Attraction of Brown Marmorated Stink Bugs, *Halyomorpha halys*, to Blooming Sunflower Semiochemicals

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ABSTRACT

I tested whether the brown marmorated stink bug (BMSB), *Halyomorpha halys*, discriminates among phenological stages of sunflower, *Helianthus annuus*. When BMSB females in a still-air laboratory experiment were offered a choice of potted sunflowers at distinct phenological stages (vegetative, pre-bloom, bloom, seeding), most females settled onto blooming plants. In moving air olfactometer experiments, testing each plant stage *versus* one another, for the attraction of BMSB females, blooming sunflowers overall were most attractive. Analyzing the headspace odorants of each plant stage revealed a marked increase of odorant abundance as plants transitioned from pre-bloom to bloom. Thirteen blooming-stage odorants elicited responses from female BMSB antennae. A synthetic blend of antennally-active odorants attracted BMSB females in laboratory olfactometer experiments, and in field settings enhanced the attractiveness of BMSB pheromone as a trap lure, particularly in spring. Sunflower semiochemicals coupled with synthetic BMSB pheromone could be developed to improve efforts to monitor and control BMSB populations.

Keywords: Brown marmorated stink bugs · Plant phenology · Sunflower semiochemicals · Olfactometer bioassays · GC-EAD · GC-MS · Monitoring

我將這份論文獻給我的父親王福祥和母親伍杏嬋。
我今天的成就是基於他們的價值觀
和無微不至的栽培及無限的支持。

[English Translation]
For my parents, Terri & Kent Wong,
whose values and efforts shaped who I am today.

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"E Pluribus Unum" – Out of Many, One

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CHAPTER 1.

GENERAL INTRODUCTION

1.1 DEPENDENCE OF INSECT HERBIVORES ON PLANT PHENOLOGY

Insect herbivores have a tightly interwoven relationship with plants, and their life cycles have adapted to synchronize with plant phenology. For insect herbivores, plants represent a trove of resources, a chance to encounter mates, a place to lay eggs, or a shelter from harsh weather (Bruce et al. 2005; Bruce and Pickett 2011). Insects with a strong dependence on a few select host plant species may live in close spatial proximity to these plants and have high phenological and temporal synchrony (Bernays and Graham 1988).

Insect dependence on host plant phenology can be viewed in relation to the four primary plant stages that attract select groups of insects: leafing (vegetative), pre-bloom, bloom, and seeding/fruiting (Cates 1980; Dinan 2001; Hilker and Meiners 2008; Jaenike 1978). The most suitable stage is typically the most attractive (Scriber 1984).

Insect reliance on the vegetative leafing stage of plants is exemplified by dipteran cecidomyiid midges. Female midges depend on young leaves or fresh shoot tips for feeding and oviposition (Cockfield and Mahr 1995; Hallett 2007; Wearing et al. 2013). Many cecidomyiid midges are agricultural pests because larval feeding on crop plants reduces the leaf surface and curtails the formation of buds which would otherwise develop into fruiting bodies (Allison et al. 1995; Fitzpatrick et al. 2018; Rhodes et al. 2014; Tewari et al. 2014; Wearing et al. 2013). For example, females of the cranberry tipworm, *Dasineura oxycoccana* (Johnson), emerge in spring coincident with the appearance of vegetative cranberry shoots (Cockfield and Mahr 1995; Fitzpatrick et al. 2018). Emergent females seek leading shoot tips of cranberry vines to oviposit because larval offspring benefit from feeding inside the soft vine tissue (Tewari et al. 2014). The larvae eventually spin a silken cocoon, pupate, metamorphose to adults, and eclose, continuing the cycle of oviposition and larval development until the cranberry vines progress to the blooming stage (Cockfield and Mahr 1995; Cook et al. 2012).

Insect reliance on plant phenology is not limited to herbivores. Parasitoids attacking herbivores also exploit plant state-dependent cues to locate hosts (De Moraes et al. 1998; Ngumbi et al. 2012; Turlings et al. 1993). For instance, the ichneumonid parasitoids *Phardis interstitialis* Thomson, *P. morionellus* Holmgr., and *Tersiolchus heterocerus* Thomson (Hymenoptera), which parasitize larvae of pollen beetles, *Meligethes* spp. (Coleoptera: Nitiduliae), exploit cues associated with the budding and blooming stages of oilseed rape, *Brassica napus* L., to locate beetle larvae (Jönsson et al. 2005). To find early-instar host larvae present on budding-stage plants and late-instar host larvae present on blooming plants, the parasitoids distinguish between the odor profiles of these plant stages and recognize the yellow color indicative of blooming oilseed rape (Jönsson et al. 2005). These parasitoids have become reliant on oilseed rape cues to indicate the time and presence of their larval hosts.

Plant phenological stages can be present for several weeks at a time, but temporal synchrony between the life cycles of insects and plants may be very short-lived and differ by only a few days between niche competitors. For example, females of the American sunflower moth *Homoeosoma electellum* (Hulst) (Lepidoptera: Pyralidae), and the banded sunflower moth, *Cochylis hospes* Walsingham (Lepidoptera: Tortricidae), both use blooming inflorescences of sunflower, *Helianthus* spp., for oviposition (Arthur and Bauer 1981; McNeil and Delisle 1989) but temporally partition the floral resource. As larvae of *C. hospes* and *H. electellum* develop best in early and late phases, respectively, of blooming inflorescences (Mphosi and Foster 2010; Mphosi 2012), both temporal niche partitioning and recognition of the most suitable inflorescence phase optimize the reproductive fitness of these heterospecific female moths (Forister 2004; Jaenike 1978; Thompson 1988).

In the seeding or fruiting stage of plants, proteins, essential amino acids and carbohydrates accumulate in fruiting bodies or embryos (Lipke and Fraenkel 1956). Insects access these nutritional resources for themselves and/or their offspring (Labandeira 1997; Sallabanks and Courtney 1992). In an evolutionary arms race between plants defending against herbivory and insects attempting to overcome plant defenses and/or outperform competitors, insects have developed specialized morphological and physiological “tools” to puncture, extract or digest plant tissue (Díaz-Fleischer et al. 2001; Keesey et al. 2015). The larvae of some species of *Drosophila* vinegar flies (Diptera: Drosophilidae) hatch within fruits selected for oviposition by their mother, and require at least ten essential plant amino acids to develop, molt and eventually become adults (Lipke and Fraenkel 1956; Royes and Robertson 1964). Females of the invasive spotted wing drosophila, *Drosophila suzukii* Matsumura, use their highly sclerotized and serrated ovipositor to lay eggs in ripe fruits, which are not yet accessible to other *Drosophila* spp. (Kenis et al. 2016), thereby reducing interspecific larval competition (Asplen et al. 2015; Dancau et al. 2017). Within a season, *Drosophila* spp. may go through several generations and use multiple host plants such as blueberries, blackberries, strawberries, and cherries (Kenis et al. 2016). As fruits ripen and ferment, they disseminate semiochemicals (message bearing chemicals), such as acetic acid, which indicate resource suitability for foraging flies (Cunningham et al. 2016). Acetic acid is now commonly used as a lure for trapping and monitoring vinegar flies (Fluegel 1981).

Context- and distance-dependent, olfactory, and/or visual plant cues guide foraging insects to their respective host plants. At long-range, olfactory cues may be more important than visual cues, particularly for polyphagous insects that seek spatially well separated host plants (Prokopy and Owens 1978). Floral patterns and colors, in contrast, inform close-range foraging decisions of plant pollinators or nectar thieves (Brodie et al. 2015; Chittka and Raine 2006; Jones and Buchmann 1974; Kunze and Gumbert 2001; Peach et al. 2019). Unlike mono- or oligophagous insects, polyphagous insects do not seem to recognize specific color hues or forms characteristic of their hosts (Prokopy and Owens 1978). All foraging insect herbivores nonetheless face the challenge not only of locating host plants but also of distinguishing between phenological stages of host plants and selecting the one stage most suitable for feeding and oviposition (McCormick et al. 2012; Webster and Cardé 2017).

Host plant semiochemicals that guide foraging insect herbivores are often secondary metabolites emanating from plants during growth (Nishida 2014; Rowan 2011). As byproducts of plant metabolism (Lortzing and Steppuhn 2016), the composition and abundance of these compounds change over time (Ishizaki et al. 2016; Jönsson et al. 2005; Rowan 2011) and indicate the presence of specific plant phenological stages (Nishida 2014; Rowan 2011). The semiochemicals that inform foraging decisions by insects may originate from different parts of a plant such as leaves, stems, buds, inflorescences, seeds or fruits (Cloonan et al. 2018; Masante-Roca et al. 2007; Metcalf and Kogan 1987; von Mérey et al. 2011), and may occur during seed germination, vegetative growth, blooming or fruiting of plants
(Karban 2008).

Semiochemicals that attract pest insects can be used to monitor and/or control pest insect populations (Mitchell 2012). Both forest and agricultural industries deploy plant-based attractants for attract-and-kill (A&K) strategies. For example, the cultural practice of felling spruce trees for colonization by the bark beetles *Ips typographus* (L.) and *Pityogenes chalcographus* Bedel (Coleoptera: Curculionidae) (Krieger 1998) exploits the semiochemical attractiveness of recently cut trees to foraging beetles, and through bark removal of infested trees enables the destruction of adult beetles and their offspring (Demirović et al. 2016). In agriculture, natural or synthetic plant semiochemical baits or lures are used on their own as attractants for pest insects, or to enhance the attractiveness of insect pheromones. For example, corn-derived sucrose or protein hydrolysates and their semiochemicals, respectively, attract tephritid fruit flies (Foster and Harris 1997; Leblanc et al. 2010), and synthetic plant semiochemicals coupled with synthetic pheromone as trap lures attract more Mediterranean fruit flies, *Ceratitis capitata*, and more female flies, than the pheromone alone (Foster and Harris 1997). This interactive effect between plant semiochemicals and pheromone inspired the development of similar lure types that have been widely adopted for fruit fly control (Leblanc et al. 2010).

Insect herbivores depend on host plants for their reproductive fitness. They rely on plant cues, and sometimes conspecifics signaling on plants, to synchronize temporally and spatially with their host plants. Polyphagous insects that move frequently between multiple host plants throughout the season are challenging to study with respect to their host preference(s) (Lamp and Zhao 1993; Masaki et al. 1984; Scriber 2002). However, with diligent observations of insect movement patterns between plants, it is possible to determine the most attractive phenological stage of potential host plants (Cook et al. 2006; Kennedy and Storer 2000). Semiochemicals of the most attractive plant stage(s) can then be identified and developed as part of an integrated pest management (IPM) strategy for herbivorous pest insects. Stink bugs (Hemiptera: Pentatomidae) are one important group of pests that fit the profile of a mobile, polyphagous pest for which plant phenology and associated odorant cues may be important for host plant location and could thus be harnessed to develop IPM tools.

1.2 LIFE HISTORY OF PENTATOMIDAE

The taxonomic moniker Pentatomidae contains the Latin word ‘penta’ (‘five’) and the Greek word ‘tomos’ (‘section’) in reference to the bugs’ five-segmented antennae (Gordh and Headrick 2001). The common term ‘stink bug’ alludes to the bugs’ ability of secreting a foul odor from their scent glands (Tsuyuki et al. 1965). This smell is thought to have the dual function of alarming nearby conspecifics and deterring predators (Krall et al. 1999; Shen and Hu 2017).

Stink bugs are mainly phytophagous but some are zoophytophagous, feeding on both plants and other insects (Hough-Goldstein and McPherson 1996; Torres et al. 2006). The most thoroughly studied stink bug species are agricultural pests (McPherson 1982). Like other hemipterans, stink bugs are hemimetabolous, developing through five nymphal instars, each larger than the last, before they mature as winged adults. Most nymphal instars can walk between host plants to continue feeding and developing (Grettenberger and Joseph 2019; Yang 2000). Winged adults disperse and seek new habitats with suitable plant resources (Lee and Leskey 2015). To locate them, stink bugs rely on plant cues (McPherson 1982).

Foraging stink bugs are guided, in part, by plant semiochemicals (Ishiwatari 1974; Lockwood and Story 1987; Pareja et al. 2007). Plants serve as: (*i*) resources rich in nutrients (House 1961; Sinclair 2015; Urbaneja-Bernat et al. 2020), water (Kerkut and Gilbert 1985) and secondary metabolites (Boppré 1984; Honda et al. 2018); (*ii*) rendezvous sites for mate encounters (Geiselhardt et al. 2012; Xu and Turlings 2018); (*iii*) oviposition sites for gravid females (Forister 2004; Jaenike 1978; Thompson 1988); (*iv*) food sources for offspring development (García-Robledo and Horvitz 2012; Scriber and Slansky Jr. 1981; Via 1986); as well as (*v*) shelter from harsh weather and natural enemies (Jones Jr. and Sullivan 1981; Mulatu et al. 2004). As most pentatomids are multivoltine and may deplete local host plant resources, they must often shift between host plants and navigate through a complex landscape in search for new hosts of varying degrees of suitability (McPherson 1982; Todd 1989).

In spring, pentatomids terminate diapause triggered by changes in temperature or photoperiod (Leather et al. 1995; Saulich and Musolin 2012; Sinclair 2015). They seek host plants to replenish their body's depleted resources (Sinclair 2015; Skillman et al. 2018), and opportunistically feed on any available vegetation including fresh plant shoots or grasses before more favorable and suitable plants become available (Jones and Sullivan 1982; Panizzi and Saraiva 1993; Velasco and Walter 1992). For some pentatomids, the plants near their emergence site in spring may become permanent hosts (Fox and Morrow 1981; Panizzi and Lucini 2017), but most polyphagous pentatomids must disperse to obtain a diverse and nutritious diet for their well-being, oogenesis and oviposition. Females failing to select suitable oviposition sites and/or poorly time oviposition, suffer adverse fitness consequences (McPherson 1982). A mother's choice of host plant for oviposition determines the resource availability for her offspring (Funayama 2004; McPherson 1982), and their opportunity to complete development without having to relocate to new host plants (Tillman et al. 2009).

Pentatomid nymphs and adults obtain nutrients through two modes of feeding, a stylet-sheath mode for intracellular penetration followed by ingesting vascular cells, and a cell-rupturing mode for consuming mesophyll or underdeveloped plant tissues, seeds and other insects (Serteyn et al. 2020; Sharma et al. 2014). The latter mode is consistently used for consuming insect prey (Cobben 1978; Lucini and Panizzi 2018). Extant phytophagous pentatomids are thought to have evolved from entomophagous ancestors, and to have become efficient plant feeders only after the maxillary barbs on their stylets were lost over evolutionary time (Cobben 1978). This hypothesis is supported by existing zoophytophagous or omnivorous pentatomids based on their stylet morphology and mode of feeding (Cobben 1978).

Phytophagous pentatomids use their stylets to drill into, or through, plant tissues such as fresh shoots, flower petals, seed shells, husks or barks before ejecting enzymes and imbibing the liquefied plant nutrients (Lucini et al. 2016; Serteyn et al. 2020). The bugs' ability to pierce through tough seed tissue makes them potential pests of even the hardest fruits and seeds such as almonds, hazelnuts, walnuts, and pistachios (Daane et al. 2005; Hedstrom et al. 2014; Lara et al. 2017; Rijal and Gyawaly 2018; Stahl et al. 2020), and enables them to adopt "new" host plants with which they have not co-evolved. Pentatomids can also exploit phloem and other plant tissues to supplement their seed diet and stay hydrated in arid environments (Cobben 1978).

As polyphagous herbivores, pentatomids have the potential to become major global pests, exemplified by the bagrada (painted) bug, *Bagrada hilaris* (Burmeister), the southern green stink bug, *Nezara viridula* (Linnaeus), and the brown marmorated stink bug, *Halyomorpha halys* Stål (Palumbo et al. 2016; Rice et al. 2014; Todd 1989). The host range of *N. viridula*, for example, surpasses 30 families of dicotyledonous plants and some monocotyledons (Knight and Gurr 2007). Similarly, *H. halys* and *B. hilaris* feed on host plants in 45 and 25 taxonomic families, respectively (Bergmann et al. 2016; Lee et al. 2013a; Palumbo et al. 2016). Both *N. viridula* and *H. halys* are pests of soybeans (Leskey, Hamilton, et al. 2012; Todd 1989; Werdin González et al. 2011), which have overlapping phenological stages with blooming and seeding plants co-occurring, and possibly for that reason, being very attractive to pentatomids (Bundy and McPherson 2000; Velasco and Walter 1992). Both *N. viridula* and *H. halys* appear as soon as plants begin to bloom, and they become abundant when plants enter the fruit-bearing stage (Bundy and McPherson 2000). In contrast, *B. hilaris* feeds exclusively on young leaves of crucifer plants (Huang et al. 2014). With such a diverse diet and host plant range, pentatomids are pests both in their native and invaded ranges (Haye et al. 2015; Sachan and Purwar 2007).

Insecticide applications are the most widely used tactic for managing pentatomid populations, but alternative control tactics are being explored. Sterile insect release (SIR) programs were highly successful for control of various pest insects (Lance and McInnis 2005), but may not be applicable for control of stink bugs. Stink bugs are costly to rear in the laboratory, and bugs released after sterilization cause feeding damage to crops (Knight and Gurr 2007; Suckling et al. 2019). The release of biological control agents, in contrast, shows greater promise for suppressing stink bug populations, at least near release sites (Corrêa-Ferreira and Moscardi 1996). As natural enemies of pentatomids, scelionid egg parasitoids have provided various degrees of stink bug suppression (Jones 1995; Laumann et al. 2008), and other parasitoids with high rates of parasitism are still considered for biological control of pentatomids (Corrêa-Ferreira and Moscardi 1996; Rice et al. 2014). However, a stage-structured matrix model re-examining the efficacy of egg parasitoids for stink bug control cautions against relying solely on these parasitoids as a stand-alone tactic and recommends instead an integrated approach for stink bug management (Abram et al. 2020). Although attractive trap crops, in general, can divert insect herbivores away from valuable cash crops (Akotsen-Mensah et al. 2017), trap crops may have limited applicability for the management of pentatomids, which readily shift host plants according to their attractiveness throughout the season (Akotsen-Mensah et al. 2017; Hokkanen 1991; Mizell et al. 2008). Frequent movement of stink bugs among host plants makes it difficult to predict pentatomid presence temporally and spatially (Lee et al. 2013b). Understanding the movement of pentatomids between host plants may be key for future population suppression efforts (Bundy and McPherson 2000; Palumbo and Carrière 2015).

Aggregation pheromones largely mediate aggregations of stink bugs on plants (Aldrich et al. 1993; Khrimian et al. 2014; Tillman et al. 2009). While sex pheromones attract only one sex, aggregation pheromones can attract both sexes, increase mating opportunities and assemble conspecifics to overcome host plant defenses (Klowden 2008). Synthetic replica of these pheromones are used in lures to detect the presence of stink bugs and to monitor population levels (Morrison et al. 2019; Palumbo et al. 2016). However, important information is still missing to better explain the population dynamics of pentatomids which seem to link to specific phenological stages of host plants (McPherson 2018; Nielsen et al. 2016; Todd 1989). Plant-derived semiochemicals guide foraging insects (Bruce and Pickett 2011), and in combination with synthetic aggregation pheromones, may become a lure that is attractive all season long (Foster and Harris 1997). Past studies have explored the use of plant semiochemicals for attraction of pentatomids (McPherson 2018), but few studies have accounted for the differential odor profiles and attractiveness of plant stages. The semiochemicals emanating from a particularly attractive plant stage could then potentially be developed as a lure for attracting and trapping overwintered stink bug adults in spring.

1.3 THE BROWN MARMORATED STINK BUG

The brown marmorated stink bug (BMSB), *Halyomorpha halys* (Hemiptera: Pentatomidae), originated from Asia and is now a pest of many agricultural crops in its invaded North American range (Leskey and Nielsen 2018). Adults can also be nuisance pests when they aggregate on or in residential homes for overwintering (Cullum et al. 2020; Inkley 2012).

The BMSB life history revolves around the presence of suitable host plants for feeding or oviposition (Rice et al. 2014). In spring, adult bugs emerge from overwintering sites including trees or residential homes in search for nearby host plants such as woody trees and shrubs to replenish their energy reserves which depleted in the course of winter (Bergmann et al. 2016; Cira et al. 2016; Skillman et al. 2018). During spring and summer, BMSBs can undergo multiple generations and move among host plants fueled by nutrient resources obtained through plant-feeding (Lee et al. 2013a; Skillman et al. 2018). Each generation begins with eggs laid on the underside of plant leaves (Rice et al. 2014). The selected host plant protects eggs from desiccation and predators and provides sustenance for emergent nymphs. Hatching almost simultaneously from an egg mass (Endo et al. 2019), first instar nymphs feed first on the surface of their egg chorion and in the process obtain essential gut symbionts deposited by their mother during oviposition (Taylor et al. 2014). The physical well-being of all five nymphal instars is dependent upon the host plant (or its surrounding) selected by their mother which – in turn – may partially depend upon the plant's phenological stage (Blaauw et al. 2019; Funayama 2004). Nymphs are incapable of flight but otherwise closely resemble adults. Nymphs and adults use their stylet mouthparts to penetrate plant tissue, rupture cells, and excrete enzyme-containing saliva before they imbibe the liquefied plant nutrients (Serteyn et al. 2020). If a host plant has become unsuitable due to senescence or depleted nutrients, nymphs may walk to nearby new hosts (Lee et al. 2014).

Adult BMSBs are capable of long-range dispersal (Lee and Leskey 2015; Wiman et al. 2014) and oviposition in new selected habitats (Webster and Cardé 2017; Zobel et al. 2016), and therefore play a critical role in the population dynamics of BMSBs. However, the cues enabling females to find and select the most suitable host plant amongst the many potential host plants are still largely unknown.

Currently, the male-produced aggregation pheromone of BMSBs is the only known attractant that elicits aggregation behavior of females and males (Khrimian et al. 2014), and may also affect host plant choice. Synthetic aggregation pheromone has been instrumental in monitoring adventive BMSB populations and led to the development of several trap designs (Krawczyk et al. 2019; Leskey, Wright, et al. 2012; Suckling et al. 2019). The efficacy of the pheromone as a monitoring tool over the course of the growing season has been demonstrated in a study conducted at multiple locations across the USA (Acebes-Doria et al. 2016a). BSBSs not only respond to the aggregation pheromone but also to various (plant) cues throughout the season. A study using a blue (435 nm) light attractant, with or without pheromone, revealed that mid-season BMSB captures were relatively low without the light cue (Rice et al. 2017). Nonetheless, in an experiment with pheromone-baited and insecticide-sprayed apple trees, fruit damage on untreated trees in the orchard perimeter 25 m apart from insecticide-sprayed trees had the same reduction in fruit damage as a fully sprayed orchard (Morrison et al. 2019), providing a proof of concept that an A&K strategy is conceivable for BMSB control, which could lower pesticide use (Krawczyk et al. 2019; Rice et al. 2017). Combining the aggregation pheromone with synthetic plant semiochemicals has the potential to further improve the efficacy of an A&K strategy (Morrison et al. 2018; Nielsen et al. 2011).

BMSBs face the challenge of locating a most suitable host plant among hundreds of potential host plants (Leskey and Nielsen 2018). Repeated shifts in host plant preference by BMSBs throughout the season have been attributed to changing host plant phenology and to inadequate nutrients provided by a single host plant species (Blaauw et al. 2019; Morrison et al. 2016b; Nielsen et al. 2016). In the mid-western US, BMSBs inflict significant damage to apple crops but cannot fully develop on apples alone (Funayama 2004). Similarly, BMSBs are major pest of peach fruits, but can develop only on a diet of both peach fruit and foliage (Acebes-Doria et al. 2016b; Pansa et al. 2013).

Host plant odorants are not necessarily attractive to BMSBs. BMSBs feed on apple fruit but fruit odorants do not enhance the attractiveness of the BSMB pheromone (Morrison et al. 2018). Conversely, soybeans are attractive to BMSBs, particularly when they transition from the full-bloom to the pod stage (Nielsen et al. 2011). Moreover, sunflower in mid but not late season was more attractive to BMSBs than sorghum, admiral pea, millet and okra (Nielsen et al. 2016).

To determine the underlying mechanisms that attract BMSBs to their host plants, it is important to select a candidate host plant and its phenological stage that is particularly attractive to BMSBs. Plants that appear attractive only in early and late season should be discounted as candidates because other plants being possibly more appealing to BMSBs are simply absent (Bergmann et al. 2016; Skillman et al. 2018). In spring, BMSBs typically abandon early-season hosts when more desired host plants become available (Nielsen and Hamilton 2009; Rice et al. 2014). In midseason, many candidate host plants exist concurrently but their relative attractiveness changes with phenological stage (Nielsen et al. 2016).

Taking all aspects into account, I have selected sunflower as the model plant species for my thesis. My specific objectives were to: (1) determine whether BMSBs discriminate between phenological stages of sunflower (vegetative, pre-bloom, bloom, seed) for settling and oviposition; (2) compare the relative attractiveness of each phenological stage to BMSBs; (3) analyze the odor profile of each stage; and (4) prepare a synthetic blend of odorants present in the most attractive stage and bioassay this blend for its attractiveness to BMSBs in laboratory and field experiments.

CHAPTER 2.

BLOOMING SUNFLOWER SEMIOCHEMICALS ENHANCE FIELD ATTRACTION OF BROWN MARMORATED STINK BUGS TO SYNTHETIC STINK BUG PHEROMONE

2.1 ABSTRACT

The polyphagous invasive brown marmorated stink bug (BMSB), *Halyomorpha halys*, reportedly discriminates among phenological stages of host plants. To determine the mechanisms underlying this ability, we selected (dwarf) sunflower, *Helianthus annuus*, as a model host plant species for BMSBs. When BMSB females in a still-air laboratory experiment were offered a choice of four potted sunflowers at distinct phenological stages (vegetative, pre-bloom, bloom, seeding), most females settled onto blooming plants but oviposited evenly on plants of all four stages. In moving-air two-choice olfactometer experiments, testing each plant stage *versus* filtered air and *versus* one another, for attraction of BMSB females, blooming sunflowers overall performed best, but no one plant stage was clearly most attractive in all experiments. Capturing and analyzing (by GC-MS) the headspace odorants of each plant stage, revealed a marked increase of odorant abundance (e.g., monoterpenes) as plants transitioned from pre-bloom to bloom. Analyzing the headspace odorant blend of blooming sunflower by gas chromatographic-electroantennographic detection (GC-EAD) revealed 13 odorants that consistently elicited responses from female BMSB antennae. An 11-component synthetic blend of these odorants attracted BMSB females in laboratory olfactometer experiments, and in field settings, enhanced the attractiveness of synthetic BMSB pheromone as a trap lure, particularly in spring (April to mid-June). A simpler yet fully effective sunflower semiochemical blend, coupled with synthetic BMSB pheromone, could be developed to improve monitoring efforts, or as an attract and kill control tactic for BMSBs to help prevent population build-up in spring and thus curtail crop damage inflicted by BMSBs.

2.2 INTRODUCTION

Host plants provide a plethora of benefits to insect herbivores. Plants serve as (*i*) resources rich in nutrients (House 1961; Sinclair 2015; Urbaneja-Bernat et al. 2020), water (Kerkut and Gilbert 1985) and secondary metabolites (Boppré 1984; Honda et al. 2018), (*ii*) rendezvous sites for mate encounters (Geiselhardt et al. 2012; Xu and Turlings 2018), (*iii*) oviposition sites for gravid females (Forister 2004; Jaenike 1978; Thompson 1988), (*iv*) food sources for offspring development (García-Robledo and Horvitz 2012; Scriber and Slansky Jr. 1981; Via 1986), as well as (*v*) shelter from harsh weather and natural enemies (Jones Jr. and Sullivan 1981; Mulatu et al. 2004).

Locating and selecting host plants is a dynamic process that changes throughout the plant and insect life cycles (Hallett 2007; Jönsson et al. 2005; Mphosi and Foster 2010). Throughout growth, maturation and senescence, plants change in form, nutrient composition and potential benefits that they provide to insect herbivores. For example, only in the blooming stage do herbaceous plants offer nectar and pollen for pollinators, and only plants in the fruiting stage provide resources for insect frugivores that specialize in raw fruits, nuts and seeds.

As plants progress through phenological stages, their visual and olfactory apparency to insect herbivores changes accordingly (Mphosi and Foster 2010; Prokopy and Owens 1978). Semiochemicals (message-bearing chemicals) associated exclusively or primarily with a distinct phenological stage may guide specific insect herbivores to these plants. For example, inflorescence semiochemicals of sunflower, *Helianthus annuus*, attract females of the American sunflower moth, *Homoeosoma electellum*, expedite maturation of their eggs, and prompt oviposition by gravid female moths on inflorescences (Arthur and Bauer 1981; McNeil and Delisle 1989). Female moths responding to these inflorescence semiochemicals essentially synchronize the development of their larval offspring with the presence of protein-rich pollen. Selecting and ovipositing on plants that maximize the survival and performance of larval offspring is particularly important for female insects whose offspring cannot readily relocate and depend on their mother's choice of host plant (Jaenike 1978; Valladores & Lawton 1991). This "mother knows best" principle likely applies to many insect herbivores.

Plant semiochemicals that attract herbivores have mostly been studied with insects that exploit single or few host plant species. For example, crucifer-specific volatile metabolites of glucosinolates attract the cabbage seed weevil, *Ceutorhynchus assimilis* (Blight et al. 1995), and 6-methoxy-2-benzoxalinone coupled with CO_2 attracts western corn rootworm larvae, *Diabrotica virgifera*, which are oligophagous on roots of maize and some other grasses (Bjostad and Hibbard 1992). Much less is known about how polyphagous insects such as stink bugs (Hemiptera: Pentatomidae) discriminate among phenological stages of their host plants.

Stink bugs are pests of many agricultural crops, including tree fruits, nuts, vegetables and row crops such as field corn and soybean (McPherson and McPherson 2000). As stink bugs commonly switch host plants throughout spring, summer and fall, they can cause damage to multiple crops (Tillman et al. 2010; Todd 1989). For example, the invasive brown marmorated stink bug (BMSB), *Halyomorpha halys*, is known to discriminate among both different host plant species as well as among different phenological stages of single host plant species (Bergmann et al. 2016; Blaauw et al. 2019; Morrison et al. 2016b; Nielsen et al. 2016). However, the underlying mechanisms of host plant recognition by BMSBs are still unknown (Morrison et al. 2018). Plant semiochemicals play an important role, although in one recent study apple and peach odorants, coupled with green leaf volatiles, failed to attract BMSBs or to enhance their attraction to the BMSB aggregation pheromone (Morrison et al. 2018), which has previously been identified (Khrimian et al. 2014). As BMSBs are attracted to host plants at distinct phenological stages (Lee et al. 2013a; Nielsen et al. 2016), the odor profile of these attractive stages warrants analysis.

Choosing a host plant highly preferred by BMSBs is the first step towards identifying plant semiochemicals attractive to BMSBs. Sunflower is a good candidate for semiochemical analyses because it is a candidate trap crop for BMSBs to protect nearby cash crops (e.g., peppers)(Soergel et al. 2015). Moreover, as trap crops, blooming sunflowers were more effective than sorghum, admiral pea, millet and okra (Nielsen et al. 2016). Among host plants capable of attracting and retaining BMSBs, blooming-stage sunflowers appear to be particularly attractive to BMSBs (Blaauw et al. 2017; Nielsen et al. 2016). Conceivably, their attractiveness is due to inflorescence semiochemicals, although visual and thermal inflorescence cues cannot be discounted.

Our objectives were to: (1) determine whether BMSBs discriminate between phenological stages of sunflower (vegetative, pre-bloom, bloom, seed) for settling and oviposition; (2) compare the relative attractiveness of each phenological stage to BMSBs; (3) analyze the odor profile of each stage; and (4) prepare a synthetic blend of odorants present in the most attractive stage and bioassay this blend for its attractiveness to BMSBs in laboratory and field experiments.

2.3 MATERIALS & METHODS

2.3.1 Insect Collection and Rearing

BMSBs were reared in the insectary of the Agassiz Research and Development Centre (ARDC), British Columbia, Canada. Annually, laboratory colonies were replenished with specimens captured in the nearby city of Chilliwack. Insects were maintained at a photoperiod of 16L:8D, 40-50% relative humidity, and a temperature of 24 ± 1 °C. Eggs were placed into separate containers (12.5 × 12.5 × 15 cm, Insect Pot; BugDorm, Tai Chung, Taiwan), and early instars provisioned with organic beans and pumpkin seeds *ad libitum*. Latter instars were transferred to mesh cages (45 × 45 × 45 cm; BugDorm), each containing two potted pepper plants and two potted fava bean plants. The bugs' diet was supplemented with pumpkin seeds *ad libitum* placed on the roof top of cages. Adults were transferred to new cages (45 × 45 × 45 cm), each containing two potted pepper plants, two potted cabbage plants, a single organic carrot, and a banana; pumpkin seeds were placed on top of cages. Adult, 2- to 3- week-old, reproductively mature females were used in experiments.

2.3.2 GROWING DWARF SUNFLOWERS

In a greenhouse at ARDC, 24 pots (15.5 cm × 16.5 cm) filled with bedding blend soil (Sumas Gro Media, Chilliwack, BC, CA) were each seeded with a single sunflower seed (var. Big Smile; *Helianthus annuus*; Johnny's Selected Seeds, ME, USA) once weekly. Seedlings were moistened with plain water and grown under a 16L:8D photoperiod, 10-40% RH, and day- and night-time temperatures of 25-27 °C and 23-25 °C, respectively. After the first pair of true leaves had formed (about one week after seeding), plants were watered with fertilizer-enriched water (18-6-20 fertilizer EC: 1.8-2.0 mS/cm, pH: 6.0-6.4; Terralink, Abbotsford, CA) until they reached the pre-bloom stage (after 6 weeks of growth). To control for powdery mildew, all plants were treated once a week with the biofungicide Rhapsody (20 ml/L; AgraQuest Inc., CA, USA). As needed, herbivore insect pests were suppressed with commercially available biological control agents. Once every month, all pots were drenched with a formulation of a nematode biological control agent (Nemasys; Becker Underwood Inc., IA, USA; mixed at 250 million per 9.5 L of water), using the greenhouse injector system.

2.3.3 PHENOLOGICAL STAGES OF SUNFLOWERS

To study the effect of sunflower phenological stage on attraction of BMSBs, four distinct phenological stages (Schneiter and Miller 1981) were selected: vegetative, pre-bloom, bloom and seed (Fig. 1A). Assignments of plants to these stages were based on specific criteria, as follows: vegetative-stage plants had a foliar diameter of ≤ 5 cm and lacked a budding flower head; pre-bloom plants had a pedicel length of > 2 cm but no visible flower petals; blooming plants displayed clearly-visible yellow petals, whereas plants at the seeding stage had already desiccated or absent flower petals and developed seed.

2.3.4 ATTRACTIVENESS OF SUNFLOWER PHENOLOGICAL STAGES TO BMSBS

2.3.4.1 *Settling and Oviposition by BMSBs on Sunflower in Four Phenological Stages*

To determine the phenological stage(s) of sunflower that female BMSBs select for feeding and oviposition, one potted plant of each stage (vegetative, pre-bloom, bloom, seed) was placed into a cage (60 × 60 × 120 cm; BioQuip Products Inc., CA, USA) at a randomly assigned position (Fig. 1A). Then, 15 females were released at the center of the cage and their position was recorded 24 h and 48 h later, counting only females in physical contact with a plant surface. Recording the position of females at two intervals enabled us to gauge the consistency of the females' plant choice over time. After 48 h, all females were returned to the lab colony not to be used in other experiments, and each plant was destructively sampled to count the number of eggs it had received. The experiment was replicated 20 times.

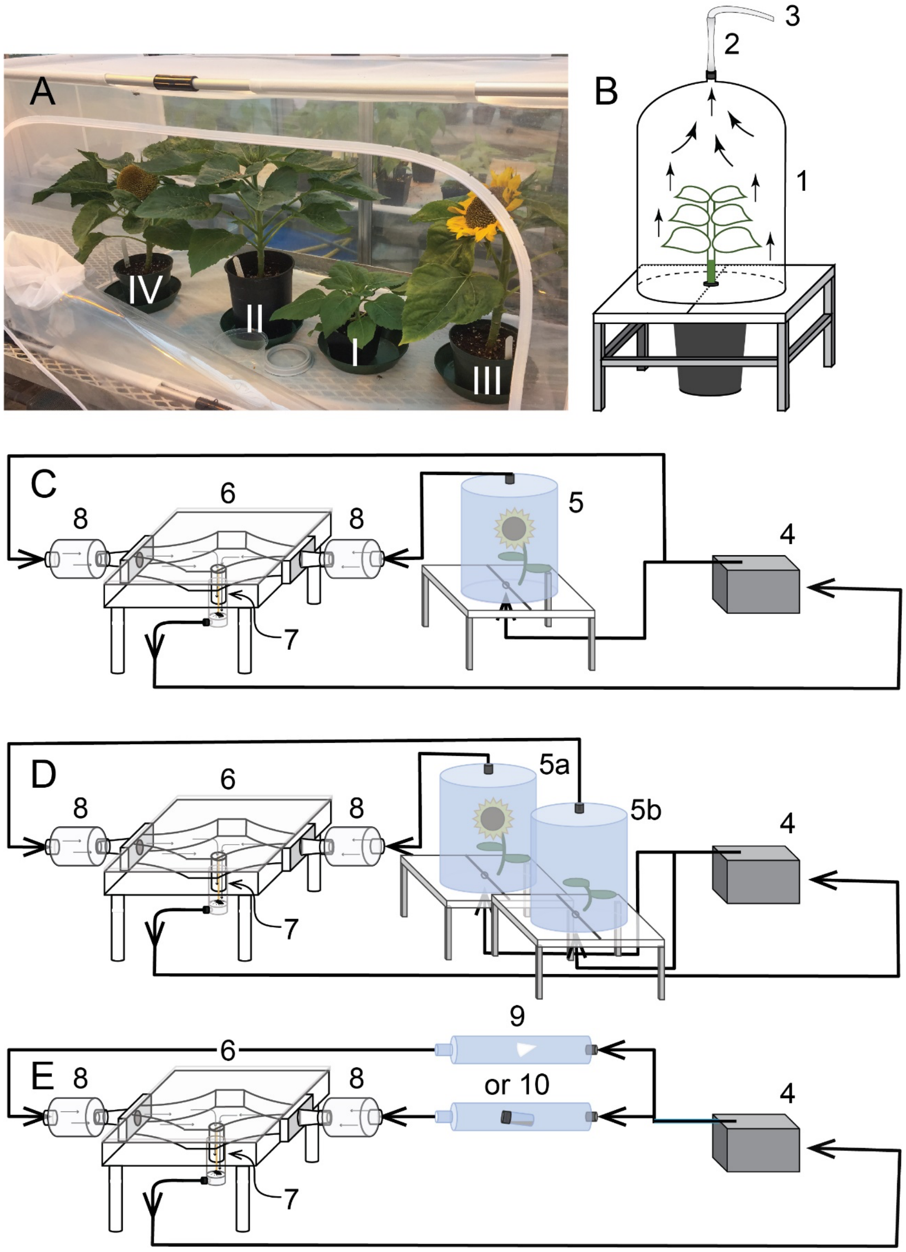

Fig. 1 Illustrations of greenhouse and laboratory experimental designs (drawings not to scale). **A**, Still-air, four-choice design offering distinct phenological stages of potted sunflower plants (I, vegetative; II, pre-bloom; III, bloom; IV, seeding) for feeding and oviposition responses of female brown marmorated stink bugs. **B**, Housing for potted sunflower plants consisting of a guillotine stand with a tall dome enclosing the plant (1), an odorant trap (2), and Teflon tubing (3) connecting the housing to the olfactometer system. **C-E**, Olfactometer system comprising an air filtration/purification station (4), various odor sources as test stimuli [one or two potted live plants (5, 5a, 5b); a synthetic odorant blend emanating either from filter paper (9) or a mineral oil formulation (10)], the olfactometer arena (6), an insect release chamber (7), and an insect trap (8), retaining stink bugs that made a decision.

2.3.4.2 *Acquisition of Sunflower Headspace Odorants*

To determine whether the four phenological stages of sunflower (vegetative, pre-bloom, bloom, seed) differ in their headspace odorants, three potted plants of each stage were transferred from the ARDC greenhouse facility to the Gries-lab at Simon Fraser University (SFU). Each plant was placed into a "guillotine" adjustable-height stand (13.6 × 13.6 × 2.5 cm; Sigma Scientific LLC, FL, USA; Fig. 1B, 1), with the entire (intact) plant enclosed within a borosilicate glass dome, and the plant stem residing in the central opening (2.5 cm diam) formed by two abutting platforms. Void space between the plant stem and the platforms was covered with a strip of activated carbon to purify the air prior to entering the dome. A vacuum pump (GAST miniature diaphragm, 15D 1150 series; IDEX Corp., MI, USA) drew carbon-filtered air at 1 L min^{-1} for 24 h through the glass dome and an odorant trap connected to an outlet at the top of the dome. The odorant trap consisted of a glass tubing (10 × 0.7 cm) containing the adsorbent Porapak Q (50 mg; 100-120 mesh; Supleco, MI, USA; Fig. 1B, 2) and was connected via teflon tubing (0.6 cm; Sigma Scientific; Fig. 1B, 3) to the vacuum pump. Plant-derived odorants were adsorbed on Porapak Q and desorbed with consecutive rinses of HPLC-grade pentane (2 mL) and ether (2 mL) stored in separate vials for analyses.

2.3.4.3 *GC-MS and GC-EAD Analyses of Sunflower Headspace Odorants*

After adding dodecyl acetate as an internal standard, each extract was concentrated to 250 µl. Aliquots (2 µl) of extracts were analyzed by coupled gas chromatography - mass spectrometry (GC-MS), using a Varian Saturn Ion Trap GC-MS (Agilent Technologies Inc., Santa Clara, CA, USA) operated in full-scan electron impact mode and fitted with a DB-5 MS column (30 m × 0.25 mm ID; Agilent J&W GC), with helium as the carrier gas (35 cm^{-1s}). The injector port was set at 250 °C, the transfer line at 280° C, and the ion trap at 200 °C. For analyses, the following temperature program was run: 50 °C for 5 min, 10 °C · min^{-1} to 280 °C (held for 10 min). Odorants were identified by comparing their retention indices (relative to straight chain alkanes) (Van Den Dool and Kratz 1963) and their mass spectra with those of authentic standards purchased from Sigma-Aldrich (St. Louis, MO, USA) or synthesized in the Gries-lab (*E*3,*E*7-4,7-dimethyl-1,3,7-nonatriene; *E*3,*E*7-4,8,12-trimethyl-trideca-1,3,7,11-tridecatetraene) following previously reported protocols (Maurer et al. 1986). All compounds were > 95% chemically pure except for ocimene (90%) which also consisted of a mixture of *cis*- and *trans*-isomers (25/75).

The absolute configuration of chiral odorants was determined on a Cyclodex B column (30 m × 0.25 mm ID; J&W Scientific, Folsom, CA, USA) in a 5890 GC. Using a split injection mode (10:1 split ratio), α-pinene, camphene, sabinene, β-pinene, and limonene were chromatographed isothermally at 80 °C, and borneol and bornyl acetate at 110 °C.

Aliquots of extracts were further analyzed by gas chromatographic-electroantennographic detection (GC-EAD), with procedures previously detailed (Arn et al., 1975; Gries et al., 2002). Briefly, the GC-EAD system consisted of a Hewlett-Packard 5890 GC fitted with a DB-5 GC column (30 m × 0.32 mm I.D.; Agilent J & W column, Agilent Technologies Inc.), with helium as the carrier gas (35 cm · s^{-1}). The injector port and flame ionization detector (FID) were set at 260 °C, and the following oven program was used: 50 °C for 1 min., then 20 °C · min^{-1} to 280 °C. For GC-EAD recordings, an antenna was carefully dislodged from a BMSB female's head and suspended between two glass capillary electrodes (1.0 × 0.58 × 100 mm; A-M Systems, Carlsborg, WA, USA) prepared to accommodate the antenna, and filled with a saline solution (Staddon and Everton 1980).

2.3.4.4 *General Design of Laboratory Olfactometer Experiments*

Attraction of BMSB females to test stimuli was tested in laboratory olfactometer experiments, with visual cues being absent or occluded. The 4–choice arena olfactometer (Sigma Scientific LLC; Fig. 1, C, D, E) was modified for 2-choice experiments and was illuminated from above with a F32T5 daylight bulb and a F32T8 plant and aquarium fluorescent light bulb (Philips, Amsterdam, NL). To deliver test stimuli originating from odor sources (potted sunflower, headspace odorant extract of sunflower, synthetic odor blend), we used pressurized and purified air. Filter-purified air (Fig. 1C, 4) moved at 1 L min $^{-1}$ through the olfactometer system entering – in sequence – the stimulus chamber(s) (Fig. 1C-E, 5, 9, 10), a barrel-shaped insect trap (Fig. 1 C-E, 8), the choice arena (Fig. 1 C-E, 6), and the insect release chamber (Fig. 1 C-E, 7), before returning to the air filter system (Fig. 1C, 4). For each replicate, a single female was placed into the release chamber fitted with a wooden stick and allowed to enter the choice arena on her own accord and to select a test stimulus. A choice was recorded when the female had entered one of the two insect traps within 45 min (in experiments testing a treatment stimulus *vs* a filtered air or mineral oil control) or within 60 min (in experiments testing two live plants). Extending the upper time limit to 60 min in choice experiments with two plants took into account that females faced difficult choices between two complex test stimuli. Following each replicate, both the arena and the traps were cleaned with Sparkleen (Fisher Scientific Comp., ON, CA) and the wooden climbing stick was replaced.

2.3.4.5 *Specific Laboratory Olfactometer Experiments*

Experiments 2-5 (n = 30 each) tested attraction of BMSB females to potted sunflower at each of four phenological stages: vegetative (Exp. 2), pre-bloom (Exp. 3), bloom (Exp. 4) and seed (Exp. 5), all *vs* filtered air. Follow-up experiments 6-11 (n = 30 each) used a full factorial design, testing the attractiveness of potted plants at each phenological stage *vs* that of each of the other three plant stages. Specifically, the vegetative stage was tested *vs* the pre-bloom, bloom, and seed stage, respectively (Exps. 6-8). Moreover, the pre-bloom stage was tested *vs* the bloom and seed stage, respectively (Exps. 9-10), and the seed stage was tested *vs* the bloom stage (Exp. 11).

Drawing on combined data of behavioral experiments 1-11 (see Results), it appeared that the bloom stage was most effective overall in prompting settling and attraction responses by female BMSBs. Moreover, there was a strong shift in the abundance and occurrence of odorants as plants transitioned from pre-bloom to bloom. Therefore, a synthetic blend (SB) of odorants was prepared that resembled the amount and ratio of natural odorants released from blooming plants during 24 h. Only those odorants (boldfaced in Table 1) that elicited antennal responses (see Results) were included in the SB. This SB was then tested for its attractiveness to BMSBs using various delivery systems. First, SB (0.1 mL) was applied onto filter paper and tested *vs* a filtered air control (Exp. 12).

To help decide whether mineral oil (MO) was suitable as a dissemination medium for SB in field experiments, we needed to determine whether MO was behaviorally benign to BMSBs and thus tested MO *vs* filtered air (Exp. 13). With evidence that MO was not attractive to BMSBs (see Results), we proceeded testing SB formulated in MO at a low dose (0.01 mL SB in 0.5 mL MO) and at a higher dose (0.1 mL SB in 0.5 mL MO) *vs* plain MO (Exps. 14, 15). The 24-h release rate of the high-dose formulation was equivalent to that of a blooming sunflower during 24 h.

Finally, to determine whether time of season affects the propensity of BMSBs to respond to the SB, we tested attraction of BMSBs exposed to a long photophase (16L:8D; laboratory colony) or a shorter photophase (11L:13D; field collected specimens) (Exps. 16, 17).

2.3.4.6 *Field Testing the Synthetic Odorant blend (SB)*

The ability of the synthetic odorant blend (SB) to attract BMSBs, or to enhance the attractiveness of a commercial BMSB pheromone lure [(3*S*,6*S*,7*R*,10*S*)- and (3*R*,6*S*,7*R*,10*S*)-10,11-epoxy-1-bisabolene-3-ol (Khrimian et al. 2014) *plus* synergistic methyl (2*E*,4*E*,6*Z*)-decatrienoate (Leskey et al. 2015) (Stink bug DUAL Lures; Trécé, Inc., OK, USA)], was tested in a field experiment in BC. The experiment was run from 26 August to 22 October 2019 when BMSB adults move from host plants to overwinter sites, and from 16 March to 03 July 2020 when BMSBs emerge from overwinter diapause and then feed on host plants. In each of three field sites (Rosedale, 49.170965, -121.830512; Chilliwack, 49.158057, -121.998131; Abbotsford, 49.003225, -122.264077), three replicates with six treatments each were set up, with $>$ 10 m spacing between replicates. In each replicate, an adhesive-coated trap (15.2 × 30.5 cm; Trécé, Inc., OK, USA) was affixed 1.2 m above ground to one of six wooden stakes which were spaced $>$ 5 m apart taking pheromone plume reach ($<$ 3 m) of pheromone-baited sticky traps into account (Kirkpatrick et al. 2019). Each trap was randomly assigned to one of six treatments: (1) commercial pheromone lure ('P'); (2) pheromone lure *plus* mineral oil ('P + MO'); (3) a synthetic blend of sunflower odorants in mineral oil ('SB in MO') (see above); (4) 'SB in MO + P'); (5) MO; and (6) an unbaited control. MO (0.5 mL), and SB (0.1 mL) formulated in 0.5 mL of MO, were each presented in a dram vial (1.5 × 4.5 cm; Fisher Scientific Comp. ON, CA) affixed to wooden stakes above the adhesive trap. As SB lures had consistent release rates for up to 14 days, lure replacement at only bi-weekly intervals was justified. All lures were rain-sheltered by a horizontal clear plastic cover (2.5 × 5 cm). Once each week for the entire duration of the field experiment, trap captures of adult BMSBs were recorded, and treatment positions within replicates were re-randomized. Traps with $>$ 10 BMSBs captured were replaced, and all other BMSBs were dislodged from the adhesive surface of traps.

2.3.5 STATISTICAL ANALYSES

Data of experiment 1, which tested feeding and oviposition choices of BMSBs on sunflower in the vegetative, pre-bloom, bloom, and seed stage, were analyzed by an exact multinomial test, comparing the bugs' choices against a theoretical choice distribution of 25:25:25:25%. This analysis was followed by a Fisher's exact test to correct for multiple comparisons with small sample sizes.

All two-choice olfactometer data (Exps. 2-17) were analyzed with a χ^2 test under the null hypothesis that BMSBs have no preference for either of the two stimuli tested.

Trap catch data of adult BMSBs in the 6-treatment field experiment (Exp. 18) were analyzed with a zero-inflated generalized linear mixed model (GLMM) with a negative binomial error distribution, using treatment as a categorical fixed factor, and site and week as categorical random factors. Likelihood ratio tests were used to assess statistical significance ($p < 0.05$). For post-hoc multiple comparisons among categorical treatments, Tukey multiple comparisons tests were run.

All statistics were run with R version 3.6.2 (R Core Team 2020) using RStudio version 1.2.5033 (RStudio Team 2016). Software packages used included 'EMT' (Menzel and Menzel 2015) for the multinomial analysis, 'car' (Fox et al. 2012) for likelihood ratio tests, and 'multcomp' (Hothorn et al. 2013), 'multcompView' (Graves et al. 2015) and 'emmeans' (Lenth et al. 2018) for Tukey multiple comparisons and extraction of model estimates and confidence intervals.

2.4 RESULTS

2.4.1 SETTLING AND OVIPOSITION OF BMSBS ON SUNFLOWER IN FOUR PHENOLOGICAL STAGES

Of the total of 300 females tested in 20 replicates of experiment 1, 154 (51.3%) and 193 (64.3%) were present on plants 24 h and 48 h, respectively, after experiment initiation. These females discriminated among the four phenological stages of potted sunflower plants that were offered (24 h: two-sided Fisher's Exact Test, $p = 0.002$; 48 h: $p = 0.0005$) (Fig. 2). Most females selected plants at the bloom stage (24 h: 70/154; 48 h: 86/193), whereas fewer females selected plants at the seed stage (24 h: 43/154; 48 h: 53/193), pre-bloom stage (24 h: 34/154; 48 h: 51/193), and vegetative stage (24 h: 7/154; 48 h: 3/193).

When plants were destructively sampled for the presence of egg masses 48 h after the experiment was initiated, the phenological stage of plants had no significant effect on the number of egg masses present (two-sided Fisher's Exact Test, $p = 0.1084$). Numerically, plants in the seed stage received more egg masses (27/81) than blooming plants (24/81), pre-blooming plants (22/81), or plants in the vegetative stage (8/81).

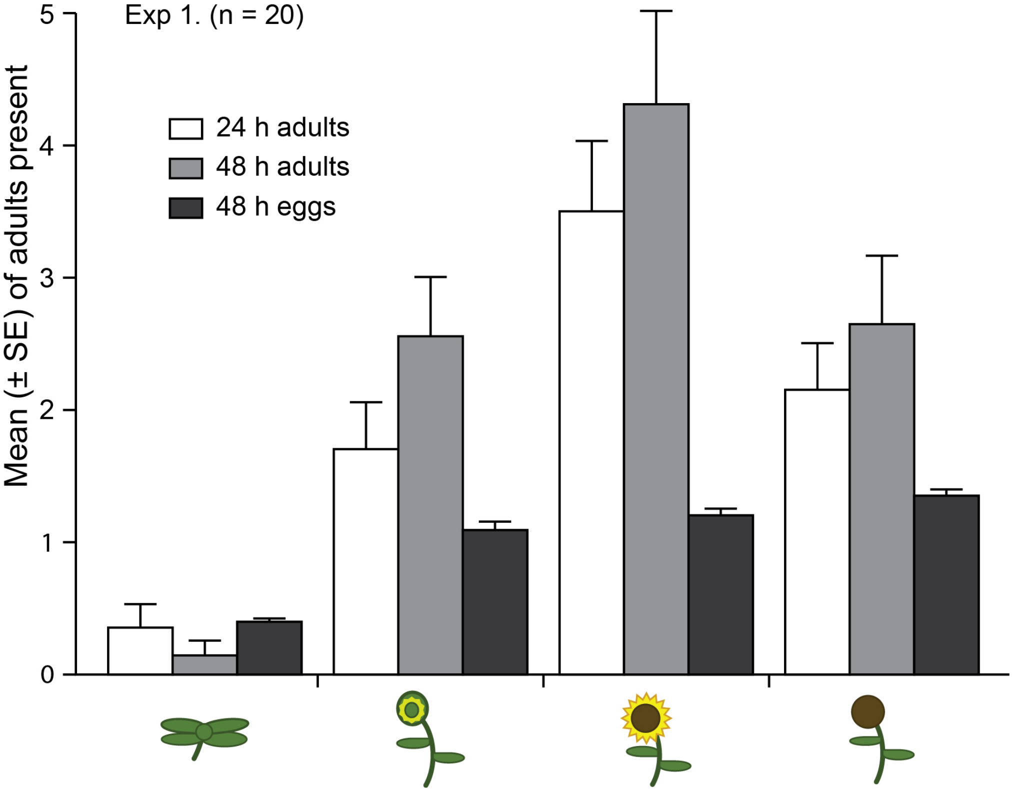

Fig. 2 Settling and oviposition by female brown marmorated stink bugs in response to concurrently offered potted sunflower plants at four phenological stages of development (from left to right: vegetative, pre-bloom, bloom, seeding) (see Fig. 1, A). Feeding/settling responses of females depended upon plant phenological stage, as recorded 24 h and 48 h after experiment initiation (24 h: two-sided Fisher's Exact Test, $p = 0.002$; 48 h: $p = 0.0005$). In contrast, plant phenological stage had no significant effect on numbers of egg masses deposited (two-sided Fisher's Exact Test, $p = 0.1084$).

2.4.2 OLFACTORY ATTRACTION OF BMSBS TO POTTED SUNFLOWERS

In olfactometer experiments 2-5 (n = 30 each; Fig. 3) with filtered air as the control stimulus and a potted sunflower plant as the treatment stimulus, the phenological stage of plants affected the females' responses. Vegetative-stage plants attracted females (Exp. 2: 17 *vs* 4, $\chi^2 = 8.05$, $p = 0.0046$), pre-bloom plants deterred females (Exp. 3: 5 *vs* 20, $\chi^2 = 9.00$, $p = 0.0027$), blooming plants (not significantly) attracted females (Exp. 4: 16 *vs* 7, $\chi^2 = 3.52$, $p = 0.06$), and seed-stage plants deterred females (Exp. 5: 6 *vs* 15, $\chi^2 = 3.86$, $p = 0.049$).

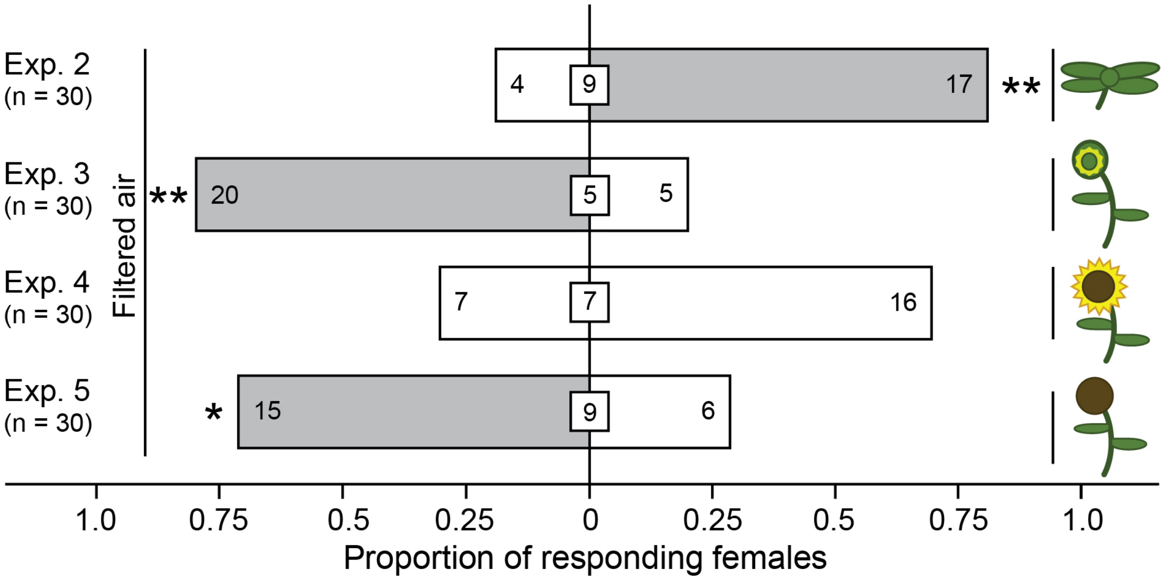

Fig. 3 Responses of adult female brown marmorated stink bugs in moving-air olfactometer experiments 2-5 (Fig. 1, C) when offered a choice between filtered air as the control stimulus and a potted sunflower plant as the treatment stimulus (for plant symbols see Fig. 3). Shown in bars and insert boxes are the number of females selecting a treatment or control stimulus and not responding to test stimuli, respectively. For each experiment, an asterisk indicates a significant preference for a test stimulus (χ^2 test; * $p \leq 0.05$, ** $p \leq 0.01$ respectively).

Comparing the attractiveness of plants head-to-head in a full factorial design (Fig. 4), pre-bloom plants (Exp. 6), but neither blooming plants (Exp. 7) nor seeding plants (Exp. 8), attracted more females than vegetative-stage plants (Exp. 6: 18 *vs* 6, $\chi^2 = 6.00$, $p = 0.0014$; Exp. 7: 7 *vs* 12, $\chi^2 = 1.32$, $p = 0.25$; Exp. 8: 16 *vs* 11, $\chi^2 = 0.93$, $p = 0.33$). Compared to pre-bloom plants, neither blooming plants (Exp. 9) nor seeding plants (Exp.10) were more attractive to females (Exp. 9: 13 *vs* 11, $\chi^2 = 0.17$, $p = 0.68$; Exp. 10: 8 *vs* 18, $\chi^2 = 3.85$, $p = 0.045$). However, blooming plants attracted more females than seeding plants (Exp. 11: 18 *vs* 7, $\chi^2 = 4.84$, $p = 0.027$).

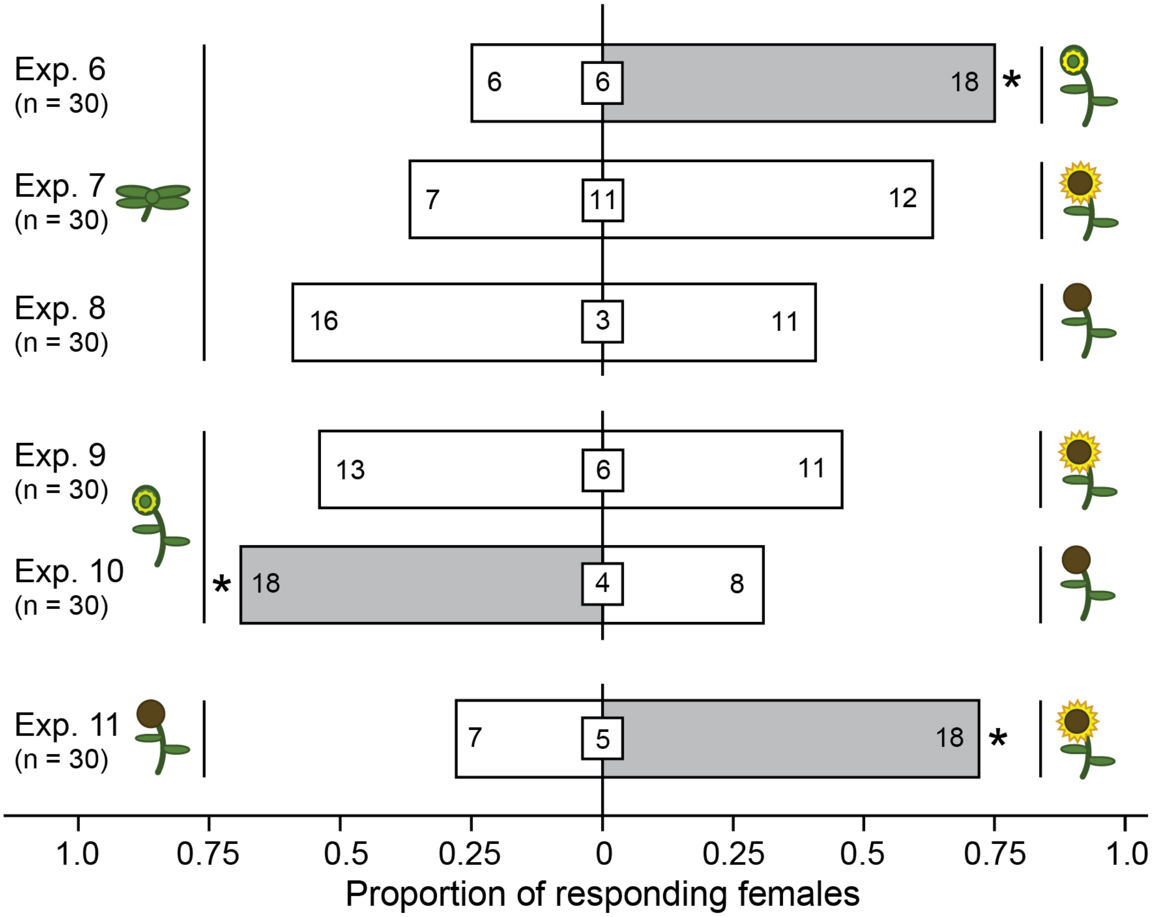

Fig. 4 Responses of adult female brown marmorated stink bugs in moving-air olfactometer experiments 6-11 (Fig. 1, D) when offered a choice between two potted sunflower plants at different stages of phenological development (for plant symbols see Fig. 3). Shown in bars and insert boxes are the number of females selecting a plant and not responding to plants, respectively. For each experiment, an asterisk (*) indicates a significant preference for a test stimulus (χ^2 test, $p \leq 0.05$).

2.4.3 GC-MS AND GC-EAD ANALYSES OF SUNFLOWER HEADSPACE ODORANTS

GC-EAD analyses of Porapak Q headspace odorant extract of blooming sunflowers revealed five monoterpene hydrocarbons (α-pinene; camphene; sabinene; β-pinene; limonene), one sesquiterpene hydrocarbon (*trans*-caryophyllene), two additional hydrocarbons (*E*3,*E*7-4,7-dimethyl-1,3,7-nonatriene; *E*3,*E*7-4,8,12-trimethyl-1,3,7,11-tridecatetraene), one alcohol (borneol), one acetate (bornyl acetate), one ether (2-methylanisole) and one aldehyde (nonanal) that consistently elicited responses from female BMSB antennae (Fig. 5). Analyzing odorants on a GC-column that separated optical isomers of EAD-active odorants further revealed that both α- and β-pinene occurred as a mixture of (+)- and (–)-isomers [α-pinene; (+)(10%)/(–)(90%); β-pinene: (+)(40%)/(–)(60%)], whereas (–)-camphene, (+)-limonene, (–)-borneol, and (–)-bornyl acetate were each present as a single optical isomer. While most odorants were present at each of the four phenological stages of sunflower, the relative abundance of these odorants changed in relation to plant stage. Particularly, α- and β-pinene, camphene and sabinene markedly increased as plants transitioned from pre-bloom to bloom (Table 1). Borneol and bornyl acetate were entirely absent at the vegetative stage and appeared at appreciable amounts only in the bloom and seed stages. Of the odorants with elevated abundance at the blooming stage, only *E*3,*E*7-4,7-dimethyl-1,3,7-nonatriene and *E*3,*E*7-4,8,12-trimethyl-1,3,7,11-tridecatetraene decreased again at the seeding stage (Table 1).

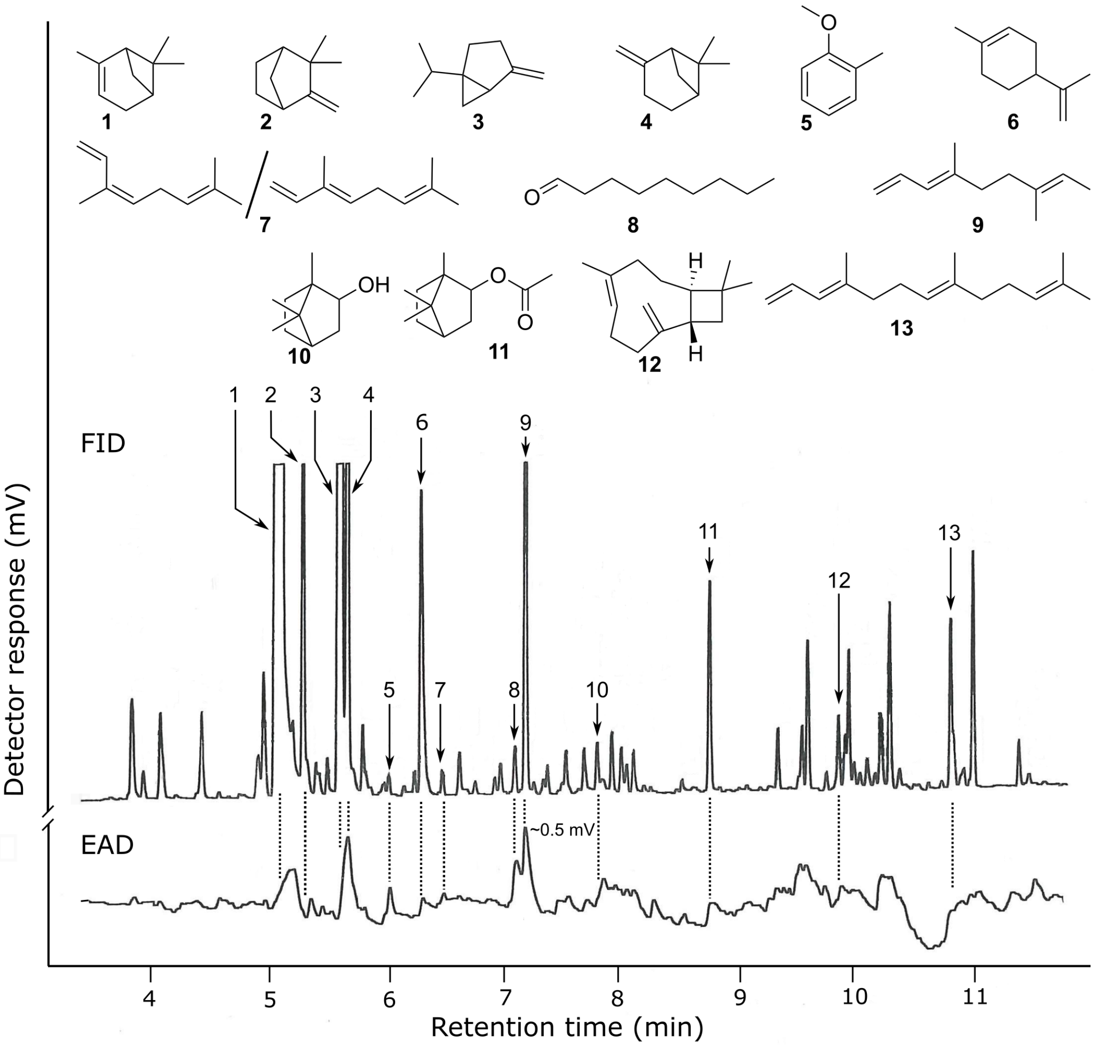

Fig. 5 Representative responses of a gas chromatographic flame ionization detector (FID) and an electroantennographic detector (EAD: antenna of a female brown marmorated stink bug) to aliquots of Porapak Q headspace odorant extract from a potted blooming sunflower. The odorants that consistently elicited antennal responses were α-pinene [(+)/(–): 10/90)] (1), (–)-camphene (2), (–)-sabinene (3), β-pinene [(+)/(–): 40/60)] (4), 2-methyl-anisole (5), (+)-limonene (6), *cis/trans*-ocimene (25/75) (7), nonanal (8), *E*3,*E*7-4,7-dimethyl-1,3,7-nonatriene (9), (–)-borneol (10), (–)-bornyl acetate (11), *trans*-caryophyllene (12), and *E*3,*E*7-4,8,12-trimethyl-trideca-1,3,7,11-tridecatetraene (13).

Table 1. Composition and amounts of odorants in headspace odorant extract of potted sunflower at four distinct phenological stages. Odorants were collected from three plants per stage for 24 h each.

	Phenological stage of potted sunflower			
Plant odorant	**Vegetative**	**Pre-bloom**	**Blooming**	**Seeding**
	Mean[1] (SEM)	Mean (SEM)	Mean (SEM)	Mean (SEM)
*Z*3-hexenol	5.2 (0.8)	3.3 (1.4)	1.0 (0.7)	1.3 (0.5)
xylene isomer 1	18.3 (13.2)	7.2 (4.4)	0.4 (0.1)	3.6 (2.7)
xylene isomer 2	81.0 (62.7)	30.1 (19.7)	2.6 (1.1)	18.0 (13.0)
xylene isomer 3	31.4 (18.7)	13.9 (4.1)	4.7 (1.7)	8.0 (3.7)
thujene	4.7 (1.1)	1.5 (0.6)	0.7 (0.1)	4.7 (1.9)
(±)-α-pinene [(-)-isomer = 90%]	88.1 (21.2)	221.5 (88.6)	**655.7 (221.5)**	**1467.4 (370.6)**
(-)-camphene	13.2 (3.2)	8.7 (2.3)	**36.6 (5.1)**	**47.1 (18.3)**
(-)-sabinene	63.3 (15.6)	44.8 (6.1)	**108.8 (18.8)**	**298.1 (87.3)**
(±)-ß-pinene [(-)-isomer = 60%]	14.9 (4.2)	10.3 (2.0)	**49.2 (16.4)**	**106.5 (27.0)**
sulcatone	7.8 (1.9)	3.4 (0.9)	8.1 (3.2)	13.2 (2.9)
unknown hydrocarbon	9.3 (2.9)	4.8 (1.9)	1.0 (0.2)	2.9 (1.1)
(+)-limonene	11.6 (2.3)	9.6 (2.1)	7.9 (0.9)	20.5 (5.8)
***cis/trans*-ocimene (30/70)**	6.3 (1.5)	1.8 (0.6)	0.7 (0.3)	0.8 (0.2)
nonanal	8.5 (1.3)	3.9 (1.5)	1.5 (0.2)	2.2 (0.8)
***E*3, *E*7-4,7-dimethyl-1,3,7-nonatriene**	20.2 (9.6)	10.4 (1.7)	21.3 (3.1)	7.3 (2.1)
verbenol	0 (0)	0 (0)	1.7 (0.4)	3.0 (1.7)
(-)-borneol	0 (0)	0 (0)	**2.7 (0.3)**	**4.7 (2.5)**
unknown hydrocarbon	54.4 (16.8)	13.3 (0.9)	4.4 (1.2)	7.2 (1.9)
decanal	9.5 (2.1)	2.5 (0.1)	0.8 (0.9)	1.6 (8.9)
(-)-bornyl acetate	0 (0)	0.4 (0.9)	**10.9 (0.1)**	**27.9 (0.6)**
unknown unsaturated hydrocarbon	59.4 (18.3)	15.1 (2.1)	4.4 (1.6)	27.5 (13.5)

	Phenological stage of potted sunflower			
Plant odorant	**Vegetative**	**Pre-bloom**	**Blooming**	**Seeding**
	Mean[1] (SEM)	Mean (SEM)	Mean (SEM)	Mean (SEM)
unknown sesquiterpene	6.4 (3.8)	7.8 (1.5)	8.5 (2.2)	3.5 (1.0)
unknown hydrocarbon	6.1 (1.7)	1.4 (0.3)	0.6 (0.3)	1.0 (0.4)
***trans*-caryophyllene**	10.1 (1.6)	6.9 (1.6)	5.6 (1.2)	4.0 (1.6)
unknown sesquiterpene	15.1 (4.3)	4.4 (1.9)	7.1 (2.4)	2.3 (0.51)
***E*3, *E*7-4,8,12-trimethyl-1,3,7,11-tridecatetraene**	4.0 (15.8)	2.9 (3.6)	**9.5 (1.1)**	**1.9 (1.9)**

Bold-faced compounds were included in a synthetic blend for lab and field testing

[1]Mean = amount (ng) of compound per gram of fresh weight of plant

2.4.4 OLFACTORY ATTRACTION OF BMSBS TO SYNTHETIC SUNFLOWER ODORANTS

The synthetic blend (SB) of blooming sunflower odorants (Table 1) attracted more stink bug females than a filtered-air control stimulus (Fig. 6, Exp. 12: 20 *vs* 4, $\chi^2 = 10.67$, $p = 0.0011$). In contrast, filtered-air and plain mineral oil (MO) as test stimuli were equally unattractive to females (Exp. 13: 9 vs 7, $\chi^2 = 0.25$, $p = 0.6171$), evidenced also by the large number of non-responding stink bugs. The SB formulated in MO at a low dose (Exp. 14) and at a higher dose (Exp. 15) attracted more stink bug females than MO alone but the effect was statistically significant only for the higher dose (Exp. 14: 16 *vs* 8, $\chi^2 = 2.67$, $p = 0.1025$; Exp. 15: 19 *vs* 5, $\chi^2 = 8.17$, $p = 0.0043$).

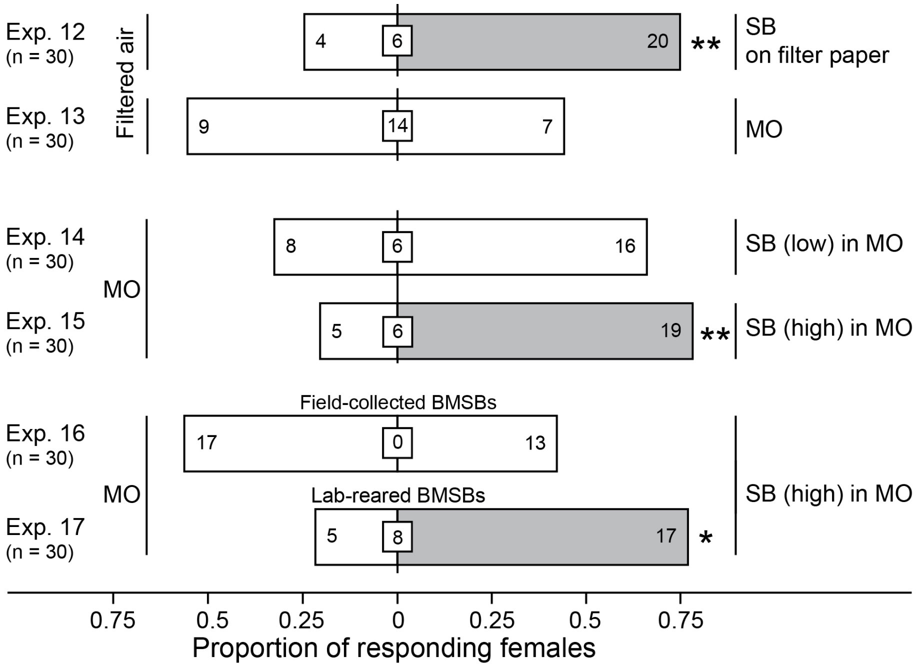

Fig. 6 Responses of adult female brown marmorated stink bugs (BMSBs) in moving-air olfactometer experiments 12-17 (Fig. 1, E) when offered a choice between a control stimulus [filtered air or plain mineral oil (MO)] and a test stimulus [synthetic blend (SB) of blooming-sunflower odorants (Table 1) applied on filter paper or formulated in MO]. Unlike females which were field-collected in the fall (October 6-9th), lab-reared females were exposed a long photoperiod (16L:8D). Shown in bars and insert boxes are the number of females selecting a treatment or control stimulus, and not responding to test stimuli, respectively. For each experiment, an asterisk indicates a significant preference for a test stimulus (χ^2 test; * $p \leq 0.05$, ** $p \leq 0.01$ respectively).

The numbers of field-captured adult BMSBs differed among the six experimental treatments tested both in the fall (26 August to 22 October) of 2019 (Type II Wald test: $\chi^2 = 137.83$; df = 5, 476; $p < 0.0001$), and in the spring/summer (16 March to 03 August) of 2020 (Type II Wald test: $\chi^2 = 106.4$; df = 5, 1070; $p < 0.0001$) (Fig. 7, Exp. 18). While the synthetic odorant blend of blooming sunflower (SB) formulated in mineral oil (MO) was not effective by itself, 'SB in MO' and synthetic pheromone ('P') in binary combination as a trap lure had an interactive effect on captures of BMSBs (see below).

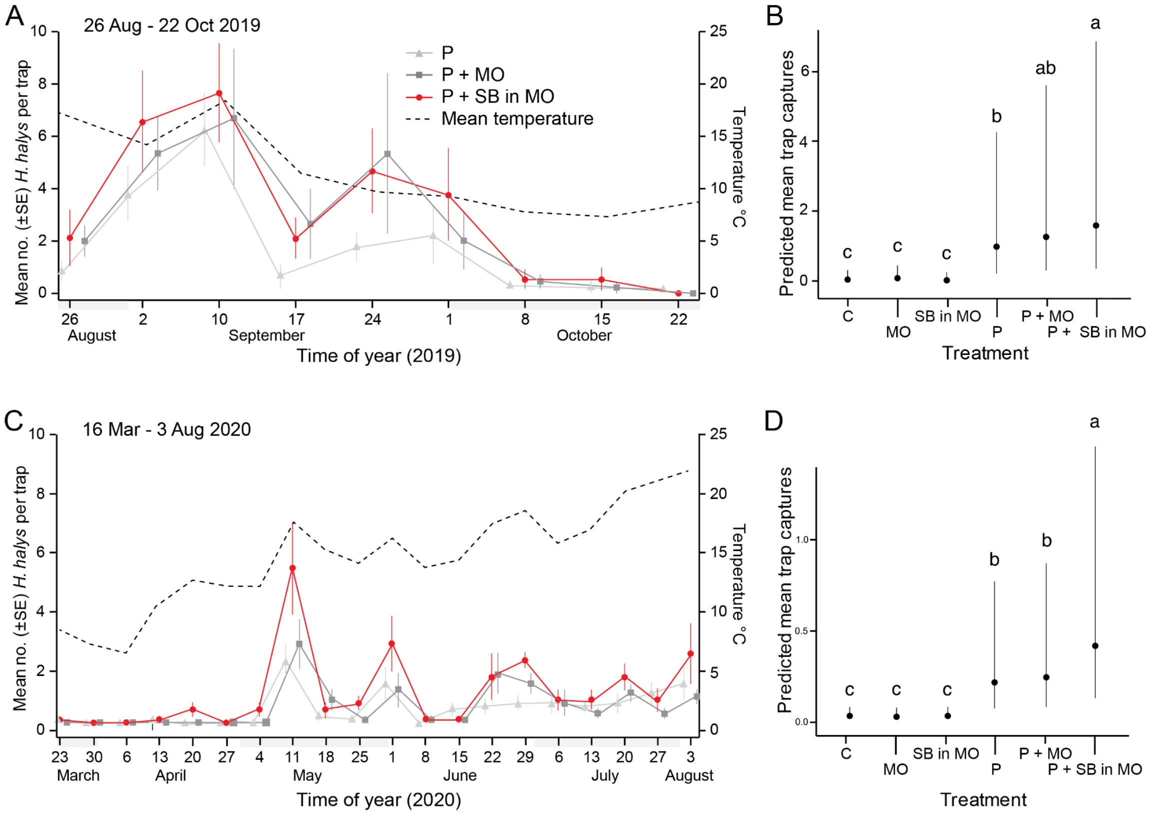

Fig. 7 Trap captures of adult brown marmorated stink bugs in a field experiment in British Columbia over time (fall 2019: panel A, spring 2020: panel C) and overall (fall 2019: panel B, spring 2020: panel D). In each of three replicates at each of three sites, traps were assigned one of six treatments: (1) an unbaited control (C), (2) mineral oil (MO), (3) a synthetic blend of sunflower odorants formulated in mineral oil (SB in MO), (4) a commercial pheromone lure (P), (5) a commercial pheromone lure plus mineral oil (P + MO), and (6) P + MO & SB in MO. Numbers of captured stink bugs (shown in panels A and C as among-site means ± SE for each date; shown in panels B and D as model predictions from the fitted GLMM ± 95% CI) differed among the six treatments both in the fall of 2019 (Type II Wald test: $\chi^2 = 137.83$, df = 5, $p < 0.0001$) and the spring/summer of 2020 ($\chi^2 = 106.4$, df = 5, $p < 0.0001$). In 2019 and 2020, traps baited with P + MO & SB in MO captured 62% and 104% more stink bugs, respectively, than traps baited with P alone (post hoc Tukey test; 2019: $p = 0.0193$; 2020: $p = 0.0001$: panels B and D; means labelled with different letters are statistically different from each other). There were 450 BMSB nymphs captured in the fall of 2019, and 33 nymphs in the spring of 2020.

In 2019, traps baited with 'SB in MO + P' in binary combination captured 62% more adult BMSBs than traps baited with ‘P’ alone (Tukey multiple comparison: $p = 0.019$). Pheromone-baited traps captured more adult BMSBs than traps baited with ‘SB in MO’ ($p < 0.0001$), fitted merely with a ‘MO’ dispenser ($p < 0.0001$), or left as unbaited controls ($p < 0.0001$). Pairwise comparisons of trap captures revealed no statistical differences between each of two pairs: ‘P *vs* P + MO’ ($p = 0.50$) and ‘P + MO *vs* P + SB in MO’ ($p = 0.69$). A total of 450 BMSB nymphs were captured in the 2019 field experiment.

In 2020, traps baited with ‘SB in MO and ‘P’ in binary combination captured 104% more adult BMSBs than traps baited with ‘P’ alone (Tukey multiple comparison: $p = 0.0001$) and 79% more adult BMSBs than traps baited with ‘P + MO’ ($p = 0.0016$). Pheromone-baited traps captured more adult BMSBs than traps baited with ‘SB in MO’ ($p < 0.0001$), fitted with a MO dispenser ($p = 0.0004$), or left as unbaited controls ($p < 0.0001$); captures between traps baited with ‘P’ or ‘P + MO’ did not differ ($p = 0.97$). A total of 33 nymphs were captured in the 2020 field experiment.

In both years of the field experiment, adult BMSB trap captures appear to peak during weeks with comparatively high ambient temperatures (Fig. 7).

2.5 DISCUSSION

Our data support the conclusion that (*i*) BMSBs discriminate between phenological stages of sunflower host plants (vegetative, pre-bloom, bloom, seeding), (*ii*) headspace odorants of these plant stages differ in amount and ratio, and (*iii*) the odor blend of blooming plants – presented in synthetic form – attracts BMSBs in laboratory bioassays, and in field settings enhances the attractiveness of synthetic BMSB pheromone. Below, we elaborate on these conclusions.

Population densities of BMSBs appear to be linked to the presence of host plants at specific phenological stages (Blaauw et al. 2019; Soergel et al. 2015). Large populations are found on seeding plants (Nielsen et al. 2016), implying that they are particularly appealing to BMSBs. In field settings, however, where most host preference studies with BMSBs were run, seeding plants often co-occur with blooming plants (Blaauw et al. 2017; Nielsen et al. 2016), making it difficult to pinpoint the stage that actually attracted BMSBs.

To determine whether BMSBs indeed discriminate between plant phenological stages, we selected (dwarf) sunflower, which is a preferred host plant of BMSBs (Nielsen et al. 2016; Soergel et al. 2015) and ran a laboratory four-choice experiment. Offering adult females a choice of plants in vegetative, pre-bloom, bloom and seed stages, and recording the number of females present on these plants as the criterion for choice of plant, we found that more females (45%) chose blooming sunflowers than pre-blooming and seeding sunflowers (22-28%) and that hardly any females (< 5%) were present on vegetative-stage plants (Fig. 2). This degree of host plant discrimination by female BMSBs was not mirrored in their choice of oviposition site. Egg masses were rather evenly distributed between all four plant stages (Fig. 2), suggesting that cues other than plant phenological stage affect oviposition choice by females, or that females "relied" on the mobility of their offspring to switch between plants which were all located in close proximity in this experiment (Fig. 2).

BMSB females sensed and behaviorally responded to sunflower odorants in olfactometer bioassays (Figs. 3, 4) but the data did not completely align with the settling choices recorded in experiment 1 (Fig. 2). For example, vegetative-stage plants which were least often settled onto by females in experiment 1, strongly attracted females in experiment 2 (Fig. 3). These data indicate that different or additional cues may guide BMSBs in the process of locating and accepting plants at a preferred physiological stage. At long range, it is generally the semiochemical profile of plants that guides foraging insects, particularly in visually complex habitats (Bruce et al. 2005; Webster and Cardé 2017). If also true for BMSBs, this would explain why plant odor alone in the absence of visual plant cues attracted BMSBs in olfactometer experiments (Figs. 3, 4). At close range, visual plant cues such as size, shape and color (Finch and Collier 2000; Rojas and

Wyatt 1999), and even polarized light reflections from foliage (Blake et al. 2019), provide additional information and likely modulate the approach trajectory (Blake et al. 2020). After alighting on a potential host plant, acceptance and onset of feeding are then contingent upon plant tactile and gustatory cues which must have been poor on vegetative-stage sunflowers which prompted few settling responses by BMSB females (Fig. 2).

Based on plant odor alone, there was no one phenological stage of sunflower that was clearly most attractive to BMSBs, but blooming plants had the "edge" when taking all data into account. Blooming plants were (*i*) significantly more attractive than seeding plants (Fig. 4, Exp. 11), (*ii*) somewhat more attractive than vegetative plants (Fig. 4, Exp. 7), (*iii*) as attractive as pre-bloom plants (Fig. 4, Exp. 9) and (*iv*) they were never repellent unlike pre-bloom and seeding plants (Fig. 3).

The odor profile among the phenological stages of sunflower markedly differed (Table 1), indicating that they could inform (long-range) foraging decisions by BMSBs. As plants transitioned from pre-bloom to bloom, monoterpenes (α-pinene, β-pinene, camphene, sabinene), bornyl acetate, *E*3,*E*7-4,7-dimethyl-1,3,7-nonatriene and *E*3,*E*7-4,8,12-trimethyl-1,3,7,11-tridecatetraene increased in abundance 2- to 27-fold. Moreover, borneol being absent in the headspace of vegetative and pre-bloom plants appeared, albeit in small quantity. As the amount of nearly all of these odorants increased even further in seeding plants (Table 1), these odorants on their own are not likely signature semiochemicals of the blooming stage. The tridecatetraene, however, may serve such signature role because it was prevalent only in the odor bouquet of blooming plants. The importance of the tridecatetraene for BMSB attraction could be tested by offering blends with or without it.

The synthetic blend of sunflower odorants for testing attraction of BMSBs in field settings was prepared according to the composition, amount and ratio of odorants in headspace odorant extracts of blooming sunflower (Table 1). The blooming stage was selected for synthetic blend preparation because this plant stage – relative to other stages – (*i*) prompted the most settling responses by females in experiment 1 (Fig. 2), elicited overall more convincing attraction of females to odor sources in olfactometer experiments (Figs. 3, 4), and (*iii*) produced the most distinct odor profile (Table 1). Moreover, if foraging BMSBs were to exploit also plant visual cues, it would likely be the bright yellow petals of blooming sunflower that enhance the attractiveness of sunflower semiochemicals. With compelling evidence that the synthetic odorant blend attracted BMSBs in olfactometers and that mineral oil could serve as a dissemination medium (Fig. 6), we proceeded testing the synthetic blend in field settings. Surprisingly, the synthetic blend on its own as a trap lure did not attract BMSBs, but it significantly enhanced the attractiveness of synthetic BMSB pheromone, particularly in spring (Fig. 7).

Failure of the synthetic odor lure on its own to attract BMSBs in field settings was likely due to the absence of plant visual cues and the presence of competing live host plants with complex semiochemical and visual cues. That both visual and olfactory plant cues guide foraging herbivores has been demonstrated in diverse insect taxa, including apple maggot flies (Epsky and Heath 1998; Morrison et al. 2016a), cabbage moths (Rojas and Wyatt 1999), and woodboring insects (Campbell and Borden 2009).

Our finding that a combined lure of BMSB pheromone and sunflower semiochemicals attracted more BMSBs than pheromone alone (Fig. 7) implies that BMSBs commonly communicate while residing on host plants. The many examples of plant odorants and aggregation or sex pheromones additively or synergistically attracting foraging insects include *Rhynchophorus* palm weevils (Gries et al. 1994), bark beetles (Deglow and Borden 1998) and fruit flies (Foster and Harris 1997).

The effectiveness of the combined BMSB pheromone and sunflower semiochemical lure was most evident in spring (Fig. 7) but became less apparent towards the fall when BMSBs begin to shift from plant foraging to hibernation mode, likely induced by a shortening photophase (Fig. 6, Exps. 16, 17). The attractiveness of this “combination lure” in spring could potentially be exploited for BMSB monitoring and management. For example, effectively attracting BMSBs in spring to (plant) surfaces treated with contact insecticide would help prevent population build-up and thus curtail crop damage throughout the growing season. Such a tactic, however, would become economically more viable if the currently complex sunflower semiochemical blend (Table 1) could be reduced to a few essential constituents without diminishing its attractiveness to BMSBs. Future research will determine whether the goal of developing a simple and effective sunflower semiochemical lure is attainable.

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