POPULATION ECOLOGY

Weed Hosts for Onion Thrips (Thysanoptera: Thripidae) and Their Potential Role in the Epidemiology of *Iris Yellow Spot Virus* in an Onion Ecosystem

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ABSTRACT Onion thrips, *Thrips tabaci* Lindeman, is a key foliage-feeding pest of onion worldwide and the principal vector of a serious onion pathogen, *Iris yellow spot virus* (IYSV). Long-term management of *T. tabaci* and IYSV will require an understanding of *T. tabaci* ecology and IYSV epidemiology in onion ecosystems. This study focused on identifying winter-annual, biennial and perennial weed species that host both *T. tabaci* and IYSV. Unlike summer-annual weeds, weeds with these habits survive overwinter and could serve as a green bridge for IYSV to survive between onion-growing seasons. *T. tabaci* larvae and adults were sampled every two weeks from 69 weed species in five areas located adjacent to onion fields in western New York in 2008 and 2009. Twenty-five of the 69 weed species were identified as hosts for *T. tabaci* larvae and populations were highest on the Brassicaceous weeds, *Barbarea vulgaris* Ait. f., *Sinapis arvensis* L., and *Thalspi arvense* L. None of these species are hosts for IYSV. Four of the 25 weed species were hosts for both *T. tabaci* larval populations and IYSV: common burdock, *Arctium minus* Bernh., dandelion, *Taraxacum officinale* G.H. Weber ex Wiggers, curly dock, *Rumex crispus* L., and chicory, *Cichorium intybus* L. Of these four weed species, *T. officinale* and *A. minus* may play an important role in the epidemiology of IYSV in New York onion fields because they may survive between onion-growing seasons, they are relatively abundant in the landscape, and they support relatively high densities of *T. tabaci*.

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

Onion thrips, *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), is a major pest of onion, *Allium cepa* L., and other *Allium* spp. worldwide (Lewis 1997). Thrips damage onion plants by feeding on leaf tissue, often leading to significant reductions in bulb yield (Fournier et al. 1995, Childers 1997). *T. tabaci* is the only thrips pest of onion in New York. Populations of *T. tabaci* overwinter in crops and weedy vegetation (North and Shelton 1986) as well as in the soil within and/or near onion fields (Larentzaki et al. 2007). Adult *T. tabaci* are observed from late March through May on volunteer onion plants (Larentzaki et al. 2007), which sprout from bulbs remaining in the field from the previous season. During this time, onion seed is planted and onion plants are transplanted in New York. Colonization of onion crops begins in June and populations are found on the crop until harvest from late-July through September. After harvest, *T. tabaci* adults have been observed on several weed species including common lambsquarters, *Chenopodium album* L., evening primrose, *Oenothera biennis* L., yellow nutsedge, *Cyperus esculentus* L., and smooth pigweed, *Amaranthus hybridus* L. (Larentzaki et al. 2007). Whether *T. tabaci* reproduce on these weeds or on other weeds in this cropping system has not been determined.

T. tabaci is the only reported vector of *Iris yellow spot virus* (IYSV) (Bunyaviridae: Tospovirus) (Kritzman et al. 2001), a serious yield-reducing pathogen of onion and other *Allium* crops worldwide (Gent et al. 2006). IYSV is transmitted by *T. tabaci* in a persistent, circulative manner (Ullman et al. 1992, Whitfield et al. 2005). Thrips are known to acquire tospoviruses as first instars and transmit them as second instars or adults (Ullman et al. 1992, Wijkamp et al. 1993). IYSV is not known to be seed-transmitted (Gent et al. 2004), nor is it easily transmitted by mechanical means (Gent et al. 2006).

IYSV was first identified in Brazil in 1981 (de Ávila et al. 1981) and has since spread to regions of onion production across the globe (Gent et al. 2006). IYSV was first detected in New York in 2006 (Hoepting et al. 2007) and has since been found throughout onion-producing regions in the state (Nault et al. 2008). In 2007 and 2008, IYSV was not detected in onion fields

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until mid-June to mid-July in New York and levels in these fields were very low until early to mid August; <12% of samples within a field tested positive at this time (Hsu et al. 2010). The incidence of IYSV in many onion fields increased dramatically during the second half of August with some fields reaching levels >90% by harvest (Hsu et al. 2010).

Potential sources of IYSV in New York recently have become better understood. IYSV may be reintroduced annually via infected onion transplants originating in states like Arizona where the virus is established (Pappu and Matheron 2008). Onion transplants imported into New York from Arizona have tested positive for IYSV (Hsu et al. 2011). Transplants account for ≈15% of New York's onion crop and only 0.04% of transplants tested positive for IYSV in 2007 and 2008 (Hsu et al. 2011).

There also are sources of IYSV that may permit this virus to bridge seasons in New York. For example, volunteer onion plants in nonrotated fields and in onion cull piles may be infected with IYSV (Hsu et al. 2011). These sources could support an early generation of onion thrips whose viruliferous adults could disperse to and infect the main onion crop. Another possible source that could enable IYSV to bridge seasons in New York includes winter-annual, biennial, or perennial weeds. In addition to onion, there are at least 46 plant species in 19 families known to host IYSV (Table 1), many of which are weed species not in the genus *Allium* (Gent et al. 2006). In 2007 and 2008, Hsu et al. (2011) tested a number of commonly occurring winter-annual, biennial, and perennial weed species for IYSV in New York. Four species tested positive including common burdock, *Arctium minus* Bernh., chicory, *Cichorium intybus* L., curly dock, *Rumex crispus* L., and dandelion, *Taraxacum officinale* G.H. Weber ex Wiggers (Table 1). The frequency of infection in each weed species was not reported.

Winter-annual, biennial, and perennial weed species could be available as hosts for *T. tabaci* early in the spring and late in the fall when the onion crop is not available as a host. These weed species would have the potential to be epidemiological bridges between cropping seasons for IYSV because they survive through the winter in New York. Potential candidates include the four species identified by Hsu et al. (2011) plus two other species: the perennial, prickly lettuce, *Lactuca serriola* L. (Sampangi and Mohan 2007), and the winter-annual, spiny sowthistle, *Sonchus asper* (L.) Hill (Nischwitz et al. 2007). Others may exist as well, but have yet to be identified.

In contrast to the aforementioned weed species, summer-annual weeds are unlikely to be significant hosts in the epidemiology of IYSV. These weeds would have to be infected by viruliferous *T. tabaci* in the summer and subsequent generations of *T. tabaci* adults would then need to disperse and transmit the virus into the onion crop. Such a scenario is conceivable if viruliferous *T. tabaci* preferentially colonize summer-annual weeds rather than onion; however, it would likely not occur until late in the season, perhaps when the onion crop is near harvest or already harvested.

The objectives of this study were to: (1) identify weed species that host *T. tabaci* larvae, especially winter-annual, biennial, and perennial species; (2) determine the overall abundance and temporal patterns of *T. tabaci* densities on weed species known to be reproductive hosts for *T. tabaci* and hosts for IYSV; and (3) identify weed species that may be the best candidates for impacting the epidemiology of IYSV in the onion ecosystem.

Materials and Methods

Sampling Location and Period. In 2008 and 2009, thrips were collected and weeds sampled from five sites located in the Elba muck region of western New York (43.1N, 78.1W), the second largest onion producing region in the state. Sites were at least 1.5 km apart. Data collection sites were selected for their proximity to onion fields and were located in areas of fallow land 10 to 50 m parallel and adjacent to onion fields. Each site was sampled in both years of this study starting several weeks before onions were colonized by thrips and ending several weeks after onions were harvested. In addition to sampling thrips on weeds, 15 onion plants in the field nearest to the weed sample site were visually inspected for *T. tabaci* larvae and the number per plant was recorded. In 2008, data were collected every 2 wk from 9 May to 30 August and again on 26 September (10 sampling dates). In 2009, data were collected every 2 wk from 18 May through 5 October (11 sampling dates). This schedule was chosen to ensure that data were collected before, during, and after the onion growing season.

Sampling Weeds and Thrips. At each of the five collection sites in both years, entire plants or leaf subsamples were collected and the numbers of *T. tabaci* adults and larvae were recorded. No more than five plants per weed species were collected per collection site. Plants within a collection site were combined to produce one composite weed species-sample per site per sampling date ($n = 5$ per sampling date). Data were represented as the number of thrips per plant per sampling date. Not all weed species were present at each site, and because of the seasonal lifecycle of some species, not all species were collected on each sample date. For example, winter-annual weeds were not usually present in July and early-August. The composite samples were placed in a 5.68 liters polypropylene container (Sterilite Corporation, Townsend, MA) and maintained in an environmental chamber at 29°C, 78% RH, and 16:8 L:D until analysis. Lids of containers were fitted with thrips-proof screen for ventilation (150×150 μm). Entire plants were collected when possible, but larger plants required the collection of a representative sub-sample of leaves. In such cases, leaf numbers were recorded for each sampled plant so thrips populations could be extrapolated to a per-plant basis for further comparisons.

Identifying *T. tabaci* from Weeds. If *T. tabaci* larvae were collected from a weed species, the weed was considered as a reproductive host. Because identification keys do not exist for *T. tabaci* larvae, thrips

Table 1. Plant species reported to be hosts of IYSV

Species	Common name	Location[a]	Reference	Habit[b]
Alstroemeriaceae				
Alstroemeria sp.	Peruvian lily	Japan	Okuda and Hanada 2001	P
Amaranthaceae				
Amaranthus retroflexus L.[c]	Redroot pigweed	Colorado	Gent et al. 2006	SA
Atriplex micrantha L.	Twoscale saltbush	Utah	Evans et al. 2009a	P
Chenopodium album L.[c]	Common lambsquarters	Oregon	Sampangi et al. 2007	SA
C. amaranticolor Coste and Reyn.	Orn. lambsquarters	Israel	Gera et al. 2002	SA
C. quinoa Willd.	Quinoa	Israel	Gera et al. 1998	SA
Gomphrena globosa L.	Globe amaranth	Israel	Mohan et al. 1991	SA
Kochia scoparia Roth	Kochia	Oregon	Sampangi et al. 2007	SA
Amaryllidaceae				
Allium spp.[c,d]	Onion, garlic, leek, etc.	Brazil	de Ávila et al. 1981	B/P/C
Clivia miniata Regel	Kaffir-lily	Japan	Jones 2005	P
Hippeastrum hybridum Herb.	Amaryllis	Israel	Gera et al. 1998	P/C
Araceae				
Scindapsus sp.	Scindapsus	Iran	Ghotbi et al. 2005	P
Asteraceae				
Arctium minus Bernh.[c]	Common burdock	New York	Hsu et al. 2011	B
Chrysanthemum sp.	Chrysanthemum	Poland	Balukiewicz and Kryczinski, 2005	P
Cichorium intybus L.[c]	Chicory	New York	Hsu et al. 2011	P
Lactuca serriola L.[c]	Prickly lettuce	Oregon	Sampangi et al. 2007	P
Sonchus asper (L.) Hill[c]	Spiny annual sowthistle	Georgia	Nischwitz et al. 2007	WA/B/P
Taraxacum officinale G.H. Weber ex Wiggers[c]	Dandelion	New York	Hsu et al. 2011	P
Cycadaceae				
Cycas sp.	Ornamental palm	Iran	Ghotbi et al. 2005	P
Fabaceae				
Vicia sativa L.	Common Vetch	Georgia	Gent et al. 2006	WA/C
Vigna unguiculata (L.) Walp.	Black-eyed pea	Iran	Ghotbi et al. 2005	C
Gentianaceae				
Eustoma grandiflorum Salisb.	Texas bluebell	Japan	Doi et al. 2003	B/P
Eustoma russellianum Salisb.	Lisianthus	Israel	Kritzman et al. 2000	P/C
Geraniaceae				
Geranium carolianum L.	Carolina geranium	Georgia	Gent et al. 2006	B
Pelargonium x hortorum L'Hér	Common geranium	Iran	Ghotbi et al. 2005	P
Iridaceae				
Iris holandica L.	Iris	Ned.	Cortês et al. 1998	P
Poaceae				
Setaria viridis (L.) P. Beauv.[c]	Green foxtail	Utah	Evans et al. 2009b	SA
Polygonaceae				
Rumex crispus L.[c]	Curly dock	New York	Hsu et al. 2011	P
Portulacaceae				
Portulaca oleracea L.[c]	Common purslane	Italy	Cosmi et al. 2003	SA
Rosaceae				
Rosa sp.	Rose	Iran	Ghotbi et al. 2005	P
Scrophulariaceae				
Linaria Canadensis (L.) Dumort.	Blue toadflax	Georgia	Gent et al. 2006	WA/B/P
Solanaceae				
Capsicum annuum L.	Pepper	Tunisia	Ben Moussa et al. 2005	C
Datura stramonium L.	Jimson weed	Israel	Gera et al. 1998	SA
Nicotiana benthamiana Domin	Ornamental tobacco	Iran	Hall et al. 1993	C
N. rustica L.	Tobacco	Brazil	Pozzer et al. 1999	C
Petunia x hybrid Juss.	Petunia	Iran	Ghotbi et al. 2005	P
Solanum lycopersicum L.	Tomato	Tunisia	Ben Moussa et al. 2005	C
S. tuberosum L.[c]	Potato	Tunisia	Ben Moussa et al. 2005	C
Themidaceae				
Bessera elegans Schult. f.	Coral drops	Japan	Jones 2005	P
Zygophyllaceae				
Tribulus terrestris L.	Puncturevine	Oregon	Sampangi et al. 2007	SA/P

[a] Location of first detection.

[b] Most common life history: B = biennial, P = perennial, WA = winter-annual, SA = summer-annual, C = crop. Combinations indicate that multiple life histories are common.

[c] Species found in the Elba Muck ecosystem, Elba, NY (43.1N, 78.1W) (E.A. Smith, unpublished data).

[d] Includes seven species of *Allium:* cultivated onion, *A. cepa* (de Ávila et al. 1981; Hall et al. 1993), shallot, *A. cepa* var. *ascalonicum* (Robene-Soustrade et al. 2006), leek, *A. porrum* (Coutts et al. 2003), garlic, *A. sativum* (Robene-Soustrade et al. 2006), and wild onions, *A. altaicum, A. pskemense,* and *A. vavilovii* (Pappu et al. 2006).

larvae were removed from plant samples and reared to the adult stage. Using a fine paintbrush, up to 30 larvae per composite weed sample were transferred to ventilated petri dishes containing sterilized leaf disks of cabbage, *Brassica oleracea* L. (Capitata group), and reared to adulthood following the procedure described in Nault et al. (2006). Based on experience rearing *T. tabaci* larvae, those larvae that were clearly not *T. tabaci* were not collected nor counted. Upon reaching the adult stage, thrips were identified and counted according to species (Moritz et al. 2001). The percentage of thrips larvae determined to be *T. tabaci* was multiplied by the total initial number of larvae in the petri dish to estimate the percentage of thrips larvae that were *T. tabaci.* These numbers were divided by the number of plants in the sample to estimate the number of *T. tabaci* larvae per plant. For example, let us say that there were 100 thrips larvae (excluding thrips that were clearly not *T. tabaci*) detected in the original container that had five plants of the same weed species. Thirty larvae were removed and placed into petri dishes until they reached adulthood. Only 24 of the 30 larvae survived to the adult stage and three of the survivors were *T. tabaci* (=3/24 or 12.5% of surviving thrips were *T. tabaci*). The final estimate of the number of *T. tabaci* in the original container was 12.5 thrips or 2.5 per plant (=12.5 thrips/5 plants). Voucher specimens are maintained in the Department of Entomology, Cornell University, NYSAES (Geneva, NY).

Weed Population Density Estimates. On each sample date, weed densities at each of the five sites were estimated by recording the number of individuals of each weed species in 0.5 × 0.5 m quadrats placed every 10 m along a 90 m linear transect parallel to the respective onion fields. Transects at each of the five collection sites occurred in the same locations both years and were adjacent to areas where weeds were collected for thrips population surveys. Numbers of plants per species in all 10 quadrats were totaled at each site and then across all sites on each sampling date. These totals were divided by the total area sampled per date (12.5 m^2) to estimate the number of plants per m^2. Weed densities are presented on a plants per hectare basis by extrapolating the mean number of plants per species on each sampling date. Values for all sampling dates were averaged to obtain an estimated season mean number of plants per hectare for each weed species.

Identifying Weed Species That May be Important in IYSV Epidemiology. A weed species that may be an important epidemiological source for IYSV must be a reproductive host for *T. tabaci,* but also may need to be relatively abundant in the landscape. The potential importance of a weed species being a source of IYSV was estimated by calculating numbers of *T. tabaci* larvae per hectare for each weed species. *T. tabaci* larval populations (larvae per plant per sampling date) on IYSV-susceptible winter-annual, biennial and perennial weed species were multiplied by each species' respective population density (plants per hectare) to determine the number of larvae per hectare per sampling date.

Results

***Larval T. tabaci* Population Survey on Weeds.** Sixty-nine winter-annual, biennial, and perennial weed species and four crop species were sampled over 2 yr. No wild *Allium* spp. were observed in this study. Twenty-five weed species and three crop species were identified as hosts for *T. tabaci* larvae (Table 2). No *T. tabaci* larvae were observed on 44 weed species and one crop species (Appendix 1). Of the 25 weed species that were hosts for *T. tabaci* larvae, only common burdock, chicory, curly dock, and dandelion are known hosts for IYSV (Hsu et al. 2011). *T. tabaci* larvae were identified on common burdock and dandelion in both 2008 and 2009, but were found on curly dock only in 2008 and on chicory only in 2009 (Fig. 1). Mean densities of *T. tabaci* larvae were highest on common burdock in 2008 and highest on both common burdock and dandelion in 2009.

Though they are not likely to be important epidemiological sources for IYSV, *T. tabaci* larvae were identified on five of 20 summer-annual weeds: redroot pigweed, *Amaranthus retroflexus* L. (Amaranthaceae), common lambsquarters (Amaranthaceae), lady's-thumb, *Persicaria maculosa* L. (Polygonaceae), wild buckwheat, *Polygonum convolvulus* L. (Polygonaceae), and green smartweed, *P. scabrum* Moench (Polygonaceae) (data available in Smith 2010).

Seasonal Dynamics of *T. tabaci* on Weeds and Onions. In 2008 and 2009, populations of *T. tabaci* were much greater on onion plants than on weeds (Figs. 2B–D). Peaks in adult *T. tabaci* populations on weeds were recorded on common burdock, chicory, curly dock, and dandelion early in the season (27 May through 15 June), and again late in the season when onions were harvested (18 August through 26 September) (Fig. 2A,B). On common burdock, peaks in adult populations occurred on 27 May, 18 August and 26 September 2008, and on 15 June and 8 September 2009. On chicory, adults were only observed on 9 June and 26 September 2008 and on 15 June and 10 August 2009. On curly dock, no observable peaks were detected in 2008 and no *T. tabaci* adults were observed in 2009. On dandelion, a peak occurred on 30 August 2008 and 21 September 2009. Adult onion thrips were present but not recorded on onion crops in 2008, but in 2009 adult populations on onion peaked to a level of 2.5 *T. tabaci* per plant on 13 July 2009 and peaked again to a level of 42.5 per plant on 8 September.

Peaks in larval populations on these weed species followed peaks in adult populations both early in the growing season (June) and during onion harvest (late August through September in 2008 and 2009, and into October in 2009) (Fig. 2C,D). On common burdock, peaks in larval populations occurred on 9 June and 18 August 2008, and on 15 June, 8 September, and 5 October 2009. On chicory, larvae were not observed in 2008, and were observed only on 10 August 2009. On curly dock, *T. tabaci* larvae were only observed on 9 June, 2008, and were not observed in 2009. On dandelion, peaks in larval populations occurred on 9 June and 30 August 2008, and on only 29 June 2009. Larval *T. tabaci* populations were first recorded on onion crops in early June of both years of this study. Populations peaked around 22 July and again on 18 August 2008, and around 27 July and 8 September 2009.

Estimated Weed Population Densities of Potential IYSV Sources. Dandelion plants were 21 and 44 times more abundant than common burdock and six and eight times more abundant than chicory in 2008 and 2009, respectively (Fig. 3). Dandelion plants were 341 times more abundant than curly dock in 2008.

Table 2. Winter-annual, biennial, and perennial weed species found to be reproductive hosts of *T. tabaci* in onion, *Allium cepa*, in western New York

Family	Common name	Habit[a]	Period[b]	Mean no. of *T. tabaci* larvae per plant[c]			
Species				2008	SE$_x$[d]	2009	SE$_x$[d]
Weed species							
Apiaceae							
Conium maculatum L.	Poison hemlock	B	All	0.54	0.36	0.52	0.23
Asclepiadaceae							
Asclepias syriaca L.	Common milkweed	P	All	0.36	0.24	0	0
Asteraceae							
Arctium minus Bernh.[e]	Common burdock	B	All	0.36	0.22	0.46	0.25
Cichorium intybus L.[e]	Chicory	P	All	0	0	0.02	0.02
Cirsium arvense (L.) Scop.	Canada thistle	P	All	0	0	0.05	0.05
Solidago Canadensis L.	Goldenrod	P	All	0.06	0.03	0.09	0.09
Taraxacum officinale G.H. Weber ex Wiggers[e]	Dandelion	P	All	0.08	0.05	0.44	0.44
Brassicaceae							
Barbarea vulgaris Ait. f.	Yellow rocket	WA/B/P	All	0.23	0.14	2.45	1.64
Capsella bursa-pastoris (L.) Medik.	Shepherd's purse	WA	Sp	0.39	0.34	0	0
Lepidium virginicum L.	Virginia pepperweed	WA	Sp, F	0.51	0.33	0.34	0.34
Raphanus raphanistrum L.	Wild radish	WA	Sp	1.80	N/A	N/A	N/A
Sinapis arvensis L.	Wild mustard	WA/B/P	All	1.07	0.52	3.42	1.73
Thlaspi arvense L.	Field pennycress	WA	Sp	0.09	0.09	2.27	2.27
Convolvulaceae							
Calystegia sepium (L.) R. Br.	Hedge bindweed	P	Sp, Su	0.04	0.04	0	0
Fabaceae							
Medicago lupulina L.	Black medic	SA/WA	All	0	0	0.13	0.12
Lamiaceae							
Lamium purpureum L.	Purple deadnettle	WA	Sp	0.04	0.04	0	0
Nepeta cataria L.	Catnip	P	All	0	0	1.14	0.64
Malvaceae							
Malva neglecta Wallr.	Common mallow	WA/B/P	All	0.54	0.50	0	0
Onagraceae							
Oenothera biennis L.	Evening primrose	B	All	0.03	0.03	0.24	0.24
Oxalidaceae							
Oxalis stricta L.	Yellow woodsorrel	P	Su, F	0.27	0.18	N/A	N/A
Plantaginaceae							
Plantago lanceolata L.	Buckhorn plantain	P	All	0	0	0.04	0.04
Poaceae							
Lolium sp.	Ryegrass	WA/B/P	Su	N/A	N/A	0.60	N/A
Polygonaceae							
Rumex crispus L.[e]	Curly dock	P	All	0.02	0.02	0	0
Scrophulariaceae							
Verbascum Thapsus L.	Common mullein	B	All	0.04	0.04	0	0
Urticaceae							
Urtica dioica L.	Stinging nettle	P	All	0.01	0.01	0	0
Crop species							
Amaryllidaceae							
Allium cepa L.[e]	Onion	B	All	27.74	18.29	14.56	4.64
Fabaceae							
Medicago sativa L.	Alfalfa	P	Sp, Su	0.10	0.10	0	0
Poaceae							
Avena sp.	Oat, winter cover crop	WA/C	F	N/A	N/A	1.40	N/A

[a] Most common life history: SA = summer-annual, WA = winter-annual, B = biennial, P = perennial, C = crop. Combinations indicate that all three life-history variations are possible and are known to occur.

[b] Period when plants were sampled, indicating prevalence in the sampling location. Sp = spring sampling (May, June), Su = summer sampling (July, Aug.), *F* = autumn sampling (Sept., Oct.), All = sampling through the duration of the onion growing season (May through Sept. and Oct.).

[c] Populations were estimated to no. of larvae per plant per sampling date except on hedge bindweed, black medic, purple deadnettle, ryegrass, common mallow, yellow woodsorrel, alfalfa, and the winter cover crop, where populations were estimated to no. of larvae per 0.0125 m^2 per sampling date. 0 = no *T. tabaci* larvae were identified (n $\geq$1 collected plant samples). N/A = no plants were sampled.

[d] Standard error of larvae per plant per sampling date or larvae per 0.0125 m^2 per sampling date. N/A = insufficient no. of samples were collected for calculation (0 or 1).

[e] Confirmed host of IYSV (Hsu et al. 2011).

Curly dock was quite rare in survey transects in 2008, and thus it is not particularly surprising that it was absent in 2009 despite its presence in the region.

Estimated Population Densities of *T. tabaci* Larvae on IYSV-Positive Weed Hosts on a Per-Area Basis. In 2008 and 2009, the estimated populations of *T. tabaci* larvae per hectare on common burdock and dandelion were considerably higher than those on chicory and curly dock (Fig. 4).

Discussion

T. tabaci larvae were detected on 25 winter-annual, biennial, and perennial weed species representing 14 families. These results indicate that despite a prefer-

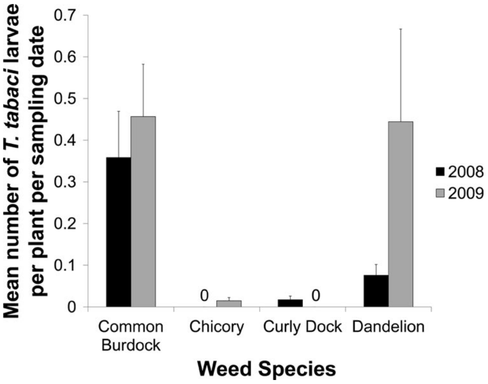

Fig. 1. Mean populations of *T. tabaci* larvae ±SE on weed species known as hosts for IYSV in 2008 and 2009 in the Elba Muck onion growing region near Elba, NY.

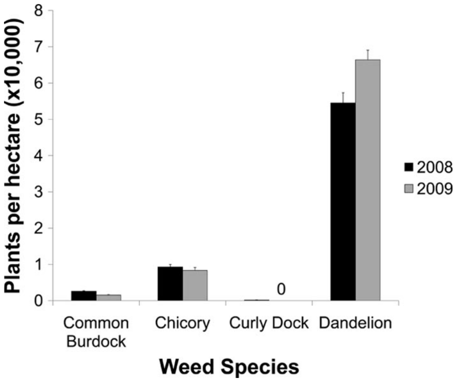

Fig. 3. Estimated population densities ±SE of weed species known as hosts for *T. tabaci* and IYSV in 2008 and 2009 in the Elba Muck onion growing region near Elba, NY.

ence for onion (Doederlein and Sites 1993), *T. tabaci* larvae can exploit a wide variety of taxonomically diverse hosts. Still, 40% (11 of 25 species) of the reproductive hosts are members of Asteraceae (five species) and Brassicaceae (six species), and 84% of *T. tabaci* larvae observed on weeds during this study were observed on members of these two taxa. Populations of *T. tabaci* larvae were most abundant on four cruciferous species, yellow rocket, *Barbarea vulgaris* Ait. f., wild radish, *Raphanus raphanistrum* L., wild mustard *Sinapis arvensis* L., and field pennycress, *Thlaspi arvense* L. Populations of *T. tabaci* larvae were greater than one larva per plant per sampling date on all four of these species, and populations on wild mustard were greater than two larvae per plant per sampling date during this study.

A number of factors are likely responsible for *T. tabaci* to use a weed species as a host. Some of these factors include attraction to plant volatiles, nutrition, a relative absence of predators, or plant architecture

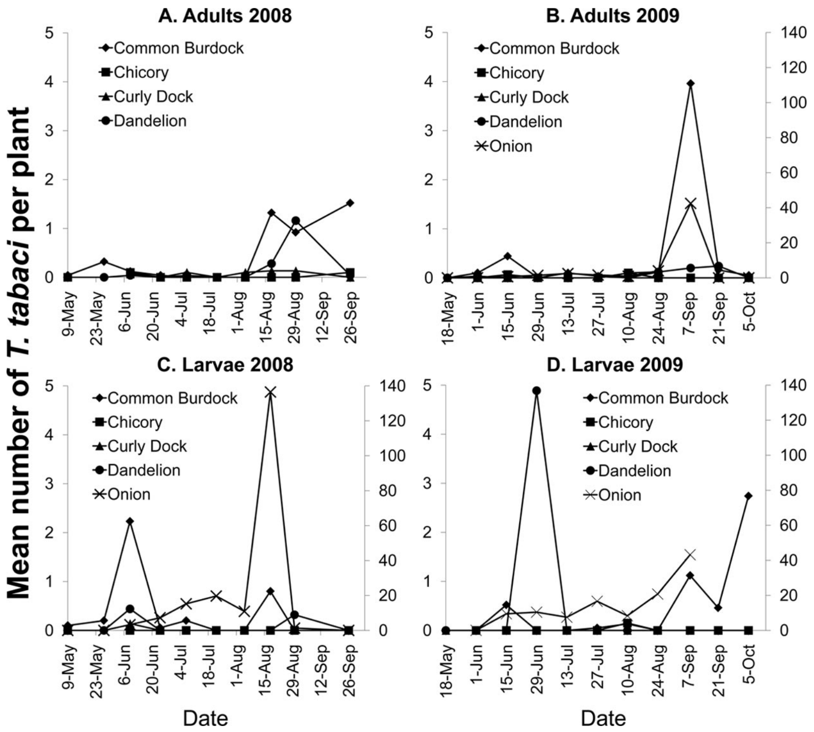

Fig. 2. Temporal population densities of *T. tabaci* adults and larvae on onion and on four weed species known to be hosts for IYSV in 2008 and 2009 in the Elba Muck onion growing region near Elba, NY. Densities of adult *T. tabaci* on onion were not recorded in 2008. The left Y axis corresponds to populations on chicory, common burdock, curly dock, and dandelion, whereas the right Y axis corresponds to populations on onion.

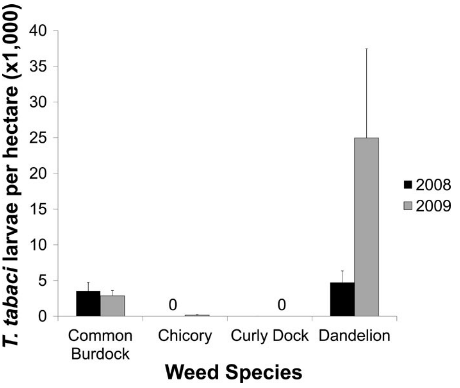

Fig. 4. Estimated abundance ±SE of *T. tabaci* larvae per hectare on IYSV-positive weed species known as hosts for IYSV in 2008 and 2009 in the Elba Muck onion growing region near Elba, NY.

that is favorable to thrips' cryptophilic and thigmotropic behavior (Lewis 1973). One of the more likely causes may be the abundance of Asteraceae and Brassicaceae species in the Elba Muck region, allowing *T. tabaci* to exploit preferable species of these two highly varied taxa. Species in the Asteraceae and Brassicaceae accounted for 22 and 9% of species in this region, respectively, and populations of species in these two families are among the highest in the region (Smith 2010).

In addition to onion, *T. tabaci* is also a major pest of cabbage crops worldwide (North and Shelton 1986, Shelton et al. 1998, Zezlina and Blazic 2003). The habit and architecture of cabbage and other cruciferous crops provide favorable habitats for *T. tabaci* as thigmophilic animals; however, this is less true for weedy crucifers. This suggests that the relative preference for weedy Brassicaceae species over other surveyed weedy species may have less to do with physical characteristics than other factors such as attraction to plant volatiles, nutritional value, or a lack of predators.

Knowledge of when *T. tabaci* use plant species during the season can provide insight into which hosts may be important in the epidemiology of IYSV. In both years of this study, populations of *T. tabaci* larvae peaked on weeds from late-May to mid-June. Because onions are seeded and transplanted in April and May, they are too small to be colonized in May and early June in most years (E.A. Smith, personal observation). Although data were not collected in March or April in either year of this study, Larentzaki et al. (2007) found *T. tabaci* on volunteer onions as early as March. This indicates that *T. tabaci* are active well before colonizing onion crops, but are concentrated on other hosts (Fig. 2). During July and early August, densities of *T. tabaci* larvae decreased in weeds, but increased in onion crops. Late in the onion growing seasons of both years, larval densities on weeds experienced a second major peak from August through October. Larentzaki et al. (2007) observed adult *T. tabaci* on weeds as late as November. Onion crops are harvested from July through September, and *T. tabaci* adults originating in onion may migrate from these fields into nearby weeds to feed and reproduce.

Weeds are largely ubiquitous in all onion growing regions. *T. tabaci* adults have been found on weeds bordering onion fields (Larentzaki et al. 2007), and at least 47 plant species in 19 families are hosts of IYSV (Table 1). Eleven of these species are non-*Allium* weed species typically found in New York onion ecosystems (E.A. Smith, personal observation), and four have tested positive for IYSV in New York (Hsu et al. 2011). Five of these 11 susceptible weed species are summer annual species in New York, but as stated previously, it is unlikely that summer-annuals contribute significantly to the epidemiology of IYSV. IYSV and tospoviruses in general are not known to be seed-transmissible, and *T. tabaci* are not likely to preferentially colonize summer-annuals and produce a viruliferous generation of *T. tabaci* until onions are harvested.

Winter-annuals, biennials, and perennials have the potential to be overwintering reservoirs for IYSV because they could be infected in the fall and remain infected in the spring. Such weed species would be considered a green bridge for the virus to survive between onion-growing seasons and could be important sources of IYSV. In this study, the four weed species, common burdock, chicory, curly dock and dandelion, were candidates as potentially important IYSV sources because they were (1) hosts of IYSV, (2) hosts for *T. tabaci* larvae, and (3) had winter-annual, biennial, or perennial life histories.

In both years of this study, common burdock and dandelion supported the most *T. tabaci* larvae compared with chicory and curly dock. Prickly lettuce is a known host of IYSV (Sampangi et al. 2007) and *T. tabaci* larvae (Chatzivassiliou et al. 2007) and is a perennial weed known to occur in agro-ecosystems in New York. However, none of the 73 prickly lettuce plants sampled in this study were hosts of *T. tabaci* larvae and 0 of 60 plants previously sampled tested positive for IYSV (Hsu et al. 2011).

Populations of *T. tabaci* larvae per hectare on common burdock and dandelion were estimated to be greater than on chicory and curly dock. These observations suggest that the potential impacts of chicory and curly dock on IYSV epidemiology in New York may be relatively inconsequential when compared with the likely impacts that common burdock and dandelion may have on IYSV epidemiology. Common burdock has been observed with high populations of *T. tabaci* larvae, but its relative infrequency in the landscape suggests that its impact on the spread of IYSV may be more localized than that of dandelion, which is ubiquitous in the onion-producing landscape in the region.

The biennial life habit of common burdock may also affect IYSV persistence. *Tomato spotted wilt virus* (TSWV) (*Bunyaviridae: Tospovirus*) is known to persist in perennial plants for multiple years (Groves et al. 2002). While similar studies have not been conducted with IYSV, this suggests that IYSV may persist in dandelion plants for multiple seasons. Conversely, common burdock survives only one winter before completing its life cycle, and an infected burdock plant is likely to be a source of inoculum for only one onion growing season. This may be especially important for IYSV persistence after cool, wet growing seasons as thrips populations are known to be negatively impacted by such conditions (Liu 2004). In addition to these reasons, the compact rosette growth habit of dandelion plants offer *T. tabaci* a suitable habitat. Moreover, dandelion may have the greatest impact on IYSV epidemiology among the candidate weed species that are likely sources for IYSV.

Knowledge of rates of acquisition and transmission of IYSV by *T. tabaci* among the most abundant weed species is important. While transmission efficiencies are unknown in weed species associated with *T. tabaci* and IYSV, Okazaki et al. (2009) evaluated acquisition and transmission rates of TSWV by *Frankliniella occidentals* (Pergande) (Thysanoptera: Thripidae) in sticky chickweed, *Cerastium glomeratum* Thuill., black nightshade, *Solanum nigrum* L., common chickweed, *Stellaria media* (L.) Vill., and *Galinsoga quadriradiata* Cav. TSWV acquisition rates by *F. occidentalis* for each species were 85.4, 73.6, 72.6, and 35.6%, respectively, and transmission rates were 76.4, 60.9, 61.3, and 29.9%, respectively. Their results indicated that weed species vary in their abilities to be sources of TSWV. IYSV and TSWV are closely related, so this degree of variability in acquisition and transmission may be likely for *T. tabaci* and weed hosts of IYSV. Analogous studies involving *T. tabaci* transmission efficiencies of IYSV from weeds to onions and vice versa will be important steps in identifying the most important weed sources of IYSV in the onion ecosystem.

More research on *T. tabaci* ecology and IYSV epidemiology is needed to develop effective management strategies. Such research should include investigation of the dispersal capabilities of *T. tabaci* and the effect of distance of weeds to onion crops on *T. tabaci* populations and IYSV incidence. Overwintering capabilities of IYSV in specific weeds as well as acquisition and transmission efficiencies should also be investigated. In particular, these findings will provide the information needed to determine if control of weeds in adjacent areas to onion fields is a worthwhile IYSV management strategy.

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Appendix 1. Winter-annual, biennial, and perennial weed species that were not determined as hosts of *T. tabaci* larvae. Weeds were sampled from the Elba Muck onion growing region near Elba, NY, in 2008 and 2009

Family Species	Common name	Habit[a]
Apiaceae		
Daucus carota L.	Wild carrot	B
Pastinaca sativa L.	Wild parsnip	B
Apocynaceae		
Apocynum cannabinum L.	Hemp dogbane	P
Asteraceae		
Achillea millefolium L.	Common yarrow	P
Centaurea stoebe L.	Spotted knapweed	P
Cirsium vulgare (Savi) Ten.	Bull thistle	B
Conyza canadensis (L.) Cronq.	Horseweed	P
Erigeron philadelphicus L.	Philadelphia fleabane	B/P
Hieracium canadense Michx	Canadian hawkweed	P
Hieracium caespitosum Dumort	Yellow hawkweed	P
Hypochaeris radicata L.	Catsear	P
Lactuca serriola L.	Prickly lettuce	SA/WA/P
Senecio vulgaris L.	Common groundsel	SA/WA
Sonchus arvensis L.	Perennial sowthistle	P
Symphyotrichum novae-angliae (L.) Nesom	New england aster	P
Brassicaceae		
Alliaria petiolata (Bieb.) Cavara & Grande	Garlic mustard	B
Descurainia sophia (L.) Webb ex Prantl	Flixweed	WA/SA
Hesperis matronalis L.	Dame's rocket	B/P
Rorippa palustris (L.) Bess.	Marsh yellow cress	SA/WA/P
Caryophyllaceae		
Cerastium fontanum Baumg.	Mouse ear chickweed	P
Saponaria officinalis L.	Bouncing bet	P
Silene latifolia Poir.	White campion	P
Dipsacaceae		
Dipsacus fullonum L.	Common teasel	B
Fabaceae		
Lotus corniculatus L.	Birdsfoot trefoil	P
Trifolium pratense L.	Red clover	P
Trifolium repens L.	White clover	P
Lamiaceae		
Lamium amplexicaule L.	Henbit	WA
Oxalidaceae		
Oxalis stricta L.	Woodsorrel	P
Phytolaccaceae		
Phytolacca americana L.	Am. pokeweed	P
Plantaginaceae		
Plantago major L.	Broadleaf plantain	P
Poaceae		
Bromus inermis Leyss.	Smooth brome	P
Bromus secalinus L.	Rye brome (cheat)	WA
Bromus tectorum L.	Downy brome	SA/WA
Dactylis glomerata L.	Orchardgrass	P
Elytrigia repens (L.) Gould	Quackgrass	P
Holcus lanatus L.	Common velvetgrass	P
Lolium multiflorum Lam.	Italian ryegrass	WA/B/P
Phleum pratense L.	Timothy	P
Phragmites australis (Cav.) Trin. Ex Steud.	Common reed	P
Poa annua L.	Annual bluegrass	WA
Poa compressa L.	Canada bluegrass	P
Ranunculaceae		
Ranunculus bulbosus L.	Bulbous buttercup	P
Rosaceae		
Potentilla norvegica L.	Rough cinquefoil	SA/WA/B/P
Potentilla recta L.	Sulphur cinquefoil	P
Rubus spp. (*R. occidentalis*, etc.)	Wild raspberry	B/P
Vitaceae		
Parthenocissus quinquefolia (L.) Planch.	Virginia creeper	P
Vitis labrusca L.	Fox grape	P

[a] SA = summer-annual, WA = winter-annual, B = biennial, P = perennial, and combinations indicate that multiple life histories are known to occur.