Thrips Settling, Oviposition and IYSV Distribution on Onion Foliage

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ABSTRACT *Thrips tabaci* Lindeman (Thysanoptera: Thripidae) adult and larval settling and oviposition on onion (*Allium cepa* L.) foliage were investigated in relation to leaf position and leaf length at prebulb plant growth stages under controlled conditions. In the laboratory, four and six adult females of *T. tabaci* were released on onion plants at three-leaf stage and six- to eight-leaf stage, respectively, and thrips egg, nymph, and adult count data were collected on each of the three inner most leaves at every 2-cm leaf segment. Thrips settling and oviposition parameters were quantified during the light period on the above ground portion of onion plants from the distal end of the bulb or leaf sheath "neck" through the tips of the foliage. Results from studies confirmed that distribution of thrips adults, nymphs, and eggs were skewed toward the base of the plant. The settling distributions of thrips adults and nymphs differed slightly from the egg distribution in that oviposition occurred all the way to the tip of the leaf while adults and nymphs were typically not observed near the tip. In a field study, the foliage was divided into three equal partitions, i.e., top, middle, basal thirds, and thrips adults by species, primarily *Frankliniella fusca* (Hinds) and *T. tabaci*, were collected from each partition to determine if there was a similar bias of all adult thrips toward the base of the plant. The results suggested that adults of different species appear to segregate along leaf length. Finally, thrips oviposition on 2-cm segments and Iris yellow spot virus positive leaf segments were quantified in the field, irrespective of thrips species. Both variables demonstrated a very similar pattern of bias toward the base of the plant and were significantly correlated.

KEY WORDS *Thrips tabaci*, *Frankliniella fusca*, Iris yellow spot virus, *Allium cepa*, Tospovirus

Onion (*Allium cepa* L.) is a high-value specialty vegetable crop in Georgia that is popular worldwide as Vidalia sweet onions. Onion, in Georgia, is grown as a winter crop in 12,000 acres with a total value of US$108,560 million in 2008 and US$82,908 million in 2009 (Boatright and McKissick 2010, National Agricultural Statistics Service [NASS] 2009). *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), also known as onion thrips, is an important pest of onions in Georgia (Sparks and Riley 2007) and worldwide (Edelson et al. 1986, Jenser and Szènàsi 2004). *T. tabaci* is the main vector of Iris Yellow Spot virus (IYSV) (Tospovirus: Bunyaviridae) (Nagata et al. 1999, Kritzman et al. 2001). Tobacco thrips, *Frankliniella fusca* (Hinds), has recently been reported to be a vector of IYSV, albeit a less competent vector than *T. tabaci* (Srinivasan et al. 2012). In Georgia, IYSV was first reported in Vidalia onions in 2003 (Mullis et al. 2004). Since its first report, IYSV was found in onion every year in the growing regions of the state. Thrips are thigmotactic and often seek narrow spaces to live and feed (Kirk 1997). In onions, the narrow spaces at the base of the neck are tightly pressed by the inner leaves, resulting in an attractive niche for thrips populations (Rossiter 1980). As the distribution of IYSV on the onion plant tends to be toward the base of the plant (Boateng and Schwartz 2013), we suspected that the presence of thrips on onion foliage, e.g., settling of adults and immatures and oviposition, would be positively correlated with IYSV distribution on the plant.

Recent studies conducted in Australia in onion fields documented the within-leaf distribution of eggs on the onion plants that demonstrated a bias toward the base of the plant (Mo et al. 2008). However, further studies have been needed in *A. cepa* to relate the distribution of settling of thrips adults, nymphs, and eggs to IYSV distribution in the plant. Virus distribution in leek, *Allium ampeloprasum* L, tends to be quite variable under field conditions (Smith et al. 2006). Unlike most tospoviruses, IYSV causes localized infection in which the virus moves less systemically (Bag et al. 2009, Pappu et al. 2009). A further complication is that isolates of IYSV can be biologically distinct in terms of symptom severity, systemic movement, and local

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distribution in leaf tissue (Bag et al. 2012). The first objective of this study was to determine the distribution of onion thrips adults, nymphs, and eggs in Georgia on the onion plant relative to leaf length under controlled conditions. The hypothesis was that all stages of thrips would exhibit a biased distribution toward the base of the onion plant, confirming the results of Mo et al. (2008). The second objective of this study was to assess the adult thrips distribution under field conditions Georgia where multiple species coexist (Riley et al. 2014). A third objective was to characterize thrips' ovipositon (irrespective of species) and percent IYSV positive onion foliage on onion foliage relative to leaf length under field conditions. The hypothesis was that the distribution of thrips eggs and IYSV in the leaf tissue would be correlated. The overriding hypothesis for the last two objectives was that all variables would similarly exhibit a distribution biased toward the base of the onion plant.

Materials and Methods

Growth Chamber Thrips Settling and Oviposition Study. The settling and oviposition of *T. tabaci* were investigated at three-leaf stage and six- to eight-leaf stage of onion plants (stages 3 and 5, respectively, Schwartz 2011) relative to leaf position L1 (inner most), L2 and L3 (outer most) for every 2 cm of the leaf length (Fig. 1) using 12 plants, each serving as a replicate. The two parameters were observed by setting up a whole plant bioassay using an insect cage measuring 47.5 by 47.5 by 47.5 cm with fine mesh screen (MegaView Science Co., Taichung, Taiwan). Onion seeds 'Pegasus Hybrid Onion' (Seminis, Oxnard, CA) were placed in germination trays and allowed to germinate and grow until the two-leaf stage 2 (Schwartz 2011) in growth chambers at 25°C. The seedlings were then transferred to the greenhouse and transplanted into 10-cm pots using "LT 5 Mix" (Sun Gro Horticulture Dist. Bellevue, WA). Before introducing the thrips, onto the stage 3 and stage 5 onion plants, the surface of the each pot was sealed with parafilm to prevent escape of thrips into the soil. Four adults of *T. tabaci* were released on stage 3 onion plants and six adults were placed on the stage 5 onion plants and placed in the insect cage. Adults were allowed to settle for 24 h. The position of thrips adults and emerging larvae on the leaf were recorded on the hour from 8:00 a.m. to 5:00 p.m. each day for 5 d (~30 min to sample leaves on all replicates). To evaluate thrips oviposition on onion plants, the same treatments were used except that thrips were allowed to oviposit for 6 d before removal of adults. Onion leaves L1 to L3 were harvested and oviposition sites were counted by following a standard lacto-phenol acid fuschin staining technique (Parella and Robb 1982, Nuessly et al. 1995). To determine the oviposition sites, the intact leaf tissues from the plant were cut from the plant base and decolorized by boiling 3–5 min in the lacto phenol acid fuschin solution under a fume hood. Stained leaves were cooled for 3–5 h, and excess stain was removed with warm water. Leaves at every 2-cm section were examined under a stereomicroscope for oviposition sites indicated by eggs and purple rings (Parella and Robb 1982).

Adult Settling Study in the Field. Ten onion plants were randomly selected in field plots at the Vidalia Onion and Vegetable Research Center (VORC), Reidsville, GA. Thrips settling on top, middle, and bottom (or basal) third leaf sections of onion plants in growth stages 5–8 (Schwartz 2011) were recorded. Observations were recorded during bulb formation and adults were counted on all leaves of the onion plant. Leaf sheaths that were dry and unwrapped around the base of the plant were not included. The locations of adults on the plant were recorded by thrips species for every 15 min starting at 8.30 a.m in the morning for 2 h. *F. fusca* adults were separated from *T. tabaci* adults based on a 10× magnification hand lens, so there was limited taxonomic accuracy in the field; however, because of strong color differences between species (Riley et al. 2011) and predominance of these two species in Vidalia onions (Riley et al. 2014), it was deemed sufficient to test for species segregation on plants.

Egg Distribution Study in the Field. For thrips egg counts, irrespective of thrips species in the field, 10 randomly selected onions plants were collected fortnightly during March, April, and May of 2009 in the field plots at the VORC. Onion plants were cut close to the ground, sealed in a zip lock 3.8-liter bag, and brought back to the Coastal Plain Experiment Station, Tifton, GA. Only the center three youngest leaves were sampled, stained, and counted for eggs. The leaf positions for all the stages of onions sampled in the onion plant were designated L1 (youngest leaf) followed by L2 and L3 (third from center). To determine the oviposition sites, the entire intact leaf was cut from the plant and the previously described lacto-phenol acid fuschin staining technique (Nuessly et al. 1995, Parella and Robb 1982) was used to count thrips eggs and egg-laying sites for every 2-cm length from the leaf collar at the base of the onion plant (Fig. 1).

IYSV Distribution in Onion Leaves. Distribution of IYSV within the onion foliage was determined from field-collected onions during the spring of 2007 and 2009 at the VORC. IYSV in mature onion plants was measured by randomly selecting the onion plants. Onion plants were cut close to the ground, sealed in a 3.8-liter zip-lock bag, and brought back to the laboratory to determine the presence of IYSV in leaf segments. In the first year, sample sites were randomly selected in the field and 90 onion plants sampled with preference given to leaves with symptomatic lesions or signs of heavy thrips feeding for IYSV testing. Each leaf was cut into 2.5-cm sections and tested for the presence of IYSV by a double antibody sandwich enzyme-linked immunosorbent assay (DAS ELISA; Clark and Adams 1977, Cortês et al. 1998). Primary antibody (anti-IYSV IgG) was used in a dilution ratio of 1:200 and the secondary antibody (anti-IYSV IgG conjugated with alkaline phosphatase) was used with the same dilution ratio (Agdia, Elkhart, IN). In the second year, 10 randomly selected

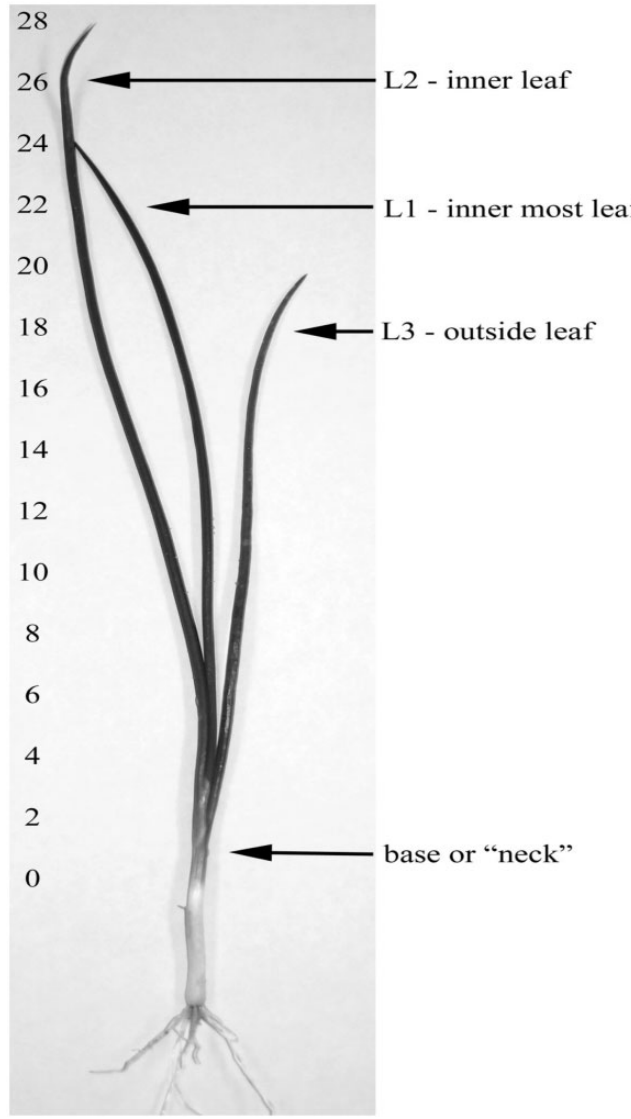

Fig. 1. Leaf positions on the onion seedling to determine settling by *T. tabaci* adults and immatures with numbers representing 2-cm sections.

onion plants were collected in April and three middle leaves from each plant were cut into 2-cm sections and tested for the presence of IYSV by DAS ELISA, as previously described.

Thrips counts from all studies were subjected to analysis of variance using a generalized linear model using PROC GLM in SAS (SAS Institute 2004, Cary, NC) with plants as replicates. Repeated measures over time were averaged, as the objective was to get as accurate a measure on the leaf segment as possible, and the analysis of variance was conducted on average counts per leaf segment. Fisher's least significant difference method was used for mean separation at a 95% confidence level.

Results

Growth Chamber Thrips Settling and Oviposition Study. *T. tabaci* adults ($F = 152$; df = 15, 329; $P < 0.001$), nymphs ($F = 12.5$; df = 15, 329; $P < 0.001$), and eggs ($F = 19.1$; df = 15, 328; $P < 0.001$) on three-leaf onion plants showed a clear preference for the base of the foliage across all leaves (Table 1). In the three-leaf onions, we considered "0" cm as the length of the contiguous leaf sheath from the distal end of the immature bulb to where the leaves separated. Settling of *T. tabaci* adults and immatures on the inner most leaf (L1) was also skewed toward the base of the plant (Fig. 2A). The adult thrips settling varied significantly across L1 leaf segments ($F = 17.1$; df = 15, 164; $P < 0.001$). On the leaf segment 2–8 cm, adults

Table 1. Settling of *T. tabaci* adults, immatures, and oviposition by leaf length

Leaf length (cm)	Three-leaf stage onion plant			Six- to eight-leaf onion plant		
	Adults	Immatures	Eggs	Adults	Immatures	Eggs
0	0.41a	0.65a	0.33e	0.55a	0.05a	1.7c
2	0.06b	0.17b	5.94b	0.06b	0.05a	9.1a
4	0.05bc	0.09bc	8.31a	0.04bc	0.02ab	8.6a
6	0.02cd	0.15bc	6.2b	0.04bcd	0.01b	6.4b
8	0.02d	0.17b	4.1c	0.03bcd	0.00b	2.9c
10	0.01de	0.12bc	3.7c	0.03bcd	0.00b	1.9cd
12	0.01de	0.12bc	2.6cd	0.02cd	0.00b	1.3de
14	0.01de	0.18b	1.5de	0.01d	0.00b	0.9ef
16	0.01de	0.12bc	1.5de	0.01d	0.00b	0.4ef
18	0.01de	0.05bc	1.4de	0.01d	0.00b	0.4ef
20	0.01de	0.00c	1.4de	0.00d	0.00b	0.3f
22	0.00de	0.00c	0.54e	0.00d	0.00b	0.1ef
24	0.00e	0.00c	0.32e	0.00d	0.00b	0.0f
26	0.00e	0.00c	0.19e	0.00d	0.00b	0.1f
28	0.00e	0.00c	0.05e	0.00d	0.00b	0.0f
30	0.00e	0.00c	0.03e	0.00d	0.00b	0.0f

The counts represent means ($n = 12$). Means within the columns are not significant if followed by the same letter (LSD, $P < 0.05$).

concentrated by 81% with less at the base and at the tip. Similarly, 61% of immature stages of thrips concentrated on leaf segment 2–8 cm with less at the base and at the tip. The immature thrips settling varied significantly across the L1 leaf segments ($F = 2.45$; df = 15, 164; $P < 0.01$). Settling of *T. tabaci* adults and immatures on L2 tended toward the middle of the plant (Fig. 2B) with only 47% of adults concentrated on leaf segment 2–8 cm and none toward the tip. However, there was not a significant effect observed with the adult thrips settling on L2 leaf segments ($F = 1.25$; df = 15, 165; $P = 0.24$). Similarly, 70% of immatures concentrated on leaf segment 6–14 cm. A significant segment effect was observed with the immature thrips settling by the L2 leaf segments ($F = 2.06$; df = 15, 165; $P < 0.01$). On the outer most leaf (L3), 60% of the adults ($F = 233$; df = 15, 165; $P < 0.001$) and 78% of the immatures ($F = 32$; df = 15, 165; $P < 0.001$) were concentrated at the base of the onion plant (Fig. 2C). Settling of *T. tabaci* adults and immatures over all leaves was skewed toward the base of the plant. Adults and immatures concentrated on the base of the leaf segment, followed by the middle, and almost none toward the tip of the leaves (Table 1).

Oviposition of *T. tabaci* by leaf length on three-leaf onion plants showed a clear preference toward the base ($F = 19.1$; df = 15, 328; $P < 0.0001$) but was more spread out over the length of the leaf (Table 1). On the inner most leaf (L1), 52% of the eggs ($F = 5.8$; df = 15, 165; $P < 0.0001$) were concentrated on the leaf segment 4–8 cm in the middle (Fig. 3A). A similar trend was seen with *T. tabaci* oviposition on L2 (Fig. 3B), with 76% of the eggs concentrated on the leaf segment 2–10 cm ($F = 8.4$; df = 15, 164; $P < 0.0001$). Oviposition of *T. tabaci* on outer most leaf (L3) exhibited a similar pattern (Fig. 3C; $F = 7.2$; df = 15, 164; $P < 0.0001$). Overall, oviposition of *T. tabaci* was similarly distributed as the adults and immature, with the difference that eggs occurred all the way to the leaf tip (Table 1).

On onion plants with six to eight leaves, the center three upright leaves were considered for observing settling and oviposition. Settling of *T. tabaci* adults ($F = 282$; df = 15, 330; $P < 0.001$) and immatures ($F = 3.9$; df = 15, 330; $P < 0.001$) on a—six- to eight-leaf onion plant was similar to that of the three-leaf onion plant, except that immatures were more clumped at the base (Table 1). On the inner most leaf (L1), 89% of the observed adults concentrated on leaf segment 2–10 cm (Fig. 4A; $F = 26$; df = 15, 165; $P < 0.001$). Also, 92% of immatures concentrated on leaf segment 2–8 cm ($F = 2.1$; df = 15, 165; $P < 0.01$). A similar trend was observed with the settling of *T. tabaci* adults on L2 (Fig. 4B) with 93% of adults concentrated on leaf segment 2–12 cm ($F = 6.3$; df = 15, 165; $P < 0.001$). No immatures were seen on the base or on tip of the leaf ($F = 0.96$; df = 15, 165; $P = 0.50$). On the leaf (L3), *T. tabaci* adults ($F = 342$; df = 15, 165; $P < 0.001$) were concentrated on the leaf segment "0" cm and 95% of immatures ($F = 3.0$; df = 15, 165; $P < 0.001$) were concentrated on leaf segment 2–8 cm (Fig. 4C). Settling of *T. tabaci* adults and immatures on the —six- to eight-leaf stage relative to leaf segment was skewed toward the base of the plant, followed by adults settling on the leaf segments < 6 cm from the base (Table 1).

Oviposition of *T. tabaci* by leaf length on six- to eight-leaf onion plant also showed the same preference toward the base of the plant ($F = 46$; df = 15, 326; $P < 0.001$). As in the case of plants with three leaves, eggs were spread out along the length of the leaf (Table 1). On the innermost leaf (L1), 73% of the eggs were concentrated on the leaf segment 2–6 cm with less in the middle and none toward the tip (Fig. 5A; $F = 13.7$; df = 15, 163; $P < 0.001$). A similar trend was observed with *T. tabaci* oviposition on L2 (Fig. 5B) with 79% of eggs concentrated on the leaf segment 2–8 cm ($F = 15.3$; df = 15, 164; $P < 0.001$). On L3, 81% of eggs were concentrated on the leaf segment 0–4 cm ($F = 7.3$; df = 15, 164; $P < 0.001$; Fig. 5C). Overall, oviposition of *T. tabaci* was skewed toward the base of the plant across all the three leaves (Table 1).

Adult Settling Study in the Field. Field study results on the distribution of thrips adults within the onion foliage recorded in the field averaged over April and May of 2009 indicated that under mixed species conditions, *T. tabaci* ($F = 25$; df = 2, 18; $P < 0.001$) appeared to occur more at the top portions of the leaf in onion plant and *F. fusca* ($F = 69$; df = 2, 17; $P < 0.001$) was more prevalent on the middle and basal portions (Fig. 6). This was possibly because of competition between these species on onion (Riley et al. 2014). The prevalence of *F. fusca* in the middle portion of the plant was associated with the leaf fold present during onion growth stages 5–8 (Schwartz 2011).

Egg Distribution Study in the Field. The summed distribution of thrips eggs, irrespective of species for the onion plants collected in the field analyzed by 2-cm leaf segments, clearly showed a distribution skewed toward the base of the onion plant (Fig. 7). Egg distribution analyzed by date starting from—two- to three-leaf stage in late February indicated that the eggs were spread out across the leaf length with 43%

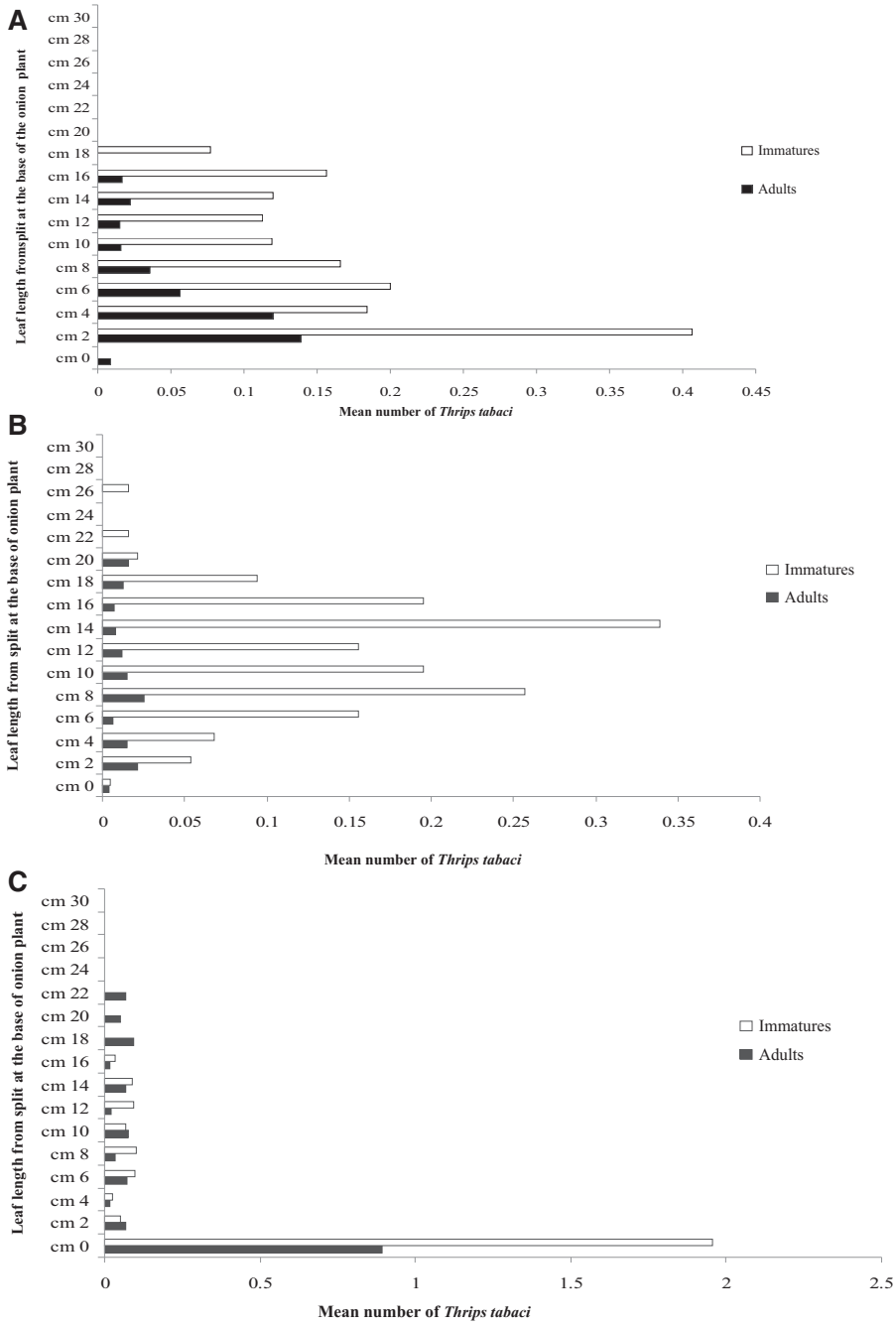

Fig. 2. Settling of *T. tabaci* adults and nymphs on (A) L1 the innermost leaf, (B) the L2 inside leaf, and (C) the outermost leaf at three-leaf stage onion plant.

of eggs concentrated on the leaf segment 2–10 cm. Eggs were spread out across the leaf length in the middle and toward the tip of the leaves. A significant leaf segment effect was observed on the distribution of thrips eggs ($F = 1.63$; df = 24, 417; $P < 0.03$). The eggs sampled during early March were found toward the base of the onion leaf with 82% of the eggs on 2–16 cm of the leaf segments, but the distribution was not significant ($F = 1.39$; df = 20, 364; $P = 0.12$). The mean number of eggs in March followed a similar distribution pattern as that of February, but was not significant ($F = 1.30$; df = 23, 600; $P = 0.16$). The distribution of eggs during late March indicated a more spread out pattern of the eggs across the leaf length with 58% of eggs concentrated on the leaf segments 14–34 cm with eggs spread out across the leaf length toward the base

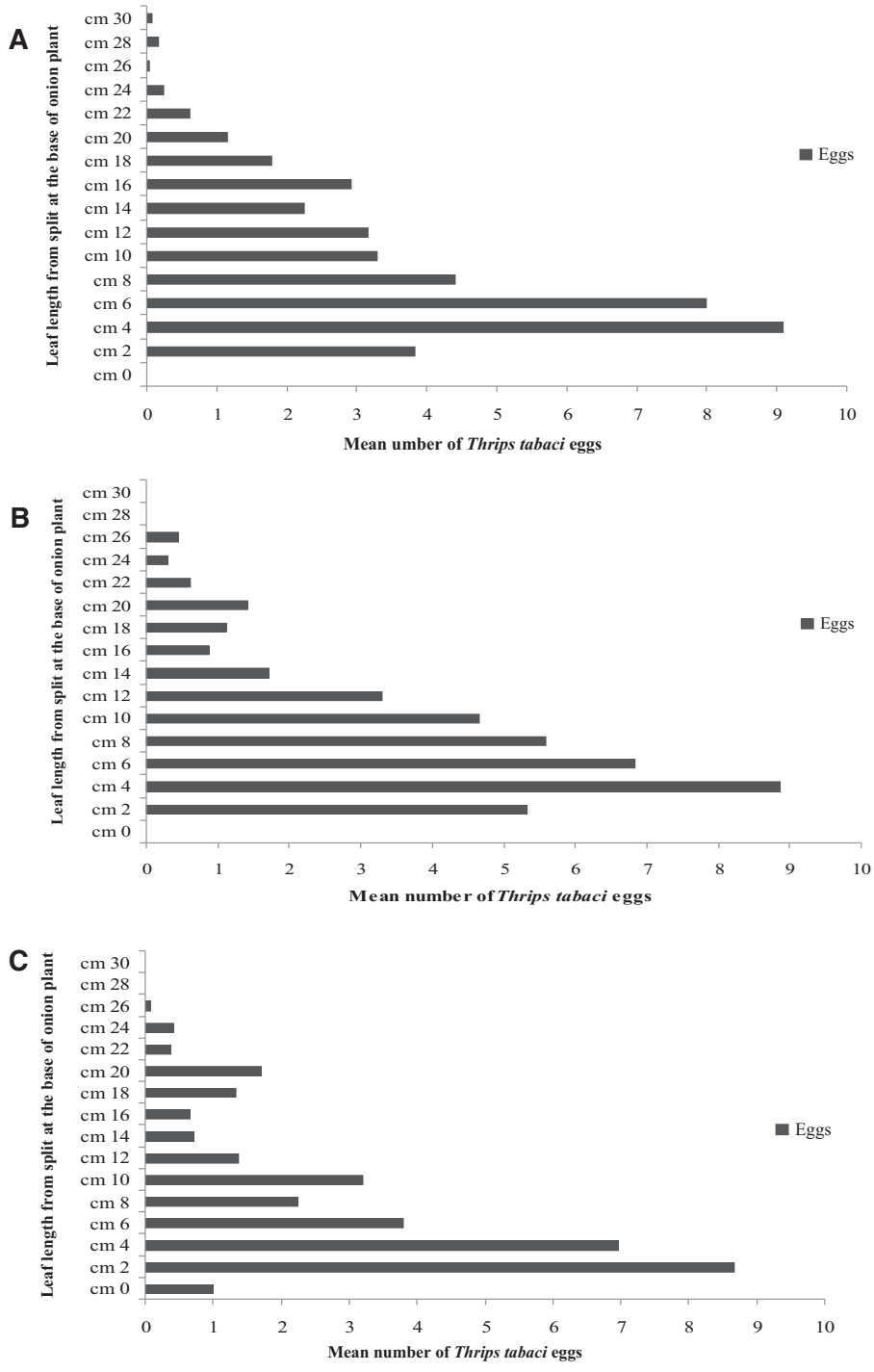

Fig. 3. Oviposition of *T. tabaci* on (A) L1 the innermost leaf, (B) L2 the inside leaf, and (C) L3 the outermost leaf at three-leaf stage onion plant.

and tip of the leaves. In March, there was a significant leaf segment effect on thrips egg distribution ($F = 1.56$; df = 30, 522; $P < 0.03$). The distribution of eggs in the field on the onion plants in April were skewed toward the base of the plant with 78% of the eggs were concentrated on the leaf segments 2–24 cm and eggs distributed to the tip of the leaves, but position effect on thrips egg distribution was not significant on that date ($F = 1.03$; df = 25, 687; $P = 0.42$). The egg distribution in late April was bimodal with 56% of eggs

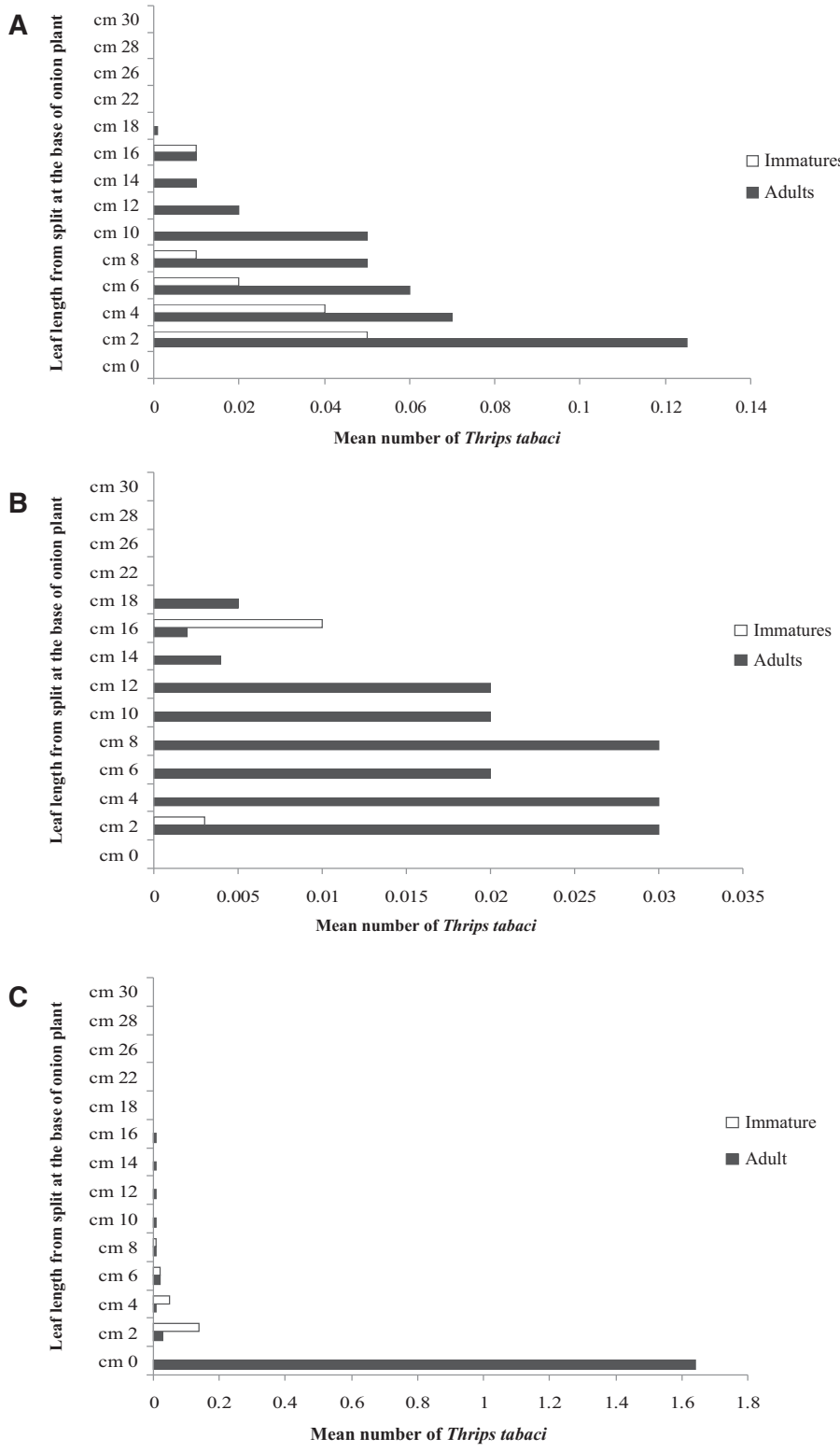

Fig. 4. Settling of *T. tabaci* adults and immatures on (A) L1 the innermost leaf, (B) L2 the inside leaf, and (C) L3 the outermost leaf at—six- to eight-leaf stage onion plant.

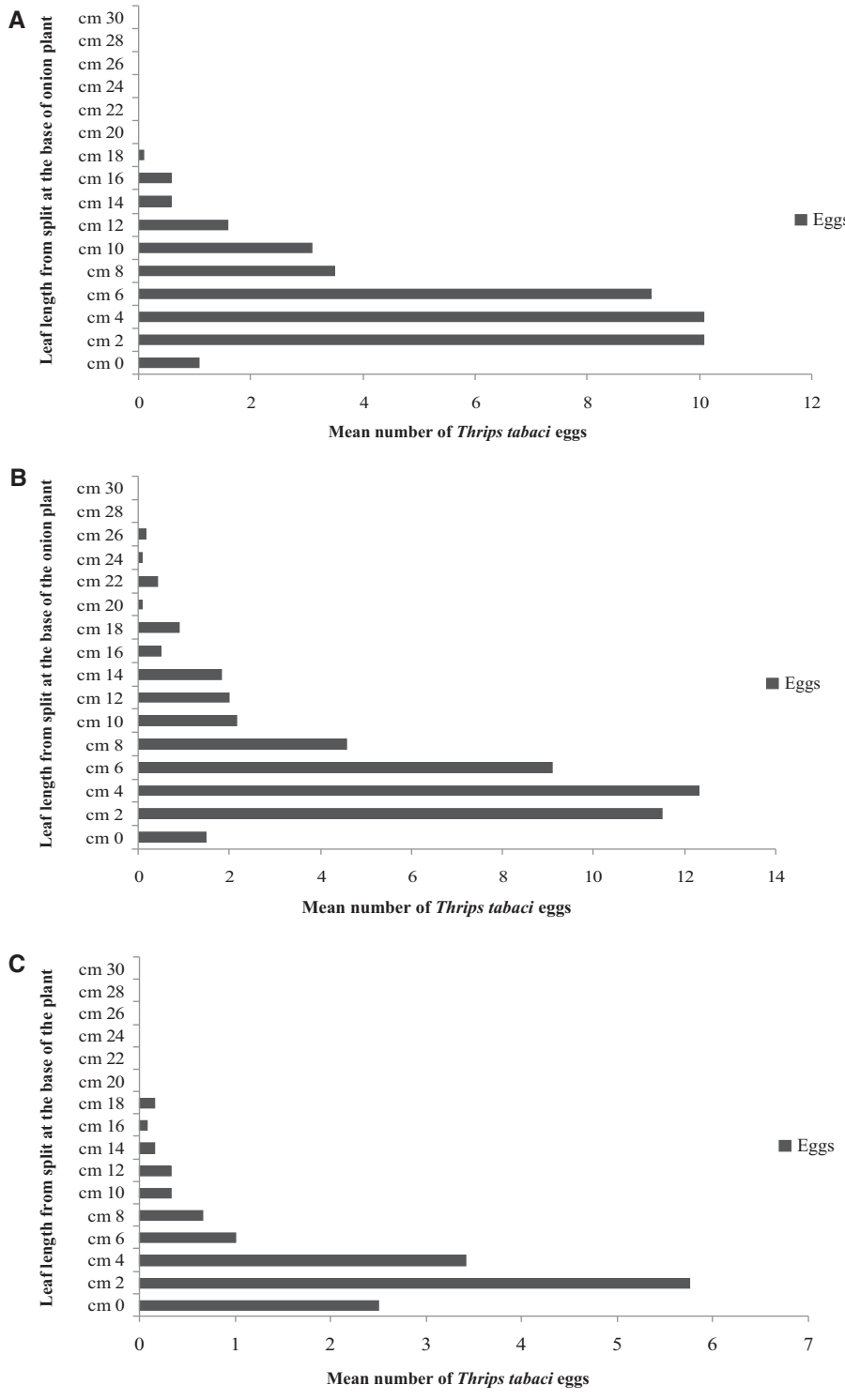

Fig. 5. Oviposition of *T. tabaci* on (A) L1 the innermost leaf, (B) L2 the inside leaf, and (C) L3 the outermost leaf at six- to eight-leaf stage onion plant.

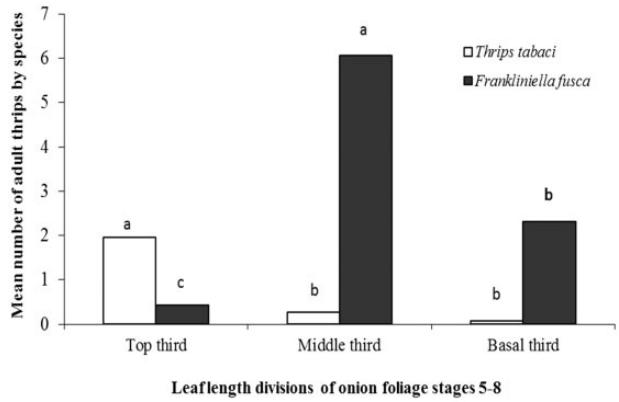

Fig. 6. Distribution of *T. tabaci* and *F. fusca* on onion plants in the field relative to leaf position for onion stages 5–8 (Schwartz 2011). Means represented by columns within species are significantly different if labeled by different letters, least significant difference (LSD) test, $P < 0.05$.

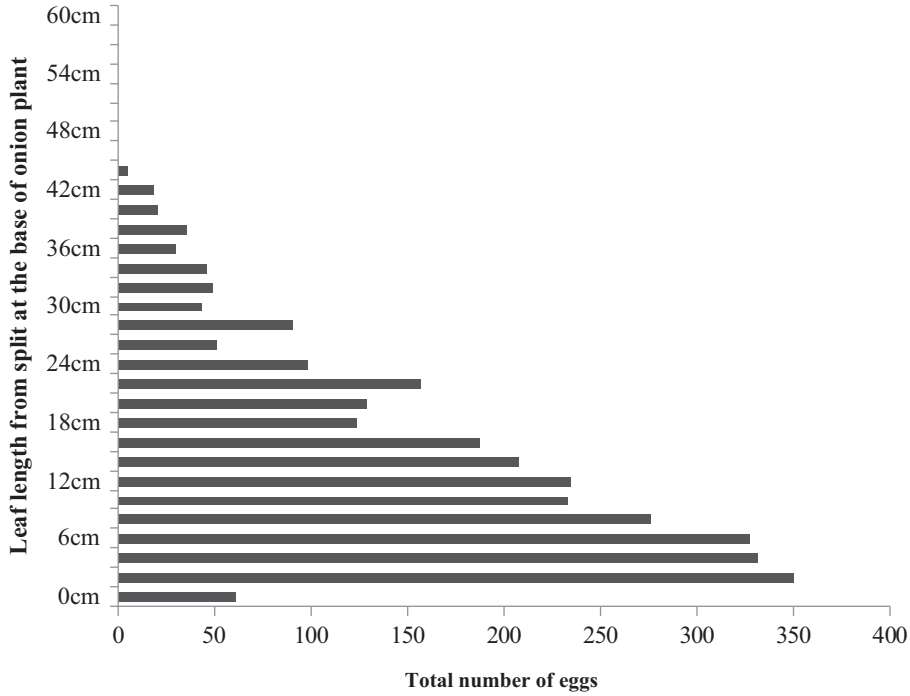

Fig. 7. Total number of thrips eggs sampled in the field relative to leaf length in 2009.

concentrated on 0–16-cm leaf segments followed by egg distribution toward the middle and tip of the leaves and the position effect on thrips egg distribution was significant ($F = 2.58$; df = 21, 416; $P < 0.001$). This is when many of the leaves in the field are "flagging," bending in the middle of the leaf to allow thrips to congregate in the leaf fold at growth stage 4 (Schwartz 2011). By the end of the season in early May, the distribution of eggs followed the earlier pattern with egg distribution skewed more toward the base of the plant with 70% of the egg distribution concentrated on 2–16-cm leaf segments with egg distribution in the middle and none toward the tip of the leaves, but the position effect was not significant ($F = 1.00$; df = 23, 456; $P = 0.47$).

The mean number of eggs distributed in the field relative to leaf position L1 were skewed toward the base of the plant with 69% of the eggs concentrated on 2–14-cm leaf segments ($F = 3.36$; df = 17, 903; $P < 0.001$). Egg distribution within the leaf position L2, followed the earlier pattern with 63% of eggs were concentrated on 2–22-cm leaf segments ($F = 1.63$; df = 30,

1514; $P < 0.02$). For the leaf L3, the distribution of eggs was strongly skewed toward the base of the plant with 91% of the eggs were concentrated on 10–18-cm leaf segments, but was not significant ($F = 0.71$; df = 23, 1161; $P = 0.84$). Over all leaves, the sum total of eggs analyzed by date, leaf position, and every 2 cm relative to the leaf length from the split at the base of the onion plant indicated that the egg distribution was skewed more toward the base of the onion plant (Fig. 7).

IYSV Distribution in Onion Leaves. Results on the distribution of IYSV within the onion foliage collected from the field samples during March 2007 indicated that IYSV was biased toward the base of onion leaf (Fig. 8A) relative to leaf length ($F = 4.30$; df = 19, 492; $P < 0.001$). The IYSV distribution within the leaf was highly variable with no leaf in which 100% of the segments tested positive, suggesting that IYSV distribution in the leaf tissue is not uniform according to DAS ELISA. Overall, the total number of IYSV positive onion leaf segments analyzed over all the leaves in March indicated that the number of IYSV positive segments were 63% higher on 5.1–15 cm leaf segments with less distribution of the virus in the middle and toward the tip of the onion leaves. Only 27.5% of the individual 2.5-cm segments ($n = 527$) tested positive with a range from 5 to 91% of the leaf segments testing positive. Results on the distribution of IYSV within the onion foliage collected from the field samples during April of 2009 indicated that the distribution of the IYSV was uneven, but still biased toward the base of the onion plant (Fig. 8B). In April, the number of onion leaf segments that tested positive were 71% more on 2–26 cm leaf segments with less number of positive leaf segments toward tip of the leaves (Fig. 8B), but the effect was not significant ($F = 1.34$; df = 25, 189; $P = 0.14$).

Comparing sums from Figs. 7 and 8A, the within-leaf distribution of eggs on the onion plants significantly correlated with the number of IYSV positive segments for the field samples tested in fall 2007 ($R = 0.92$; $P < 0.001$). Thus, there were some similarities between egg and IYSV distributions within the plant relative to leaf length in the onion plant.

Discussion

The distribution of thrips oviposition by leaf length was skewed toward the base of the plant, similar to that reported by Mo et al. (2008). However, in this study, the distribution of adults and immatures was even more biased toward the base of the plant than eggs. Differences between the mobile and immobile stages of thrips could simply relate to eggs being a cumulative measure of activity. Thrips are generally thigmotactic, preferring to spend time in or near tightly protected spaces on the plant surface, such as on the side of folded leaf surfaces or in tightly wrapped leaf sheaths for protection from predators such as *Orius* spp. (Kirk 1997). In the early stages of the plant growth, the onion leaves are straight (Schwartz 2011). As the plants mature, leaves begin to have extensive leaf folding, which provides additional protected spaces for thrips higher up on the leaf tube. In stage 5 onion plants, the distribution of eggs still occurred significantly toward the base of the plant. The adult settling data showed that, although clumped at the base, thrips must be spending some time out on the leaf laying eggs. Our data indicated that the distribution of thrips nymphs was more similar to the egg distribution in the onion plant studies. Thus, immatures might be taking more time to migrate to the protected sheaths than adults.

In the field, the adult thrips species analyzed over both the dates and leaf positions suggested that *T. tabaci* spatially segregated from *F. fusca* along leaf length. The distribution of *T. tabaci* and *F. fusca* by time indicated that there was no temporal displacement of thrips species. Both the species were observed on the onion more during the morning hours between 8:45 to 9:30 a.m. than in the later part of the day, similar to that reported by Sites et al. (1991). Based on these limited late season observations, it appears that *T. tabaci* and *F. fusca* have a tendency to segregate along leaf length in the field possibly because of thrips competition (Paini et al. 2008, Riley et al. 2014).

Within-leaf distribution of thrips eggs in the field was skewed more toward the base of the onion plant. Results on the distribution of IYSV within the onion foliage collected from the field samples in Georgia during 2007 and 2009 indicated that IYSV is consistently limited in the onion leaves. However, the number of onion leaf segments that tested IYSV-positive per leaf from the base of the plant in the field samples was biased toward the base of the onion plant with less number of positive IYSV leaf segments in the middle and toward the tip of the leaves. This is consistent with the findings of Boateng and Schwartz (2013), who reported more IYSV titer in the basal third of sampled onion foliage. Smith et al. (2006) reported a different distribution of IYSV in leek, but the plant structure is slightly different in leek, and thrips distribution will also likely be affected by this structure. Also, IYSV biotypes could differ in the level of systemic movement (Bag et al. 2012). In this study, results show that distribution of detectable virus in onion leaves is associated with thrips' presence on the foliage. Bag et al. (2012) demonstrated that local IYSV lesions eventually coalesce and render leaves necrotic by 40 days post inoculation. We propose that the distribution of IYSV in onion leaf tissue is highly associated with thrips presence on the leaf, i.e., IYSV has initially limited systemic distribution in the onion plants and is concentrated near the points of thrips settling, oviposition, and feeding.

Management of thrips in onions has shifted from controlling thrips to prevent direct feeding damage (Childers 1997) and the subsequent reduction of bulb size (Riley and Batal 1998) to additional concerns associated with plant virus transmission (Gent et al. 2006, Pappu et al. 2009, Pozzer et al. 1999). IYSV was documented in Georgia in 2004 (Mullis et al. 2004) and was primarily associated with the thrips vector *T. tabaci*

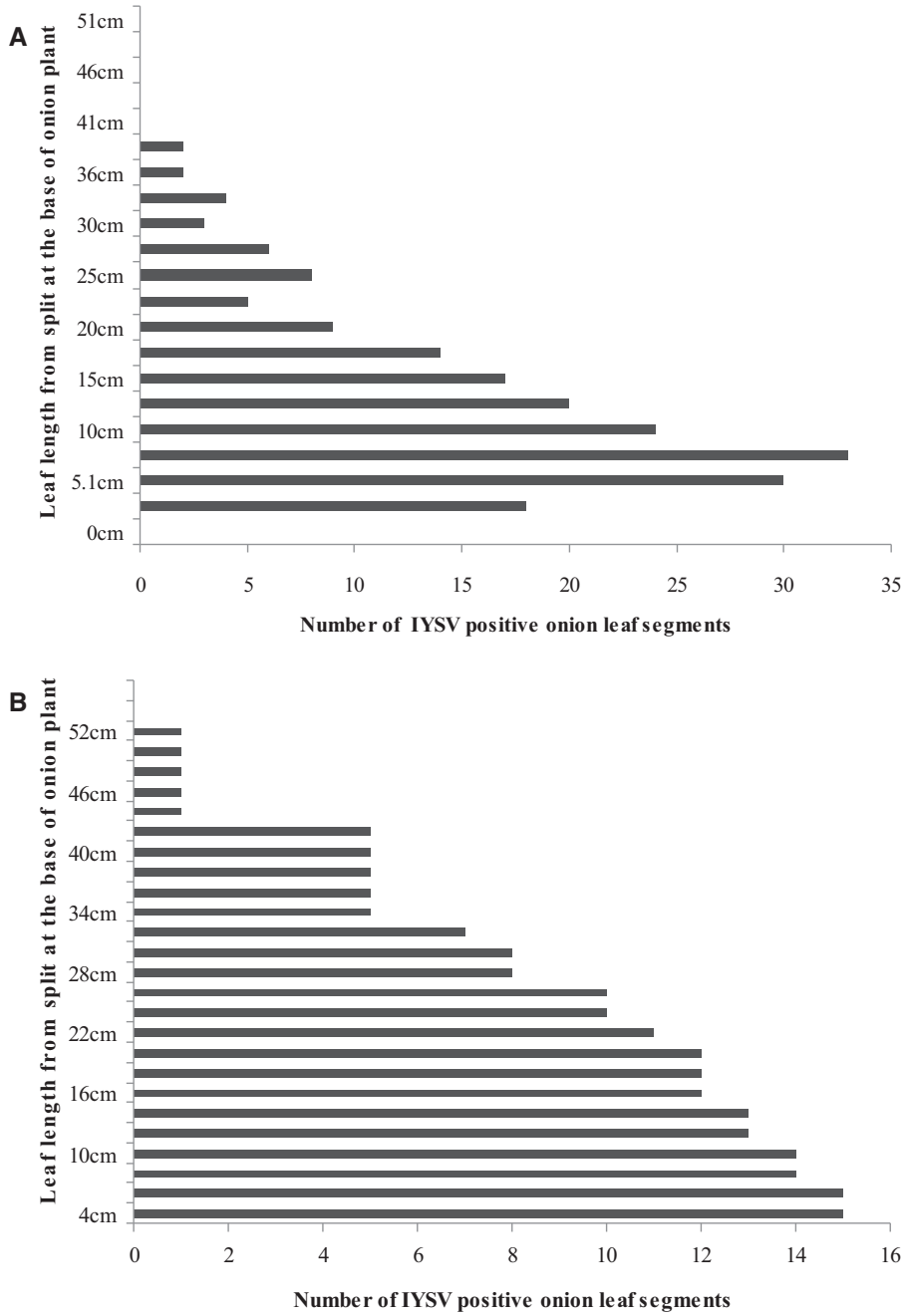

Fig. 8. Total IYSV-positive leaf segments per length of onion leaf sampled in the field during (A) March 2007 ($n = 33$ plants) and (B) over both dates in the field during 2009 ($n = 30$ plants).

(Nischwitz et al. 2007). *T. tabaci* has increased in the past decade in Georgia, but occurs in smaller proportions than *F. fusca* in the Vidalia onion production area (Riley et al. 2014). Economic loss due to IYSV in Georgia has not yet been reported, even though the virus is present in the Vidalia onions, as recorded in this study. Winter or cool season production of Georgia's onion may offer some protection from losses due to IYSV either directly through reduced plant–virus interaction or indirectly by cooler temperatures favoring *F. fusca* (Riley et al 2014), a less efficient vector of IYSV (Srinivasan et al. 2012). We suspected that the distribution of the virus in the plant was spatially associated with the distribution and frequency of the thrips vectors. If so, a reduction of thrips could directly impact the intensity and distribution of IYSV in the crop.

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