ABSTRACT A micro-cage bioassay was developed to test the effect of slash pine pollen (Pinus elliottii Engelm.) supplementation to a whole onion plant (Allium cepa L. variety Pegasus) diet on thrips (Thysanoptera: Thripidae) reproductive parameters. Frankliniella fusca (Hinds) females were placed on two to three-leaf stage onion seedling under a treatment of either slash pine (Pinus elliottii Engelm.) pollen dusting (a pollen supplement) or no pollen treatment. Adult survival, net oviposition, and offspring produced over a series of ten 2-d intervals were recorded. From these values, $l_x$, $l_xm_x$, and $R_v$ values were constructed. A trimodal distribution of oviposition was observed with the pollen supplement. Increased oviposition rates led to higher female offspring production per female and to a four-fold increase in $F.$ fusca net reproduction on pollen-treated onions.

KEY WORDS Frankliniella fusca, thrips reproduction, life table, onion, pollen

Thrips have been described as opportunists: able to survive on poor hosts until nutritionally superior hosts are available, whereupon increased reproduction leads to rapidly accelerating population growth (Mound and Teulon 1995). Although nutritional requirements and host preferences vary among species, nutritious thrips hosts have been characterized as rich in available amino acids (Fennah 1963, Kirk 1997, Brodebeck et al. 2001). Pollen grains contain some of the highest amino acid, or dietary nitrogen, levels of plant parts accessible to thrips—much higher than most leaf foliage (Virtanen and Kari 1955, Kirk 1995)—and thus could be a nutritious supplement to a thrips diet. Multiple species of thrips have been observed consuming pollen (Kirk 1995). In fact, pollen supplementation has increased developmental and reproductive rates in many thrips species. The following thrips species exhibited a significant increase in oviposition rates with pollen supplementation: Cera
tothripoides cameroni Bagnall (Kirk 1985), Cerato-
thrips ericae (Haliday) (Kirk 1985), Frankliniella in-
tonsa (Trybom) (Murai and Ishii 1982), F. schultzei
(Trybom) (Annadurai and Morrison 1987), Kako-
thrips pisicorouos (Westw.) (Kirk 1985), Taeniothrips inconsequens (Uzel) (Leskey et al. 1997), Thrips juc-
cipennis Haliday (Kirk 1985), T. imaginis Bagnall (An
drewartha and Kilpatrick 1951), T. obscuratus (Craw-
ford) (Teulon and Penman 1991), and F. occidentalis
(Pergande) (Hulshof et al. 2003), and F. fusca (Hinds)
(Riley et al. 2007).

Not all species respond to an equal effect, however. For example, the effect of pollen on tobacco thrips, F. fusca, reproduction was not as pronounced as that of western flower thrips, F. occidentalis (Riley et al. 2007). Riley et al. (2007) found that pine pollen dusted on tomato (Solanum lycopersicum L.) and peanut (Arachis hypogaea L.) leaves significantly increased western flower thrips oviposition rates by $\approx200\%$, yet those of tobacco thrips were increased significantly on peanut to a lesser degree and not significantly increased on tomato. This might be expected, because we have observed the tobacco thrips to be primarily a foliage feeder. Based on these data, we suspect tobacco thrips to have lower dietary nitrogen requirements for reproduction than western flower thrips. Even so, as variations in foliar nitrogen content and host quality occur among crops, tobacco thrips could exhibit an increase in reproduction with a high-nitro-
gen dietary supplement, such as pollen, on host foliage with relatively lower nitrogen content.

The tobacco thrips is an important pest of onions (Allium cepa L.) in Georgia (Riley and Batal 1998). Onions are an economically important crop in Georgia, grown on 12,000 acres of land with a production value of over $20$ million in 2008 (NASS 2009). Although tobacco thrips reproduce slowly through the winter on Georgia onions, they increase through early spring to reach peak population size in March (Riley and Batal 2000). In Georgia tomato, tobacco thrips and western flower thrips peak in April to May (Riley and Pappu 2000, 2004). Understanding the stimuli that contribute to this large springtime population growth in tobacco thrips can result in better prediction of population dynamics.

One possible factor affecting western flower and tobacco thrips population dynamics during early
spring in the Southeast is an annual pollen deposition event, the bulk of which originates from pine trees (Dorman and Barber 1956, O'Shaughnessy 1988). It is likely that tobacco thrips reproductive rates increase in late winter or early spring with increasing temperature, but the timing of the seasonal population density increase also follows the pine pollen dehiscence event in the southeast (Dorman and Barber 1956). In southern Georgia, pine pollen dehiscence begins in late January/early February and lasts through April into May (Wakeley 1954). Throughout this period, it settles on all surfaces, including plant hosts of thrips. It is possible that pine pollen availability on plant foliage induces greater reproduction in tobacco thrips in the spring (Riley et al. 2007).

This study evaluated the effects of pine pollen supplementation in an onion diet on tobacco thrips population development, through a life table bioassay method using live plants. Onions were used both because tobacco thrips populations increase in field crops during the early spring and because live onion seedlings could be contained inside a micro-cage for thrips. Western flower and tobacco thrips have a noted feeding preference for whole, intact plant foliage (Chitturi et al. 2006), which more closely approximates field conditions than discs or excised leaves. A method using live plants. Onions were used both because tobacco thrips populations increase in field crops during the early spring and because live onion seedlings could be contained inside a micro-cage for thrips. Western flower and tobacco thrips have a noted feeding preference for whole, intact plant foliage (Chitturi et al. 2006), which more closely approximates field conditions than discs or excised leaves. A micro-plant held inside a micro-cage provided live plant material long enough to measure thrips life table parameters. In this study, tobacco thrips were placed on two-to three-leaf onion seedlings (Allium cepa L. variety pegasus) with and without slash pine pollen (Pinus elliottii Engelm.) and contained in micro-centrifuge tubes while the insects' life table parameters were measured. It was hypothesized that net reproduction of tobacco thrips would increase on the onion tissue diet with a supplement of pine pollen.

Materials and Methods

**Thrips Colony.** The tobacco thrips colony was initiated from adult male and female thrips collected from peanut fields in Tifton, Tift Co., GA, during Spring 2006 and supplemented with additional thrips from the same location in Summer 2008. The tobacco thrips colony was maintained on green beans (Phaseolus vulgaris L.) in 473-ml plastic deli cups (Loomans et al. 1999) with 150-μm openings (Fisher, Pittsburgh, PA) to isolate pollen from debris. The pollen was stored in sealed glass vials at 3°C.

**Micro-Cages.** Micro-cages were constructed of centrifuge tubes (Central Research, Athens, GA) with 1.5-ml capacity. The 0.5-cm-diameter opening was covered by a copper mesh screen (TWP, Berkeley, CA) with 76-μm openings. Insects generally cannot pass through screens with holes smaller than their thoracic diameter (Bethke and Paine 1991). Because female tobacco thrips thoracic diameters are ~145–150 μm (Johansen 2002, Robb et al. 2005) and males’ thoraxes are only slightly smaller, the mesh screen allowed air to circulate without allowing thrips to escape the cage. Each micro-cage contained a two- to three-leaf onion seedling (Allium cepa L. variety pegasus). Damp cotton was placed under the trimmed onion roots in the tube bottom to keep the onions alive. Onions under the pollen treatment were lightly dusted at an approximate rate of 1 mg for every 70 onions before placement into the tubes. Micro-cages were placed upright in a styrofoam base in separate slots and not specifically paired. Fifty micro-cages under each treatment fit in each base. All micro-cages were kept in a growth chamber under the uniform conditions of 25°C, 94% RH, and 24-h daylight.

**Procedures.** Experimental design was a split plot with pollen versus no pollen supplementation as the main plot variables and a time interval ranging from 2 to 20 d as the subplot variables. Two runs of 10 micro-cages/onion replicates under each treatment were made, generating 20 total replicates per treatment. Two adult female tobacco thrips, or two progenitors, were placed inside a micro-cage on an untreated or pollen-treated onion. Thus, sample size was 40 adult female thrips. The progenitors were placed on onion foliage within micro-cages using a round size 3 craft brush (Robert Simmons, New York, NY) and transferred every 2 d to a new micro-cage/onion under similar treatment for a total of 20 d. Progenitor mortality was observed every 2 d. After the progenitors’ occupation of a micro-cage, the number of eggs and larval and adult offspring produced were observed on onions under both treatments. However, the method used to quantify oviposition killed onion tissue and was necessary to conduct before hatching occurred for greater egg identification accuracy. Because of this, either the oviposition in an onion’s tissues or the larval and adult offspring hatching from and surviving on a particular onion was quantified. These data were used to construct a life table and generate net reproduction values for each treatment type.

Oviposition was quantified in 40% of the treatment replicates (eight onions from each treatment and 2-d time interval). Eggs in the onion tissue were stained using a lacto phenol-acid fuchsin staining technique similar to one elaborated by Nuesly et al. (1995) and first described by Simonet and Pienkowski (1977). Onion leaflets were separated from the bulb, and all onion tissue was boiled for 3–4 min in a 1:2:1:1:1 solution of 10% lactic acid, 50% glycerin solution, distilled water, saturated phenol buffered at pH 4.3, and 1 g/liter of acid fuchsin high purity biological stain. Chemicals were obtained from Fisher. Stained leaves were allowed to cool for 3–5 h, and excess...
stain was rinsed off with warm tap water. Stained eggs were observed in onion tissue under a stereo microscope.

Larval and adult offspring were quantified in 60% of treatment replicates (12 onions from each treatment and 2-d time interval). Because of the thrips’ tendency to crawl into onion crevices, offspring were not easily observable to monitor developmental rates. To view all possible thrips on an onion, the leaves had to be gently opened and separated, thus damaging or killing the plant. Rather than repeatedly quantifying the larvæ in an onion and placing them back on the damaged seedling, a single observation of larval thrips was made. All larvae were extracted from an onion, quantified, and transferred to a fresh onion seedling under similar treatment to ensure thrips had access to the living tissue of an intact plant on which to feed. Based on life table data compiled by Lowry et al. (1992) describing development time of tobacco thrips on peanut, a time period was estimated that would ensure that all larvae would have had ample time to hatch from eggs. We estimated that 8.1 ± 0.2 d after egg deposition would be required for 100% hatch at 25°C. Therefore, larvae were quantified in onions and transferred to fresh seedlings 9 d after the end of the 2-d ovipositional period. After 18 d—ample time to allow thrips to develop into adults at 25°C (Lowry et al. 1992)—the remaining 60% of treatment replicate onions (12 onions from each treatment and 2-d time interval under) were removed and taken apart to count all adult male and female progeny.

Mean Eggs and Offspring per Female. Mean eggs, larvae, and male plus female adults produced per female were calculated for each 2-d time interval under both treatments. Analysis of variance (ANOVA) for the effect of pollen treatment (main plot) and interval (subplot) on the eggs, nymphs, and male and female adults produced per female were analyzed using PROC GLM (SAS Institute 1990) with a split plot design model. Fisher least significant difference (LSD) method was used for determining interval differences using PROC GLM with α = 0.05.

R₀ Calculations. R₀ values were calculated in one of two ways. First, overall R₀ value was generated per treatment over all replicates. Second, four R₀ values were calculated for groups of three replicates, and a mean R₀ was generated per treatment. The first calculation was generated from a larger body of data gathered from all replicates of a treatment, creating a more rigorous R₀ value. The multiple R₀ values calculated were less rigorous, being generated from data of a subset of treatment replicates, but allowed for the calculation of a mean R₀ per treatment and comparison analysis of treatment effect on R₀.

To generate one R₀ value for each treatment, l₁ and m₁ values first had to be calculated. The l₁ values were calculated for each 2-d time interval under each treatment. To determine l₁ values, the percent surviving progenitors during a given time interval was multiplied by the percentage of thrips surviving from egg to adult emergence. Ideally, a single generation of females would be observed from first larval instar throughout adulthood for egg and offspring production and mortality data in the life table bioassay. However, because of time constraints, the percentage of thrips surviving from egg to adult for each time interval were used from the second generation and multiplied with the percentage of surviving first generation progenitors for each time interval to make a complete data set. The percentage of thrips surviving from egg to adult for each time interval was determined by dividing mean total offspring surviving through adult emergence per female by the mean eggs produced per female. Next, l₁m₁ values were determined for each time interval and summed to generate R₀ values. To determine l₁m₁ values, l₁ was multiplied by m₁, which was the product of an average proportion of females in the population and mean eggs per female for a time interval. The proportions of females in the populations were determined by dividing total adult female offspring by total adult offspring per time interval. The sum of l₁m₁ values for each time interval in a treatment yielded one R₀ value for each treatment.

The second calculation of four R₀ values per treatment involved calculating l₁ values for each time interval in a treatment in the same way as described above, but using the average replicate values of four groups of three replicates. Replicates for both egg and larval/adult data sets were randomly assigned to a group using a random numbers table. The four m₁ values per time interval were generated from the product of egg count data, and an average proportion of females in the population from the smaller group of three experiment replicates. These values were multiplied by the l₁ values of the corresponding time interval in a treatment. The four m₁ values were calculated from four separate average population proportions of females and four individual mean eggs produced per female values for each time interval in a treatment. There were 12 replicates of onions from which the proportion of female offspring in populations were calculated. Four average female population proportion values were generated for each time interval by random grouping of three replicates. Additionally, the egg count data (destructive sample) were collected from four groups of two replicates. Four mean eggs produced per female values were generated for each treatment by processing the egg count data in random groups of two replicates. To generate the m₁ values for each time interval per treatment, proportion of females in the population and mean eggs produced per female values generated from each corresponding replicate group were multiplied. For example, the average proportion of females in the population generated from the first replicate group was multiplied by the mean eggs produced per female generated from the first replicate group, and then the second replicate population’s average proportion of females was multiplied by the second replicate group’s mean eggs produced per female value, and so on. Each of the l₁m₁ values from one of the four replicate groups in each treatment’s time interval were added together for an R₀ value.
The four Rₙ values were analyzed using PROC ANOVA (SAS Institute 1990). To determine treatment differences, Fisher LSD method was implemented using PROC ANOVA with α = 0.05. Because identical experiments provided similar results, the ANOVA was conducted over experiments using all replicates.

Results

Mean Eggs and Offspring per Female. Mean values of total eggs ($F = 17.5, \text{df} = 1.7, P = 0.0041$), larvae ($F = 31.3, \text{df} = 1.11, P = 0.0002$), male adults ($F = 8.66, \text{df} = 1.11, P = 0.0134$), and female adults produced per female ($F = 21.8, \text{df} = 1.11, P = 0.0007$) were significantly greater under the pine pollen supplementation treatment (Table 1). The eggs, larvae, adult females, and adult males per female produced during the first 10-d interval were contrasted to the later 10-d interval because it appeared that the pollen supplement not only increased overall reproduction (Fig. 1) but specifically increased the production of female thrips from eggs laid later in the ovipositional period (Table 2). Also, the production of eggs per female remained high throughout the experiment, whereas egg production on untreated onions decreased. This meant that egg production was higher under the pollen treatment by 2.5-fold during the first half of the experiment and by 4.4-fold during the latter half of the experiment (Table 2).

The distribution of mean eggs produced per female throughout the 20-d oviposition period was fairly flat
in the untreated onions ($F = 1.37$, df = 9.63, $P = 0.22$; Table 3), with slightly more eggs produced at the 2–6 d after initiating the test (Fig. 1). The pollen treatment resulted in trimodal egg counts for the tobacco thrips, exhibiting peak values around days 2–4, 8–10, and 14–18 ($F = 2.11$, df = 9.63, $P = 0.0419$; Table 4). Eggs produced per female rebounded to similar high levels three times during the ovipositional period, suggesting that the nutritional supplement of pollen directly affected egg production. This increase in mean values of total eggs in the later 10 d of the ovipositional period ($F = 14.0$, df = 1.7, $P = 0.0072$), coincided with increased numbers of larvae ($F = 22$, df = 1.10, $P = 0.0009$), and female adults produced from the eggs during this period ($F = 11.1$, df = 1.10, $P = 0.0076$; Table 2).

**R₀ Calculations.** There was a marked difference in tobacco thrips reproduction between the two treatments (Tables 1–4). Under the pollen treatment, the $R₀$ value was 4.68, which was 3.4-fold larger than the untreated $R₀$ value of 1.39. Using the four subgroups per treatment, the mean $R₀$ value for the pollen treatment was 3.81, significantly (eight-fold) larger than that of untreated onion, which was 0.478 ($F = 7.31$, df = 1.7, $P = 0.035$; Table 1).

**Discussion**

Using this bioassay, tobacco thrips reproduction increased 3.4- to 8-fold with slash pine pollen supplementation in an onion plant diet. The bioassay technique effectively retained the thrips and kept both the thrips and onion plants alive long enough to measure life table parameters for thrips on onions. One problem that remained was that oviposition counts could only be taken using a destructive sampling method. The egg-staining procedure killed all onion and thrips egg tissues. A nondestructive method to quantify oviposition would allow for more accurate life table analyses. Additionally, it was very difficult to locate larvae for observation on the onions, because they had the tendency to hide and feed inside the onion crevices. The onions could not be pulled apart without damaging onion tissue, so after quantifying the larvae, they had to be transferred to fresh onions. Last, because of time constraints, the $l_x$ values were generated with data from two generations with different rearing procedures. It was assumed that the effects of rearing procedures would not be significant enough to mask treatment effects; however, for greater accuracy of net reproduction calculation, such values should be generated from data arising from one generation. The amount of pollen applied during this experiment (1 mg per 70 onion plants, typically planted on $\approx$1 m²) is well within the range of what can be expected for pine pollen deposition in the field in Georgia (0–500 mg/m²; D.G.R., unpublished data). It is probable that rainfall events remove some pollen grains from plants, so the availability of pollen could vary dramatically over the spring with weather. Regardless of these problems, the bioassay method allowed the study of pollen supplementation effects on thrips life table parameters and could be useful in future studies.

<table>
<thead>
<tr>
<th>Table 2. Mean <em>F. fusca</em> eggs, larvae, female adults, and male adults per female for the beginning interval (0–10 d) and ending interval (12–20 d) by pollen treatments</th>
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Means within columns within interval with the same letter are not significantly different (LSD, $P < 0.05$).

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<tr>
<th>Table 3. Mean <em>F. fusca</em> eggs per female, proportion of females in the pop, $l_x$, $l_xm_x$, and $R₀$ for each 2-d interval on untreated onions</th>
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Means within columns with the same letter are not statistically significant (LSD, $P < 0.05$).

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<tr>
<th>Table 4. Mean <em>F. fusca</em> eggs per female, proportion of females in the pop, $l_x$, $l_xm_x$, and $R₀$ for each 2-d interval on pine pollentreated onions</th>
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Means within columns with the same letter are not statistically significant (LSD, $P < 0.05$).
Pollination deposition on onion plants, along with other known important factors such as temperature increases and lack of rainfall (Morsello et al. 2008), could help explain increasing thrips populations during March, April, and May in Vidalia onion and tomato fields. During this study, mean values of eggs produced per female rebounded to similar high levels three times during the ovipositional period around intervals of 6, 10, and 18 d in pollen-treated onions. The peak values are more than three-fold higher in pollen-treated onions than corresponding values in untreated onions, suggesting that the nutritional supplement of pollen directly affected egg production (Table 4).

Coinciding with mean egg production peaks in the latter 10 d of the experiment, the mean values of larval offspring produced per female remained high and female adult offspring produced per female increased under the pollen treatment (Table 2). This could suggest multiple mechanisms for the increase in tobacco thrips with pine pollen diet supplementation in onions, such as inducing a greater proportion of females in the population, increased adult longevity, or decreased developmental time. The western flower thrips has exhibited decreased developmental time and increased adult longevity with pollen supplementation in a plant diet (Murai and Ishii 1982, Trichilo and Leigh 1988), but these effects have not been noted in tobacco thrips. It is not clear whether dietary nutrition has an effect on western flower or tobacco thrips sex ratios.

Furthermore, although pine pollen supplementation induced significantly greater reproduction in tobacco thrips in onions, western flower thrips have been shown to react to pine pollen supplementation with equal or greater increases in reproduction or oviposition on common crop host tissues such as cucumber, tomato, and peanut (Hulshof and Vänninen 1999, 2002; Hulshof et al. 2003; Riley et al. 2007). Flower-feeding thrips, such as the western flower thrips, could affect even stronger responses to pine pollen deposition than the typically foliage-feeding tobacco thrips, resulting in an even greater population explosion during the spring pollen deposition event in the South. As such, concurrent thrips population fluctuations in the field would also need to be observed, because pollen supplementation could effect thrips reproduction to various degrees depending on thrips species. Life table analyses of other thrips species could allow a more in-depth comparison of specific responses to pollen supplementation.

Certain additional nutrients supplied to tobacco thrips through pollen that were lacking in onion likely accounts for the 3.4-fold increase in net reproduction. It would be of interest to assess nitrogen content of plant hosts along with tobacco thrips reproduction on a host plant diet with and without a pollen treatment. Although there is significant variation in leaf percent nitrogen levels depending on fertilizer application and crop season, percent nitrogen in onion leaf ranges from around 2.6 to 5.0 (Brown 1981), roughly comparable to a range of percent nitrogen values found in tomato leaves (Orth and Harkness 1962). The experiment was not designed to analyze onion leaf nitrogen content. Pollen supplementation may have a greater treatment effect on tobacco thrips in a poorer host plant diet, explaining why tobacco thrips oviposition significantly increased on pollen-treated peanut but not tomato leaves (Riley et al. 2007). If this is the case, the onion seedlings used in this study may have had lower nitrogen levels relative to the tomato leaves used in the study by Riley et al. (2007). Additionally, pine pollen deposition on poor-quality thrips hosts in the field may make them more attractive to certain thrips in the field. Pine pollen deposition on peanut and tomato leaf discs was found to significantly increase settling behavior in western flower thrips but not in tobacco thrips (Chitturi et al. 2006). Tobacco thrips settling behavior was not significantly increased overall, but a notable increase in settling with pollen treatment on peanut and not tomato may suggest that poorer-quality hosts can be made more attractive to tobacco thrips with pine pollen supplementation.

Tobacco thrips have a very large host plant range, encompassing a variety of crops (Newsom et al. 1953, Salguero Navas et al. 1991, Chamberlin et al. 1992, Eckel et al. 1996, Toapanta et al. 1996). This, combined with a short generation time and the potential for high oviposition rates, enables a tobacco thrips population to quite rapidly increase. A thrips generation time is roughly 2 wk. If tobacco thrips respond to pine pollen supplementation on onion crops with a net reproduction similar to the 4.68 calculated with this study, field populations would increase exponentially—more than quadrupling in size every 2 wk—after a pollen deposition event. Because pollen deluncrince begins in late January/early February in southern Georgia, pine pollen settling on onion crops could plausibly induce a large increase in tobacco thrips net reproduction during the early spring, when young crops are most vulnerable to tomato spotted wilt virus (TSWV). Further understanding of this relationship may allow for better prediction and control of pest thrips population dynamics and thus decrease TSWV damage in crops.

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