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Combining Cultural Tactics and Insecticides for the Management of the Sweetpotato Whitefly, *Bemisia tabaci* MEAM1, and Viruses in Yellow Squash

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Abstract: The sweetpotato whitefly, *Bemisia tabaci* MEAM1 Gennadius (Hemiptera: Aleyrodidae), and the complex of viruses it transmits are major limiting factors to squash production in the southeastern United States. At this time, insecticides are extensively relied upon for the management of whiteflies and, indirectly, whitefly-transmitted viruses. The development of a multi-faceted, integrated pest management (IPM) program is needed to increase the sustainability and profitability of squash production. Experiments in 2018 and 2019 evaluated the effects of insect exclusion netting (IEN) in combination with selected pesticides on whitefly population dynamics and virus incidence in greenhouse-grown squash seedlings. Field experiments from 2018 to 2021 evaluated the effects of mulch type (UV-reflective mulch, live mulch, and white plastic mulch), row covers, and insecticides on whitefly population dynamics, silver leaf disorder (SSL) intensity, virus symptom severity, and marketable yield. IEN significantly reduced whiteflies and virus incidence on squash seedlings in the greenhouse study. In the field mulch study, lower whitefly abundance and SSL intensity, as well as reduced virus symptom severity, were observed in plots with reflective mulch compared with white plastic or live mulch. In the insecticide/row cover study, whitefly abundance, SSL intensity, and virus symptom severity were lowest in the row cover and cyantraniliprole- and flupyradifurone-treated plots. Field plots with row covers and those with UV-reflective mulch consistently produced the greatest marketable yields. These findings demonstrate that growers can reduce whitefly and virus pressure and preserve yields in squash production in the southeastern United States by combining cultural and chemical tactics, including row covers, UV-reflective mulch, and select insecticides.

Keywords: whiteflies; whitefly-transmitted viruses; integrated pest management; cultural control; cucurbit leaf crumple virus; cucurbit yellow stunting disorder virus

1. Introduction

Southeastern states, including Georgia and Florida, are among the top producers of fresh market yellow and zucchini squash (*Cucurbita pepo* L.) in the United States, with a market valued at USD 37.6 million in 2019 [1]. The majority of Georgia's yellow and zucchini squash (hereafter referred to as squash) are grown in the fall season, during which pressure from pests and pathogens is typically higher than in the spring [2–4]. The sweetpotato whitefly, *Bemisia tabaci* Gennadius MEAM1 (Hemiptera: Aleyrodidae), is arguably one of the most important pests of squash. Feeding by whitefly nymphs results in squash silverleaf disorder (SSL), a reversible physiological disorder that reduces photosynthesis, stunts plants, and diminishes fruit quality [5–8]. Feeding by whiteflies also results in the transmission of plant viruses, which can be severely yield-limiting. Yield losses from *B. tabaci* and whitefly-transmitted viruses, combined with management actions, cost growers tens of millions of dollars each year [9–11].

A complex of at least two whitefly-transmitted viruses impacts squash in Georgia, viz., cucurbit leaf crumple virus (CuLCrV) and cucurbit yellow stunting disorder virus (CYSDV) [4]. Both viruses are relatively new to Georgia. CuLCrV was first documented in the U.S. in 1998–1999 in Arizona, Texas, and California, and it was found in Florida and Georgia in 2006 and 2009, respectively [12–15]. CYSDV was first observed in California and Arizona in 2006 and in Georgia in 2016 [16,17]. Cucurbit leaf crumple virus is in the genus *Begomovirus* and family *Geminiviridae*, and Cucurbit yellow stunting disorder virus is in the genus *Crinivirus* and family *Closteroviridae* [18,19]. CuLCrV is transmitted in a persistent and circulative manner by whiteflies [20–23]. The acquisition access period (AAP), inoculation access period (IAP), and latent period each take hours to days [24]. CYSDV is transmitted by whiteflies in a semi-persistent and non-circulative manner [25,26]. Criniviruses, such as CYSDV, have shorter AAPs and IAPs (minutes to hours) than begomoviruses, with no latent period before they can be inoculated to a susceptible host [25,27,28]. Whiteflies can acquire and transmit multiple viruses at once, and thus, both viruses are often observed as mixed infection in squash, resulting in more severe symptoms [4,24].

Squash seedling/transplant production in open greenhouses is a common practice that often leaves plants vulnerable to virus infection at their most susceptible stage. This can result in the establishment of vector reservoirs and virus inoculum sources once infected seedlings are transplanted into the field [29–33]. Resistant crop varieties offer the best protection against whiteflies and viruses, but there are no commercially available squash varieties with resistance to whiteflies and/or CuLCrV and CYSDV [3,34,35]. Insecticide use, often multiple applications per week, is the norm for whitefly and virus management, indirectly [35,36]. However, most insecticides, despite suppressing whiteflies, do not reduce virus transmission, as one or a few viruliferous whiteflies past the latent period can readily inoculate a susceptible squash plant within minutes of feeding [37,38].

The current management strategy of prophylactic and frequent insecticide applications can also increase risks of insecticide resistance development. *Bemisia tabaci* MEAM1 populations around the world have developed resistance to nearly all insecticide classes used [37,39–42]. Such indiscriminate insecticide applications pose risks to applicators, non-target organisms, and the environment, and can negatively impact the biological control of pests by natural enemies. Reflective mulch can disorient whiteflies and prevent landing on transplanted seedlings by reflecting visible and UV light [43–46]. Living mulches, such as buckwheat, clover, perennial peanut, yellow mustard, cowpea, and sorghum have also been shown to effectively reduce whitefly abundance, SSL intensity, and virus incidence in crops [32,47–49]. In addition, row covers and other methods of physical exclusion have been shown to be extremely effective in protecting greenhouse seedlings and direct-seeded plants in the first few weeks of the growing season [33,46,50–53]. Despite the effectiveness of reflective mulch and row covers, they are seldom used in commercial squash production in the southeastern U.S.

At this time, there is no single management tactic that is effective enough to suppress whiteflies and reduce the transmission of viruses in Georgia and other southeastern states. Therefore, an integrated pest management (IPM) program comprised of existing cultural and chemical tactics aimed at pre- and post-transplant protection is essential to limit yield losses and maintain sustainability. The first objective of this study was to evaluate the effect of insect exclusion netting (IEN), either alone or in combination with insecticides, in greenhouse production of squash seedlings. The second objective was to evaluate UV-reflective and live mulches, as well as insecticides in combination with row covers, under open field conditions. One greenhouse and two field trials were conducted over four field seasons (2018–2021) with the goal of developing a combination of reduced-risk tactics to mitigate yield loss and enhance sustainability in squash production.

2. Materials and Methods

2.1. Evaluation of Pre-Plant Seedling Protection Tactics (Greenhouse)

Greenhouse experiments were performed in 2018 and 2019 to evaluate the effects of insecticide/acibenzolar-S-methyl applications and physical exclusion of whiteflies on whitefly population dynamics and virus incidence in squash seedlings. Experiments were performed at the University of Georgia (UGA) Coastal Plain Experiment Station in Tifton, GA, USA, in a non-insect-proof, temperature-controlled polytunnel enclosed with double-layer plastic sheeting. Roll-up sides opened automatically for ventilation. Squash seeds (cultivar 'Gold Star'; Johnny's Selected Seeds, Fairfield, ME, USA) were planted in seed trays (~64 plants) with Sta-Green potting mix (Lowe's®, Moorseville, NC, USA) and were arranged on top of greenhouse benches in a split-plot design with five replicates. The main plot factor was the presence or absence of IEN, which is an equivalent to row cover when used in the field. The subplot factor was insecticide/acibenzolar-S-methyl treatment (Table 1).

Table 1. Pesticide treatments, years, and application rates from greenhouse and field experiments performed at the University of Georgia Coastal Plain Experiment Station in Tifton, GA, USA.

Trial	Active Ingredient	Trade Name	IRAC Sub-Group [a]	Year				Application Rate Per Hectare
				2018	2019	2020	2021	
Greenhouse [b]	Cyantraniliprole	Verimark	28 Diamide	✓	✓			0.95 kg
	Acibenzolar-S-methyl	Actigard	-	✓	✓			17.51 g
	Terpene constituents of *Chenopodium ambrosioides* near *ambrosioides* extract	Requiem Prime	UNE Botanical essence with unknown/uncertain MoA	✓	✓			4.68 L
Field (Row cover/insecticide only)	Imidacloprid	Admire Pro	4A Neonicotinoid	✓	✓	✓	✓	0.73 L
	Cyantraniliprole	Exirel	28 Diamide	✓	✓	✓	✓	1.50 L
	Flupyradifurone	Sivanto Prime	4D Butenolide	✓	✓	✓	✓	1.02 L
	Terpene constituents of *Chenopodium ambrosioides* near *ambrosioides* extract	Requiem Prime	UNE botanical essence with unknown/uncertain MoA	✓	✓	✓	✓	7.01 L
	Chromobacterium subtsugae strain PRAA4–1	Grandevo WDG	-	✓	✓	✓	✓	3.36 kg
	Paraffinic oil	JMS Stylet-Oil	-	✓	✓	✓	✓	14.03 L
	Afidopyropen	Sefina	9D Pyropropene			✓	✓	1.02 L
	Spirotetramat + pyriproxyfen	Senstar	23 Tetronic/tetramic acid derivative; 7C pyriproxyfen			✓	✓	0.73 L

[a] Insecticide Resistance Action Committee (IRAC) classification scheme represents mode of action (MoA) [54].
[b] Greenhouse experiments only performed in 2018–2019.

Benches were spaced 0.6 m apart, with a 1.8 m aisle down the center of the greenhouse. IEN (0.35 mm × 0.35 mm; Dubois Agrinovation, Saint-Rémi, QC, Canada) was installed over PVC hoops and completely enclosed the seedling trays in each main plot. Insecticides/acibenzolar-S-methyl were applied as soil drenches approximately one week after planting. Plants were irrigated at the soil line as needed. Greenhouse conditions were 24 °C, 60% relative humidity, and 13:11 (L:D) h photoperiod.

In 2018 and 2019, plants were sampled once for whitefly eggs, nymphs, and adults at approximately 15 days after planting. Adult whiteflies were counted in situ on the abaxial sides of two randomly selected leaves from each replicate. Two additional leaves were removed from each replicate and taken to the Virus-Vector Interactions Laboratory in Tifton, GA, where eggs and immature whiteflies were counted at 20X magnification under a dissection microscope (Leica Microsystems, Wetzlar, Germany). Leaf samples were stored in a refrigerator at 3–5 °C until processing. All plants were visually screened for virus symptoms two to three weeks after planting. All plants exhibiting virus symptoms were tested to confirm CuLCrV infection. DNA was extracted and polymerase chain reaction (PCR) was conducted using virus-specific primer sets and established protocols [24]. The percent virus incidence in each replicate was calculated.

2.2. Evaluation of Post-plant Protection Tactics (Field)

2.2.1. General

All field experiments were conducted at the UGA Coastal Plain Experiment Station in Tifton, GA, USA. Experimental plots were constructed in accordance with standard commercial practices. Rows were tilled with a KMC 6800 ripper bedder and fertilized with 10-10-10 fertilizer (500 lb./ac.) before beds were shaped. A tractor mounted Kennco micro-combo plastic layer (Kennco Manufacturing, Inc., Ruskin, FL, USA) was used to shape raised beds, lay irrigation tape, and apply plastic mulch (DNM Ag Supply, Inc., Calabasas, CA, USA) to each bed. Raised beds in all trials in all years were 0.81 m wide with 1.8 m wide row middles. Beds were fumigated with Pic-Clor 60 (Trical, Inc., Hollister, CA, USA) approximately three weeks prior to planting. Planting holes at 30.5 cm spacing were cut along the center of each bed using a hand-powered, spiked wheel planter. Plots were irrigated as needed.

2.2.2. Evaluation of Mulch Types

Field experiments were performed in 2018, 2019, 2020, and 2021 to evaluate the effects of UV-reflective plastic mulch, white plastic mulch, and live mulch on whitefly abundance, SSL intensity, virus symptom severity, and marketable yield. Three-row plots were used for this trial in all years. Plots (replicates) were approximately 6 m in length with 3 m buffers between adjacent plots in a row. Treatments in all years were arranged in a randomized complete block design with four replicates. Treatments included: (1) UV-reflective mulch; (2) live mulch (buckwheat, *Fagopyrum esculentum*) plus white plastic mulch; and (3) white plastic mulch. The white mulch treatment was considered the control/grower standard. Buckwheat seeds were seeded directly between and outside each row in the three-row plots, two to three weeks before squash was planted. In 2021, buckwheat was re-seeded one week after initial seeding due to low germination. Buckwheat plants were also irrigated through drip lines. Yellow squash seeds (cultivar 'Gold Star') were seeded directly into pre-made planting holes in late August to early September of each year.

Whitefly abundance was measured weekly for three to six weeks beginning in September of each year. In 2018 and 2019, adult samples were taken by gently turning ten squash leaves per plot and counting adult whiteflies in situ on the abaxial side of each leaf. In 2020 and 2021, adult samples were taken by turning five leaves per plot and taking an image of the abaxial side of each leaf using an iPhone 7/iPhone SE/iPhone XR camera (Apple®, Inc., Cupertino, CA, USA). Adult whiteflies were counted by examining sample photos on a desktop computer. To measure whitefly egg and nymph abundances, five leaves were randomly collected per plot, stored in labeled zipper bags (Great Value, Walmart, Bentonville, AR, USA), and transported in a cooler to the Virus-Vector Interactions Laboratory in Tifton, GA (2019) or Griffin, GA (2020 and 2021). Leaf samples were stored in a refrigerator at 3–5 °C until processing. The number of eggs and nymphs in a 2.54 cm^2 area on the abaxial side of each leaf were counted at 20X magnification under a dissection microscope (Leica Microsystems, Wetzlar, Germany). Eggs and nymphs were only counted to an upper limit of 200 individuals per leaf. Abundances of whitefly eggs and nymphs were not measured in 2018.

SSL intensity and virus symptom severity ratings were performed once at the end of each season. The SSL intensity in each plot was rated on a 1–5 scale in all years, as follows: 1 = 0–20% of plants exhibiting SSL symptoms; 2 = 21–40% of plants exhibiting SSL symptoms; 3 = 41–60% of plants exhibiting SSL symptoms; 4 = 61–80% of plants exhibiting SSL symptoms; and 5 = 81–100% of plants exhibiting SSL symptoms. The severity of virus symptoms was rated on a 1–5 scale in all years, as follows: 1 = no visible symptoms; 2 = $\leq$ 50% of plants showing leaves with minimal curling symptoms and early chlorosis; 3 = > 50% of plants showing leaves with minimal curling and early chlorosis; 4 = $\leq$ 50% of plants showing leaves with severe curling, yellowing, or stunting; 5 = > 50% of plants showing severe curling, yellowing, or stunting [34]. Symptomatic plant samples were randomly selected from plots to confirm CuLCrV and/or CYSDV infection. DNA and RNA were extracted, and PCR and RT-PCR were conducted using virus-specific primer sets and established protocols [24].

In all years, yield was measured by harvesting squash fruits of marketable size ($\geq$15 cm in length) every 2–4 days and classifying as "marketable" or "non-marketable" (non-marketable data not included in analysis). Fruits were considered non-marketable when they exhibited virus symptoms, such as green streaking and mosaic discoloration, wrinkling due to poor pollination, or distorted shape. The number of fruits in each category was recorded.

2.2.3. Evaluation of Row Covers and Insecticides

Field experiments were performed in 2018, 2019, 2020, and 2021 to evaluate the effects of insecticides and physical exclusion of whiteflies (row covers) on whitefly abundance, SSL intensity, virus symptom severity, and marketable yield. Single row plots were used in all years. Plots (replicates) were 6.0–7.6 m in length with 1.5–3.0 m buffers between adjacent plots within a row. Yellow squash seeds (cultivar 'Gold Star') were seeded directly into pre-made planting holes in late August to early September of each year. Treatments in all years were arranged in a randomized complete block design with four replicates. Insecticide treatments evaluated in all years are listed in Table 1. Row covers (0.35 mm $\times$ 0.35 mm; Dubois Agrinovation, Saint-Rémi, QC, Canada) were installed over PVC hoops at the time squash was planted and were removed three weeks after planting or at the emergence of female flowers, whichever occurred earlier. No insecticide sprays were undertaken for the row cover treatment until the covers were removed. Cyantraniliprole (Exirel; FMC Ag US, Philadelphia, PA, USA) was applied weekly following removal of row covers. All insecticides were applied as foliar sprays using a CO_2-powered backpack sprayer at the rate of 300–468 L per hectare using cone tip nozzles (TeeJet Technologies, Wheaton, IL, USA). In each year, insecticide applications were made weekly for four to six weeks.

Whitefly abundance was measured weekly for three to seven weeks beginning in September of each year. Samples of adult and immature whiteflies were collected and processed as described under the mulch trial methods. The population dynamics of whitefly eggs and nymphs were not measured in 2018.

The SSL intensity and virus symptom severity were rated using the scales previously described. SSL intensity was not measured in 2019. Virus symptom severity was rated once at the end of each season. Symptomatic plant samples were randomly selected from plots to confirm CuLCrV and/or CYSDV infection. DNA and RNA were extracted, and PCR and RT-PCR were conducted using virus-specific primer sets and established protocols [24]. To measure yield in all years, squash fruits were harvested, classified as marketable/non-marketable, and counted as previously described.

2.3. Data Analysis

End-of-season ratings of virus symptom severity, SSL intensity, whitefly counts, and marketable yield were analyzed with a generalized linear mixed model using PROC GLIM-

MIX in SAS 9.4 software (SAS Institute Inc., Cary, NC, USA). The number of eggs, nymphs, and adult whiteflies, as well as the number of marketable fruits, were fitted to a Poisson distribution. Virus symptom severity and SSL intensity data were fitted to a Gaussian distribution. For the greenhouse study, the use of IEN, insecticide/acibenzolar-S-methyl, and their interaction were considered fixed effects. For the mulch evaluation study, mulch type was considered as a fixed effect. For the insecticide study, treatment (insecticides, row cover) was the fixed effect. Treatment effects and their interaction (interaction term in greenhouse study only) were considered significant at $p \leq 0.05$. Multiple mean comparisons were performed using the Tukey method. Means were considered to be significantly different at $p \leq 0.05$.

3. Results

3.1. Evaluation of Pre-Plant Seedling Protection Tactics (Greenhouse)

The use of IEN on squash seedlings significantly impacted the number of whitefly eggs, nymphs, and adults observed (Table 2). Squash seedlings grown under IEN had fewer whiteflies compared with non-covered seedlings, with the mean number of whitefly adults being nearly zero in both years (Table 3).

Table 2. Effect of treatments and their interaction on the number of whiteflies on squash seedlings grown in the greenhouse at the University of Georgia Coastal Plain Experiment Station in Tifton, GA, USA, in 2018 and 2019.

Treatments	df	2018		2019	
		F	*p* > *F*	*F*	*p* > *F*
Number of whitefly eggs					
Insect exclusion netting (IEN)	1,72	57.57	<0.0001	72.39	<0.0001
Insecticide/acibenzolar-S-methyl	3,72	0.75	0.5260	0.42	0.7390
IEN*Insecticide/acibenzolar-S-methyl	3,72	0.81	0.4940	1.20	0.3140
Number of whitefly nymphs					
IEN	1,72	11.53	0.0011	14.43	0.0003
Insecticide/acibenzolar-S-methyl	3,72	0.36	0.7840	1.37	0.2577
IEN*Insecticide/acibenzolar-S-methyl	3,72	0.43	0.7317	1.30	0.2812
Number of whitefly adults					
IEN	1,72	79.93	<0.0001	216.00	<0.0001
Insecticide/acibenzolar-S-methyl	3,72	6.50	0.0006	22.90	<0.0001
IEN*Insecticide/acibenzolar-S-methyl	3,72	6.50	0.0006	17.88	<0.0001

Data were subjected to analysis of variance using generalized linear mixed models, α = 0.05. Asterisk indicates an interaction.

Table 3. Effect of insect exclusion netting (IEN), insecticide/acibenzolar-S-methyl, and their interactions on the number of whitefly eggs, nymphs, and adults on squash seedlings grown in the greenhouse at the University of Georgia Coastal Plain Experiment Station in Tifton, GA, USA, in 2018 and 2019.

Treatments	Eggs [a]		Nymphs [a]		Adults [a]	
	2018	2019	2018	2019	2018	2019
Main plot (IEN)						
IEN	0.25b	1.80b	0.18b	0.28b	0.00b	0.13b
No IEN	34.38a	15.25a	4.13a	2.73a	1.10a	2.23a
Subplot (Insecticide/acibenzolar-S-methyl)						
Non-treated control	21.65a	9.75a	1.80a	0.90a	0.95a	2.15a
Acibenzolar-S-methyl (17.51 g/ha)	12.20a	8.65a	2.20a	2.05a	0.60ab	0.70b
Terpene constituents of *Chenopodium ambrosioides* near *ambrosioides* extract (4.68 L/ha)	17.35a	8.45a	1.50a	2.25a	0.20b	0.70b
Cyantraniliprole (0.95 kg/ha)	18.05a	7.25a	3.10a	0.80a	0.45b	1.15b

Table 3. *Cont.*

Treatments	Eggs [a]		Nymphs [a]		Adults [a]	
	2018	2019	2018	2019	2018	2019
IEN*Insecticide/acibenzolar-S-methyl						
No IEN: Non-treated control	43.10a	17.90a	3.60a	1.50ab	1.90a	4.10a
No IEN: Acibenzolar-S-methyl	23.90a	12.90ab	3.70a	3.30ab	1.20ab	1.40b
No IEN: Terpene constituents of *Chenopodium ambrosioides* near *ambrosioides* extract	34.40a	16.10a	3.00a	4.50ab	0.40cd	1.40b
No IEN: Cyantraniliprole	43.10a	14.10ab	6.20a	1.60ab	0.90bc	2.00b
IEN: Non-treated control	0.20b	1.60c	0.00a	0.30b	0.00d	0.20c
IEN: Acibenzolar-S-methyl	0.50b	4.40bc	0.70a	0.80ab	0.00d	0.00c
IEN: Terpene constituents of *Chenopodium ambrosioides* near *ambrosioides* extract	0.30b	0.80c	0.00a	0.00b	0.00d	0.00c
IEN: Cyantraniliprole	0.00b	0.40c	0.00a	0.00b	0.00d	0.30c

Data were subjected to analysis of variance using generalized linear mixed models, $\alpha = 0.05$. Treatment means within columns followed by the same letter are not significantly different (Tukey, $p < 0.05$). [a] Data represent average number of whiteflies per leaf. Asterisk indicates an interaction.

The insecticide/acibenzolar-S-methyl treatments and the interaction between IEN and insecticide/acibenzolar-S-methyl both had a significant effect on the number of adult whiteflies observed but not on the number of eggs and nymphs (Table 2). Among non-covered seedlings, the number of adult whiteflies was consistently lower on seedlings treated with *Chenopodium ambrosioides* near *ambrosioides* extract (Requiem Prime) and cyantraniliprole (Verimark), the two insecticides included in the study (Table 3). It is not surprising that acibenzolar-S-methyl (Actigard) had no effect on whitefly abundance, as this product induces plant resistance to pathogens and does not have direct pesticidal activity. The number of whiteflies did not vary significantly among insecticide/acibenzolar-S-methyl treatments in seedlings grown under IEN, as the IEN nearly eliminated whitefly abundance on plants.

In 2018, the use of IEN ($F_{1,32} = 10.95$, $p > F = 0.0023$) and insecticides/acibenzolar-S-methyl ($F_{3,32} = 6.92$, $p > F = 0.0010$) each had a significant effect on the percent incidence of CuLCrV. The interaction between IEN and insecticide/acibenzolar-S-methyl did not have an effect on CuLCrV ($F_{3,32} = 1.17$, $p > F = 0.3367$). The use of IEN reduced virus incidence in seedlings by half, compared with those grown without IEN (Table 4). However, CuLCrV incidence was higher in seedlings treated with acibenzolar-S-methyl and *Chenopodium ambrosioides* near *ambrosioides* extract compared with the non-treated control and cyantraniliprole. No CuLCrV was detected in the 2019 greenhouse experiment.

Table 4. Effect of IEN, insecticide/acibenzolar-S-methyl, and their interaction on percent incidence of cucurbit leaf crumple virus (CuLCrV) in squash seedlings grown in the greenhouse at the University of Georgia Coastal Plain Experiment Station in Tifton, GA, USA, in 2018 [a].

Treatments by Level	Percent CuLCrV Incidence [b]
Main plot (IEN)	
IEN	2.89b
No IEN	5.39a
Subplot (Insecticide/acibenzolar-S-methyl)	
Non-treated control	2.50b
Acibenzolar-S-methyl (17.51 g/ha)	5.94a
Terpene constituents of *Chenopodium ambrosioides* near *ambrosioides* extract (4.68 L/ha)	5.78a
Cyantraniliprole (0.95 kg/ha)	2.34b
IEN *Insecticide/acibenzolar-S-methyl	
No IEN: Non-treated control	3.13ab
No IEN: Acibenzolar-S-methyl	7.81a

Table 4. *Cont.*

Treatments by Level	**Percent CuLCrV Incidence** [b]
No IEN: Terpene constituents of *Chenopodium ambrosioides* near *ambrosioides* extract	7.81a
No IEN: Cyantraniliprole	2.81b
IEN: Non-treated control	1.88b
IEN: Acibenzolar-S-methyl	4.06ab
IEN: Terpene constituents of *Chenopodium ambrosioides* near *ambrosioides* extract	3.75ab
IEN: Cyantraniliprole	1.88b

Data were subjected to analysis of variance using generalized linear mixed models, $\alpha = 0.05$. Treatment means within columns followed by the same letter are not significantly different (Tukey, $p < 0.05$). [a] No virus infection was observed in 2019. [b] Data represent average percent incidence per plot. Asterisk indicates an interaction.

3.2. Evaluation of Post-Plant Protection Tactics (Field)

3.2.1. Evaluation of Mulch Types

Mulch type had a significant effect on the number of whitefly eggs, nymphs, and adults over the multi-year study (Table 5). There were significantly fewer whitefly nymphs and adults in squash grown on UV-reflective mulch compared with white plastic and live mulch (Figure 1). Fewer whitefly eggs were observed in plants grown on white plastic in 2019 and with live mulch and UV-reflective mulch in 2020, but the effects were inconsistent across years. Mulch type also had a significant effect on the intensity of SSL in two out of four years. In 2018 and 2021, SSL was less intense in plots with UV-reflective mulch (Figure 1). The intensity of SSL was not different in the other two years. The symptom severity of virus infection was lower among infected plants on plots with UV-reflective mulch in 2018 and in live mulch and UV-reflective mulch treatments in 2019 (Figure 1).

Table 5. Effect of mulch type on whiteflies, squash silverleaf disorder (SSL) intensity, virus symptom severity, and marketable yield in yellow squash grown in 2018, 2019, 2020, and 2021 at the University of Georgia Coastal Plain Experiment Station in Tifton, GA, USA.

Response Variable	**2018**			**2019**			**2020**			**2021**		
	df	***F***	***p* > *F***	**df**	***F***	***p* > *F***	**df**	***F***	***p* > *F***	**df**	***F***	***p* > *F***
Whitefly eggs [a]	-	-	-	2,56	4.32	0.0179	2,235	5.38	0.0055	2,341	31.58	<0.0001
Whitefly nymphs [a]	-	-	-	2,57	7.02	0.0019	2,235	14.48	<0.0001	2,341	2.82	0.0118
Whitefly adults	2,357	26.38	0.0011	2,717	1.38	0.3208	2,286	18.61	<0.0001	2,342	7.57	0.0006
SSL intensity	2,9	9.80	0.0129	2,9	2.33	0.1780	2,9	1.88	0.1680	2,9	22.23	<0.0001
Virus symptom severity	2,9	16.71	0.0035	2,9	3.67	0.0911	2,9	2.37	0.1090	2,9	0.95	0.4010
Yield	2,9	5.08	0.0333	2,9	64.71	<0.0001	2,33	13.06	<0.0001	2,33	6.83	0.0052

Data were subjected to analysis of variance using generalized linear mixed models, $\alpha = 0.05$. [a] Data were not collected in 2018.

Mulch had a consistent effect on the number of marketable fruits harvested throughout all years. Plants grown in plots with UV-reflective mulch produced the greatest number of marketable squash fruits (Figure 1). In three out of four years of the study, the number of marketable fruits in plots with UV-reflective mulch was more than twice the amount harvested in the white plastic and live mulch plots.

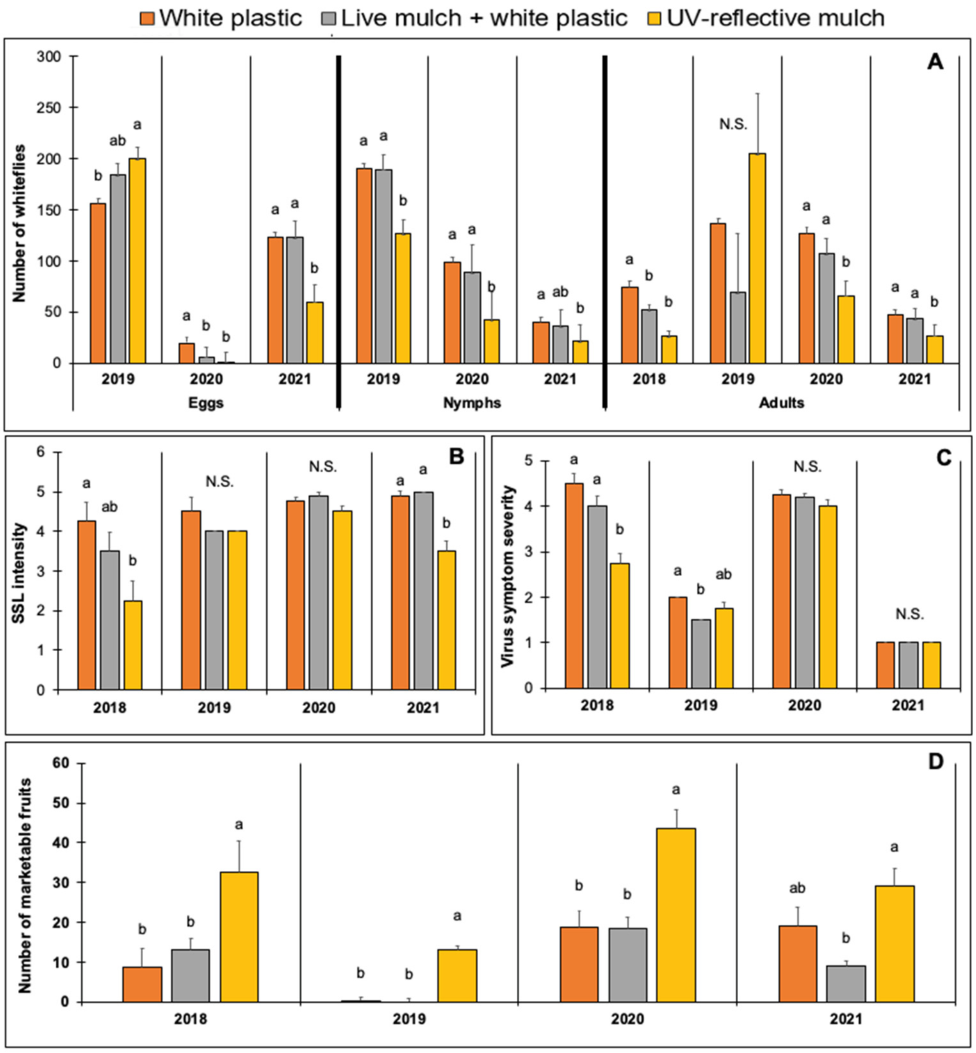

Figure 1. Effect of mulch type on the number of immature whiteflies (per 2.54 cm^2) and adult whiteflies (per leaf) (**A**). Squash silverleaf disorder (SSL) intensity (**B**). Severity of whitefly-transmitted virus symptoms (**C**). The number of marketable fruits per plot of yellow squash grown in field trials conducted in 2018, 2019, 2020, and 2021 at the University of Georgia Coastal Plain Experiment Station in Tifton, GA, USA (**D**). Data were subjected to analysis of variance using generalized linear mixed models, $\alpha = 0.05$. Treatment means followed by the same letter are not significantly different (Tukey, $p < 0.05$). N.S. = means not significantly different.

3.2.2. Evaluation of Row Covers and Insecticides

The treatments had significant effects on abundances of whitefly eggs, nymphs, and adults (Table 6). The number of whitefly eggs was consistently greatest in non-treated plots and plots treated with *Chromobacterium subtsugae* (Grandevo WDG) (Figure 2). In 2019 and 2020, the fewest whitefly eggs were observed in plots with row covers. Compared with the non-treated control, significantly fewer whitefly eggs were observed in plots treated with imidacloprid (Admire Pro), cyantraniliprole (Exirel), flupyradifurone (Sivanto Prime), afidopyropen (Sefina), and spirotetramat plus pyriproxyfen (Senstar) in two out of the three years that whitefly eggs were recorded. Similarly, there were fewer nymphs in plots with row covers and those treated with cyantraniliprole, flupyradifurone, paraffinic oil (JMS Stylet-Oil), afidopyropen, and spirotetramat plus pyriproxyfen compared with the non-treated control (Figure 2). The abundances of nymphs in plots treated with *Chromobacterium subtsugae* and *Chenopodium ambrosioides* near *ambrosioides* extract were not significantly different than the non-treated control. The number of adult whiteflies also varied among treatments. In three out of the four years, significantly fewer adult whiteflies were recorded in plots with row covers and those treated with cyantraniliprole, flupyradifurone, *Chenopodium ambrosioides* near *ambrosioides* extract, and Paraffinic oil. The non-treated plots, as well as plots treated with imidacloprid and *Chromobacterium subtsugae*, had the greatest number of adult whiteflies (Figure 2).

Table 6. Effect of treatment (insecticide or row cover) on whiteflies, squash silverleaf disorder (SSL) intensity, virus symptom severity, and marketable yield in yellow squash grown in 2018, 2019, 2020, and 2021 at the University of Georgia Coastal Plain Experiment Station in Tifton, GA, USA.

Response Variable	**2018**			**2019**			**2020**			**2021**		
	df	***F***	***p* > *F***	**df**	***F***	***p* > *F***	**df**	***F***	***p* > *F***	**df**	***F***	***p* > *F***
Whitefly eggs [a]	-	-	-	7,755	10.82	<0.0001	9,1160	46.45	<0.0001	9,1154	11.71	<0.0001
Whitefly nymphs [a]	-	-	-	7,755	7.40	0.0002	9,1160	8.75	<0.0001	9,1189	16.22	<0.0001
Whitefly adults	7,952	52.28	<0.0001	7,1536	2.73	0.0349	9,1184	26.22	<0.0001	9,1189	18.71	<0.0001
SSL intensity [b]	7,24	1.69	0.1657	-	-	-	9,30	114.40	<0.0001	9,30	69.34	<0.0001
Virus severity	7,24	19.80	<0.0001	7,24	22.41	<0.0001	9,30	159.40	<0.0001	9,30	0.92	0.519
Yield	7,24	33.88	<0.0001	7,24	9.80	<0.0001	9,30	56.81	<0.0001	9,30	1.63	0.151

Data were subjected to analysis of variance using generalized linear mixed models, $\alpha = 0.05$. [a] Data were not collected in 2018. [b] Data were not collected in 2019.

The intensity of SSL varied among treatments in two out of the three years that data were collected (Table 6). In 2020 and 2021, SSL was less intense in plots with row covers and those treated with cyantraniliprole and flupyradifurone (Figure 3). In these three treatments, the mean SSL intensity was rated <1 at the end of the growing season. SSL was severe in plots treated with *Chenopodium ambrosioides* near *ambrosioides* extract, *Chromobacterium subtsugae*, paraffinic oil, and imidacloprid.

Treatments influenced virus symptom severity (Table 6). In three out of four years, virus symptoms were least severe among plots with row covers (Figure 3). In 2019 and 2020, plots treated with cyantraniliprole and flupyradifurone also had lower virus symptom severity compared with the non-treated control. The severity of virus symptoms did not vary significantly among treatments in 2021, due to low virus pressure.

Plots with row covers consistently produced the greatest number of marketable fruits in three out of four years (Figure 3). In contrast, the lowest yields were observed in plots treated with imidacloprid, *Chenopodium ambrosioides* near *ambrosioides* extract, *Chromobacterium subtsugae*, and paraffinic oil, and the non-treated control. The number of marketable fruits was not different among treatments in 2021.

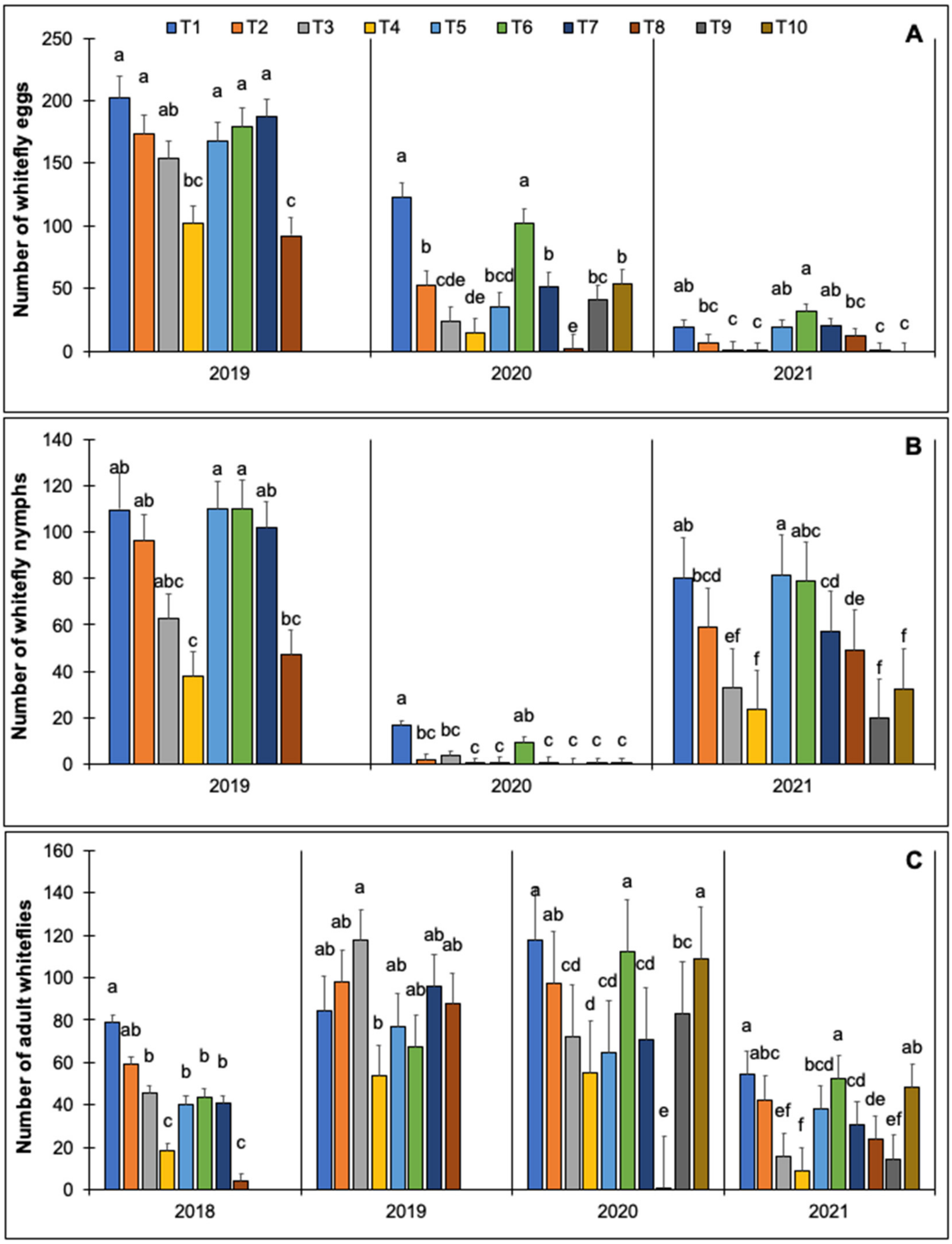

Figure 2. Effect of insecticides and row covers followed by insecticide application on the number of whitefly eggs (per 2.54 cm^2) (**A**). Nymphs (per 2.54 cm^2) (**B**) and adults (per leaf) (**C**) observed in yellow squash grown in field trials conducted in 2018, 2019, 2020, and 2021 at the University of Georgia Coastal Plain Experiment Station in Tifton, GA, USA. Whitefly egg and nymph data were not collected in 2018. Only treatments T1-T8 were included in 2018 and 2019. All treatments (T1–T10) were included in 2020 and 2021. The treatments are as follows: T1 = non-treated control, T2 = imidacloprid (0.73 L/ha), T3 = cyantraniliprole (1.50 L/ha), T4 = flupyradifurone (1.02 L/ha), T5 = terpene constituents of *Chenopodium ambrosioides* near *ambrosioides* extract (7.01 L/ha), T6 = *Chromobacterium subtsugae* (3.36 kg/ha), T7 = paraffinic oil (14.03 L/ha), T8 = row cover followed by cyantraniliprole (1.50 L/ha), T9 = afidopyropen (1.02 L/ha), and T10 = spirotetramat plus pyriproxyfen (0.73 L/ha). Data were subjected to analysis of variance using generalized linear mixed models, $\alpha = 0.05$. Treatment means followed by the same letter are not significantly different (Tukey, $p < 0.05$).

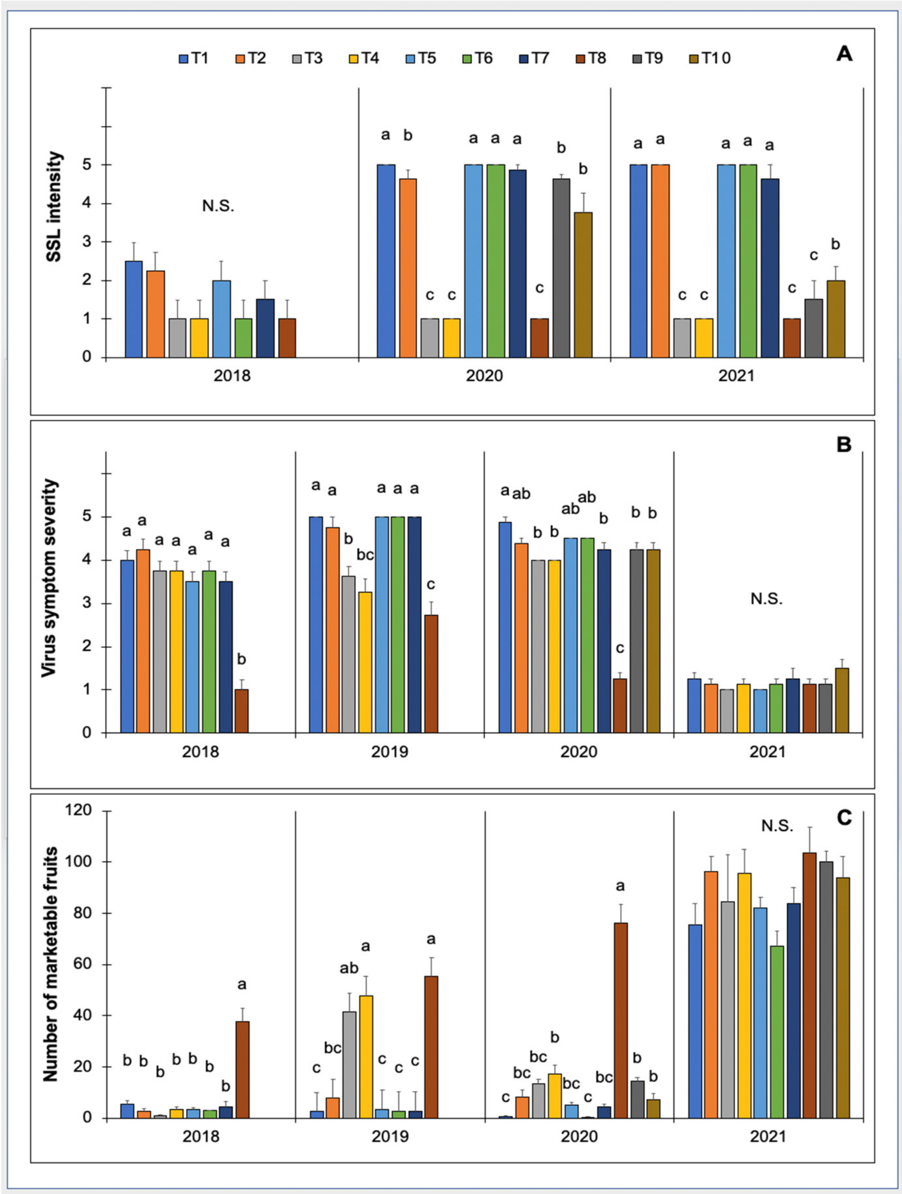

Figure 3. Effect of insecticides and row cover followed by insecticide application on squash silverleaf disorder (SSL) intensity (data not collected in 2019) (**A**). Severity of whitefly-transmitted virus symptoms (**B**). The number of marketable fruits in yellow squash grown in field trials conducted in 2018, 2019, 2020, and 2021 at the University of Georgia Coastal Plain Experiment Station in Tifton, GA (**C**). Only treatments T1-T8 were included in 2018 and 2019. All treatments (T1–T10) were included in 2020 and 2021. The treatments are as follows: T1 = non-treated control, T2 = imidacloprid (0.73 L/ha), T3 = cyantraniliprole (1.50 L/ha), T4 = flupyradifurone (1.02 L/ha), T5 = terpene constituents of *Chenopodium ambrosioides* near *ambrosioides* extract (7.01 L/ha), T6 = *Chromobacterium subtsugae* (3.36 kg/ha), T7 = paraffinic oil (14.03 L/ha), T8 = row cover followed by cyantraniliprole (1.50 L/ha), T9 = afidopyropen (1.02 L/ha), and T10 = spirotetramat plus pyriproxyfen (0.73 L/ha). Data were subjected to analysis of variance using generalized linear mixed models, $\alpha = 0.05$. Treatment means followed by the same letter are not significantly different (Tukey, $p < 0.05$). N.S. = means not significantly different.

4. Discussion

Bemisia tabaci MEAM1 and whitefly-transmitted viruses are the biggest limiting factors to profitable and sustainable yellow and zucchini squash production in Georgia, United

States. In this study, several management tactics aimed at reducing the impacts of *B. tabaci* MEAM1 and whitefly-transmitted viruses were evaluated. This study demonstrated that adequate management measures in seedling greenhouses are key to minimizing virus inoculum sources in the field. Additionally, this study evaluated UV-reflective and live mulches, row covers, and insecticides in the field over four consecutive field seasons. The outcomes revealed that protection methods and insecticides helped manage whitefly populations and, to some extent, virus symptom severity. The benefits of these management tactics led to an increase in yield that was most prominent during the seasons when virus pressure was highest.

Whitefly-transmitted viruses are emerging worldwide [55], and the southeastern United States is no exception to this global trend. Mixed infections of CuLCrV, CYSDV, and cucurbit chlorotic yellows virus (CCYV) were found to be widespread in cucurbit fields in Georgia in 2021 [4,56]. Squash silverleaf disorder (SSL), a physiological disorder resulting from whitefly feeding, also affects squash production [5,43]. Yellow and zucchini squash varieties with resistance or tolerance to whiteflies and/or whitefly-transmitted viruses are not commercially available [34,35]. Current management programs for whiteflies and whitefly-transmitted viruses rely heavily on insecticides [37,42,57]. There is not a single management tactic available that can effectively reduce whitefly-mediated transmission of viruses to desirable levels. This study intended to offset this critically important need by evaluating a number of management tactics with the goal of developing IPM recommendations for yellow and zucchini squash production in the southeastern United States.

The first step to reducing virus pressure and the resulting reduction in yield is to avoid introducing virus-infected seedlings into the field. Squash seedlings are typically grown in open greenhouses without any insect exclusion materials. Consequently, virus-infected seedlings may be transplanted into fields, facilitating rapid secondary spread of viruses after planting. The IEN used in this study was effective in reducing whitefly abundance and virus incidence in the greenhouse study. The insecticides cyantraniliprole and terpene constituents of *Chenopodium ambrosioides* near *ambrosioides* extract also reduced the number of whitefly adults on seedlings, although cyantraniliprole alone reduced virus incidence. Acibenzolar-S-methyl, a salicylic acid analog, does not have insecticidal properties but is known to induce plant defenses against viruses by activating the salicylic acid pathway [58–60]. While fewer adult whiteflies were observed in the acibenzolar-S-methyl treatment compared with the non-treated control in our study, the former did not reduce virus incidence in squash seedlings. It is possible that the timing of our acibenzolar-S-methyl application could be optimized to improve virus protection [59], or that multiple applications may be necessary for suppressing CuLCrV-induced symptoms on squash seedlings [60]. The greenhouse experiment in this study demonstrated that seedling infection in open greenhouses could be minimized with the use of IEN in conjunction with insecticides.

In addition to transplant seedling protection, an effective IPM program should include tactics that reduce whitefly abundance and virus inoculum in the transplanted field. Previous studies have shown that different mulch types can have varying effects on whiteflies and virus transmission [38,43,45,49,61,62]. Summers and Stapleton [43] observed fewer whitefly adults and nymphs in squash plots with UV-reflective mulch than in bare-ground plots and found that reflective mulch was as effective for whitefly management as imidacloprid. In our study, the use of UV-reflective plastic mulch reduced the number of immature and adult whiteflies and significantly reduced SSL intensity (Figure 4). Marketable yield was doubled in plots with UV-reflective mulch compared with live mulch and white plastic. Reflective mulch may have encouraged yield increases by several complementary mechanisms: (1) by repelling whiteflies and reducing direct feeding injury and SSL intensity [43]; (2) by reducing virus transmission due to reduced feeding [38,45,61]; and (3) by radiating additional light energy onto plants, which augments photosynthesis and growth [45,63–65]. Although UV-reflective mulch has been shown to reduce virus pressure in squash [66,67], reduced virus severity was only detected in one year of our study. This was likely due to explosive whitefly populations in the experimental area and the fact that a single viruliferous whitefly can transmit the virus to a susceptible host plant [68–70].

Figure 4. Reduced squash silverleaf disorder (SSL) intensity observed on yellow squash plants grown on UV-reflective mulch (**left**) compared with white plastic mulch (**right**) in a trial at the University of Georgia Coastal Plain Experiment Station in Tifton, GA, USA.

Live mulch intercropped with white plastic mulch only reduced adult whitefly abundance as effectively as the UV-reflective mulch in the 2018 season. This effect did not extend to abundances of whitefly eggs and nymphs, virus symptom severity, SSL intensity, or yield, and no effects of live mulch were observed in 2019, 2020, or 2021. Similarly, Frank and Liburd [48] did not observe reduced whitefly abundance or virus incidence in plots with live mulch. However, other studies have found that plantings with live mulch had comparable whitefly abundances, virus incidences, and yields to reflective mulch and even insecticide treatments [49,61]. Flowering live mulches can increase the abundances of natural enemies that attack whiteflies, such as hover flies (Diptera: Syrphidae), predatory wasps (Hymenoptera: Scoliidae, Sphecidae, Eumenidae, Vespidae), and lady beetles (Coleoptera: Coccinellidae [47,48,71–73]. Poor germination and growth of buckwheat in at least two years of our study due to heavy rains may have negatively impacted natural enemy populations and, subsequently, whitefly populations.

Insect-proof row covers installed immediately after planting were equally or more effective than insecticides in reducing whitefly abundance, SSL intensity, and virus symptom severity in squash plants. Additionally, protecting young plants with row covers dramatically increased marketable yield, while the insecticide treatments alone had little to no effect. Webb and Linda [33] and Costa et al. [51] saw similar reductions in whitefly abundance and SSL intensity, as well as increases in yield when squash was protected using row covers. Other studies have also seen virus incidence reduction with the use of row covers [50,51]. Row covers also exclude other pests that can cause additional injury and yield reductions [33,50]. The use of row covers in squash production is relatively new in the southeastern United States but is already practiced for frost protection in crops such as strawberries [74,75].

Insecticides have effectively reduced whitefly abundance and SSL intensity in squash in other studies [37,61,76]. Of the insecticides tested in our field trials, cyantraniliprole and flupyradifurone offered the best protection against adult whiteflies. Afidopyropen and spirotetramat plus pyriproxyfen also provided protection against whitefly nymphs. All four products have different modes of action (Table 1) and represent alternatives to commonly used neonicotinoids, such as imidacloprid. Some insecticides can also help prevent virus infection under certain conditions, including cyantraniliprole and flupyradifurone [36,39,53,77–82]. In this study, reduced virus symptom severity, but not virus incidence, was observed in plots treated with cyantraniliprole and flupyradifurone compared with the non-treated control. Virus infection was ubiquitous in the trials, often reaching 100%. Unlike many conventional insecticides that rely only on toxic activity against the vector, cyantraniliprole and flupyradifurone rapidly inhibit vector feeding, potentially limiting virus transmission [37,78,81,83–86]. Thus, insecticide applications remain an important part of IPM programs for whiteflies and viruses. However, reliance on insecticides is not recommended, as most insecticides do not impact virus incidence in the long-term, and insecticide resistance in whitefly populations is a major concern [37,38]. There is already evidence that *B. tabaci* MEAM1 populations in the southeastern United States have developed high levels of resistance to the commonly used neonicotinoids imidacloprid and thiamethoxam, with varying tolerances to pyrethroids, flupyradifurone, buprofezin, and dinotefuran [41,87,88].

With no "silver bullet" for managing whitefly-transmitted viruses in squash, a combination of multiple tactics with additive effects is the most effective management approach at this time. Combining the use of row covers and UV-reflective plastic mulch with effective insecticides may help achieve optimum control and ensure profitable yields until virus-resistant squash varieties become available [48,49,61,79,82]. Besides improving the management of whiteflies and viruses, integrating these cultural management practices can reduce reliance on insecticides and lessen resistance development risks [62]. These practices can be implemented by both small- and large-scale growers and may also be effective in other crops, such as watermelon, where squash vein yellowing virus, another whitefly-transmitted virus causing vine decline in watermelon, is common [79,80,89,90].

5. Conclusions

The protection of squash seedlings in greenhouses and in the field is essential for reducing whitefly and virus pressure and ensuring profitable yields. IEN/row covers were extremely effective for reducing whitefly feeding and virus symptom severity in both greenhouse and field settings. UV-reflective mulch also helped reduce whitefly pressure and SSL symptoms and led to increases in yield. Most of the insecticides tested were not as effective for managing whiteflies and viruses as the use of IEN/row covers. Until whitefly- or virus-resistant squash varieties become available, a combination of cultural and chemical tactics is required to mitigate virus-induced risks and yield losses in squash production in the southeastern United States.

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