Temporal Dynamics of Iris Yellow Spot Virus and Its Vector, *Thrips tabaci* (Thysanoptera: Thripidae), in Seeded and Transplanted Onion Fields

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ABSTRACT Onion thrips, *Thrips tabaci* (Lindeman) (Thysanoptera: Thripidae), can reduce onion bulb yield and transmit iris yellow spot virus (IYSV) (Bunyaviridae: Tospovirus), which can cause additional yield losses. In New York, onions are planted using seeds and imported transplants. IYSV is not seed transmitted, but infected transplants have been found in other U.S. states. Transplants are also larger than seeded onions early in the season, and thrips, some of which may be viruliferous, may preferentially colonize larger plants. Limited information is available on the temporal dynamics of IYSV and its vector in onion fields. In 2007 and 2008, *T. tabaci* and IYSV levels were monitored in six seeded and six transplanted fields. We found significantly more thrips in transplanted fields early in the season, but by the end of the season seeded fields had higher levels of IYSV. The percentage of sample sites with IYSV-infected plants remained low (<12%) until August, when infection levels increased dramatically in some fields. The densities of adult and larval thrips in August and September were better predictors of final IYSV levels than early season thrips densities. For 2007 and 2008, the time onions were harvested may have been more important in determining IYSV levels than whether the onions were seeded or transplanted. Viruliferous thrips emigrating from harvested onion fields into nonharvested ones may be increasing the primary spread of IYSV in late-harvested onions. Managing *T. tabaci* populations before harvest, and manipulating the spatial arrangement of fields based on harvest date could mitigate the spread of IYSV.

KEY WORDS *Thrips tabaci*, Tospovirus, epidemiology, management, *Allium cepa*

Onion thrips, *Thrips tabaci* (Lindeman) (Thysanoptera: Thripidae), is a major pest of dry bulb onion, *Allium cepa* (L.), in New York. Larvae and adults feed directly on leaves damaging plant tissue and reducing photosynthesis, resulting in smaller bulbs and lower marketable yields. In New York, severe thrips damage can reduce bulb yield by 33% or more (Nault and Shelton 2008).

T. tabaci has become an even greater concern to onion growers across the U.S. because of their ability to transmit an invasive tospovirus, iris yellow spot virus (IYSV) (Bunyaviridae: Tospovirus). Thrips are the only vectors of tospoviruses, and *T. tabaci* is the only known vector of IYSV (Cortês et al. 1998, Nagata et al. 1999a, Pozzer et al. 1999, Kritzman et al. 2001). IYSV is not transmitted through onion seeds (Kritzman et al. 2001, Robène-Soustrade et al. 2006). Thrips that develop on plants infected with a tospovirus can acquire the virus in their early larval stages (Jones 2005, Whitfield et al. 2005), and acquisition rates decrease as larvae mature (Nagata et al. 1999b, van de Wetering et al. 1999, Chatzivassiliou et al. 2002). Once acquired, tospoviruses propagate in their vector and are persistently transmitted, and viruliferous thrips are capable of spreading the virus for the rest of their lives (Ullman 2002, Jones 2005, Whitfield et al. 2005). Aviruliferous thrips cannot acquire a tospovirus as adults (Jones 2005, Whitfield et al. 2005).

IYSV was first detected in the U.S. in Idaho in 1989 (Hall et al. 1993). Since 2000, IYSV has been confirmed in most onion production areas in the United States (Hall et al. 1993, Schwartz et al. 2002, Abad et al. 2003, Moyer et al. 2003, Creamer et al. 2004, du Toit et al. 2004a, Mullis et al. 2004, Crowe and Pappu 2005, Miller et al. 2006, Pappu and Matheron 2008) and provinces in Canada (Hoepting et al. 2008). In New York, IYSV was first detected in 2006 (Hoepting et al. 2007). A survey of onion fields in western New York in late 2006 found IYSV-infected plants in 37 of 41 fields (Fuchs et al. 2007). In 2007, a more extensive survey found IYSV-infected plants in every major onion growing region in

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New York (Nault et al. 2008a). IYSV can cause significant yield losses and grade reductions in onion bulb and seed crops (Pozzer et al. 1999; Gent et al. 2004a, 2004b; du Toit et al. 2004b; Gent et al. 2006; Poole et al. 2007; Shock et al. 2008). The potential impact of IYSV on New York's onion industry is unclear and may depend on how early and quickly the virus spreads within a field.

Dry bulb onions in New York are planted in April and May and bulbs are harvested in the late summer and fall; no onions are grown over the winter in New York. Approximately 85% of the onion crop is grown from seed and 15% is grown from transplanted onions, most of which are imported from Arizona. In Colorado, between 0.4–5% of onion transplant seedling lots imported from Arizona and California had symptoms of IYSV, and 18–91% of the seedling lots sampled were infested with *T. tabaci* (Gent et al. 2006). At the start of our study, the role of transplants as a potential source of IYSV in New York was not known. Imported transplant onions could be infected with IYSV when they arrive or they could harbor viruliferous thrips. Thus, IYSV might be detected in transplanted fields earlier in the season than in fields grown from seed.

In addition, onion plants started from transplants are usually farther ahead in development than plants started from seed. Transplanted onions are generally larger in size than seeded onions, and this size difference is most evident early in the season. The larger plants in transplanted onion fields may be preferentially colonized by early season *T. tabaci*. There are a number of early season plants in New York's onion system that could serve as inoculum sources for IYSV. In 2007 and 2008, IYSV-infected volunteer onion plants were found in the spring in onion fields and onion cull piles in New York (Nault et al. 2008b). Many weeds in New York and in other states have also been confirmed as host plants for IYSV (Gent et al. 2006; Fuchs et al. 2007; Nischwitz et al. 2007; Sampangi et al. 2007; Nault et al. 2008b; Schwartz et al. 2008b; Evans et al. 2009a, 2009b). Schwartz et al. (2008b) demonstrated that *T. tabaci* that developed on IYSV-infected weeds and became viruliferous could transmit IYSV to uninfected onion seedlings. Preferential colonization of the larger plants in transplanted fields by early season thrips, some of which may be viruliferous, might also increase the risk of transplanted onions becoming infected sooner than seeded onions.

Although IYSV might be detected sooner in transplanted onion fields, transplanted onion fields may be at lower risk of yield losses from IYSV. While seeded and transplanted onions are planted simultaneously in New York, most transplanted fields are harvested before seeded ones, and transplanted fields may be harvested before the virus spreads through the field and/or before symptoms affect bulb development. Schwartz et al. (2004) suggested that the incubation period from infection by IYSV to symptom expression might be 30 d or longer. Seeded fields may be at a greater risk of yield loss because plants started from seeds are in the fields longer allowing more time for symptoms to develop. In addition, seeded fields might be at higher risk for higher infection levels at the end of the season if viruliferous adult *T. tabaci* emigrating from senescing plants in harvested fields colonize and spread the virus in fields that are still green and growing.

The purpose of this project was to compare thrips populations and IYSV infection levels in seeded and transplanted onion fields in New York. Specific objectives were to: (1) identify differences in colonization by comparing *T. tabaci* densities in seeded and transplanted onions early in the season; (2) document the spread of IYSV by monitoring IYSV levels over time in seeded and transplanted onion fields; (3) test whether IYSV levels at the end of the season were higher in seeded or transplanted fields; and, (4) determine whether *T. tabaci* densities could be used to predict IYSV levels at the end of the season.

Methods and Materials

Onion Fields and Sampling Strategy. Commercial onion fields located in western New York were used. Seeded and transplanted onion fields of the same variety were blocked in pairs that were managed by the same grower to minimize variation because of pest management practices, except one pair in 2008, which was managed by two separate growers. Pairs of fields were within close proximity to each other. Six pairs of fields were sampled in each year. Fields ranged between 60–80 m wide and each field was separated into six transects. Distances between transects varied depending on the width of the field. Within each transect, 8–10 sample locations were used, spaced ≈23–34 m apart depending on the length of the field. This divided each field into a grid with 50–60 sections per field. Sample grid sections were held constant within each field for each sample date, while the exact sample location varied within the grid between sample dates.

In 2007, a pair of seeded and transplanted fields representing each of six varieties (days to maturity) was used: 'Highlander' (88), 'Sherman' (95), 'Milestone' (106), 'Santana' (115), 'Red Bull' (118), and 'Sedona' (118). The Highlander, Sherman, Santana, and Sedona fields were located in the Elba Muck in Orleans County, and the Milestone and Red Bull fields were located in the Linwood Muck in Genesee County. Thrips counts were made every 2 wk from 11 June through 4 September (seven sample dates). Plant samples for IYSV analyses were taken every 2 wk from 9 July through 4 September (five sample dates).

In 2008, all 12 fields were located in the Elba Muck. There were two pairs of Milestone and Red Bull fields, and one pair each of Sedona and 'Red Zeppelin' (115 d to maturity) fields. Thrips counts were taken every 2 wk from 9 June to 20 August 2008, and then weekly from 20 August to 5 September 2008 (eight sample dates). Plant samples for IYSV analyses were taken every 2 wk from 9 June through 4 August, and then weekly from 4 August to 5 September (nine sample dates).

All fields were sampled twice for *T. tabaci* before insecticide spray programs were initiated. Foliar applications of registered insecticides (Reiners and Petzoldt 2009) were then used multiple times during the season to manage thrips populations. Despite the use of insecticides in the fields sampled, thrips were prevalent all season long in both years.

Plant and Thrips Samples. At each sample site, one plant was pulled and all larval and adult thrips on the plant were counted and recorded separately. In New York, *T. tabaci* is by far the dominant species on onions, precluding the need to differentiate among other species during sampling (Gangloff 1999). To test for IYSV, an additional four plants were pulled within a 4 m radius of the first plant and the five plants were combined. Plants were selected arbitrarily, not based on the presence or absence of symptoms. Depending on the number of sample sites in the field, 250–300 plants per field were removed from the field on each sample date for analysis. All plants were maintained in a cold storage facility (7.2°C) until analysis. In the last 2 wk of the season, we did not count thrips on plants after the bulbs were undercut and lifted because this practice dislodges thrips from the plants. However, we were able to collect plant material for IYSV analyses in some of those fields.

Testing for IYSV. A double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) was used to determine whether a plant was infected with IYSV. A standard protocol, commercially available antibodies, and positive and negative controls for IYSV in onions were used based on the manufacturer's recommendations (Agdia Inc., Elkhard, IN). All samples and controls were tested in duplicate wells and the mean of the two readings was used for analysis.

Plants from each site were analyzed as a 5-plant composite sample. In 2007, a thin lateral slice of leaf tissue from the middle section of each plant leaf was used. In 2008, based on preliminary studies showing that newer leaves were more likely to react positively for IYSV using DAS-ELISA than older leaves (C.L.H., unpublished data), the outermost four leaves of each plant were removed and a thin lateral slice of leaf tissue from the middle section of only the central leaves (=youngest leaves) was used. This sampling method is conservative because IYSV does not appear to be detectable in all leaves of *Allium* spp. using DAS-ELISA (Gent et al. 2006, Smith et al. 2006). The spatial heterogeneity of IYSV in onion plants means there is a potential for false negative results resulting in an underestimate of virus incidence.

Plant tissue samples were 1 g and were ground 1:10 (wt:vol) in general extraction buffer (Agdia Inc.). Reactions were stopped after 20 min using 3.0 N sodium hydroxide (NaOH). Optical density (OD) readings were taken at 405 nm using an MRX Microplate Absorbance Reader and Revelation software (DYNEX Technologies, Chantilly, VA).

Sample data were separated into two populations to determine whether a sample was considered positive for IYSV. First, the mean OD reading for the negative controls for each plate was subtracted from the mean OD readings for each sample on the plate to control for any variation between plates. The resulting data were transformed using ln ([sample * 1000] + 100). The distribution of transformed samples was separated into negative and positive populations using "normalmixEM" (R Project 2008), an expectation-maximization (EM) algorithm for mixtures of univariate normal distributions that separates data into two populations (McLachlan and Peel 2000). The population with the lower mean OD reading was considered the negative population. A threshold, *t*, was calculated using the estimated mean of the negative population (0 = 4.721) plus four times the estimated standard deviation of the negative population (SD = 0.207). If a Gaussian distribution is an appropriate assumption, this threshold, $t = 5.549$, would capture 99.99% of the negative data, minimizing the probability that a negative sample would be incorrectly classified as positive for the virus. Samples with a ln-transformed value greater than $t = 5.549$ were classified as positive for IYSV. The estimated mean for the negative population calculated using "normalmixEM" was robust to changes in the mean and/or standard deviation of the positive population. Data are presented in terms of the percentage of sites with plants that reacted positively for IYSV within each field over time.

Statistical Analyses. All statistical analyses were done using PROC MIXED (SAS Institute 2002) unless noted otherwise. Variety was used as the random factor and was not included in the model statements. The denominator degrees of freedom were calculated using Kenward-Roger methods (Kenward and Roger 1997). The proportion of sites with IYSV-infected plants in each field was transformed using a logit transformation, ln ([proportion positive + c] / [1 - proportion positive + c]), where $c = 0.001$, and thrips counts were transformed using ln (thrips count + 0.001) before regression analyses. Nonsignificant interaction terms were dropped during model development. Nonsignificant main effect terms were included if including those terms resulted in a final model with a lower residual variance compared with models that excluded those terms.

The following designations of thrips densities were used in the analyses: cumulative number of thrips larvae and adults counted over the season, larval densities early in the season, adult densities early in the season, larval densities late in the season, and adult densities late in the season. To standardize cumulative thrips densities for comparisons, total larval and adult thrips counts per field were divided by the number of sites and the number of thrips sample dates for each field. Early thrips densities were calculated as the total number of thrips larvae or adults counted per field on the first two sample dates, before any pesticide applications were made in any of the fields. Field totals were standardized by dividing by the number of sites per field and the number of thrips sample dates. Late thrips densities were calculated as the total number of larval or adult thrips counted per field between 6 August and 4 September 2007, and between 4 August

and 5 September 2008, and field totals were standardized by dividing by the number of sites and the number of thrips sample dates for each field. In regressions using late densities of larvae and adults, the Highlander variety was harvested before 6 August 2007, so no late thrips data were collected. Consequently, the Highlander pair of fields was excluded from some analyses and N was adjusted accordingly.

There was a potential for the four thrips categories, larval and adult densities early and late in the season, to be correlated. An analysis was done using PROC REG (SAS Institute 2002) to test for collinearity between these four categories with final levels of IYSV as the response variable. Results showed that none of the four categories had a variance inflation factor >10 or a condition index >10. We concluded that collinearity would not be a significant problem for regressions that included all four thrips categories.

Thrips Densities in Seeded and Transplanted Fields. Larval and adult thrips densities over time in seeded and transplanted fields were compared graphically. Relative proportions of larvae and adults were calculated over time and compared between 2007 and 2008.

Differences in *larval* and *adult thrips densities* between seeded and transplanted fields early in the season and late in the season were analyzed using regression models that included *year*, *Julian date* of the last thrips sample before harvest, *field type* (seeded or transplanted) and the two-way interaction between *field type* and *year* as predictors.

For the 2008 data only, increases in thrips populations over time were further analyzed using PROC REG (SAS Institute 2002), with *Julian date* of each thrips sample as the predictor and *thrips densities* on that date as the response. An exponential growth model was used and thrips counts were ln-transformed to create a linear model. The season was divided into two periods, June/July, consisting of the four sample dates between 9 June and 21 July, and August/September, consisting of the remaining sample dates between 4 August and 5 September. Thrips were divided into two categories, larvae or adults. Mean slopes were calculated as estimates of growth rates, and 95% confidence intervals for slopes were calculated for each regression.

IYSV Levels Over Time. The proportion of sites testing positive for IYSV over time in each field was compared graphically between field types and years. The first date IYSV was detected in each field was recorded.

Effects of Thrips Densities and Field Type on IYSV Levels. To determine whether the proportion of sites with IYSV-infected plants was higher in seeded or transplanted fields, and whether thrips densities were a significant predictor for final IYSV levels, only sample dates for which both IYSV and thrips data were available were used. The regression model response, *IYSV level*, was the proportion of sites that had plants that reacted positively for IYSV on the last sample date in which thrips data existed.

The first analysis used *cumulative larval thrips densities*, *cumulative adult thrips densities*, *year*, *Julian date* of the last thrips sample, and *field type* as main effects, and included all of the two-way interaction terms involving *field type* and *year*. Subsequent analyses used the four categories of thrips, *early* and *late larval thrips densities*, and *early* and *late adult thrips densities*, instead of cumulative thrips densities, to identify which categories were significant in predicting final *IYSV levels*. These analyses used all four thrips categories, *year*, *Julian date* of the last thrips sample, and *field type* as the main effects, and included all of the two-way interaction terms involving *field type*, and the two-way interaction terms between *year* and the four *thrips categories*.

Relative Importance of Thrips Categories in Predicting IYSV. Model subsets were used to compare the relative importance of the four thrips categories, *early* and *late larval* and *adult densities*. The base model included *Julian date* of the last thrips sample before harvest and *field type*. Data from each year were analyzed separately. The unexplained residual variance resulting from this base model was then compared against a base model plus one of the four thrips categories. Each thrips category was analyzed separately. The relative importance of each thrips category was ranked based on the amount of residual variance that category explained above the base model. To allow equitable comparisons between early and late thrips populations in 2007, the Highlander fields were excluded from the data set used in both regressions.

Results

Thrips Densities Over Time. Thrips densities increased over the course of the season in both years even though fields were receiving insecticide sprays throughout the season (Fig. 1). Peaks in mean larval densities per plant occurred in mid July and late August. Mean larval and adult densities were higher in transplanted fields early in the season and higher in seeded fields later in the season. Larval densities in many of the fields exceeded 10 larvae per plant between 20 August and 5 September in both years. Adult thrips densities remained low for most fields in 2007, but in 2008 adult densities in 11 out of 15 samples exceeded 10 adults per plant between 20 August and 5 September. There was more variation in both larval and adult densities between fields in August and September 2007 compared with the levels of variation in thrips densities between fields in August and September 2008.

The proportion of larvae to adults over time showed two distinct peaks in relative densities of adults, one in mid to late June and a second peak in August (Fig. 2). The proportion of adults increased to >50% by the end of the season in 2008, but not in 2007.

Early Season Thrips Densities. Transplanted fields had more thrips early in the season compared with seeded fields (Fig. 1). The difference was significant for *early larvae* (Fig. 3) (*field type:* $N = 24$; $F = 5.62$; df = 1, 18.1; $P = 0.029$) and marginally significant for

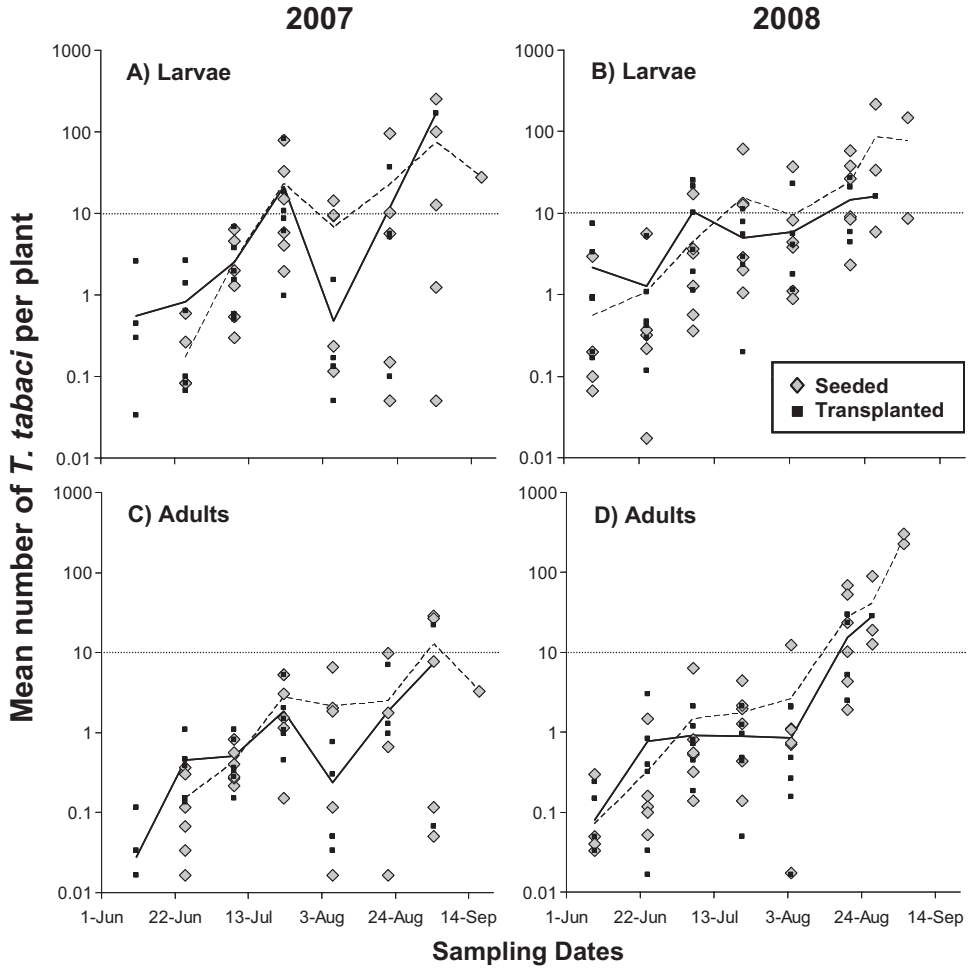

Fig. 1. Density of *T. tabaci* larvae (A and B) and adults (C and D) in 12 onion fields in 2007 and 2008. Dashed line, mean densities in seeded fields; solid line, mean densities in transplanted fields.

early adults (Fig. 3) (*field type:* $N = 24$; $F = 4.28$; df = 1, 15.8; $P = 0.055$).

There were no significant interactions between *field type* and *year*, and *year* was not significant in either analysis so data from both years were analyzed together in both analyses. The model with the lowest residual variance for *early larvae* included *year*, *Julian date*, and *field type*, though *Julian date* was not significant (Table 1). The model with the lowest residual variance for *early adults* included only *field type* (Table 1).

Late Season Thrips Densities. Fields harvested later in the season had higher mean densities of thrips than earlier harvested fields (Fig. 1). *Year* was significant in regressions using both *late larvae* and *late adults* as the response variables; there were significantly more late larvae in 2007 compared with 2008 (Fig. 4) (*year:* $N = 22$; $F = 6.00$; df = 1, 16.1; $P = 0.026$), and significantly more late adults in 2008 than in 2007 (Fig. 4) (*year:* $N = 22$; $F = 30.42$; df = 1, 14.6; $P < 0.001$). Consequently, each thrips category was analyzed separately by year. There was no significant interaction between *field type* and *year*.

For *late larval thrips* there were significant positive relationships between thrips densities and *Julian date* of the last thrips sample, samples taken later in the season had significantly higher larval populations in both years (2007, *Julian date:* $N = 10$; $F = 24.37$; df = 1, 4.04; $P = 0.008$; 2008, *Julian date:* $N = 12$; $F = 8.37$; df = 1, 10; $P = 0.016$). *Field type* was not significant in either year. The models with the lowest residual variance for *late larvae* in both 2007 and 2008 included only *Julian date* (Table 1).

For *late adult thrips densities* in 2007, neither *Julian date* nor *field type* was a significant predictor. In 2008, *Julian date* was significant and, similar to 2008 *late larvae*, the relationship between *Julian date* and *late adult thrips densities* was positive (Table 1) (2008, *Julian date:* $N = 12$; $F = 9.69$; df = 1, 7.6; $P = 0.015$). *Field type* was not significant in 2008, though the model with the lowest residual variance for *late adults* in 2008 included *Julian date* and *field type* (Table 1).

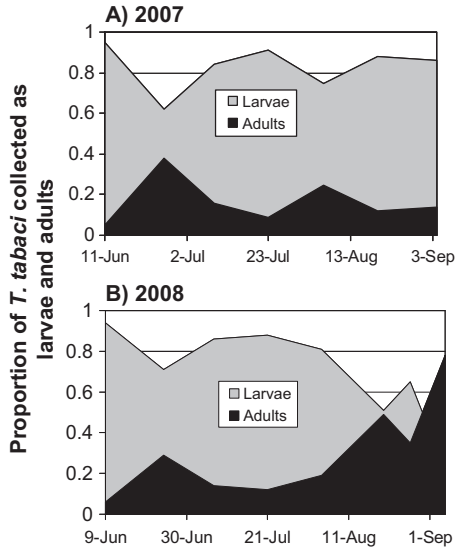

Fig. 2. Relative proportions of larvae to adult *T. tabaci* in onion fields over time in 2007 (A) and 2008 (B).

Thrips Population Growth Rates. The growth rates for adult thrips populations were higher than the growth rates for larvae in both time periods (Table 2). The highest mean rate of increase was for adults in the August/September period. The 95% confidence interval for the population growth rate for adults in the August/September period had minimal overlap with growth rates for larvae in June/July, larvae in August/September and adults in June/July. All four regressions using *June/July larvae* and *adults*, and *August/September larvae* and *adults* were significant, though the exponential growth models provided a better fit for *adults* than for *larvae* (Table 2).

IYSV Levels Over Time. IYSV was detected first in seeded fields in 2007 (9 July) using DAS-ELISA. In 2008, IYSV was detected in both field types at the same time and a month earlier than in 2007 (9 June) (Fig. 5). There was no clear pattern suggesting that IYSV was more likely to be detected earlier or spread faster in one or the other field type, even though transplanted fields had significantly more thrips early in the season.

Table 1. Final models and parameter estimates for six separate mixed model regression analyses testing the significance of year, Julian date of the last sample before harvest and field type on densities of *T. tabaci*

Response variable	Intercept	Year	Julian date	Field type[a]
Early larvae[b]	−2223.03	1.1145	−0.0648	−1.8639
Early adults[b]	−1.8338	N/A	N/A	−0.9640
Late larvae 2007[c]	−32.0239	N/A	0.1366	N/A
Late larvae 2008[c]	−45.6012	N/A	0.2021	N/A
Late adults 2007[c]	N/A	N/A	N/A	N/A
Late adults 2008[c]	−44.0549	N/A	0.1947	0.9048

[a] The default field type was seeded. A negative value means thrips densities were lower in seeded fields compared with transplanted fields, a positive value means thrips densities were higher in seeded fields.
[b] Early larvae and adults are the total no. thrips counted per field on the first two sample dates divided by the no. of sites per field.
[c] Late larvae and adults are the total no. thrips counted per field between 4 Aug. and 5 Sept. 2008, divided by the no. of sites and the no. thrips sample dates for that field.
N/A, the term was not included in the final model.

IYSV levels were low for the beginning of both years before increasing substantially in some fields during August (Fig. 5). In 2007, only three fields had sites that tested positive for IYSV before 6 August, and <2% of the sites tested positive in each field. On 6 August, IYSV was detected in five of the 12 fields. Only one field had high levels of IYSV by the end of the season (91.7% of the sites in the seeded Sherman field had IYSV-infected plants). In the seeded Highlander field, we did not find IYSV in any of the sites throughout the sampling period.

In 2008, we found IYSV in four fields on the very first sample date, 9 June; two were seeded fields and two were transplanted fields. The percentage of sites with IYSV-infected plants remained low (<12%) in all 12 fields until the last sample date in July. After 21 July, IYSV levels increased until nine of the 12 fields had IYSV-infected plants in 20% or more of the sites sampled. The lowest consistent IYSV levels were in three of the Milestone fields, which had IYSV-infected plants in only 0–8.3% of the sites in each field. The

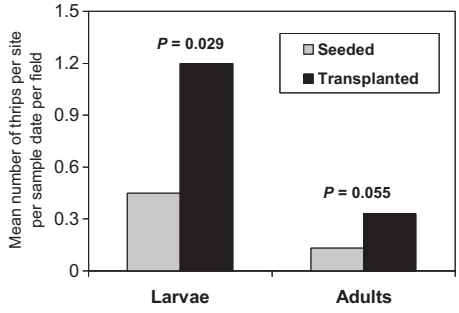

Fig. 3. Mean number of *T. tabaci* larvae and adults found in seeded and transplanted onion fields early in the season (during the first two sample dates in June).

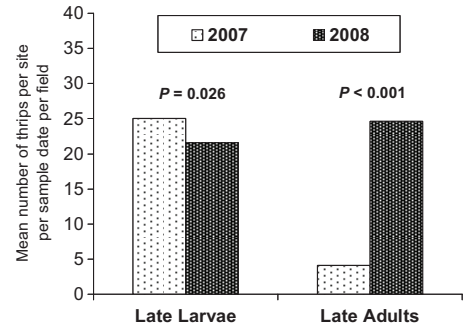

Fig. 4. Mean number of *T. tabaci* larvae and adults found late in the season (during August and September) in 2007 and 2008.

Table 2. Results from four separate linear regression analyses estimating the rate of increase (slope estimate) in *T. tabaci* larval and adult populations over time in 2008

Time[a]	Thrips	N[b]	Slope estimate	95% confidence interval	t	P	R^2
June/July	Larvae	54	0.096	(0.049, 0.144)	4.06	0.002	0.241
Aug./Sept.	Larvae	32	0.113	(0.026, 0.199)	2.66	0.012	0.191
June/July	Adults	54	0.116	(0.070, 0.162)	5.07	<0.001	0.331
Aug./Sept.	Adults	32	0.187	(0.137, 0.238)	7.56	<0.001	0.656

[a] The growing season was split into two periods: June/July, consisting of thrips samples taken between 9 June and 21 July, and Aug./Sept., consisting of thrips samples taken between 4 Aug. and 5 Sept.
[b] *N*, total no. samples taken in the sample period (no. fields × no. sample dates).

highest levels of IYSV were found in a transplanted Red Bull field; 96.7% of the sites had IYSV-infected plants on the last sampling date before harvest.

In general, IYSV-infected plants were asymptomatic in June. The first plants with IYSV-symptoms were found in early July in both 2007 and 2008 and were found in transplanted fields (C.A.H., unpublished data). Symptomatic plants were not very common in either field type until late July/early August (C.L.H., unpublished data).

Effects of Thrips Densities and Field Type on IYSV. *Cumulative adult thrips* were a significant predictor of final *IYSV levels*, the greater the density of adult thrips the higher the percentage of sites testing positive for IYSV on the last sample date (*cumulative adults:* $N = 24; F = 27.13; \mathrm{df} = 1, 18.9; P < 0.001$). *Cumulative larval*

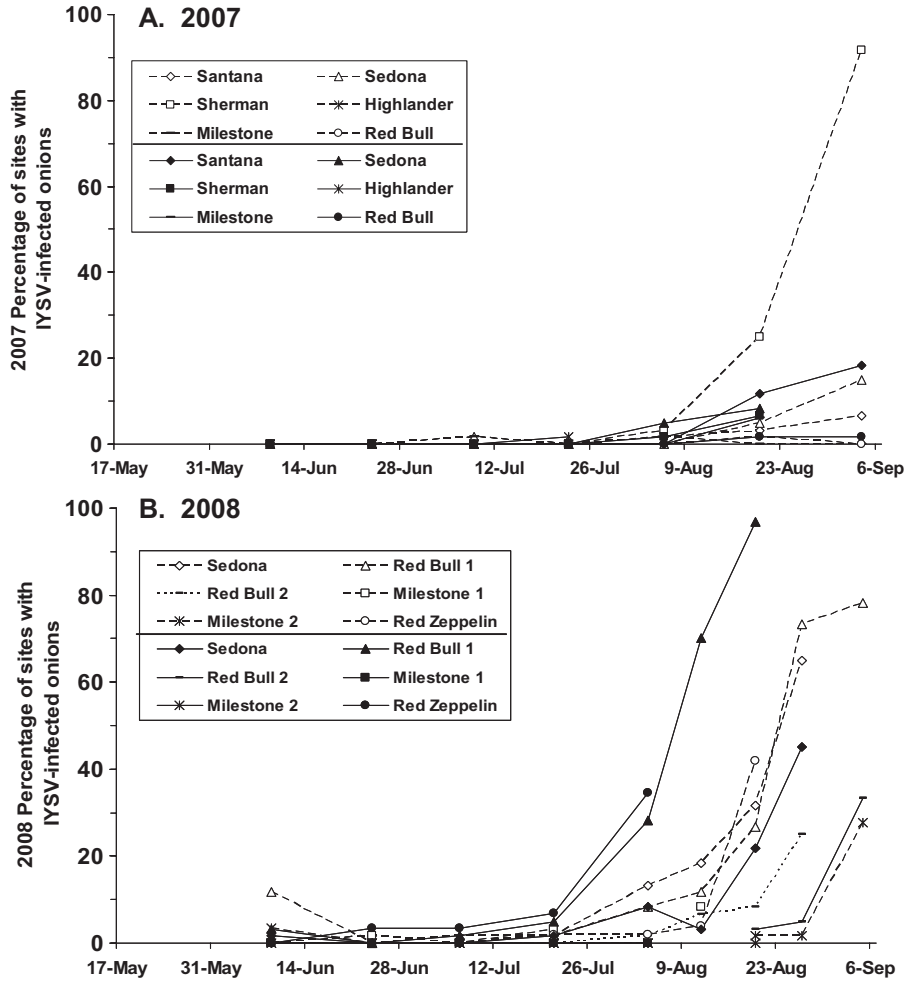

Fig. 5. Percentage of sites with IYSV-infected onions in 12 commercial fields in New York monitored in 2007 (A) and 2008 (B). Open symbols and dashed lines, seeded fields; closed symbols and solid lines, transplanted fields.

Table 3. Results of a mixed model regression testing the significance of Julian date of the last sample before harvest, field type, and early and late larval and adult densities of *T. tabaci* on final IYSV levels in 12 commercial onion fields

Independent variable	Regression ($N = 12$)			Parameter estimate
	df[a]	F	P	
Julian date[b]	1, 1	47,721	0.0029	0.2519
Field type[c]	1, 1	247	0.0405	2.6260
Early larvae[d]	1, 1	842,464	0.0007	3.2590
Early adults[d]	1, 1	7,654	0.0073	0.6216
Late larvae[e]	1, 1	4,291	0.0097	−1.0305
Late adults[e]	1, 1	188	0.0463	1.2063
Early larvae × Field type	1, 1	12,089	0.0058	−2.8962
Late adults × Field type	1, 1	573	0.0266	−1.1412

[a] Degrees of freedom are calculated using methods proposed by Kenward and Roger (1997).

[b] Julian date is the last date a thrips sample was collected from a field.

[c] Field type is either a seeded or a transplanted field. The default field type was seeded. A negative value means IYSV levels were lower in seeded fields compared with transplanted fields, a positive value means IYSV levels were higher in seeded fields.

[d] Early larvae and adults are the total no. thrips counted per field on the first two sample dates divided by the no. sites per field.

[e] Late larvae and adults are the total no. thrips counted per field between 4 Aug. and 5 Sept. 2008, divided by the no. sites and the no. thrips sample dates for that field.

densities, and *year*, *Julian date*, and *field type* were not significant predictors of final *IYSV levels.* The model with the lowest residual variance included *field type* and *cumulative adults*, though *field type* was not significant [*IYSV level* = −2.6422(intercept) − 1.0233(*field type* = *seeded*) + 1.2627(*cumulative adults*)].

Results of analyses including the four separate categories of thrips densities simultaneously were more complicated. There were significant interactions between *year* and *early larval densities*, between *year* and *late larval densities*, and between *year* and *adult densities*, so data from each year were analyzed separately.

For 2007, there were no significant interaction terms. There was a significant positive relationship between *late adult thrips densities* and final *IYSV levels;* higher late adult densities resulted in higher IYSV levels (*late adults:* $N = 10$; $F = 13.42$; df = 1, 6.0; $P = 0.011$). All other terms, *Julian date*, *field type*, and *early larval, early adult* and *late larval densities*, were not significant. The model with the lowest residual variance included *field type*, *early larval density*, and *late adult density*, though *field type* and *early larval density* were not significant [*IYSV level* = −2.6254(*intercept*) − 2.2038(*field type* = *seeded*) − 0.4074(*early larvae*) + 0.8809(*late adults*)].

For 2008, there were significant interactions between *field type* and *early larval densities*, and between *field type* and *late adult densities*, and all main effects in the model were significant (Table 3). It was not possible to analyze the data separately by field type when the model included all four thrips categories. Regression results shown are for the model that included both significant interactions.

For *early larvae* and *late adult T. tabaci*, there was a stronger positive relationship between thrips densities and final *IYSV levels* in transplanted fields than in seeded fields; the higher the density of early larvae or late adults, the higher the final level of IYSV in transplanted fields. For seeded fields, the relationships were also positive but weaker with significantly shallower slopes.

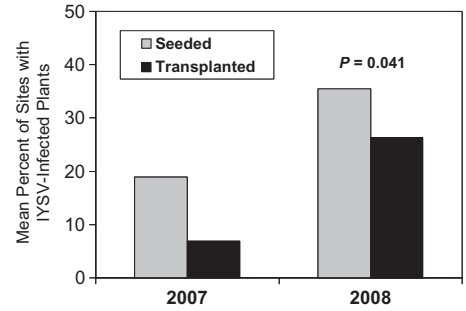

Fig. 6. Mean percent of sites with IYSV-infected plants in seeded and transplanted onion fields at the end of the season in 2007 and 2008.

Early adult thrips density also had a significant positive relationship with final *IYSV level* ($P < 0.001$) and the relationship did not depend on field type. For *late larval thrips densities*, the relationship with final *IYSV levels* was also significant but negative in both field types, the lower the larval density the higher the final level of IYSV ($P < 0.010$).

Overall there were significantly higher levels of IYSV in seeded fields than in transplanted fields ($P = 0.041$) (Fig. 6). *Julian date* of the last sample was also significant ($P = 0.003$), indicating that there were higher levels of IYSV in fields harvested later in the season.

Relative Importance of Thrips Categories in Predicting Final Levels of IYSV. In 2007, *late adult thrips densities* were more important in predicting final levels of IYSV than the other three thrips categories (Table 4). However, the differences in the amount of residual variance explained by each thrips category were not very large. This result was similar to the regression results when all four categories of thrips were simultaneously included in the model and only *late adult thrips density* was identified as a significant predictor.

In 2008, the significant interactions between *thrips categories* and *field type* were considered and the relative significance of individual thrips categories was analyzed separately by field type. For seeded fields in 2008, *late larval thrips densities* were the most important predictor of final *IYSV levels* (Table 4). Unlike the 2007 analysis, there was a large difference between the residual variance explained by *late larval densities* compared with the residual variance explained by the other three thrips categories in predicting final levels of IYSV. For transplanted fields, *late adult thrips densities* were the most important predictor and the differences in residual variance explained by *late adult densities* and the other three thrips categories were large (Table 4); *late adult densities* explained considerably more of the variation in the data than the next most important predictor. The second most important predictor of final *IYSV levels* in both 2007 and 2008 was *early larval densities* (Table 4).

Table 4. A ranking of the relative importance of four categories of *T. tabaci* in predicting final IYSV levels in commercial onion fields in western New York in 2007 and 2008

Ranking	Variable	Residual variance[a]
2007	Base model (Julian + field type), $N^b = 10$	4.89
1	Base model + late adults	4.21
2	Base model + early larvae	5.10
3	Base model + early adults	5.41
4	Base model + late larvae	5.51
2008, Seeded fields	Base model (Julian), $N = 6$	0.79
1	Base model + late larvae	<0.0001
2	Base model + early larvae	0.24
3	Base model + late adults	1.05
4	Base model + early adults	1.07
2008, Transplanted fields	Base model (Julian), $N = 6$	10.97
1	Base model + late adults	<0.0001
2	Base model + early larvae	2.39
3	Base model + early adults	7.83
4	Base model + late larvae	11.71

[a] The residual variance is the amount of variation that is not explained by the regression model. The category with the lowest residual variance is considered the most important category because it explains more of the variance in the data.

[b] The Highlander variety was harvested before late thrips data were collected so this pair of fields is excluded from the analyses reducing *N* from 12 to 10.

Discussion

There were more *T. tabaci* larvae and adults in transplanted fields compared with seeded fields early in the season. Transplanted onions may have arrived already infested with *T. tabaci* from their point of origin, or they may have been preferentially colonized by native *T. tabaci*, or both. In New York, transplanted fields are usually the first onion fields in the production system to be treated with insecticides for managing *T. tabaci* infestations (B.A.N., unpublished data), and this grower practice seems appropriate based on our data.

We hypothesized that transplanted fields might be at greater risk for higher levels of IYSV than seeded fields, but this was not the case. Both field types showed evidence of infection at the same time and there was no consistent pattern suggesting that virus levels increased faster in one field type compared with the other; IYSV remained at low levels in both field types in June and July. Though transplanted fields had higher initial densities of thrips early in the season and symptomatic plants were found first in transplanted fields, by the end of the season seeded fields had significantly higher levels of IYSV than transplanted fields. However, this situation could change if the proportion of transplants infected with IYSV imported into New York increases.

The relationship between thrips densities and IYSV levels was complicated. When both years were combined, and total thrips densities were considered, only cumulative adult thrips densities were a significant predictor of final IYSV levels, cumulative larval densities and field type were not significant. Separating thrips into early and late larvae and adults and analyzing each year separately revealed that late season larval and adult densities were more important in predicting final IYSV levels than early season larval and adult densities. In 2007, late adult thrips densities were the most important thrips category predicting final IYSV levels; the more adult thrips present late in the season the greater the percentage of sites with IYSV. In 2008, the relative importance of each thrips category depended on field type. Late larval thrips density was the most important thrips category in seeded fields but, in this case, the relationship was negative; one of the seeded fields, the one with highest level of IYSV, had a relatively low level of thrips larvae late in the season and this one field influenced the direction of the relationship. In transplanted fields, late adult thrips density was the most important predictor and the relationship was positive, as in 2007. Early larval densities were consistently the second most important thrips category, but early adult densities did not explain much of the variation in the data.

It was more difficult to assess the relative importance of field type, *Julian date* of the last sample, and thrips densities on final IYSV levels because these variables were confounded. The mean *Julian date* of the last sample taken before harvest in transplanted fields was day 230.6, and for seeded fields it was more than 1 wk later at day 239.7. We found a significant relationship between *Julian date* of the last sample before harvest and late larval and late adult thrips densities; the longer plants were in the field, the larger the late thrips populations. We also found a trend in final IYSV levels and field type; seeded fields had higher levels of IYSV than transplanted fields, and field type was significant in 2008, but not in 2007. It is possible that harvest date and late season thrips densities may be more important in determining final IYSV levels than field type. Schwartz et al. (2004) observed that very early maturing onion cultivars tended to have a lower incidence of IYSV.

There were low levels of IYSV throughout June and July of both years (<12% of sites in each field had IYSV-infected plants). This suggests that the initial primary spread of IYSV from inoculum sources into onion fields by *T. tabaci* occurred infrequently in 2007 and 2008. If there was secondary spread of the virus within fields during June and July, it was spatially localized and occurred at a smaller scale than the distances between our sample sites. Gent et al. (2004) found limited positive spatial autocorrelation in IYSV incidence in two fields sampled in Colorado ≈7 d before harvest and concluded that secondary spread was limited. Schwartz et al. (2008a) also found low levels of spatial autocorrelation of IYSV incidence and concluded that there was limited secondary spread. Fichtner et al. (2004) suggested that the spatial dependency of IYSV occurred over very short distances. In field variety trials in Washington, du Toit (2005) found a gradient in incidence and severity of IYSV that was attributed to immigration of viruliferous adults from adjacent vegetation, and suggested that there

was limited secondary movement of viruliferous thrips within onion fields. This corresponds with data collected on *T. tabaci* and tospoviruses in other crops. In Greece, *T. tabaci* in tobacco are the primary vector of tomato spotted wilt virus (TSWV) (Bunyaviridae: Tospovirus), and the dispersal behavior of viruliferous *T. tabaci* resulted in a very limited and localized pattern of secondary spread (Chatzivassiliou 2008). TSWV in other crops, where multiple thrips species are vectors including *T. tabaci*, is also considered to have only limited secondary spread (Latham and Jones 1997, Coutts et al. 2004). Similar to TSWV, the spread of IYSV by *T. tabaci* in onion may be monocyclic, but increasing levels of IYSV late in the season have not been tested for spatial autocorrelation yet to confirm this hypothesis.

Though we did not collect *T. tabaci* dispersal data, the rate at which adult thrips populations increased between August and September was much greater than the population growth rate for adults between June and July, and there was very little overlap between the 95% confidence intervals. This was not true for larvae, where the 95% population growth rate confidence intervals for June/July and August/September had considerable overlap. These results suggest that adult immigration into fields late in the season may be increasing adult densities in unharvested fields above that expected by within field reproduction rates alone. This is supported by data showing *T. tabaci* often have two peak flights in New York, one in May and one in August. The first peak in May is the result of *T. tabaci* migrating from neighboring fields of alfalfa/red clover and wheat into onion fields (Gangloff 1999). As onion fields are harvested in August, the second peak in adult flight may be caused by an increase in adult dispersal from senescing onion fields into onion fields that are still growing.

August was also the time when the proportion of sites with IYSV-infected plants began to increase rapidly. This was particularly true in 2008, when we detected dramatic increases in virus levels in a number of fields (e.g., in a seeded Red Bull field the percentage of sites with IYSV-infected plants increased from 27 to 73% between 20 and 27 August 2008). In addition, overall levels of IYSV were much higher in 2008 compared with 2007. This might be related to the significantly higher populations of late adult *T. tabaci* found in 2008, and the higher ratio of adults-to-larvae observed in 2008 compared with 2007. Once their native fields are harvested in late July/early August, viruliferous adults may move to nearby unharvested fields, increasing the spread of IYSV.

Another potential explanation for the increase in IYSV levels in August may be a change in the efficiency of the *T. tabaci* population that transmits IYSV. *T. tabaci* in onion fields have multiple reproductive modes in New York: thelytoky, the production of unfertilized females by females; arrhenotoky, the production of males from unfertilized eggs and females from fertilized eggs; and deuterotoky, the production of males and females by unfertilized eggs (Nault et al. 2006). In general, NY populations of *T. tabaci* in June and July are primarily thelytokous, with very few males produced. By August, the populations shift to primarily arrhenotokous and/or deuterotokous (Nault et al. 2006). Chatzivassiliou et al. (2002) showed that arrhenotokous populations of *T. tabaci* collected from leeks were able to transmit TSWV, while thrips from thelytokous populations collected from leek were nonvectors. Within arrhenotokous populations collected from tobacco, male *T. tabaci* had a higher successful transmission rate of TSWV than females (Chatzivassiliou et al. 2007). There are no data available on the relative transmission efficacy of thelytokous and arrhenotokous populations of *T. tabaci* and IYSV in New York. Additional research is needed to understand the relative importance of reproductive mode and other factors that affect vector competence and transmission efficacy, such as virus isolates (Paliwal 1974, Tedeschi et al. 2001), host plants (Chatzivassiliou et al. 2002), genetic inheritance (Cabrera-La Rosa and Kennedy 2007), and physiological barriers (Nagata et al. 1999b).

Implications for Management. Transplanted onion fields had significantly higher levels of thrips early in the season, and there was a positive relationship between early larval thrips densities in transplanted fields and final levels of IYSV. This suggests that management of thrips early in the season in transplanted fields may help prevent high levels of IYSV late in the season in those fields. However, late season occurrences of IYSV in transplanted fields may not impact bulb grades or yields because few plants showed IYSV symptoms that could affect photosynthesis and bulb development before harvest, and most of the plants that reacted positively for IYSV using DAS-ELISA were asymptomatic (C.L.H., unpublished data). Reducing thrips populations late in the season in transplanted fields may be the most important management strategy for IYSV because of the potential impact emigrating viruliferous thrips can have on neighboring fields once the transplanted fields are harvested. Viruliferous thrips that disperse from harvested fields and colonize adjacent fields can rapidly increase the primary spread of IYSV in those fields.

In general, onion growers in New York do not attempt to manage thrips in fields 1–2 wks before harvest because >30–50% of the leaves have collapsed, and adequate spray coverage for thrips control is not possible. During this time, larvae can complete development on infected plants and may be dramatically increasing the population of viruliferous adults. If future studies show that IYSV negatively impacts onion yields in New York, growers may consider more aggressive thrips control measures in early harvested fields to prevent viruliferous adults from moving the virus to onions that are still developing.

In addition, the Elba muck and many of the onion producing areas in the Great Lakes region of the U.S. resemble spatial checkerboards of early- and late-harvested onion fields. This spatial pattern enables adults emigrating from harvested fields to travel a short distance to find a field that is still growing. Concentrating fields that will be harvested around the same time in the same geographic location may minimize immigra-

tion of IYSV-infected adults into fields that are not harvested, and slow the spread of IYSV to those fields. Results from small-plot studies of thrips that are vectors of TSWV (*T. tabaci*, western flower thrips, *Frankliniella occidentalis* [Pergande], and the tomato thrips, *F. schultzei* [Trybom]) suggested that 23 m was a 'safe' planting distance to successfully limit the dispersal of viruliferous thrips from potential TSWV sources to the pepper crop (Latham and Jones 1997). These studies also found a more frequent spread of TSWV to sites downwind from the infection source. Manipulating the spatial arrangement of onion fields based on harvest date and the most prevalent wind direction may be another cultural control option onion growers can use to help mitigate the impact of this invasive pathogen.

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