OXFORD

Striped cucumber Beetle and Western Striped Cucumber Beetle (Coleoptera: Chrysomelidae)

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Subject Editor: Thomas Kuhar

Received 27 August 2020; Editorial decision 5 November 2020

Abstract

The striped cucumber beetle [StCB; *Acalymma vittatum* (F) (Coleoptera: Chrysomelidae)] and the western striped cucumber beetle [WStCB; *Acalymma trivittatum* (Mannerheim)] are closely related species of herbivores endemic to North America that specialize on Cucurbitaceae plants. StCB and WStCB are key pests of cucurbit crops that can reduce quantity and quality of yield or even kill plants, especially seedlings, by feeding and by vectoring pathogens. Insecticides can be used to control StCB and WStCB, but a number of more selective nonchemical management methods are also available to help control these pests. Here, we describe the biology, life stages, and damage caused by StCB and WStCB and discuss methods for managing these pests in cucurbit crops.

Key words: bacterial wilt, cucumber beetle, Cucurbitaceae, integrated pest management

The striped cucumber beetle (StCB), Acalymma vittatum (F.) (Coleoptera: Chrysomelidae), and the western striped cucumber beetle (WStCB), Acalymma trivittatum (Mannerheim), are closely related specialist herbivores (Eben and Espinosa de Los Monteros 2013). They are both native to North America and feed primarily on plants in the family Cucurbitaceae, which contains many wild species native to North America. StCB is found east of the Rocky Mountains from Texas to southern Canada (Fig. 1), where squash (C. pepo ssp. ovifera) has been cultivated for at least five millennia (Smith and Yarnell 2009). Throughout this region, StCB is a key pest of cucurbit crops that causes feeding damage and vectors pathogens of major diseases. Pest severity is most pronounced in the northeastern and midwestern United States and eastern Canada, where it is the primary pest of cucurbits. WStCB inhabits the western and southwestern United States, parts of Texas, and most areas of Mexico, and is similar in biology and the damage it causes (Capinera 2020). Prior to cultivation of cucurbits in the Pacific states, the wild cucurbit genus Marah (manroots) was the presumed host of WStCB (Smith 1966). WStCB is of the greatest economic importance in California, where a large number of cucurbits are produced. Muskmelon production in the northern and north-central part of the state is particularly affected by WStCB. While the two species share many similarities, differences in production systems and pathogen presence between eastern and western North America create some variation in pest status.

Damage

Both StCB and WStCB can damage cucurbit crops across much of the growing season (Table 1), but damage varies across species of cultivated cucurbits, as well as by region and cultural practices. A number of studies have investigated beetle preference for host plant species to understand host susceptibility (Howe et al. 1972, Bach 1980, Eben et al. 1997, Smyth et al. 2002, Brzozowski et al. 2016). However, preference can be driven by a number of factors, including volatiles (Lewis et al. 1990, Andrews et al. 2007, Gardner et al. 2015), cucurbitacin content (Chambliss and Jones 1966), and flower size (Theis et al. 2014), and cucurbit varieties differ in their tolerance of feeding injury (Hoffmann et al. 2000). Therefore, it is difficult to link differential host preference directly to crop susceptibility or tolerance.

Early season damage is typically more severe with StCB than WStCB because of the former species vectors pathogens. Adult StCB feeds on cotyledons, foliage, and stems of plants, which can kill young seedlings and weaken older plants (Fig. 2a,b). Adults also feed on flowers, inhibiting successful pollination and fruit set (Fig. 2c). Larvae feed on the roots of cucurbit plants, which can impede root development (Diver and Hinman 2008) and can spread the fungal pathogen *Fusarium oxysporum*, resulting in *Fusarium* wilt (Latin and Reed 1985). StCB adults can vector squash mosaic virus and *Phoma cucurbitacearum*, the fungal pathogen that causes

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Figure 1. Geographic occurrence of *Acalymma vittatum and A. trivittatum*. Redrawn and partially revised in color from Munroe and Smith (1980). Highlighted dots are additions. Texas, New Mexico, and Arizona records are corrected by based on text records (Munroe and Smith 1980, pp. 37, 46–47) for both species. Munroe and Smith (1980) text for *A. vittatum* lists range as 'Canada to Northern Mexico'(p.7) but does not list any records from Mexico. Smith (1966) states that *A. vittatum* does not occur in Mexico. Guatemalan records shown on map for *A. trivittatum* are not recorded in text on page 37. Utah records (Garland, Green River, Moab) of *A. trivittatum* added thanks to R. Davis and D. Alston, USU, with single record of *A. vittatum* (Munroe and Smith 1980, p. 47) deleted. Montana (Billings, Culbertson, Scoby, Custer Co.) and Wyoming (Buffalo) records from MSU collections, thanks to M. Ivie. No records found from Idaho, thanks to J. Clements. Saskatchewan (Verwood) and PEI (Cherry Valley) records confirmed by H. Douglas, Canadian National Collection, AAFC Ottawa. Reported absent in Fraser River valley BC by provincial personnel; no confirmed records for BC or AK.

black rot (Diver and Hinman 2008, Sharma et al. 2016). Perhaps most importantly, StCB vectors the bacterium Erwinia tracheiphila (E.F. Smith), which causes bacterial wilt (Fig. 3). Bacterial wilt is a major threat to cucurbit production in the Midwest, mid-Atlantic, and northeast regions of the United States and southern Ontario and Quebec (Saalau Rojas et al. 2015). Its symptoms include wilting followed by foliar necrosis, and plants infected with bacterial wilt often die before they produce fruit (Salau Rojas et al. 2015). Erwinia tracheiphila overwinters in the gut of the beetles and is transmitted when beetles feed in leaves and nectaries and defecate onto fresh feeding wounds (Sasu et al. 2010). Up to 10% of overwintering beetles harbor E. tracheiphila and transmit it upon spring emergence (Brust 1997a, Fleischer et al. 1999). Although serological assays have suggested that noncucurbit herbaceous weed species can contain E. tracheiphila, researchers have been unable to re-isolate E. tracheiphila from these species (de Mackiewicz et al. 1998). Thus, adult StCBs are assumed to be the primary overwintering reservoirs of E. tracheiphila. Cultivars of cucurbits are differentially susceptible to bacterial wilt (Brust and

Rane 1995, Brust 1997b). It is impossible to stop disease progression once a plant is infected, so managing cucumber beetles is the primary means of managing bacterial wilt.

Similar to the StCB, the WStCB damages an array of cucurbits. The most severe and economically important damage by WStCB in commercial fields typically occurs in fresh-market muskmelon fields, although severe problems can occur with other cucurbits, especially in smaller-scale and organic production systems. Adult WStCB can move into freshly planted fields, defoliate plants, and damage and kill seedlings. Plants are generally more tolerant of feeding once they are established (4-5 leaf stage). More importantly for melons, adult WStCB causes major cosmetic damage to fruit by feeding on rinds, creating scars, and rendering fruit unmarketable (Michelbacher et al. 1953, California Melon Research Board and California Specialty Crops Council 2016). WStCB typically prefers melons over other cucurbits, and prefers honeydew melons over other varieties of melons (Michelbacher et al. 1953, Alston and Worwood 2012, PMSP 2016). Immature melons without a hardened rind are most susceptible. Adult WStCB hide under fruit and feed on the rind, causing damage

Crop	Species	Comments on beetle interactions
Crops with no or low susceptibility to bacterial wilt ^d Watermolons	Citrullus lanatus	
Bitter melons	Citrullus sob. & Momordica sop.	
Cushaw pumpkin	Cucurbita argyrosperma	
Buttercup squash	Cucurbita maxima	preferred by beetles but generally considered tolerant of adult feeding
Hubbard squash		
Kubocha squash		
French/Turk's turban gourd		
Butternut squash	Cucurbita moschata	C. maxima is preferred over C. moschata and has been used as trap crop for it
Acorn squash	<i>Cucurbita pepo</i> ssp. <i>ovifera</i> (includes ssp. <i>texana</i>)	higher thresholds for beetles due to lower wilt susceptibility; beetles prefer subspe-
Pattypan squash		cies <i>pepo</i> , at least when both sspp. are present ^b
Crookneck squash		
Ornamental gourds (most)		
Pumpkin	Cucurbita pepo ssp. pepo	higher thresholds for beetles due to lower wilt susceptibility; beetles prefer subspe-
Cocozelle squash		cies <i>pepo</i> over <i>ovifera</i> , at least when both sspp. are present ^b
Straightneck squash		
Zucchini		
Crops with high susceptibility to bacterial wilt ^a		
Cucumber	Cucumis sativus	low threshold for beetles due to high wilt susceptibility
Cantaloupe, muskmelon	Cucumis melo	low threshold for beetles due to wilt; damage to rinds and increased risk of fungal
Honeydew melon		rot increase susceptibility
Other miscellaneous cucurbits		
Bottle gourd	Lagenaria siceraria	
Chayote	Sechium edule	
Loofah	Luffa spp.	
Snake gourd	Trichosanthes cucumerina	
Cassabanana or musk cucumber	Sicana odorifera	
Wax gourd	Benincasa hispida	
^a Erwinia tracheiphila. Hoffmann and Zitter 1994. ^b Brzozowski et al. (2016).		

Table 1. Commonly cultivated cucurbits and preference of Acalymma vittatum and A. trivittatum, and bacterial wilt susceptibility (Cucurbit taxonomy from Chomicki et al. 2020)



Figure 2. Adult feeding on (a) cotyledons, (b) leaves, (c) flowers, and (d) muskmelon rind. All photos except 2c, by Whitney Cranshaw, Colorado State University, Bugwood.org. Photo 2c by D. Gordon E. Robertson, Ottawa, Ontario.



Figure 3. Symptoms of cucumber beetle vectored bacterial wilt, *Erwinia tracheiphila*, on winter squash. Photo by G. Higgins, University of Massachusetts Vegetable Program.

where the fruit touches the soil (Fig. 2d). As the melons increase in size, the damage expands and raised scars form. Adults oviposit in fields they colonize, although root feeding by larvae tends to not be an issue in fresh market melon fields. Larvae, when abundant, also feed on the undersides of melons and can create scarring damage similar to that of adults (Michelbacher et al. 1953), although this

damage is of less consequence than adult damage in conventional production. There are no records or published reports of bacterial wilt in western states, so the spread of the pathogen is not a component of the damage WStCB causes (Shapiro et al. 2018). However, WStCB can vector squash mosaic virus (Diver and Hinman 2008).

Life Cycle and Description

Of the two species, the life cycle of StCB has been better described, although the two species are fairly similar. StCB overwinter as adults in or near cucurbit fields in leaf litter or in the top 2–3 cm of soil, and become active in spring when temperatures exceed 12°C (Radin and Drummond 1994). Adults emerge before cucurbits are available as host plants, and feed on pollen, petals, and foliage of alternative host plants, including trees and shrubs in the Rosaceae family, until cucurbits emerge. Eggs are laid at the base of cucurbit plants below the soil surface 10–20 d after mating. When eggs hatch, larvae move to the roots to feed, pupate in the soil, and emerge as the next generation of adults. The number of generations each year ranges from one in northern latitudes to three in the southernmost latitudes (Capinera 2020).

WStCB also overwinter as adults in or near cucurbit fields, including underneath tree bark and leaf litter (Pedersen 2009). They become active as early as mid-February in northern California (Pedersen 2009). Cucurbit hosts are often not readily available in the environment during winter and early spring, so adults likely feed on alternative hosts, although the identity of these hosts is not well described. The WStCB is a multivoltine species with up to three generations per summer in the Sacramento Valley (Pedersen 2009). Like the StCB, the WStCB depends on cucurbits to complete its lifecycle.

Eggs

Eggs of both species are yellow or orange, oval-shaped, and average 0.50 mm long \times 0.36 mm wide. StCB eggs are laid in clusters of up to four eggs (Ellers-Kirk and Fleischer 2006). A female can lay up to 1,500 eggs over her lifetime (Diver and Hinman 2008). The egg stage lasts 5–9 d before hatching (Evans and Renkema 2018).

Larvae

StCB and WStCB larvae are wormlike, white or yellowish-white, and have a dark brown head capsule (Fig. 4). Larvae pass through three instars over 11–45 d (Diver and Hinman 2008). First instar larvae measure approximately 1.5 mm long, and third instar larvae can be up to 12 mm long (Capinera 2020).

Pupae

StCB and WStCB pupae are white and 8–10 mm long (Houser and Balduf 1925). They reside in the soil near the base of the host plant. The pupal stage lasts 7–10 d (Dill and Kirby 2016).



Figure 4. Larvae of striped cucumber beetle on cantaloupe rind. Photo by Whitney Cranshaw, Colorado State University, Bugwood.org.



Figure 5. Adult striped cucumber beetle, *Acalymma vittatum*. Photo by Susan Mahr, Wisconsin Master Gardener Program.

Adults

Adults of both species measure approximately 7 mm long (Capinera 2020). They have a brown or black head, yellow prothorax, and black abdomen (Figs. 5 and 6). Elytra are pale to dark yellow and have three longitudinal black stripes over their entire length. Legs in StCB are generally pale with patellas, tarsi, fore tibia, and dorsal apex of femora dark, whereas most WStCB have legs dark brown to black with only the base of femora pale. Males of the two species are distinguished by genitalia, but females and insects in the field may be difficult to distinguish where the ranges overlap, particularly in Texas (Munroe and Smith 1980). Male StCB emit a pheromone (vittatalactone) attractive to both males and females (Smyth and Hoffmann 2003, Morris et al. 2005). Cucurbitacins, the characteristic bitter components of cucurbits, are phagostimulants and arrestants for StCB (Smyth et al. 2002, Metcalf AND Lampman 1989) and presumably for WStCB.

Adult striped cucumber beetles are often confused in the field with western corn rootworm (*Diabrotica virgifera virgifera* LeConte) where their ranges overlap. Western corn rootworm adults (Fig. 7a,b) are longer and have yellow-green (not black) abdomens. Their black and yellow stripes do not extend the full length of the elytra (Hoffman and Zitter 1994) and their legs are solid black (Diver and Hinman 2008). Beetles in the genus *Lema*, particularly *Lema daturaphila* Kogan and Goeden (Fig. 7c), are also sometimes mistaken for StCB. These feed on potato, tomatillo, and other nightshade-family plants; they are larger than cucumber beetles and have an orange abdomen and wide yellow stripes on the elytra (Eaton 2015).

Management

Although many farmers use prophylactic treatments for StCB, threshold-based management programs result in lower pesticide use and enhanced pollinator service, thereby reducing net costs relative to prophylactic treatment programs (Ternest et al. 2020). StCB economic thresholds differ by crop type, variety, geographical region, and plant age (Diver and Hinman 2008). Field studies in upstate New York suggested damage thresholds of 20% leaf damage for cotyledon and 50% leaf damage for first through third-leaf winter squash (Cucurbita moschata; Ayyappath et al. 2002). For pumpkin (Cucurbita pepo), a treatment threshold of 60% leaf area damage over the entire field was proposed (Hoffmann et al. 2003). Studies in Indiana found that cantaloupe growers in the Midwestern United States should begin to apply control measures at a population density of one beetle per plant (Brust and Foster 1999). Meanwhile, in New England, it has been recommended that infestations not be allowed to exceed one beetle for every two plants in crops most susceptible to bacterial wilt, and that they not exceed 1-2 beetles per



Figure 6. Adult western striped cucumber beetle, *Acalymma trivittatum*. Photo by I. Grettenberger, Davis, California



Figure 7. Similar species: (a, b) Adult western corn rootworm, *Diabrotica virgifera virgifera* (photo by Stephen Ausmus, USDA ARS D1910-33, and Tom Hlavaty, USDA ARS K1289-17), and (c) Adult threelined potato beetle, *Lema daturaphila* (photo by Tom Murray, Bolton, Massachusetts).

plant for the less susceptible crops (e.g., butternut squash; Hazzard and Cavanaugh 2010). However, crop and region-specific thresholds for managing StCB are not well-established.

For WStCB, economic thresholds similarly differ by crop type, variety, and plant age, although established thresholds are often not available. California has a stringent threshold for conventional muskmelon production. Typically, if one beetle is found in a conventional melon field, the field is treated with insecticides (PMSP 2016). Damage thresholds are also lowest in conventional muskmelon fields with fruit destined for domestic fresh market sale or export. The threshold depends on the strength of markets, but is often a single scarred area 20–25 mm in diameter. Organic operations tend to exhibit higher damage levels likely due to a lack of effective or practical control options, and varieties susceptible to scarring are sometimes avoided (Vinchesi-Vahl, unpublished).

Chemical Control

Organophosphates, carbamates, pyrethroids, and neonicotinoids are often used to manage StCB on cucurbit crops, particularly during the seedling stage when plants are most susceptible to foliar injury and pathogen introduction (Sharma et al. 2016). Growers commonly use systemic neonicotinoids at planting, either as a seed treatment or applied as a soil drench, because this approach provides longer residual protection of seedlings than a foliar application (MacIntyre Allen et al. 2001, Jasinski et al. 2009). Seed treatments are particularly attractive to growers, as this approach requires no additional labor and uses less pesticide than foliar or soil applications. However, synthetic insecticides can have nontarget effects, including adverse effects on native pollinator populations (Gill et al. 2012, Whitehorn et al. 2012). Because cucurbit crops depend on pollinators for fruit set, the detrimental effects of insecticides on pollinators can reduce yield as well (Brust and Foster 1995). Moreover, beetles can develop resistance to synthetic insecticides; therefore, these insecticides should be used sparingly and in combination with other control methods.

Kaolin clay, pyrethrins, and spinosyns are registered for use in organic systems. Kaolin clay is an insect repellent and deterrent, and should be applied before beetles arrive because it will prevent beetles from recognizing the plant (Hazzard and Cavanagh 2010). Pyrethrin is a naturally occurring, broad-spectrum insecticide. However, pyr-ethrin should be applied with caution because it can kill beneficial organisms in addition to the target pest, disrupting the management of other pests (Sharma et al. 2016). Spinosad is a general feeding deterrent and toxin; however, not all spinosad formulations are approved for certified organic production (Snyder 2019). Insecticides are sometimes used in combination with a feeding stimulant (Seaman et al. 2013, Tillman et al. 2015, Gardner et al. 2018) so that beetles are enticed to feed and subsequently killed.

It is difficult to control WStCB adults with foliar insecticides when the beetles are protected underneath the fruit. However, insecticides continue to be the most successful approach to management of cucumber beetles in conventionally grown melon crops, although insecticide resistance is a concern. Seedlings may be treated with carbamates to prevent stand loss from feeding early in the season, and neonicotinoids and pyrethroids are used throughout the season. Sprays are typically applied at night to limit pollinator toxicity. Currently, insecticide seed treatments are not used for WStCB.

In organic cucurbit production in California, spinosad is generally reserved for higher-value crops (i.e., watermelon) because it is expensive and used when producers need to target more than one pest. Kaolin clay and diatomaceous earth are also commonly used as an early-season beetle deterrent. For melons with a complex rind like cantaloupes, the residue of kaolin clay is an issue once they develop netting, so its use is often discontinued at that point. During the fruiting stage, strongly scented oils such as rosemary and cedar oil are sometimes used to prevent damage to fruit (Vinchesi-Vahl, unpublished).

Biological Control

The tachinid fly *Celatoria setosa* (Coquillet), an *Acalymma* specialist (Toepfer et al. 2008), and the braconid wasp *Centistes diabroticae* (Gahan) parasitize adult StCB (Toepfer et al. 2009, Smyth and Hoffmann 2010, Coco et al. 2020; Fig. 8). However, the efficacy of these parasitoids in controlling StCB in cucurbit fields is not known. Predatory carabid beetles and lycosid spiders have been shown to reduce StCB densities (Snyder and Wise 2001). The presence of the lycosid spider *Rabidosa rabida* was found to reduce StCB feeding rates and to increase emigration from plants (Williams and Wise 2003), indicating that StCB antipredator responses could help to reduce crop damage. A recent study also found that coccinellid beetles can be important predators of StCB (Mabin et al. 2020). The nematode Steinernema riobravis caused a ~50% decrease in StCB larval survival under commercial field conditions in both organic and conventional soil management systems (Ellers-Kirk et al. 2000). Another nematode, Howardula begnina, can affect female longevity and fecundity, although H. begnina infection rates are low (Capinera 2020). In a recent study in Pennsylvania, a potentially undescribed Howardula species was found to parasitize and damage organs of StCB (Coco et al. 2020). There is also evidence to suggest that Heterorhabditis spp. and Neoaplectana carpocapsae can reduce emergence of StCB (Reed et al. 1986). In addition, StCB is known to be a host to the intracellular bacterial pathogen Wolbachia. This suggests the potential for Wolbachia to be used as a biological control, although it has never been attempted (Toepfer et al. 2009).

The WStCB is also parasitized by the tachinids *C. setosa* and *C. compressa* (Wulp) (Eben & Barbercheck 1996, Toepfer et al. 2008, Pedersen 2009). The role of generalist predators in suppressing WStCB populations is not well known.



Figure 8. (a) Celatoria diabroticae (Shimer) (female tachinid fly, closely related to *C. setosa*, emerged from the closely related host western spotted cucumber beetle (*Diabrotica undecimpunctata undecimpunctata* Mannerheim)), photo by Joyce Gross, San Leandro, California; (b) Celatoria setosa (Coquillet) (Diptera: Tachinidae), mounted specimen, photo by Angela Coco and Carolyn Trietsch, Frost Museum, Penn State University, courtesy Maggie Lewis. and (c,d) Centistes diabroticae (braconid wasp, Hymenoptera: Braconidae) (c) with spotted cucumber beetle, *Diabrotica undecimpunctata*); photo by StefanToepfer, CABI, Delémont, Jura, Switzerland; (d) close-up of mounted specimen, photo by Angela Coco and Carolyn Trietsch, Frost Museum, Penn State University, courtesy Maggie Lewis.

Cultural and Mechanical Control

Given the potential for beetles to develop resistance and the adverse environmental impacts associated with synthetic insecticide use, and the inconsistent efficacy of organic insecticides, additional methods are needed to manage cucumber beetles. Cultural and mechanical practices are useful as part of an integrated management program for long-term pest control. These methods can alter the time and level of crop exposure to pests, reduce pest reproductive ability, and physically keep pests off of crops. The practices that we describe here can be applied to both StCB and WStCB; however, the efficacy of these practices is much better studied in StCB than in WStCB. In addition, because WStCB is of greatest concern in California, where large-scale conventional agriculture is predominant, many of these practices may not be economically feasible for WStCB control.

Crop Rotation

Both species overwinter near fields planted with cucurbit crops the prior year. Pest problems can be reduced by planting the new cucurbit crop as far as possible from last year's crop. However, given the high mobility of StCB, crop rotation is likely insufficient in controlling StCB on its own (Snyder 2019). Managing volunteer cucurbits in nearby fields can also prevent populations from developing outside a cucurbit field and then moving in.

Transplant Instead of Direct Seed

Plants are most susceptible to feeding damage during their early developmental stages (Brewer et al. 1987). Transplanting rather than direct-seeding cucurbit crops, while significantly more expensive, limits exposure to cucumber beetles when the plant is most susceptible. Moreover, this minimizes the period of time in a given field that cucumber beetles have to build their populations and that disease symptoms can develop (where disease is an issue).

Perimeter Trap Crops

Perimeter trap cropping consists of planting a border crop that is more attractive to a pest than the main crop so that the pest preferentially colonizes the border crop, protecting the main crop from damage. The use of trap crops can eliminate or reduce insecticide use, often by limiting necessary insecticide application only to the border. Blue Hubbard, buttercup squash, and zucchini are all highly attractive to StCB (Adler and Hazzard 2009, Cavanagh et al. 2009). As border crops, they can effectively control StCB while reducing the need for insecticides. It is important to avoid using trap crops that promote spread of bacterial wilt. Trap cropping may not work if beetle populations are too high or if the main crop is highly preferred. It has had only limited adoption due to its need to dedicate cropland to less marketable trap crops, and/or the necessity of managing pest populations on the trap crop to avoid pest movement to the main crop.

Intercropping

Specialist herbivores tend to be more abundant in simple than in diverse habitats, so intercropping can be used to reduce such pest pressure. StCB densities were lower in cucumbers (*Cucumis sativus*) in a polyculture with corn (*Zea mays*) and broccoli (*Brassica oleracea*) than they were in a monoculture of cucumbers (Bach 1980). Companion plants that are repellant to cucumber beetles (radish, tansy, and nasturtium) or that attract beneficial insects (buckwheat, cowpea, and sweet clover) were also found to reduce StCB populations (Cline et al. 2008). Zucchini fields intercropped with sunn

hemp had significantly fewer StCB than bare-ground zucchini fields (Hinds and Hooks 2013).

Natural Mulches and Composts

Natural mulches can benefit crop production by improving soil nutrient levels and by supporting beneficial insect communities. Populations of StCB were found to be significantly lower on cucumber plants treated with food waste vermicompost than on cucumber plants treated with inorganic fertilizer (Yardim et al. 2006). Straw mulch may also help suppress StCB populations by reducing interplant movement and by helping to support predator populations (Snyder 2019).

Physical Barriers

Floating row covers can be used as a barrier to keep StCB off plants during the early stages of plant growth. Row covers on muskmelon have been found to decrease bacterial wilt incidence and increase yield (Mueller et al. 2006, Caudle et al. 2013). Planting on black plastic mulch can also limit oviposition and reduce the survival of StCB larvae (Necibi et al. 1992). Row covers must be removed when plants begin flowering to allow for pollination, but plants are able to tolerate moderate pest levels by this stage. One disadvantage of row covers is that they create favorable conditions for weed growth during the most susceptible stage of cucurbit development. Many organic systems use a combination of row covers and weedsuppressing mulches to manage insect pests and weeds simultaneously (Diver and Hinman 2008).

Mass Trapping

Mass trapping uses synthetic chemical attractants, including sex and aggregation pheromones and host plant volatiles, as lures to trap insects (El-Sayed et al. 2006, Gregg et al. 2018). Attractants are often combined with a killing agent to reduce the pest population, in which case the system is called 'attract and kill'. Traps baited with commercially available synthetic mixtures of Cucurbita blossom volatiles have successfully attracted StCB and WStCB adults in field studies (Lewis et al. 1990, Jackson et al. 2005, Pedersen 2009, Piñero 2018). Lures targeting StCB typically include three componentstrimethoxybenzene, indole, and cinnamaldehyde-abbreviated TIC. Lures targeting WStCB have included benzyl alcohol, indole, and βionone. However, traps with synthetic floral volatiles can attract and capture pollinators (Meagher et al. 1999), an undesirable nontarget effect. It is currently unknown which Cucurbita blossom volatiles may attract pollinators, and what trap designs might aggravate or mitigate this effect. Conversely, pheromone lures can provide a species-specific attractant with limited nontarget effects. Pheromone traps are not currently available for cucumber beetle management. However, preliminary work has shown that traps baited with a synthetic mixture of eight isomers of the male-produced aggregation pheromone, vittatalactone, attract large numbers of adult StCB (Weber 2018). This suggests that vittatalactone could precisely target this pest and reduce beetle populations through an attractand-kill system, possibly in combination with cucurbitacins as a phagostimulant (Weber 2018).

References Cited

Adler, L. S., and R. V. Hazzard. 2009. Comparison of perimeter trap crop varieties: effects on herbivory, pollination, and yield in butternut squash. Environ. Entomol. 38: 207–215.

- Alston, D. G., and D. R. Worwood. 2012. Western striped cucumber beetle and western spotted cucumber beetle (*Acalymma trivittatum* and *Diabrotica* undecipunctata undecipunctata). Utah State University Extension and Utah Plant Pest Diagnostic Laboratory, Logan, UT. www.utahpests.usu.edu.
- Andrews, E. S., N. Theis, and L. S. Adler. 2007. Pollinator and herbivore attraction to *Cucurbita* floral volatiles. J. Chem. Ecol. 33: 1682–1691.
- Ayyappath, R., M. P. Hoffmann, and J. Gardner. 2002. Effect of striped cucumber beetle (Coleoptera: Chrysomelidae) foliar feeding on winter squash injury and yield. J. Entomol. Sci. 37: 236–243.
- Bach, C. E. 1980. Effects of plant-density and diversity on the populationdynamics of a specialist herbivore, the striped cucumber beetle *Acalymma vittata*. Ecology 61: 1515–1530.
- Brewer, M. J., R. N. Story, and V. N. Wright. 1987. Development of summer squash seedlings damaged by striped and spotted cucumber beetles (Coleoptera: Chrysomelidae). J. Econ. Entomol. 80: 104–1009.
- Brust, G. E. 1997a. Seasonal variation in percentage of striped cucumber beetles (Coleoptera: Chrysomelidae) that vector *Erwinia tracheiphila*. Environ. Entomol. 26: 580–584.
- Brust, G. E. 1997b. Interaction of *Erwinia tracheiphila* and muskmelon plants. Environ. Entomol. 26: 849–854.
- Brust, G. E., and R. E. Foster. 1995. Semiochemical-based toxic baits for control of striped cucumber beetle (Coleoptera, Chrysomelidae) in cantaloupe. J. Econ. Entomol. 88: 112–116.
- Brust, G. E., and R. E. Foster. 1999. New economic threshold for striped cucumber beetle (Coleoptera: Chrysomelidae) in cantaloupe in the midwest. J. Econ. Entomol. 92: 936–940.
- Brust, G. E., and K. K. Rane. 1995. Differential occurrence of bacterial wilt in muskmelon due to preferential striped cucumber beetle feeding. HortScience. 30: 1043–1045.
- Brzozowski, L., B. M. Leckie, J. Gardner, M. P. Hoffmann, and M. Mazourek. 2016. Curcurbita pepo subspecies delineates striped cucumber beetle (Acalymma vittatum) preference. Hortic. Res. 3: 16028.
- California Melon Research Board and California Specialty Crops Council. 2016. Pest Management Strategic Plan for Cantaloupe, Honeydew and Mixed Melon Production in California. Prepared for USDA and US EPA. https://ipmdata.ipmcenters.org/documents/pmsps/2016%20CA%20 Melon%20PMSP.pdf
- Capinera, J. L. 2020. Handbook of vegetable pests, 2nd ed. Academic Press, Cambridge, MA.
- Caudle, J. R., T. Coolong, M. A. Williams, P. Vincelli, and R. Bessin. 2013. Development of an organic muskmelon production system against bacterial wilt disease. Acta Hortic. 1001: 249–254.
- Cavanagh, A., R. Hazzard, L. S. Adler, and J. Boucher. 2009. Using trap crops for control of *Acalymma vittatum* (Coleoptera: Chrysomelidae) reduces insecticide use in butternut squash. J. Econ. Entomol. 102: 1101–1107.
- Chambliss, O. L., and C. M. Jones. 1966. Cucurbitacins: specific insect attractants in Cucurbitaceae. Science. 153: 1392–1393.
- Chomicki, G., H. Schaefer, and S. S. Renner. 2020. Origin and domestication of Cucurbitaceae crops: insights from phylogenies, genomics, and archaeology. New Phytol. 226: 1240–1255.
- Cline, G. R., J. D. Sedlacek, S. L. Hillman, S. K. Parker, and A. F. Silvernail. 2008. Organic management of cucumber beetles in watermelon and muskmelon production. HortTechnology. 18: 436–444.
- Coco, A. M., M. T. Lewis, S. J. Fleischer, and J. F. Tooker. 2020. Parasitoids, nematodes, and protists in populations of striped cucumber beetle (Coleoptera: Chrysomelidae). Environ. Entomol. doi: 10.1093/ec/nvaa116
- Dill, J. F., and C. A. Kirby. 2016. Striped cucumber beetle. Pest Management Fact Sheet 5038. University of Maine. https://extension.umaine.edu/ipm/ ipddl/publications/5038e/
- Diver, S., and T. Hinman. 2008. Cucumber beetles: organic and biorational integrated pest management. National Center for Appropriate Technology, Butte, MT. www.attra.ncat.org.
- Eaton, A. T. 2015. Three-lined potato beetle. Univ. of New Hampshire Coop. Extn., Durham, NH.
- Eben, A., M. E. Barbercheck, and A. S. Martin. 1997. Mexican diabroticite beetles: II. Test for preference of cucurbit hosts by *Acalymma* and *Diabrotica* spp. Entomol. Exp. Appl. 82: 63–72.

- Eben, A., and A. Espinosa de Los Monteros. 2013. Tempo and mode of evolutionary radiation in Diabroticina beetles (genera Acalymma, Cerotoma, and Diabrotica). ZooKeys. 332: 207–321.
- Ellers-Kirk, C., and S. J. Fleischer. 2006. Development and life table of *Acalymma vittatum* (Coleoptera: Chrysomelidae), a vector of *Erwinia* tracheiphila in cucurbits. Environ. Entomol. 35: 875–880.
- Ellers-Kirk, C. D., S. J. Fleischer, R. H. Snyder, and J. P. Lynch. 2000. Potential of entomopathogenic nematodes for biological control of *Acalymma vittatum* (Coleoptera: Chrysomelidae) in cucumbers grown in conventional and organic soil management systems. J. Econ. Entomol. 93: 605–612.
- El-Sayed, A. M., D. M. Suckling, C. H. Wearing, and J. A. Byers. 2006. Potential of mass trapping for long-term pest management and eradication of invasive species. J. Econ. Entomol. 99: 1550–1564.
- Evans, B. G., and J. M. Renkema. 2018. Striped cucumber beetle Acalymma vittatum F. (Insecta: Coleoptera: Chrysomelidae). Department of Entomology and Nematology, UF/IFAS Extension. https://edis.ifas.ufl.edu/ in1215
- Fleischer, S. J., D. de Mackiewicz, F. E. Gildow, and F. L. Lukezic. 1999. Serological estimates of the seasonal dynamics of *Erwinia tracheiphila* in *Acalymma vittata* (Coleoptera: Chrysomelidae). Environ. Entomol. 28: 470–476.
- Gardner, J., M. P. Hoffmann, and M. Mazourek. 2015. Striped cucumber beetle (Coleoptera: Chrysomelidae) aggregation in response to cultivar and flowering. Environ. Entomol. 44: 309–316.
- Gardner, J., A. L. Seaman, and M. P. Hoffman. 2018. Laboratory bioassay evaluation of insecticides allowed for organic production against striped cucumber beetle, 2015. Arthropod. Manag. Tests 43: 1–2.
- Gill, R. J., O. Ramos-Rodriguez, and N. E. Raine. 2012. Combined pesticide exposure severely affects individual- and colony-level traits in bees. Nature. 491: 105–108.
- Gregg, P. C., A. P. Del Socorro, and P. J. Landolt. 2018. Advances in attractand-kill for agricultural pests: beyond pheromones. Annu. Rev. Entomol. 63: 453–470.
- Hazzard, R., and A. Cavanagh. 2010. Managing striped cucumber beetle in vine crops. The Centre for Agriculture, Food and the Environment, the College of Natural Sciences, University of Massachusetts Amherst, MA. https://extension.umass.edu/vegetable/articles/ managing-striped- cucumber-beetle-vine-crops
- Hinds, J., and C. R. R. Hooks. 2013. Population dynamics of arthropods in a sunn hemp zucchini interplanting system. Crop Prot. 53: 6–12.
- Hoffmann, M. P., and T. A. Zitter. 1994. Cucumber beetles, corn rootworms, and bacterial wilt in cucurbits. Department of Plant Pathology, Cornell University, Ithaca, NY. http://vegetablemdonline.ppath.cornell.edu/ factsheets/Cucurbit_Beetles.htm
- Hoffmann, M. P., R. Ayyappath, and J. J. Kirkwyland. 2000. Yield response of pumpkin and winter squash to simulated cucumber beetle (Coleoptera: Chrysomelidae) feeding injury. J. Econ. Entomol. 93: 136–140.
- Hoffmann, M. P., R. Ayyappath, and J. Gardner. 2003. Effect of striped cucumber beetle (Coleoptera: Chrysomelidae) foliar feeding on pumpkin yield. J. Entomol. Sci. 38: 439–448.
- Houser, J. S., and W. V. Balduf. 1925. The striped cucumber beetles: Diabrotica vittata F. Ohio Agricultural Experimental Station Bulletin. 388: 241–364.
- Howe, W. L., E. Zdarkova, and A. M. Rhodes. 1972. Host preferences of *Acalymma vittatum* (Coleoptera: Chrysomelidae) among certain Cucurbitaceae. Ann. Entomol. Soc. Am. 65: 372–374.
- Jackson, D. M., K. A. Sorensen, C. E. Sorenson, and R. N. Story. 2005. Monitoring cucumber beetles in sweetpotato and cucurbits with kairomone-baited traps. J. Econ. Entomol. 98: 159–170.
- Jasinski, J., M. Darr, E. Ozkan, and R. Precheur. 2009. Applying imidacloprid via a precision banding system to control striped cucumber beetle (Coleoptera: Chrysomelidae) in cucurbits. J. Econ. Entomol. 102: 2255–2264.
- Latin, R. X., and G. L. Reed. 1985. Effect of root feeding by striped cucumber beetle larvae on the incidence and severity of Fusarium wilt of muskmelon. Phytopathology 75: 209–212.
- Lewis, P. A., R. L. Lampman, and R. L. Metcalf. 1990. Kairomonal attractants for *Acalymma vittatum* (Coleoptera: Chrysomelidae). Environ. Entomol. 19: 8–14.

- Mabin, M. D., C. Welty, and M. M. Gardiner. 2020. Predator richness predicts pest suppression within organic and conventional summer squash (*Cucurbita pepo* L. Cucurbitales: Cucurbitaceae). Agr. Ecosyst. Environ. 287: 106689.
- de Mackiewicz, D., F. E. Gildow, M. Blua, S. J. Fleischer, and F. L. Lukezic. 1998. Herbaceous weeds are not ecologically important reservoirs of *Erwinia tracheiphila*. Plant Dis. 82: 521–529.
- Mac Intyre Allen, J. K., C. D. Scott-Dupree, J. H. Tolman, and C. R. Harris. 2001. Evaluation of application methods for the chemical control of striped cucumber beetle (Coleoptera: Chrysomelidae) attacking seedling cucurbits. J. Veg. Crop Prod. 7: 83–95.
- Meagher, R. L. Jr, and E. R. Mitchell. 1999. Nontarget hymenoptera collected in pheromone- and synthetic floral volatile-baited traps. Environ. Entomol. 28: 367–371.
- Metcalf, R. L., and R. L. Lampman. 1989. The chemical ecology of diabroticites and Cucurbitaceae. Experientia. 45: 240–247.
- Michelbacher, A. E., W. W. Middlekauff, and O. G. Bacon. 1953. Cucumber beetles attacking melons in Northern California. J. Econ. Entomol. 46: 489–494.
- Morris, B. D., R. R. Smyth, S. P. Foster, M. P. Hoffmann, W. L. Roelofs, S. Franke, and W. Francke. 2005. Vittatalactone, a β-lactone from the striped cucumber beetle, *Acalymma vittatum.* J. Nat. Prod 68: 26–30.
- Mueller, D. S., M. L. Gleason, A. J. Sisson, and J. M. Massman. 2006. Effect of row covers on suppression of bacterial wilt of muskmelon in Iowa. Online. Plant Health Progress. 7: 1–10.
- Munroe, D. D., and R. F. Smith. 1980. A revision of the systematics of Acalymma sensu stricto Barber (Coleoptera: Chrysomelidae) from North America including Mexico. Mem. Entomol. Soc. Canada. 112: 1–92.
- Necibi, S., B. A. Barrett, and J. W. Johnson. 1992. Effects of a black plastic mulch on soil and plant dispersal of cucumber beetles, *Acalymma vittatum*(E) and *Diabrotica undecimpunctata howardi* Barber (Coleoptera: Chrysomelidae), on melons. J. Agric. Entomol. 9: 129–135.
- Pedersen, A. B. 2009. Improved integrated pest management of two cucumber beetle species (Coleoptera: Chrysomelidae) in California melon agroecosystems. M.S. thesis, University of California Davis, Davis, CA.
- Piñero, J. C. 2018. A comparative assessment of the response of two species of cucumber beetles (Coleoptera: Chrysomelidae) to visual and olfactory cues and prospects for mass trapping. J. Econ. Entomol. 111: 1439–1445.
- Radin, A. M., and F. A. Drummond. 1994. Patterns of initial colonization of cucurbits, reproductive activity, and dispersion of striped cucumber beetle, *Acalymma vittata* (F.) (Coleoptera: Chrysomelidae). J. Agric. Entomol. 11:115–123.
- Reed, D. K., G. L. Reed, and C. S. Creighton. 1986. Introduction of entomogenous nematodes in to trickle irrigation systems to control striped cucumber beetle (Coleoptera: Chrysomelidae). J. Econ. Entomol. 79: 1330–1333.
- Saalau Rojas, E. S., J. C. Batzer, G. A. Beattie, S. J. Fleischer, L. R. Shapiro, M. A. Williams, R. Bessin, B. D. Bruton, T. J. Boucher, L. C. H. Jesse, *et al.* 2015. Bacterial wilt of cucurbits: resurrecting a classic pathosystem. Plant Dis. 99: 564–574.
- Sasu, M. A., I. Seidl-Adams, K. Wall, J. A. Winsor, and A. G. Stephenson. 2010. Floral transmission of *Erwinia tracheiphila* by cucumber beetles in wild *Cucurbita pepo*. Environ. Entomol. 39: 140–148.
- Seaman, A. J., H. Lange, and A. M. Shelton. 2013. Striped cucumber control with insecticides allowed for organic production, 2012. Arthropod. Manag, Tests 38: 1–2.
- Shapiro, L. R., J. N. Paulson, B. J. Arnold, E. D. Scully, O. Zhaxybayeva, N. E. Pierce, J. Rocha, V. Klepac-Ceraj, K. Holton, and R. Kolter. 2018. An introduced crop plant is driving diversification of the virulent bacterial pathogen *Erwinia tracheiphila*. mBio. 9: e01307–e01318.

- Sharma, A., C. Rana, and K. Shiwani. 2016. Important insect pests of cucurbits and their management, pp.327–360. In M. Pessarakli (ed.), Handbook of cucurbits: growth, cultural practices and physiology, 1st ed. CRC Press, Boca Raton, FL.
- Smith, R. F. 1966. Distributional patterns of selected western North American insects: The distribution of diabroticites in western North America. Bull. Ent. Soc. Am. 12: 108–110.
- Smith, B. D., and R. A. Yarnell. 2009. Initial formation of an indigenous crop complex in eastern North America at 3800 B.P. Proc. Natl. Acad. Sci. U. S. A. 106: 6561–6566.
- Smyth, R. R., and M. P. Hoffmann. 2003. A male-produced aggregation pheromone facilitating *Acalymma vittatum* [F.] (Coleoptera: Chrysomelidae) early-season host plant colonization. J. Insect Behav. 16: 347–359.
- Smyth, R. R., and M. P. Hoffmann. 2010. Seasonal incidence of two co-occurring adult parasitoids of *Acalymma vittatum* in New York State: *Centistes (Syrrhizus) diabroticae* and *Celatoria setosa*. BioControl. 55: 219–228.
- Smyth, R. R., D. W. Tallamy, J. A. A. Renwick, and M. P. Hoffmann. 2002. Effects of age, sex, and dietary history on response to cucurbitacin in *Acalymma vittatum*. Entomol. Exp. Appl. 104: 69–78.
- Snyder, W. E. Managing cucumber beetles in organic farming systems. Department of Entomology, Washington State University; 2019.https:// eorganic.org/node/5307.
- Snyder, W. E., and D. H. Wise. 2001. Contrasting trophic cascades generated by a community of generalist predators. Ecology 82: 1571–1583.
- Ternest, J. J., L. L. Ingwell, R. E. Foster, and I. Kaplan. 2020. Comparing prophylactic versus threshold-based insecticide programs for striped cucumber beetle (Coleoptera: Chrysomelidae) management in watermelon. J. Econ. Entomol. 113: 872–881.
- Theis, N., N. A. Barber, S. D. Gillespie, R. V. Hazzard, and L. S. Adler. 2014. Attracting mutualists and antagonists: plant trait variation explains the distribution of specialist floral herbivores and pollinators on crops and wild gourds. Am. J. Bot. 101: 1314–1322.
- Tillman, J., A. Nair, M. Gleason, and J. Batzer. 2015. Evaluating strip tillage and row cover use in organic and conventional muskmelon production. HortTechnology. 25: 487–495.
- Toepfer, S., G. Cabrera Walsh, A. Eben, R. Alvarez-Zagoya, T. Haye, F. Zhang, and U. Kuhlmann. 2008. A critical evaluation of host ranges of parasitoids of the subtribe Diabroticina (Coleoptera: Chrysomelidae: Galerucinae: Luperini) using field and laboratory host records. Biocontrol Sci. Techn. 18: 483–504.
- Toepfer, S., T. Haye, M. Erlandson, M. Goettel, J. G. Lundgren, R. G. Kleespies, D. C. Weber, G. Cabrera Walsh, A. Peters, R.-U. Ehlers, *et al.* 2009. A review of the natural enemies of beetles in the subtribe Diabroticina (Coleoptera: Chrysomelidae): implications for sustainable pest management. Biocontrol Sci. Techn. 19: 1–65.
- Weber, D. C. 2018. Field attraction of striped cucumber beetles to a synthetic vittatalactone mixture. J. Econ. Entomol. 111: 2988–2991.
- Whitehorn, P. R., S. O'Connor, F. L. Wackers, and D. Goulson. 2012. Neonicotinoid pesticide reduces bumble bee colony growth and queen production. Science. 336: 351–352.
- Williams, J. L., and D. H. Wise. 2003. Avoidance of wolf spiders (Araneae: Lycosidae) by striped cucumber beetles (Coleoptera: Chrysomelidae): laboratory and field studies. Environ. Entomol. 32: 633–640.
- Yardim, E. N., N. Q. Arancon, C. A. Edwards, T. J. Oliver, and R. J. Byrne. 2006. Suppression of tomato hornworm (Manduca quinquemaculata) and cucumber beetles (Acalymma vittatum and Diabrotica undecimpunctata) populations and damage by vermicomposts. Pedobiologia. 50: 23–29.