems that carry the pest from southern states. *F. tritici* is also quite common in New York (EAS, personal observation), indicating that weather systems are also carrying these thrips to New York. While *T. tabaci* overwinter in New York (Larentzaki et al. 2007), it is possible that weather systems are also bringing *T. tabaci* from other regions into the state.

Seasonal population dynamics of dispersing *T. tabaci* differed between years. Densities observed on both plants and traps increased predictably during the season in 2012, while densities in 2013 were different. Early-season densities were higher in 2013 than in 2012, but mid-season densities on both plants and traps in 2013 decreased by >50% before rebounding late season. However, it appears that mid-season densities had decreased to a point that prevented late season populations from reaching levels observed in 2012. $DD_{11.5°C}$ at the time of early-season sampling were greater in 2013 than in 2012; however, mid- and late season $DD_{11.5°C}$ were higher in 2012 than in 2013. These discrepancies were reflected in *T. tabaci* densities on traps and in crops in all seasons of this study. In addition to lower accumulated $DD_{11.5°C}$, the Elba Muck region experienced a particularly rainy spring (between early and mid-season sampling periods) in 2013 (EAS, personal observation), which is likely responsible for the decrease in *T. tabaci* densities observed by mid-season 2013. Indeed, heavy rains are known to cause sharp declines in thrips populations (North and Shelton 1986) and negatively impact dispersal (Morsello et al. 2008).

The impact of immediate weather conditions on *T. tabaci* dispersal behaviors is not known. Lewis (1964) observed that several species of thrips prefer to fly when it is "sunny, settled weather with slight convection and a maximum temperature of at least 20°C"; however, the weather conditions under which *T. tabaci* tend to disperse are not known.

In both years of this study, early season detection of IYSV in *T. tabaci* adults was much lower (between 2 and 3% of captured *T. tabaci*) than later in the season (more than 20 times greater). Hsu et al. (2011) observed similar increasing trends in IYSV incidence through the season in onion crops. Localized populations of viruliferous *T. tabaci* likely dispersed within onion fields, as well as from early-maturing onion crops that senesced into adjacent late-maturing crops, thereby increasing the proportion of infected plants in these late-maturing fields. Late-season immigration of viruliferous *T. tabaci* from other onion-growing regions also may contribute to IYSV incidence late in the season. Investigating the patterns of *T. tabaci* emigration and immigration between specific onion fields late in the growing season will allow us to better understand the effect of *T. tabaci* dispersal on IYSV epidemiology in onion crops. Additionally, potential dispersal of *T. tabaci* from other crop and noncrop hosts into onion fields during the season is not known. Knowledge of such seasonal dispersal patterns could inform the development of management strategies for *T. tabaci* and IYSV in onion.

The proportions of IYSV-positive *T. tabaci* collected from traps on UAVs late in the season were much lower than those collected from pole-mounted sticky cards late in the season. While collection methods differed, we do not think that this alone would explain the differences in IYSV detection. Perhaps, viruliferous *T. tabaci* may behave differently from those that are not, and may be less inclined to fly at altitudes or in conditions that would lead to their breaching the SBL threshold and being carried aloft. While *altitude* was not a significant effect for viruliferous individuals collected on pole-mounted traps, perhaps 6 m was not high enough to detect this difference. Alternatively, it's possible that a relatively higher proportion of *T. tabaci* collected on UAV traps may have originated from hosts not infected with IYSV, outside the muck region.

While many *T. tabaci* in our study tested positive for IYSV, it is not known what proportion were capable of transmitting the virus and what proportion had just fed on an IYSV-infected host (i.e., gut contents included infected host material, but no virus in the salivary glands). Our testing for IYSV targeted the N gene rather than the NSs gene, which can be used as an indicator of IYSV transmissibility (Bag et al. 2010). Bag et al. (2014) observed that the proportion of *T. tabaci* testing positive for IYSV that are actually transmitters can vary throughout the season; however, all IYSV-positive populations yielded a proportion of individuals capable of transmission (~5–75%). It is reasonable to expect similar percentages of *T. tabaci* capable of IYSV transmission in our study.

While *T. tabaci* show a clear tendency toward trivial dispersal and that plant to plant and field to field movement may be important in developing management strategies, many thrips breach the SBL threshold and potentially travel long distances. Thus, it is almost certain that some *T. tabaci* in New York onion fields originated a long distance away, possibly from other onion-producing regions, and it will be important for

future research to focus on the impact and significance of long-distance dispersal to crops. Considering parthenogenesis is *T. tabaci*'s primary reproductive strategy (Lewis 1997), long-distance dispersal of thrips has implications for refining insecticide resistance management and IYSV-management strategies. Resistant individuals may spread across great distances over a short period, imparting resistant alleles that may persist in regions where they have settled. Epidemiological implications for *T. tabaci*-transmitted crop pathogens are more complex. Tospoviruses are not known to be transovarially transmissible (Wijkamp et al. 1996) and IYSV acquisition and transmission rates are highly varied in *T. tabaci* (Inoue et al. 2010). Thus, the effect of *T. tabaci* dispersal on IYSV epidemiology may be relatively variable through the onion-growing season. Long-distance dispersal may contribute to IYSV introduction in an onion crop, but the predominance of trivial dispersal by *T. tabaci* during the onion-growing season is likely facilitating IYSV outbreaks among fields within contiguous growing regions.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Acknowledgments

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