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Twospotted Spider Mite Preference and Performance on Day-Neutral Strawberry in New York and Role of Structural Characteristics in Plant Susceptibility

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Additional index words: *Tetranychus urticae*, host plant resistance, cultural control, integrated pest management, plant breeding

Abstract

Growing strawberries (*Fragaria* x *ananassa* Duch.) under plastic low tunnels is increasing in popularity among growers in the northeastern U.S. despite reports of higher *Tetranychus urticae* Koch (TSSM) pressure in this system. This study evaluated differences in susceptibility to TSSM among cultivars that are commonly planted in the Northeast. A second objective was to quantify differences in key structural characteristics (trichome density, leaflet area, average number of leaflets, and total above-ground biomass) that may contribute to variation in cultivar susceptibility to TSSM. We evaluated TSSM preference and performance using leaf disc and whole plant assays in the lab/greenhouse, and in the field at several commercial sites. Performance tests conducted on leaf discs yielded inconclusive results, but 'Albion' and especially 'Seascape' were identified as the least preferred cultivars by TSSM when assessed on whole plants. Of the structural characteristics measured, total above-ground biomass was the best predictor of TSSM number per leaflet, with larger plants having lower TSSM counts on leaflets. Total numbers of TSSM on whole plants were also higher on 'Seascape' which was the smallest cultivar tested in our study in terms of plant weight and leaflet area. However, there was no correlation between TSSM counts per leaflet and yield for any of the cultivars tested in the field. We discuss potential explanations for these results with implications on TSSM management under low tunnels.

Strawberry growers in the Northeast have several options for expanding their business and increasing yield. First, growers can plant day-neutral cultivars that will fruit continuously throughout the summer and fall and during the first year of planting if temperatures are between 4 – 30 °C. When planted in annual plasticulture systems, yields from day-neutral cultivars can be larger than traditional June-bearing cultivars and can add several weeks of production (Petran et al., 2017). Second, day-neutral cultivars can be planted under high or low plastic tunnels that provide additional benefits including season extension and protection from disease and some insects (Orde et al., 2018; Orde and Sideman, 2019; Willden et al., 2021). Indeed, several studies in the Northeast and Midwest observed a 10-50% greater proportion of marketable yield under low tunnels compared to open beds (Lewers et al., 2017; Petran et al., 2017; Pritts and McDermott, 2016; Willden et al., 2021). Due to these benefits, an increasing number of growers are adopting tunnel production of day-neutral cultivars in the Northeast, with most producing 'Albion', 'San Andreas' and 'Seascape' under low tunnels (Orde and Sideman, 2019).

A primary concern for day-neutral strawberry production under plastic tunnels is increased presence of twospotted spider mite (*Tetranychus urticae* Koch), but TSSM impacts on yield in this system, especially in the Northeastern U.S., is unclear (Costa et al., 2017; Ingwell et al., 2017; Willden et al., 2021). Twospotted spider mite, hereby referred to as 'TSSM', thrives under warm and dry conditions provided by protective tunnels

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and is able to reach high population densities by late summer when day-neutrals are still producing fruit. TSSM is an extreme generalist herbivore that can feed on over 4000 host plant species worldwide, many of which are important crops (Grbić et al., 2011; Migeon et al., 2012). Although TSSM rapidly accepts and adapts to novel host plants (Snoeck et al., 2018; Sousa et al., 2019), preference and performance of TSSM can vary by plant species, even at the cultivar level for a single species (Greco et al., 2006; Puspitarini et al., 2021; Xu et al., 2019). For strawberry, many studies have evaluated TSSM preference and performance on various cultivars, but none have directly compared those that are relevant to the Northeast (Dana et al., 2018; de Resende et al., 2020; Ferrer et al., 1993; Figueiredo et al., 2013; Giménez-Ferrer et al., 1994; Gong et al., 2018; Rezaie et al., 2013; Steinite and Ievinsh, 2003).

Variability in TSSM performance is likely tied to host plant quality, a metric that includes presence of constitutive and induced plant defenses (including both structural and chemical barriers), and nutrient availability (Santamaria et al., 2020; War et al., 2012). These defenses can reduce pest abundance or injury or improve tolerance to injury upon infestation. A recent meta-analysis determined that plant susceptibility to herbivores across 40 plant species was more correlated with variation in plant life-history traits, gross morphological traits and physical defenses rather than chemical defenses, such as secondary metabolites (Carmona et al., 2011). Physical plant defenses in strawberry largely include increased leaf hairiness, presence of glandular and non-glandular trichomes, and leaf texture (Kishaba et al., 1972; Liu et al., 2020). Trichomes, particularly those that are glandular, are often described as important plant defenses against TSSM in strawberry (de Resende et al., 2020; Esteca et al., 2017; Luczynski et al., 1990), despite contradictory reports of positive or neutral associations between TSSM performance and leaf pubescence (Gong et al., 2018; Gugole Ottaviano et al., 2013; Kishaba et al., 1972; Steinite and Ievinsh, 2003). Plant size could also be an important morphological trait in strawberry that contributes to TSSM tolerance. Larger plants could better tolerate TSSM presence by thinning population densities and feeding intensity on leaves (Carmona et al., 2011; Castells et al., 2016). The role of key physical defenses (trichomes) and morphological traits (plant size) in predicting TSSM performance is largely unknown for day-neutral strawberry cultivars.

As growers increase adoption of protected culture production practices of day-neutral cultivars, additional management efforts will be necessary against TSSM. Risks of pesticide resistance is exceptionally high for TSSM, thus alternative management options will be greatly needed (Van Leeuwen et al., 2015, 2010). Plant selection is an important facet of integrated pest management (IPM), and if done carefully can reduce the need for additional management tactics. It is currently unclear which day-neutral strawberry cultivars grown in Northeast are least preferred by TSSM, and such information would be a useful to IPM programs. The objective of this study was to first determine trends of TSSM preference and performance on several day neutral cultivars that are relevant to growers in the Northeast. A second objective was to describe how varying trichome density and plant size (biomass, leaflet area, and number of leaflets) may contribute to cultivar susceptibility.

Materials and Methods

Plant and colony maintenance. TSSM used in all experiments were reared on whole bean plants (*Phaseolus vulgaris* L.) in growth chambers for over 40 years before experimentation. Only mated adult females were used in all experiments. Rearing of host plants and TSSM occurred at 25 C and 70% RH. Ten-day-old bean plants were fed to TSSM twice per week. Day-neutral strawberry cultivars used for lab, field and greenhouse experiments at Cornell AgriTech were supplied by Nourse Farms, Whatley MA. For lab and greenhouse experiments, strawberry plants were potted in 3 L containers as bare roots and grown under greenhouse conditions for 4 weeks. Plants were hand watered twice weekly and fertilized once per week using a 20-20-20 fertilizer (Jack's Professional, JR Peters, Inc.) at the rate of 2.1g·L-1 of water. Runners and flowers were cut daily. Mature plants, with a minimum of 4 leaves, were selected for experiments.

Oviposition and offspring development on leaf discs. Strawberry cultivars used for oviposition experiments on leaf discs included 'Monterey', 'Albion', 'Cabrillo', 'Portola', 'San Andreas', 'Seascape' and 'Sweet Ann'. Leaflets from each cultivar were collected from similarly aged plants grown in the greenhouse. A 25 mm diameter leaf disc was cut from the center of each leaflet using a punch press and placed abaxial side up on water-soaked cotton in covered Petri dishes. Two similarly aged TSSM females reared on bean plants were then placed onto each strawberry leaf disc using a fine brush. Twenty replicates of each cultivar were tested, split between two trials separated by 2 weeks. After 24 h, TSSM females were removed and the number of oviposited eggs counted. Every 2-3 days thereafter, the number of hatched nymphs and adults were counted until adults began laying eggs, which occurred 11 days post inoculation.

Cultivar choice tests on leaf discs. Strawberry cultivars included in choice trials included 'Portola', 'Albion', 'Seascape' and 'San Andreas'. Similarly aged leaflets from each cultivar were harvested from greenhouse-grown plants. Square 5 cm2 sections were cut along the midvein of each leaflet. Each of the four cultivar sections were randomized in space, and placed abaxial side up onto water-soaked cotton (Gastonia, NC) so leaf margins were touching (Fig. 1). A total 32 replicates, or arenas were included in this experiment, and 6 arenas were randomly selected to be monitored by EthoVision XT tracking software (Noldus Information Technology, Wageningen, Netherlands). A single TSSM adult female was placed on a parafilm platform at the center of the arena and allowed to move among the cultivar choices. Six replicates were monitored using EthoVision to determine short-term movement patterns. The "darker" subject color at 30 sensitivity and the differencing method was used in detection settings of EthoVision to discriminate TSSM from the leaf background. Each cultivar was included as a separate zone within each arena. The distance moved (cm) was determined for each cultivar zone after a 90 min period for EthoVision arenas. At 48 h post inoculation, the number of eggs deposited on each cultivar was counted.

Impacts of artificial trichomes on TSSM movement and oviposition on leaf discs. Leaf disc experiments were conducted to simulate the effect of added trichomes on movement patterns and oviposition capacity of TSSM females using EthoVision tracking. Leaf disc arenas were cut from bean, a preferred low-trichome host of TSSM, and 'Albion' strawberry, a moderately preferred host plant with a relatively high trichome density. Each leaf disc was 25 mm in diameter and a random half was selected for the added trichome treatment. A small amount of cotton (same as above) was used as the artificial trichome source and was spread evenly over half of the leaf disc following methods by Roda et al. 2001 (Fig 1). A single individual TSSM was inoculated onto each of the four treatments (bean or strawberry, with or without added trichomes) and observed using EthoVision tracking for a 1 h interval. The same detection settings were used as described above, with additional zones of no-trichome and added-trichome for those that received trichomes (Fig. 1B). Samples were then incubated at 25 C, 70 % RH for 24 h after which the number of oviposited TSSM eggs were counted.

Greenhouse experiments on whole plants. Greenhouse experiments were conducted to determine TSSM performance on whole plants in controlled greenhouse conditions.

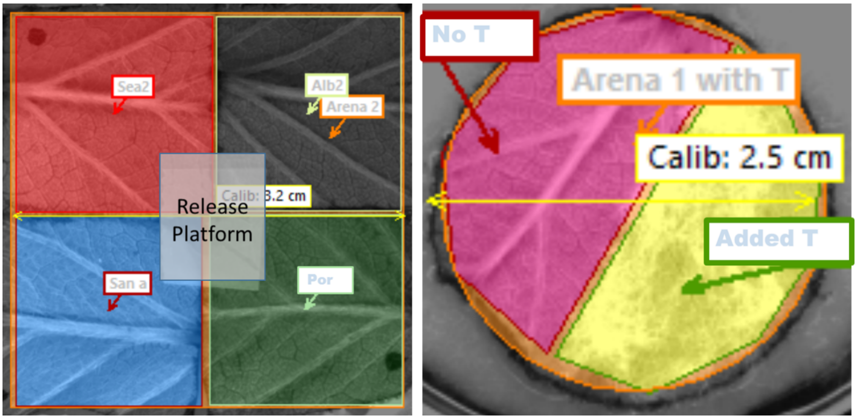

Figure 1. EthoVision arena design for TSSM preference on four cultivars (left) and with and without artificial trichomes (right). Both arenas were constructed using cut leaf sections. Four cultivars were used for the preference test (left) where leaf sections were flushed together and a single TSSM female was placed onto the platform that bordered each cultivar. EthoVision tracking was used to determine movement of the mite on each cultivar. The "Added T" section on the right panel demonstrates where artificial trichomes were added to the arena to determine TSSM preference for glabrous verses trichome dense leaf surfaces.

Day-neutral cultivars 'Albion', 'Monterey', 'Portola', 'San Andreas' and 'Seascape' were potted and maintained using methods described above, and randomly selected for greenhouse experiments once they matured. Four plants of a cultivar were moved into individual 160 µm aperture BugDorms (MegaView Science CO., Ltd., Taichung, Taiwan) and placed close together so foliage overlapped. A total of 18 replicates of each cultivar treatment was included in this experiment, split between two trials that occurred two weeks apart. For each trial, an even number of replicates for each treatment was blocked by location in the greenhouse to account for variances in location on TSSM population dynamics.

Sixteen TSSM adult females were then placed onto plants within dorms, spaced evenly between plants. Destructive sampling was conducted at 14 and 21 days post inoculation by harvesting 4 leaflets from each plant and brushing their contents onto soapy plates that were viewed under a dissecting microscope (Macmillan and Costello, 2015). The numbers of TSSM eggs and motiles per leaflet was estimated. To estimate the number of TSSM present on whole plants, the average number of TSSM per leaflet was multiplied by the number of leaflets present on each plant.

Comparing plant structural characteristics and impact on TSSM in greenhouse experiment. After 21 days, the above plants used for estimating TSSM counts were also measured for average leaflet area, leaflet number, trichome density on leaflets, and plant biomass. For measuring leaflet area, two similarly-aged center leaflets were collected from a random subsample of 5 plants of each cultivar and measured using LeafByte (Getman-Pickering et al., 2020). Trichome density was also measured on these leaflets using the imaging software ImageJ (Schneider et al 2021). To estimate trichome density, a linear 1 cm section of the center of the midvein on the abaxial leaf surface and a 50 mm2 section of the leaf surface adjacent to the midvein was photographed and uploaded to ImageJ. The number of trichomes and leaf hairs present at each location was counted in ImageJ using cell counter. To estimate plant biomass, all above ground plant parts (including the leaflets used for leaflet area and trichome estimates) were collected and dried in brown paper bags for 24 h at 70 C to determine relative differences in biomass among the cultivars.

Field experiments: Research site. This experiment took place at a research farm located on the Cornell AgriTech campus in Geneva, NY. During June 2019, plots of 'Albion', 'Seascape', and 'Portola' were planted as bare roots in plots using a randomized complete block design. Each plot consisted of 20 plants of a cultivar planted in a double staggered row along a 3 m raised bed section that was covered in white plastic mulch. A replicate of each cultivar was planted under a single low tunnel (location of each plot was randomized), which served as a block. Plastic used to construct low tunnels was a standard Dubois 1.5 mil film with perforations on each side (Trioplast AB, distributed by Dubois Agrinovations, Saint-Rémi, Canada). Each plot within a tunnel was spaced 3 m apart. Eighteen replicate plots of each cultivar were planted under 18 tunnels, resulting in total of 54 plots. Plants were drip-irrigated twice per week and fertilized with 20-20-20 fertilizer weekly at a rate of 0.56 g N / m2. To facilitate optimal plant growth, runners were cut weekly during the entire season and flowers picked weekly during the first month. When low tunnels were constructed, one side of the plastic remained down while the opposite side was raised or lowered if rain or high temperatures were forecasted. No pesticides or biocontrol agents were applied during the season, although predatory mites appeared naturally.

During late-July, half of the tunnels were randomly inoculated with supplemental twospotted spider mites to standardize spider mite colonization. Each plot within selected tunnels received 40 adult twospotted spider mite females. Every two weeks after spider mite inoculation, 10 leaflets from each plot were indiscriminately selected and brought back to the lab to determine mite counts per leaflet. These leaflets were brushed onto soapy plates and observed under a dissecting microscope for the presence of twospotted spider mites. Strawberries were harvested weekly from early August to early November in 2019. Average total yield per plant was determined by dividing total weight per plot by the number of plants present across sampling dates. The proportion of marketable yield was determined by dividing the number of marketable berries (i.e., those with minimal damage and > 5 g) from the total number collected.

Field experiments: Monitoring at commercial farms. Two commercial farms were selected to compare differences in counts of naturally occurring TSSM among day-neutral cultivars grown under low tunnels. The first site "Commercial 1" was located in western NY (Wayne County) and the second "Commercial 2" was located in eastern NY (Rensselaer County). The day-neutral cultivars 'Albion', 'San Andreas', and 'Seascape' were planted at both commercial sites on continuous raised beds under Dubois plastic. Plants were managed similarly to research plants above, following recommendations by Pritts and McDermott (2016). Pesticides and biocontrol agents were applied as needed at both sites to manage TSSM and other pests. Each cultivar was planted along individual parallel rows, and four 3 m sections of each cultivar row were flagged as replicate plots at both sites. Each plot contained 20 plants and were spaced 6 m from other plots. Every 2 weeks, 10 leaflets from each plot were collected and processed using the same method described above to determine differences in TSSM counts per leaflet. Note that cultivars were not randomly blocked at commercial sites, therefore replicates in these experiments are not truly independent. This planting design is typical of commercial strawberry fields but it important to acknowledge this statistical flaw.

Statistics. Analyses were conducted in R (R version 3.5.1; R Core Team. Vienna, Austria 2020). Data for lab no-choice and choice experiments on leaf discs were analyzed using a generalized linear mixed effect models with a Poisson and a negative binomial distribution, respectively (packages 'lme4' and

'MASS'). These experiments were conducted on single leaf discs using single *T. urticae* adults and blocked by trial, therefore trial was included as a random effect for both experiments, and mite ID was used as an additional random effect for the choice test. Fixed effects for both lab experiments included cultivar treatment and time post inoculation. To compare the proportion of individuals that survived to different life stages in no-choice tests, and the proportion of females present on specific cultivars for choice tests, similar mixed models were used with a binomial logistic regression.

To compare TSSM counts, yield and plant structural characteristics (plant biomass, leaflet area, average number of leaflets, and trichome density) on whole plants for greenhouse experiments, linear mixed effect models were used with a log transformation of TSSM counts and yield. No transformations were used for plant structure models, but a generalized mixed effects model with a gamma distribution was used for comparing average number of leaflets among cultivars to account for violation of normality assumptions. To describe the direct effects of plant size (plant biomass, average number of leaflets, leaflet area and trichome density) on TSSM count, structural equation modeling with a path analysis (package 'lavaan' [Rosseel, 2012]) was used. In the same analysis, we also included the direct relationships of plant structural characteristics and TSSM counts on plant yield. Because we found no significant correlations among plant structural characteristics and yield, we removed these paths from the analysis to simplify the model.

Field data were analyzed for each site (commercial site 1, 2, and the research site) separately. For commercial sites 1 and 2, a generalized mixed effect model with negative binomial distribution was used to compare TSSM counts per leaflet among 'Albion', 'Seascape' and 'San Andreas'. TSSM counts at the research site was analyzed using a linear mixed effect model with a log transformation. Yield per plant (g) was analyzed at all sites using a generalized mixed effect model with a gamma distribution. Random effects for all field models included row to account for blocking and replicate plot and date to account for repeated measures.

For all linear mixed effect models, F-tests were fit using a residual maximum likelihood estimations (REML) to estimate variance components with random effects. Model simplification was employed for all data analyses, where non-significant interactions of main effects were dropped to determine the most parsimonious model. A Tukey's multiple comparisons test (package 'emmeans') was used to compare pairwise differences among fixed effects and estimated marginal means for all variables. Estimated marginal means and standard errors from models were used to generate all figures.

Results

Oviposition and offspring development on leaf discs. The average number of eggs laid by mated foundress TSSM females on leaf discs over 24 hr ranged between 7 – 11 eggs and did not vary among the cultivars (Table 1). The majority of eggs hatched after 4-6 days in incubation, but the proportion of those that successfully reached the nymph stage varied significantly by cultivar (Fig. 2: $\chi 2 = 21.11$, df = 6, $p < 0.01$). The lowest egg-nymph survival rate occurred on 'Sweet Ann', followed by 'Portola', 'Cabrillo', 'Monterey', 'Seascape', 'San Andreas', and finally the highest survival rate was observed on 'Albion' (Fig. 2). The only comparisons that were statistically different were 'Sweet Ann' versus 'Albion', 'San Andreas', 'Seascape' or 'Monterey'. The proportion of nymphs that survived to adulthood was not impacted by cultivar (Fig. 2: $\chi 2 = 3.55$, df = 6, $p = 0.74$). Cultivar differences in survival rates from egg-nymphs resulted in fewer nymphs and adults present on leaf discs at 6, 8 and 11 days after oviposition (Table 1).

Cultivar choice tests on leaf discs. When given a choice to feed and oviposit on 'Albion', 'Portola', 'San Andreas', or 'Seascape', there was no clear preference in TSSM foraging or oviposition on any cultivar (Figs. 3, 4; oviposition: $\chi2 = 2.52$, df = 3, $p = 0.50$; walking distance: $\chi2 = 4.59$, df = 3, $p = 0.20$).

Table 1. Estimated marginal means (± SE) of the number of individuals present at each life stage during 11 d on each cultivar. Each of the five data sections represents data collected at separate time intervals for a single data set. Means followed by common letters do not differ at the 5 % level of significance by Tukey's test for multiple comparisons. The absence of letters indicate no differences among all means within a time block.

		Eggs		Nymphs		Adults	
Cultivar	Time (d)	Mean	SE	Average	SE	Mean	SE
Albion	1	9.05	1.05	0	0	0	0
Cabrillo	1	12.34	1.33	0	0	0	0
Monterey	1	11.59	1.28	0	0	0	0
Portola	1	8.85	1.04	0	0	0	0
San And.	1	10.84	1.19	0	0	0	0
Seascape	1	9.78	1.13	0	0	0	0
Swt.Ann	1	8.68	0.99	0	0	0	0
		$\chi2 = 9.41$, $p = 0.15$		ND		ND	
Albion	4	8.29	0.91	0	0	0	0
Cabrillo	4	10.4	1.05	0.08	0.05	0	0
Monterey	4	10.26	1.06	0.04	0.04	0	0
Portola	4	7.33	0.83	0.04	0.04	0	0
San And.	4	9.41	0.98	0	0	0	0
Seascape	4	9.17	0.98	0	0	0	0
Swt. Ann	4	7.39	0.81	0	0	0	0
		$\chi2 = 10.96$, $p = 0.08$		ND		ND	
Albion	6	0.1	0.07	**6.25 (AB)**	**0.98**	0	0
Cabrillo	6	0.26	0.15	**6.93 (A)**	**1.05**	0	0
Monterey	6	0.13	0.08	**7.23 (A)**	**1.11**	0.04	0.04
Portola	6	0.09	0.06	**5.03 (AB)**	**0.82**	0.09	0.06
San And.	6	0.23	0.13	**7.61 (A)**	**1.13**	0	0
Seascape	6	0.37	0.19	**6.34 (AB)**	**0.99**	0	0
Swt. Ann	6	0.52	0.27	**3.23 (B)**	**0.57**	0	0
		$\chi2 = 8.52$, $p = 0.20$		**$\chi2 = 18.75$, $p < 0.01$**		ND	
Albion	8	0.02	0.02	**9.55 (A)**	**1.29**	0	0
Cabrillo	8	0.07	0.06	**9.71 (A)**	**1.25**	0.05	0.04
Monterey	8	0.08	0.08	**10.47 (A)**	**1.36**	0.11	0.06
Portola	8	0.03	0.03	**7.64 (AB)**	**1.05**	0.11	0.06
San And.	8	0.07	0.06	**9.95 (A)**	**1.27**	0	0
Seascape	8	0.03	0.03	**8.84 (A)**	**1.21**	0.06	0.04
Swt. Ann	8	0.13	0.12	**4.62 (B)**	**0.69**	0	0
		$\chi2 = 4.30$, $p = 0.63$		**$\chi2 = 23.31$, $p < 0.01$**		$\chi2 = 0.64$, $p = 0.99$	
Albion	11	0	0	0.54	0.23	**6.66 (AB)**	**1.22**
Cabrillo	11	0	0	0.83	0.31	**5.52 (AB)**	**0.094**
Monterey	11	0	0	0.67	0.29	**8.16 (A)**	**1.34**
Portola	11	0	0	0.19	0.11	**6.3 (AB)**	**1.08**
San And.	11	0	0	0.51	0.21	**7.86 (A)**	**1.27**
Seascape	11	0	0	0.45	0.19	**5.65 (AB)**	**0.98**
Swt. Ann	11	0	0	0.41	0.18	**3.59 (B)**	**0.66**
		ND		$\chi2 = 6.09$, $p = 0.41$		**$\chi2 = 14.84$, $p = 0.02$**	

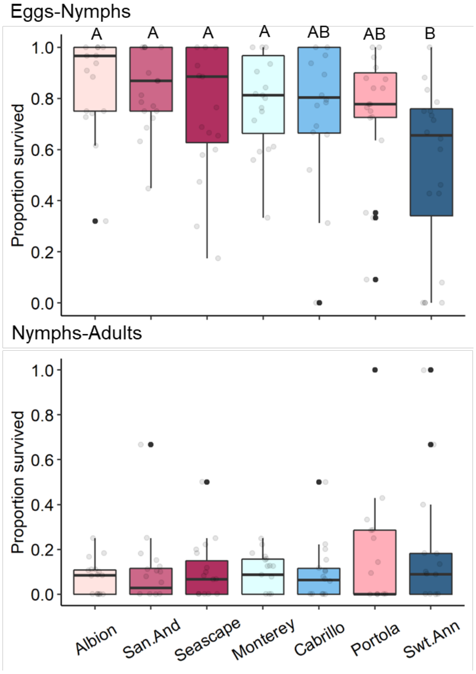

Figure 2. Raw data of the mean ± SE proportion of TSSM that survived from eggs to nymphs (top), and from nymphs to adults (bottom) on leaf discs of each cultivar. Different letters for the top panel indicate significant differences in survival based on a Tukey's test for multiple comparisons (p < 0.05). No differences were observed among treatments for nymph-adult survival.

TSSM traveled an average distance of 183.42 ± 32.68 cm as measured by EthoVision during a 1 hr interval, but moved equally among the cultivars. During subsequent observations after EthoVision tracking, we observed a moderate preference for 'Portola' at 5 hr, but overall preference compared to remaining cultivars was not statistically significant at any time interval ($\chi 2 = 0.99$, df = 3, $p = 0.80$).

Impacts of artificial trichomes on TSSM movement and oviposition on leaf discs. Single TSSM females moved an average distance of 97.25 ± 16.52 cm during a 1 hour interval on bean or strawberry discs. There was little difference in overall TSSM movement between the plant species ($F_{1,59} = 0.11$, $p = 0.74$), or between discs with or without additional trichomes ($F_{1, 52} = 1.04$, $p = 0.31$). However, for the discs with additional trichomes, most of their movement occurred on the zone where the trichomes were located (Fig. 4; $F_{1, 8} = 10.80$, $p = 0.01$). The number of eggs laid by TSSM females was consistently higher on bean (10.52 ± 4.59 eggs) compared to strawberry (8.49 ± 4.69 eggs), but this difference was not significant ($F_{1, 79} = 2.08$, $p = 0.15$). Added trichomes also had no impact on TSSM egg laying (F1, 79 = 0.02, p = 0.87), but some preference for ovipositing in trichomes was observed ($F_{1, 59} = 3.57$, $p = 0.06$).

Greenhouse experiments on whole plants: TSSM counts and yield. After 21 days in incubation, TSSM numbers ranged between 11-30 motiles per leaflet and varied significantly by cultivar (Fig. 5; $F_{4, 77} = 4.91$, $p < 0.01$). Highest leaflet counts were observed on

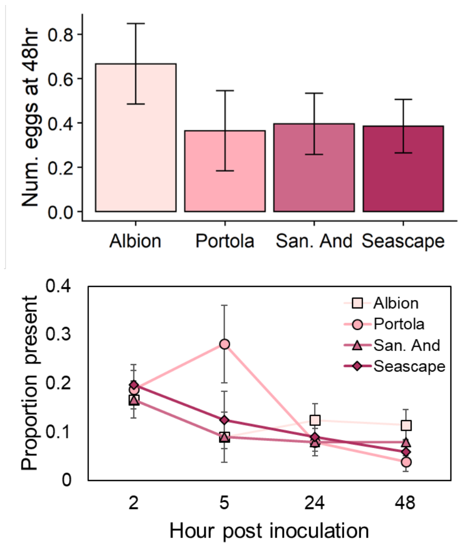

Figure 3. Model estimated (± SE) mean eggs oviposited by single TSSM females on cultivars Albion, Portola, San Andreas and Seascape after 48 h in incubation (top) and the proportion of TSSM females that were observed foraging on each cultivar at 2, 5, 24 and 48 h post inoculation for choice tests. No differences among means were present for either observation.

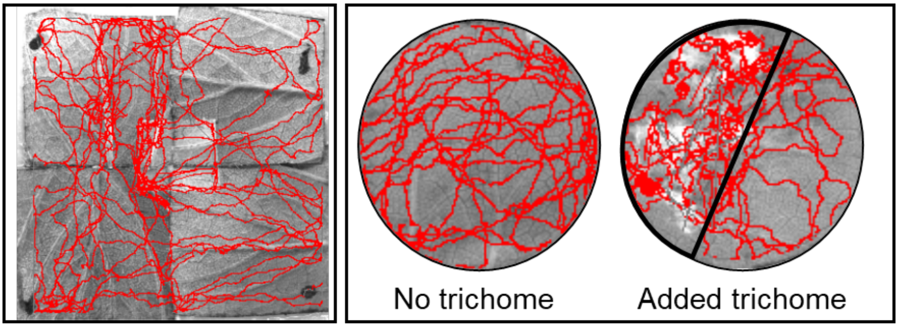

Figure 4. Representative arenas that demonstrate the non-preference for cultivars (left) for choice tests, and a preference for movement within artificial trichomes (right) from EthoVision tracking on leaf disc arenas. The black-outlined semicircle represents the region where artificial trichomes were added. Data were summarized over a 1 hr interval for both experiments.

cultivars 'Seascape' and 'Albion', followed by 'San Andreas', 'Portola' and 'Monterey'. The significant effect of cultivar was driven by the considerably higher counts on 'Seascape' compared to 'San Andreas', 'Portola', 'Monterey' and to a lesser extent 'Albion' (Fig. 5). The estimated total number of TSSM per plant followed a similar trend where counts were highest on 'Seascape' ($F_{4, 77} = 4.96$, $p < 0.01$); however, counts did not differ between 'Albion' and remaining cultivars ($p > 0.05$). When TSSM were present on plants, yield was not impacted by differences in counts per leaflet within and between cultivars ($\chi 2 = 3.24$, df = 3, $p = 0.52$).

Comparing plant structural characteristics and impact on TSSM in greenhouse experiment. Comparisons of plant structural characteristics indicate significant difference among the cultivars in plant biomass ($F_{4, 69} = 53.03$, $p < 0.01$), leaflet area ($F_{4, 45} = 17.38$, $p < 0.01$), average number of leaflets ($\chi 2 = 88.93$, df = 3, $p < 0.01$) and average number of trichomes ($F_{4, 25} = 3.32$, $p = 0.02$). 'Albion' and 'Seascape' were consistently the smallest plants in terms of plant biomass, number of leaflets present, and leaflet area, while 'Portola' was the largest (Table 2). 'Monterey' and 'San Andreas' were consistently mid-sized among the cultivars. Trichome density was similar among 'Portola', 'San Andreas', 'Al-

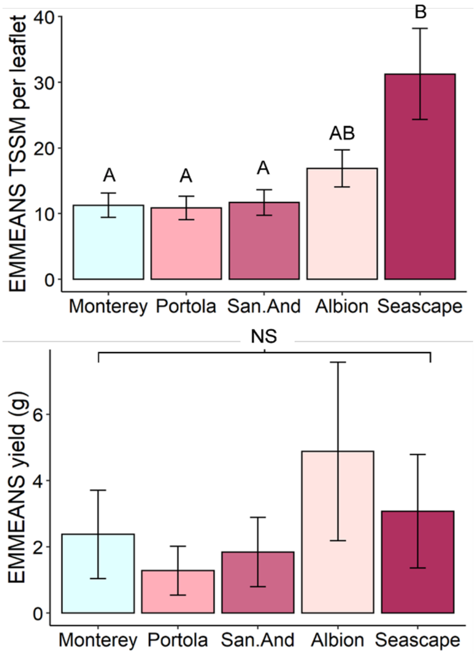

Figure 5. Model estimated means (± SE) of the number of TSSM per leaflet (top) and plant yield (bottom) on whole plants of 5 strawberry cultivars 21 d after TSSM inoculation for greenhouse experiments. Four plants were inoculated with 16 TSSM females. Means between cultivars represented by common letters do not differ at the 5 % level of significance by Tukey's test for multiple comparisons. No significant differences in yield were observed among cultivars.

Table 2. Model estimated means (± SE) of above ground biomass, average leaflet area, average number of leaflets and average trichome density among five strawberry cultivars. Common 'Group' letters do not differ at the 5 % level of significance by Tukey's test for multiple comparisons.

Above ground biomass (g)

	emmeans	SE	Group
Seascape	5.26	0.58	A
Albion	5.86	0.42	A
Monterey	8.48	0.45	B
San Andreas	8.70	0.43	B
Portola	11.73	0.45	C

Average leaflet area (cm^2)

	emmeans	SE	Group
Seascape	32.10	1.38	A
Albion	32.40	1.25	A
Monterey	38.10	1.54	B
San Andreas	39.50	1.32	B
Portola	46.00	1.38	C

Average num. leaflets

	emmeans	SE	Group
Albion	16.00	0.98	A
Seascape	16.70	1.36	AB
San Andreas	19.90	1.28	B
Monterey	21.70	1.43	B
Portola	31.00	2.33	C

Average trichome density

	emmeans	SE	Group
Monterey	54.80	10.6	A
Seascape	67.60	10.25	AB
Albion	85.90	10.45	AB
Portola	88.80	11.02	AB
San Andreas	104.20	13.53	B

bion' and 'Seascape', but was significantly lower for 'Monterey' compared to 'San Andreas' that had the highest trichome density. The path analysis revealed little evidence for significant correlations between these plant structural characteristics and TSSM counts per leaflet (Fig. 6; $\chi 2 = 5.17$, df = 3, $p = 0.15$). The strength of the relationship between variables is determined by the path coefficient, which is summarized alongside coefficients and significant p-value indicators on Fig. 6. Among them, there was a nearly significant negative effect of plant biomass and TSSM counts per leaflet, in that heavier plants were correlated with lower TSSM densities. Plant biomass was highly predicted by leaflet area and average leaflet number, but neither leaflet area nor leaflet number had a significant direct effect on TSSM counts per leaflet. Additional pathways were included in the model to describe correlations between plant structural characteristics and yield, but none resulted in significant relationships and were thus not pictured in Fig. 6 for simplicity.

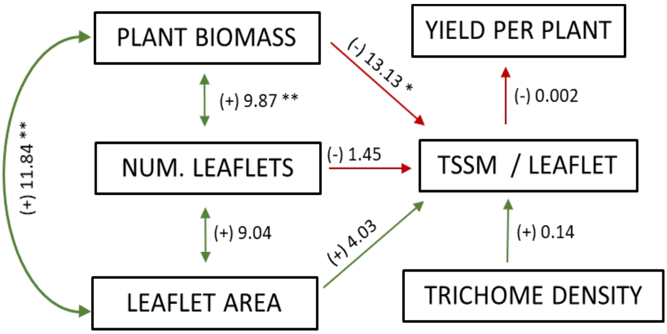

Figure 6. A conceptual path analysis illustrating the effects of structural plant characteristics (plant biomass, average number of leaflets, leaflet area and trichome density on TSSM density, and TSSM density impacts on yield. Path coefficients are untransformed and represent relative strength of the interaction. Directionality of the interaction is indicated by the direction of the arrow, with green (+) arrows indicating positive correlations, while red (-) arrows indicate a negative correlation. Double headedarrows indicate covariance between variables. A single asterisk (*) represent marginal significance ($p < 0.10$) and double asterisks (**) represent significance $p < 0.05$.

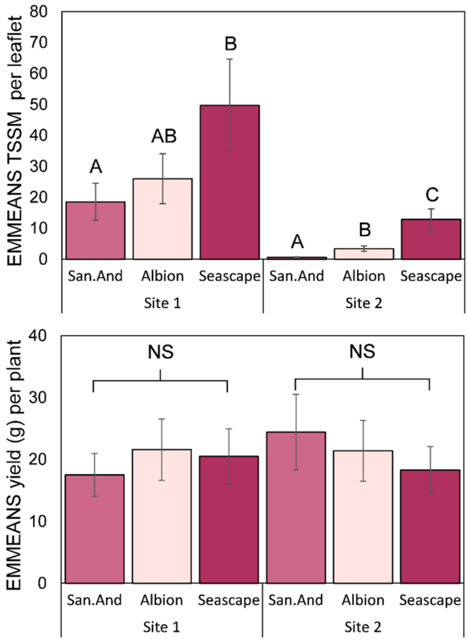

Figure 7. Model estimated means (± SE) of TSSM density per leaflet (top) and yield per plant (bottom) among cultivars evaluated at two commercial sites during the 2019 field season. TSSM density represents weekly averages collected during the season (July – Oct). Means followed by common letters do not differ at the 5 % level of significance by Tukey's test for multiple comparisons.

Field experiments at research site and commercial farms. The number of naturally occurring TSSM at commercial strawberry farms varied significantly by cultivar during the 2019 season for both sites observed (Site 1; $\chi 2 = 6.02$, df = 2, $p = 0.04$; Site 2: $\chi 2 = 13.19$, df = 2, $p < 0.01$). For both sites, 'Seascape' had a 47-73% higher number of TSSM per leaflet compared to 'Albion', and a 62-95% higher number compared to 'San Andreas' (Fig. 7). TSSM counts per leaflet were also highest on 'Seascape' at the research site, but comparisons among 'Seascape', 'Portola' and 'Albion' were not statistically significant (not pictured; $\chi 2 = 2.37$, df = 2, $p = 0.31$). Season averaged strawberry yield per plant ranged between 17-24 g and did not differ among sites and cultivars (Cultivar: $\chi 2 = 2.23$, df = 3, $p = 0.52$; Site: $\chi 2 = 1.46$, df = 2, $p = 0.48$). The average proportion of marketable fruit among all sites was 0.45 ± 0.39 and also did not vary by site or cultivar (Cultivar: $\chi 2 = 5.76$, df = 3, $p = 0.12$; Site: $\chi 2 = 4.52$, df = 2, $p = 0.10$).

Discussion

To meet increasing market expectations, strawberry growers in the northeastern U.S. have the opportunity to adopt protected culture growing practices using day-neutrals. In past studies, growing day-neutrals under low tunnels resulted in higher and more marketable yield and a longer growing season with minimal impact on the presence of beneficial predators, parasitoids and pollinators (Anderson et al., 2019; Lewers et al., 2017; Maughan et al., 2014; Orde et al., 2018; Sorkel et al., 2006; Willden et al., 2022). However, a tradeoff associated with this system is a greater risk of severe TSSM infestation under low tunnels compared to the open field (Costa et al., 2017; Willden et al., 2021). Results of this study indicate that cultivar selection could be a useful cultural control tactic for managing TSSM under low tunnels, and that plant biomass is the best predicator of TSSM tolerance among the structural characteristics measured in this study.

Plants can counter attacks from herbivores using several defense mechanisms that include structural defenses (trichomes, hairs, leaf thickness, plant size, and ratio of susceptible plant parts, etc.), chemical defenses (secondary metabolites that impact pest behavior and physiology, or herbivore-induce plant volatiles that attract natural enemies), and nutrition availability (War et al., 2012). These defenses can simultaneously contribute to pest resistance (prevent insect herbivory) or tolerance (ability of a plant to withstand herbivory). Although chemical defenses play an important role in determining a plant's susceptibility to herbivory, there is some evidence that structural defenses are the leading mechanisms of resistance and tolerance against herbivores (Carmona et al., 2011). In this study, we described the role of structural defenses among strawberry cultivars that can contribute to resistance (trichomes) or tolerance (plant size) against TSSM.

Our lab experiments on survival, preference, and oviposition by TSSM did not reveal consistent trends in TSSM preference or performance among cultivars at the leaf scale. This indicates that structural characteristics of the leaf (e.g., density of trichomes, leaf thickness, surface texture, etc.) are either poor predictors of TSSM performance, or that they do not vary enough among strawberry cultivars to elicit a clear response. Despite past studies that report a positive correlation between TSSM resistance and trichome density (de Resende et al., 2020; Esteca et al., 2017; Luczynski et al., 1990), others report the opposite effect or no correlation between TSSM resistance and trichome density (Gong et al., 2018; Gugole Ottaviano et al., 2013; Kishaba et al., 1972). Steinite and Ievinsh (2003) and Figueiredo et al. (2013) conclude that TSSM resistance to strawberry cultivars is likely tied to the density of glandular trichomes rather than non-glandular trichomes, which might explain some of this variability. In our study, the density of non-glandular trichomes also varied among cultivars, but with no impact on TSSM counts or oviposition. However, we did see more movement and higher oviposition preference within artificial trichomes on strawberry compared to control zones. Overall, these results support that non-glandular trichomes are unlikely mechanisms of resistance to TSSM in strawberry, but may play an important role when variation in trichome density is more conspicuous.

Population dynamics on whole plants did result in consistent differences among cultivars in greenhouse and field experiments. 'Seascape' supported higher numbers of TSSM on whole plants, followed closely by 'Albion', and finally 'San Andreas.' This trend was also consistent at two independent commercial low tunnel strawberry sites, although it is important to note that plots at commercial sites were not randomized within in the field and therefore statistical interpretation should be made with caution. It is possible that mechanisms for TSSM resistance occurs at the whole plant scale (e.g. plant size), or that defense at the leaf scale is stronger on intact leaves. Indeed, mechanical damage from cutting leaf discs for bioassays could release sequestered alkaloids and terpenoids and alter defense response to TSSM (Schmelz et al., 2001). Nutrient availability would also vary between intact or excised leaves (van Emden and Bashford, 1976). It is therefore likely that differences in TSSM resistance would vary between experiments on leaf discs and whole plants, and comparisons between them should be made with caution.

When comparing plant size among the cultivars, 'Albion' and 'Seascape' were consistently smaller compared to 'Monterey', 'Portola' and 'San Andreas' in terms of above ground biomass, leaflet area, and average number of leaflets present. However, these measurements are likely to vary under varying environmental conditions that should be carefully considered (Massetani et al. 2014). In our study 'Seascape', the smallest cultivar observed, consistently supported higher TSSM leaflet densities and counts on whole plants. Total biomass was negatively correlated with TSSM counts per leaflet, and was the strongest predictor of TSSM counts in our path model. This indicates that a large above ground biomass (greater than 5.86 g, as inferred from Table 2) could reduce TSSM density on strawberry leaflets, which may contribute to plant tolerance by reducing TSSM feeding intensity and damage potential (Tehri et al., 2014; Tiffin, 2000). Morphological traits not measured in this study but contribute to total biomass are petiole and peduncle biomass. In strawberries, petioles connect leaves to the crown and peduncles connect fruit to the crown. These connection points could assist in TSSM dispersal within a plant, and could therefore be correlated with TSSM density at the leaf scale (Aguilar-

Fenollosa et al., 2016; Strong et al., 1999). Curiously, counts on whole plants were similar among all cultivars, except for 'Seascape' that supported especially high densities. This lends some support to our hypothesis that large plants dilute TSSM numbers on leaflets. Regardless of cultivar differences in TSSM counts, we observed similar yield and proportions of marketable fruit among cultivars in all experiments. Because our studies were conducted when TSSM were present and did not include comparisons between infested and noninfested plants within each cultivar, interpretations of this result should be made with caution. However, past studies conducted on individual strawberry cultivars to compare TSSM density impacts on yield also observed little differences in yield despite exceeding action thresholds of 5 mites per leaflet (English-Loeb and Hesler, 2004). Another study in Florida, where mite pressure is high relative to the Northeast, found that 50-80 mites per leaf were required before yield reductions were detected (Nyoike and Liburd, 2013). Therefore, although cultivar differences in TSSM performance was detected in this study, the impact on yield in growing systems of New York and other northeastern regions is unclear and requires further investigation.

Conclusions

We conducted a series of lab, greenhouse, and field experiments to determine the relative preference and performance of TSSM on day-neutral cultivars relevant to growers in the northeastern U.S. Leaf disc assays were inconclusive, but experiments conducted on whole plants at several sites identified 'Seascape' and 'Albion' as the most susceptible of the cultivars. We conducted a path analysis to determine correlations between plant structural characteristics (trichome density, leaflet area, average number of leaflets, and total above-ground biomass) and TSSM counts per leaflet to describe possible mechanisms of TSSM resistance or tolerance. Of these, above-ground biomass was the strongest predictor where smaller plants were associated with higher TSSM counts per leaflet. However, increased TSSM presence on leaflets did not result in detectable reductions in yield. This study provides useful information in using cultivar choice as an IPM tactic against TSSM on protected culture strawberry in the Northeast.

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