Herbivore-induced volatile emissions are altered by soil legacy effects in cereal cropping systems

Shealyn C. Malone · David K. Weaver · Tim F. Seipel · Fabian D. Menalled · Megan L. Hofland · Justin B. Runyon · Amy M. Trowbridge

Abstract

Aims (main purpose and research question) Soil properties, including microbial composition and nutrient availability, can influence the emissions of plant volatile organic compounds (VOCs) that serve as host-location cues for insect pests and their natural enemies. Agricultural practices have profound effects on soil properties, but how these influence crop VOCs remains largely unknown. The aim of this study was to investigate the effect of agricultural practices on constitutive and herbivore-induced VOC emissions by a major staple crop through soil legacy effects.

Methods In a full factorial experiment, we measured VOC emissions by wheat (*Triticum aestivum*) grown in soil inoculum from wheat-fallow or wheat-cover crop rotations that was subjected to feeding by larval *Cephus cinctus*.

Results (main findings) Under herbivory, plants grown in cover crop inoculum emitted greater total VOCs, including higher concentrations of 2-pentadecanone, an insect repellent, and nonanal, a compound important in the recruitment of natural enemies. Plants grown in fallow inoculum showed no differences in emissions whether under herbivory or not. Soil inoculum did not influence VOC emissions of plants in the absence of larval feeding.

Conclusions These results suggest that agricultural practices influence crop VOC emissions through soil legacy effects. Additionally, crops grown in wheat-fallow rotations may be less successful recruiting natural enemies of pests through herbivore-induced VOC signaling.

Abbreviations Volatile organic compounds (VOCs); herbivore-induced plant volatiles (HIPV); green leaf volatiles (GLVs); northern Great Plains (NGP); wheat stem sawfly (WSS); gas chromatography-mass spectrometry (GC-MS); non-metric multidimensional scaling (NMDS); generalized linear mixed-effects model (GLMM).

Keywords Crop rotations · Plant-soil feedbacks · Indirect defense · *Triticum aestivum* · *Cephus cinctus* · Pest management

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Abbreviations

VOCs	Volatile organic compounds
HIPV	herbivore-induced plant volatiles
GLVs	green leaf volatiles
NGP	northern Great Plains

WSS   wheat stem sawfly
GC-MS   gas chromatography-mass spectrometry
NMDS   non-metric multidimensional scaling
GLMM   generalized linear mixed-effects model

Introduction

Plant volatile organic compounds (VOCs) have multiple ecological roles including attracting pollinators, acting as cues for foraging herbivores, and functioning as direct and indirect defense against herbivores (Dudareva et al. 2013; Heil 2014; Heil and Karban 2010; Parachnowitsch and Manson 2015). Given their central role in mediating plant-insect interactions, it is no surprise that many forms of pest management employ plant VOCs to influence the behavior of pests and their natural enemies (Pickett and Khan 2016; Shrivastava et al. 2010). For example, trap crops, or unharvested crops planted around the protected field, emit attractive VOCs that 'intercept' pests before they damage the cash crop (Adler and Hazzard 2009; Buteler et al. 2010; Morrill et al. 2001). Intercropping, the simultaneous cultivation of multiple plant species, can lower pest pressure by masking volatile cues necessary for pests to locate appropriate hosts (Lopes et al. 2016). Additionally, specific crop varieties are known to differ in constitutive, or always present VOC emissions, making them less attractive to pests compared to other varieties of the same crop species (Buteler and Weaver 2012; Weaver et al. 2009). Crop varieties may also vary in VOCs emitted upon herbivore attack, also known as herbivore-induced plant volatiles (HIPVs), influencing their ability to recruit natural enemies (Kappers et al. 2011; Rasmann et al. 2005). Exciting evidence suggests that pest management utilizing plant volatiles can be applied to existing farming practices through the concept of plant-soil feedbacks (Kaplan et al. 2018; Mutyambai et al. 2019).

Plant-soil feedbacks occur when plants alter soil properties, which in turn, influence subsequent plant growth and performance (Bever 1994; Kulmanski et al. 2008; Wardle et al. 2004). While plant-soil feedbacks can influence soil nutrients, chemistry, moisture, physical structure, and macrofauna, many of these feedbacks are mediated by microbes in the soil (Putten et al. 2013; Wang et al. 2019). Through their root exudates, plants recruit and inhibit different bacteria and fungi,

shaping distinct microbiomes (Babin et al. 2019; Frasier et al. 2016) that ultimately influence the growth and performance of plants grown subsequently in the same soil. As such, plant-soil feedbacks are inherent features of existing agricultural practices, in particular, the use of cover crops in crop rotations (Mariotte et al. 2018; Vukicevich et al. 2016).

Unlike cash crops which are planted for harvest, cover crops are traditionally planted to manage soil erosion, fertility, and water, and to abate weeds, pests, and diseases (Fageria et al. 2005). However, cover crops may provide additional modes of pest management to the subsequent crop through their impact on the soil (Kaplan et al. 2018). Compared to fallow practices, cover crops, and the way in which they are managed, cause significant shifts in soil properties, including increased microbial abundance, activity, and diversity (Kim et al. 2020; Lupwayi et al. 1998), improved soil structure (Fageria et al. 2005), and increased nutrient availability (Blanco-Canqui et al. 2013; Fageria et al. 2005). Diversified management of cover crops, such as cover crop termination via grazing, is also likely to increase nutrient availability and soil microbe diversity through nutrient-rich manure inputs by grazers (Hartmann et al. 2015; Navarro-Noya et al. 2013). Therefore, cover crops and management practices have the potential to differentially influence the performance of the subsequent cash crop through plant-soil feedbacks, particularly when compared to traditional fallow rotations (Kaplan et al. 2018; Pineda et al. 2017).

While it has long been recognized that cover crops may decrease negative plant-soil feedbacks (i.e. 'soil sicknesses'), recent work has focused on using cover crops to promote beneficial plant-soil feedbacks that improve the pest resistance of plants (Huang et al. 2013; Kaplan et al. 2018; Pineda et al. 2017). Specifically, cover crops may improve nutrient availability for the cash crop or increase the presence of beneficial soil microbes that can prime cash crop defense pathways (Gouinguené and Turlings 2002; Sharifi et al. 2018). Indeed, such beneficial effects have been demonstrated in various agricultural systems. For example, organically managed soils (Blundell et al. 2020) and the use of mycorrhizal-associated cover crops (Murrell et al. 2019) have been shown to reduce plant attractiveness to pests through increased foliar chemical defense. While these and other studies demonstrate that agricultural soils can influence plant-insect interactions through changes to foliar chemistry (Carrillo et al. 2019; Ingerslew and

Kaplan 2018), how they may alter constitutive and herbivore-induced VOC emissions is largely unknown.

Here, we evaluate how soil legacy effects, driven by plant-soil feedbacks and management practices in contrasting agricultural practices, alter constitutive and herbivore-induced VOC emissions by wheat (*Triticum aestivum* L.), a major crop of the northern Great Plains (NGP; Fig. 1). Wheat grown in the NGP faces intense pest pressure from the wheat stem sawfly (WSS; *Cephus cinctus* Norton), a stem-mining pest that causes $350 million dollars of lost revenue annually in North America (Beres et al. 2011). Females use volatile cues to locate appropriate plant hosts where they oviposit eggs into the stems of wheat and other grasses (Buteler and Weaver 2012; Piesik et al. 2008; Weaver et al. 2009). Upon hatching, the developing larvae mine and feed upon the parenchyma of the stem throughout the growing season, which impairs photosynthesis and movement of assimilate to the developing seed head (Delaney et al. 2010; Macedo et al. 2007). Destructive feeding increases via larval boring through stem nodes over the growing season resulting in reduced grain quality, protein content, and grain yield (Ainslie 1929; Morrill and Kushnak 1996). Like many plants that elicit herbivore-induced defense mechanisms, wheat infested with larvae generally emit altered VOCs (Peck 2004; Pérez 2009; but see Piesik et al., 2009), some of which are used as host location cues by braconid parasitoids, natural enemies of the WSS (Pérez 2009). Braconid parasitoids can effectively reduce WSS populations and lower yield loss by providing high irreplaceable larval mortality (Buteler et al. 2015; Buteler et al. 2008; Peterson et al. 2011); however, this is contingent upon adequate parasitoid abundance which can have significant spatial and management-driven variability (Peterson et al. 2011; Runyon et al. 2002; Weaver et al. 2004). Thus, agricultural practices have the potential to improve the biological control of WSS through improved VOC signaling and subsequent parasitoid recruitment.

Understanding the potential of cover crop rotations to influence crop VOCs will help inform whether agricultural practices might be leveraged to enhance pest-resistance in crops. In this study, we assess the influence of the cropping system and subsequent herbivory on the chemical plasticity of wheat VOC emissions in a full factorial greenhouse experiment. Wheat plants were grown in sterilized soil mixed with live soil inoculum from established rotations: (1) wheat-

fallow or (2) wheat-cover crop rotations terminated by grazing cattle to represent low and high diversity cropping systems, respectively. To observe the effect of crop rotation on constitutive and induced volatiles of wheat, we measured VOCs emitted by WSS-infested and uninfested wheat plants grown in soil from the two different cropping systems. We hypothesized that (1) larval feeding would increase VOC emissions by wheat relative to constitutive VOCs. Furthermore, given that more diverse cropping systems increase the potential for beneficial soil legacy effects, including the priming of defenses through beneficial plant-microbe associations and increased nutrient availability, we hypothesized that (2) wheat grown in cover crop inoculum would produce greater amounts of constitutive and induced VOCs compared to wheat grown in fallow inoculum.

Materials and methods

Soil collection

Soil was collected from the Northern Agriculture Research Center located south of Havre, MT (48°29'48.8"N, 109°48'10.4"W). The site is a water-limited agroecosystem of the Northern Great Plains (NGP) with an average annual precipitation of 305 mm. Average annual high and low temperatures at the site are 13.6 and 0.0 °C, respectively (Western Regional Climate Center 2020). Since 2012, two replicate fields (40 m x 360 m, each) have been planted in an alternating rotation of winter wheat (*Triticum aestivum* L., Judee variety) with either cover crop mixtures or fallow (Fig. 1). Within each field, each treatment is randomly repeated in 3 separate plots (8 m x 14 m). The location of each treatment was randomized in 2012 and has been maintained through time.

This study used inoculums of soil collected from low and high diversity cropping systems: (1) winter wheat rotated with fallow and (2) winter wheat rotated with a 7-species mixture of cover crops that was terminated by grazing cattle. Hereafter, soil from these cropping systems will be referred to as 'fallow inoculum' and 'cover crop inoculum', respectively. The cover crop mixture consisted of radish (*Raphanus raphanistrum* L.), lentil (*Lens culinaris* Medikus), field pea (*Pisum sativum* L.), oat (*Avena sativa* L.), turnip (*Brassica rapa* L.), sorghum x sudan grass (*Sorghum drummondii* Nees ex.
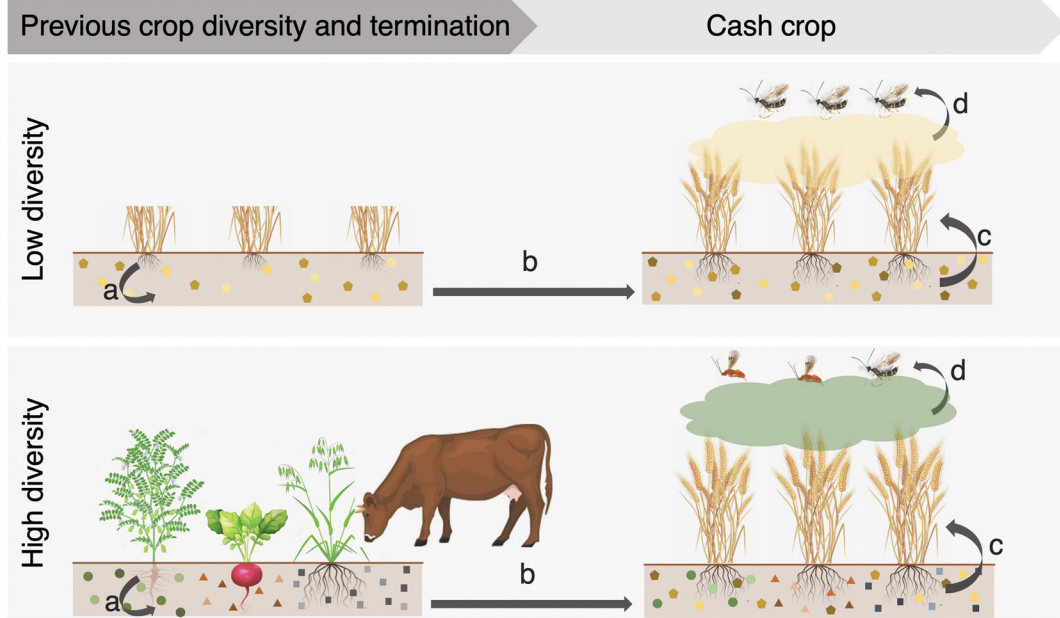
Fig. 1 Experimental framework and overarching hypothesis. Crop rotations have the potential to modify crop-pest interactions through their soil legacy effects. (**a**) High diversity rotations influence soil properties, such as microbial abundance and nutrient availability, differentially than low diversity rotations. (**b**) Soil properties persist into the next growing season where they (**c**) interact with subsequent crops, potentially modifying VOC emissions. (**d**) Altered VOCs may differentially attract pests and their natural enemies, conferring different levels of pest resistance of crops

Steud.), and soybean (*Glycine max* L.). Species were selected based on USDA-ARS recommendations for the NGP and represent a range of functional groups with potential for the provision of various ecosystem services (https://www.ars.usda.gov/plains-area/mandan-nd/ngprl/docs/cover-crop-chart/). Cover crop plots were planted mid-May and terminated early-July to protect soil moisture, as practiced in the region (O'Dea et al. 2013). Termination of cover crops was achieved by targeted cattle grazing, an ecologically based management approach to enhance economic and environmental sustainability of growing cover crops (McKenzie et al. 2017; Thiessen Martens and Entz 2011). Both cropping systems were spot treated with glyphosate to manage rare postharvest weeds during July and September.

Soil collection occurred on 2018 July 4 immediately before cattle grazing to attain peak season microbe diversity (Ishaq et al. 2017). We collected soil that would be planted in wheat later that fall; thus, soil was collected from plots that were either planted in cover crops or laid fallow, depending on the rotation. Surface litter was cleared and approximately 2,000 g of soil was collected to a depth of 30 cm with a sterilized shovel at three random locations within each plot. Bags of soil were stored on ice and transported back to Montana State University (Bozeman, MT) where all samples of a single soil type were homogenized and stored at -18 °C until later use in the greenhouse.

Plant growth

Wheat seeds of the commonly grown spring wheat cultivar Reeder were collected from a single spike grown in Big Sandy, MT during fall of 2018 and grown to maturity in the Montana State University Plant Growth Center. We used these genetically identical seeds to control for chemotypic variation between plants (Gouinguené et al. 2001). Mature seeds were surface-sterilized in 5% bleach, rinsed twice with deionized water, allowed to dry completely, and stored at -18 °C until planting. Upon planting, seeds were sown in washed and sterilized conical pots in a 1:1 mix of autoclaved Sunshine Mix #1 soil (Gro Horticulture Inc., Bellevue, WA) and MSU soil with a 15%-by-mass inoculum of live field soil. Previous studies conducted in agroecosystems have shown that a small amount of inoculum allows the evaluation of the impact of biologically mediated plant-soil feedbacks on ecosystem

processes (Brinkman et al. 2010; Menalled et al. 2020; Seipel et al. 2019). Sunshine Mix #1 soil is comprised of Canadian sphagnum peat moss, perlite, vermiculite, starter nutrient charge, wetting agent, and dolomitic lime. MSU soil is equal parts of Bozeman silt loam soil, washed concrete sand, and Canadian sphagnum peat moss. AquaGro 2000 g wetting agent (Aquatrols, Paulsboro, NJ) was blended in at one pound per cubic yard of soil mix and aerated steam pasteurized at 80 °C for 45 min.

To minimize any effect of variation in plant development stage on infestation and VOC emissions, we planted one cohort of plants each week from late March 2019 to early May 2019. During each planting, 600 g of soil inoculum were homogenized in 3400 g of sterilized soil and divided equally between 30 conical pots (17.8 cm height x 6.9 cm diameter; Stuewe & Sons, Tangent, OR). This was repeated for the second soil type, always sterilizing equipment in between each treatment with 70% isopropyl alcohol.

Plants were fertilized biweekly with 60 ml of 20-20-20 (N-P-K, 50 ppm) fertilizer (Peters General Purpose Fertilizer, Allentown, PA) starting 3 weeks after planting. We fertilized at a 50% rate of 50 ppm compared to the standard rate of 100 ppm to preserve the functional diversity inherent in the field inoculum while also ensuring plants received nutrients necessary for development. While fertilizers are known to affect microbial community structure and biomass (Donnison et al. 2000; Sarathchandra et al. 2001), low fertilizer rates have been shown to preserve the functional diversity of soil microbial communities (Marschner et al. 2003). The position of plants was randomized to control for environmental variations along the greenhouse bench. Plants were watered *ad libitum* and grown in a greenhouse with supplemental light (GE Multi-Vapor MVR1000/C/U, GE Lighting, Cleveland, OH) under a 15 L:9 D photoperiod. Mean daytime temperatures were 22 °C and mean night temperatures were 20 °C ($\pm$ 1.5°C).

Wheat stem sawfly (WSS) collection and infestation

WSS larvae were collected from naturally occurring populations near Amsterdam-Churchill, MT (45°45'26.8"N 111°24'13.4"W). Wheat stubs—in which larvae diapause—were collected from heavily infested fields in the fall of 2018 and spring of 2019. Stubs were stored in plastic Ziplock bags at 0 °C for a

minimum of 100 days to facilitate completion of larval diapause. Approximately three weeks prior to infestation, stubs were transferred to perforated plastic containers where adults were held at room temperature (22–27 °C) until adult emergence began. WSS adults are sexually mature and females do not require copulation to oviposit (Holmes 1977), thus, newly emerged adults could be used immediately to infest plants. To ensure newly emerged females were used, we removed all adults from the plastic container every 24 h. These adults were immediately used for infestation and any surplus adults were stored in Mason glass jars at 2 °C for up to two days for later use before they were discarded.

We exposed plants to adult WSS at stem elongation (Zadoks growth stages 32–34; Zadoks et al. 1974) when wheat is first susceptible to infestation under field conditions (Buteler et al. 2010; Weaver et al. 2009). Individual transparent polycarbonate cylindrical cages (60–65 cm x 3.8 cm) were placed over each plant to be infested. The top of the cage was covered in cloth-mesh and sterilized soil was placed around the bottom of the cage to prevent adults from escaping. Each cage had three cloth-mesh covered holes (3.8 cm diameter) distributed along its length for air circulation, and an additional 1 cm diameter hole, plugged with removable cotton cloth through which adults were introduced. One male and three female adults were added to each cage for a three-day oviposition period. Cages were also placed over control plants, but no adults were added. After infestation, the cages and adults were removed.

Volatile organic compound (VOC) collections

Volatiles were collected immediately after anthesis and the onset of milk development (Zadoks growth stage 71), which was approximately 21 days post-infestation. The sampling system allowed collection of VOCs from 12 plants each day. As such, on each sample day we collected VOCs from 12 individual plants: six plants grown in each soil inoculum, four of which had been exposed to adults and two of which had not. We chose to expose more than half of the plants because infestation is variable and cryptic, and this ensured we had an adequate number of infested plants for analysis. We collected VOCs two to four times a week from a total of 238 plants. We sampled from late May through early July, always infesting plants 19–22 days before VOC sampling.

For each VOC collection, plants were placed in 1 L glass collection chambers in a volatile collection system (VCS, Analytical Research Systems, Inc., Gainesville, FL) as previously described by Piesik et al. (2006). The apparatus features 12 glass chambers attached to a volatile collection port on one end and open on the other end to enclose one individual plant per chamber. Chambers were placed atop Teflon guillotine stands, which separated plant roots and potting soil from the collection chamber. Gaps between the plant stem and Teflon guillotines were filled with cotton to prevent soil VOCs from entering the collection chamber. Purified, humidified air was delivered at a rate of 1.0 L min^{-1} over the plants and the flow and pressure were maintained by a regulated vacuum pump. Two volatile collector traps—one purge trap and one sample trap—containing 30 mg of HayeSep Q solid-phase adsorbent (Sigma Scientific, Gainesville, FL) were inserted into each volatile collection port. In order to clear ambient air from the chamber, air was initially collected on purge traps for 10 min before switching to the sample traps. Both the purge and the sample traps were set to a flow rate of 1.0 L min^{-1}. We collected volatiles on the sample traps for 8 h from approximately 9:00 to 17:00 each day. After sampling, volatile collection traps were removed, wrapped in aluminum foil, and eluted within 24 h (see below).

To account for the effects of environmental variables on VOC emissions, Thermochron temperature sensors (Maxim Integrated, San Jose, CA) were placed in each chamber and set to measure temperature every five minutes. Photosynthetically active radiation (PAR), measured every hour, was acquired from the local university weather station. Both temperature data (over the 8 h sampling period) and PAR data (from start of day until the end of the sampling period) were averaged to yield a cumulative value for each of the variables per sampling day. To normalize emissions for comparison, we used these cumulative values to calculate basal emission volatile rates standardized to 30 °C according to Guenther (1997).

After VOC collections, plants were cut at the base of the stem to determine aboveground biomass. To determine whether plants were infested, stems were split along their length with a scalpel. Plants were considered infested when one or more larvae (alive or dead) and/or frass were observed in any stem of the plant. For all infested plants, larvae were always present in the main stem, and of these plants only 3% had larvae present in additional tillers. Therefore, we focused on infestation occurring in the main stem. For each infested main stem, we measured the proportion of stem bored (length of stem bored / total length of stem), proportion of internodes bored (internodes bored / total internodes), and the total mass of live larvae present. Plants exposed to adults that were not infested were initially characterized as 'exposed' but later aggregated with control plants due to no difference in total volatiles ($F_{1,113.6} = 0.027$, $P = 0.87$).

Analysis and identification of VOCs

We determined the identities and relative amounts of VOCs using gas chromatography-mass spectrometry (GC-MS). Volatile traps were eluted with 200 µl of methylene chloride (Fisher Scientific, Fair Lawn, NJ). 10 µl of a 30 ng µL^{-1} solution of nonyl acetate (Sigma-Aldrich, Saint Louis, MO) in methylene chloride was added as an internal standard following elution and samples were stored at -70 °C until analysis. For chemical analysis, 3 µl of each sample was injected onto an Agilent Technologies 6890 GC-5973 MS fitted with an HP-5MS column (30 m x 0.25 mm, 0.25 µm film thickness; J&W Scientific, Folsom, CA). Helium was used as the carrier gas at a flow rate of 1.2 mL min^{-1} and injector temperature was set to 250 °C. The oven profile consisted of an initial temperature of 50 °C followed by a ramp of 5 °C min^{-1} to 200 °C, then a second ramp of 25 °C min^{-1} to 280 °C. Volatile compounds were identified by comparing retention times and mass spectra with commercial standards using ChemStation software (Agilent Technologies, Wilmington, DE) and the NIST Mass Spectral Library (National Institute of Standards and Technology, Gaithersburg, MD). All standards were purchased from Sigma Aldrich (Saint Louis, MO) with the exception of decanal and β-ocimene (The Good Scents Company, Oak Creek, WI). When we could not identify compounds with commercial standards, we used the mass spectra to determine the compound family (i.e. monoterpene, alkane, etc.) (Table 1). We quantified the relative concentrations of each compound by comparing its peak area with that of the internal standard, nonyl acetate, in order to determine nonyl acetate equivalents. Concentrations of volatile compounds were standardized for the number of hours for which they were collected and for aboveground plant biomass (ng g^{-1} h^{-1}). In total, we collected the VOC emissions of 238 plants. For seven of these, we could not accurately determine peak areas and they were

omitted from our analysis. Thus, we quantified the relative VOC emissions for 231 plants ($n_{Fallow/Uninfested}$ = 66, $n_{Fallow/Infested}$ = 51, $n_{Cover/Uninfested}$ = 68, $n_{Cover/Infested}$ = 46).

Data analysis

We performed all analyses in R version 3.5.2 (R Core Team, 2018). Raw emission rates were converted to basal emission rates standardized to 30 °C using cumulative temperature and PAR from each volatile collection (Guenther 1997). We assessed the relative (nonyl acetate equivalent) emissions of individual compounds and their sum, hereafter called 'total VOCs'. Given the relative quantification of all compounds to a single internal standard, the reported emission rates are not absolute values and results are discussed as relative differences in VOC emissions among treatments. To compare the effects of soil inoculum and infestation on induced VOC emissions, we fit linear mixed models using the 'lmer' function in the 'lm4' package (Bates et al. 2015). Measures of individual or total VOCs were the dependent variables and soil inoculum, infestation, and their interactions were fixed effects. Sample day was used as a random effect to account for day-to-day variability in other unmeasured environmental factors from each trial. All response variables were transformed as needed to meet the assumption of normality and homoskedasticity. To assess if cropping system, infestation, and their interaction accounted for variation, we performed Type III ANOVA using the 'anova' function in the 'lmerTest' package (Kuznetsova et al. 2017). When our fixed effects accounted for variation, we compared post-hoc differences using pairwise Tukey comparisons with the 'emmeans' function (Lenth et al. 2020).

We evaluated differences in the volatile community composition among soil inoculum, infestation, and their interaction using permutational multivariate ANOVA (PERMANOVA; Anderson et al. 2017; Oksanen et al. 2019). To do so, we calculated dissimilarities among treatments using the Bray-Curtis metric with the 'vegdist' function in the 'vegan' package (Oksanen et al. 2019).

To evaluate the probability of infestation by soil inoculum for plants exposed to adults, we used a generalized linear mixed-effects model (GLMM) with soil inoculum as the fixed effect, sample day as the random effect, and infestation as the response variable. To do

this, we calculated the mean odds of plant infestation when exposed to adults using the 'glmer' function in the 'lme4' package using a binomial error distribution (Bates et al. 2015). Plant biomass was modeled using a linear mixed model using the 'lmer' function in the 'lm4' package with soil, infestation, and their interaction as fixed effects and sample day as a random effect (Bates et al. 2015). We used Pearson's correlation test to assess the influence of soil type on the proportion of stem length bored, proportion of internodes bored, and total live larval mass.

Results

A total of 26 volatile compounds were quantified using GC-MS analysis from the headspace of wheat plants. Volatile compounds quantified include five monoterpenes, two sesquiterpenes, nine alkanes, five ketones, three aldehydes, one green leaf volatile (GLV), and one irregular terpene (Table 1). Plants grown in different soil inoculums emitted the same 26 compounds but in different relative amounts. The overall VOC composition varied in response to the interaction of soil inoculum and larval feeding (PERMANOVA Infestation x Soil: $F_{1, 104}$ = 2.91, P = 0.034), though it only explained a small amount of variation among treatments (R^2 = 0.03). Total relative VOC emissions also varied in response to the interaction of soil and feeding (Fig. 2; Soil x Infestation: $F_{1, 211.8}$ = 5.78, P = 0.017), and sample day explained a significant amount of the overall variation (variance explained by fixed effects, R_m^2 = 0.03; variance explained by entire model, R_c^2 = 0.33).

Constitutively, soil inoculum did not influence VOC emissions (t_{210} = 0.62, P = 0.926) and regardless of soil inoculum, plants emitted an average of 13.53 ng gFW^{-1} h^{-1} total constitutive VOCs (95% CI: 11.04 to 16.60 ng gFW^{-1} h^{-1}). We found that in the absence of feeding injury plants did not differ in their emissions of individual volatile compounds (Table 1). We observed no effect of soil inoculum on the probability of infestation for plants exposed to ovipositing females (F_1 = 0.53, P = 0.469). Infestation rates were 65% (95% CI: 54–75%) for wheat grown in fallow inoculum and 60% (95% CI: 48–70%) for wheat grown in cover crop inoculum.

Induced VOC emissions caused by larval feeding varied among soil inoculum. VOC emissions did not

Table 1 Constitutive and induced mean emission rates (ng nonyl acetate equivalents $gFW^{-1} h^{-1}$) and 95% CI (enclosed in brackets) of total compounds, families of compounds, and individual compounds, in response to larval feeding by soil treatment

Compound	ID[1]	Fallow		Cover	
		− WSS	+ WSS	− WSS	+ WSS
Total		13.92[a] (11.35, 17.09)	12.55[a] (10.09, 15.60)	13.14[ab] (10.72, 16.10)	16.85[b] (13.49, 21.06)
Monoterpenes		1.02[a] (0.83, 1.26)	1.02[a] (0.82, 1.28)	1.11[a] (0.90, 1.37)	1.22[a] (0.98, 1.53)
β-pinene	SS	0.15[a] (0.12, 0.19)	0.16[a] (0.12, 0.19)	0.17[a] (0.14, 0.20)	0.19[a] (0.15, 0.23)
Limonene	SS	0.18[a] (0.14, 0.22)	0.15[a] (0.11, 0.19)	0.15[a] (0.11, 0.19)	0.18[a] (0.14, 0.23)
β-ocimene	SS	0.31[a] (0.23, 0.40)	0.34[a] (0.25, 0.45)	0.41[a] (0.31, 0.52)	0.37[a] (0.27, 0.48)
linalool	SS	0.21[a] (0.17, 0.26)	0.19[a] (0.16, 0.24)	0.22[a] (0.18, 0.28)	0.25[a] (0.20, 0.31)
MT1[2]	NIST	0.15[a] (0.10, 0.20)	0.16[a] (0.11, 0.22)	0.17[a] (0.12, 0.23)	0.21[a] (0.15, 0.28)
Sesquiterpenes		1.62[a] (1.18, 2.22)	1.46[a] (1.05, 2.02)	1.70[a] (1.24, 2.32)	1.90[a] (1.36, 2.65)
ST1[3]	NIST	0.40[a] (0.24, 0.62)	0.37[a] (0.21, 0.59)	0.33[a] (0.18, 0.53)	0.43[a] (0.24, 0.66)
ST2[3]	NIST	0.10[a] (0.07, 0.14)	0.09[a] (0.06, 0.13)	0.09[a] (0.06, 0.13)	0.13[a] (0.09, 0.18)
Alkanes		1.72[a] (1.43, 2.08)	1.63[a] (1.33, 1.98)	1.98[ab] (1.64, 2.39)	2.20[b] (1.79, 2.69)
ALK1[4]	NIST	0.10[a] (0.08, 0.12)	0.11[a] (0.08, 0.13)	0.12[a] (0.10, 0.15)	0.12[a] (0.10, 0.15)
ALK2[4]	NIST	0.11[a] (0.09, 0.14)	0.11[a] (0.09, 0.14)	0.13[ab] (0.10, 0.16)	0.15[b] (0.12, 0.18)
ALK3[4]	NIST	0.39[a] (0.33, 0.47)	0.39[a] (0.32, 0.47)	0.47[ab] (0.39, 0.57)	0.51[b] (0.42, 0.62)
ALK4[4]	NIST	0.12[a] (0.10, 0.16)	0.13[a] (0.10, 0.17)	0.15[a] (0.12, 0.19)	0.16[a] (0.13, 0.20)
ALK5[4]	NIST	0.12[a] (0.08, 0.16)	0.11[a] (0.08, 0.16)	0.14[a] (0.10, 0.18)	0.14[a] (0.10, 0.19)
Tridecane	SS	0.29[a] (0.24, 0.35)	0.29[a] (0.24, 0.35)	0.36[ab] (0.30, 0.43)	0.40[b] (0.33, 0.49)
ALK6[4]	NIST	0.50[a] (0.41, 0.60)	0.47[a] (0.38, 0.57)	0.58[a] (0.48, 0.68)	0.58[a] (0.47, 0.69)
Tetradecane	SS	0.25[a] (0.21, 0.31)	0.24[a] (0.19, 0.29)	0.29[ab] (0.23, 0.35)	0.31[b] (0.25, 0.39)
ALK7[4]	NIST	0.27[a] (0.20, 0.36)	0.25[a] (0.17, 0.34)	0.29[a] (0.21, 0.37)	0.38[a] (0.28, 0.50)
Ketones		6.69[a] (5.18, 8.63)	6.20[a] (4.69, 8.21)	6.07[a] (4.80, 7.67)	8.30[a] (6.29, 10.95)
6-methyl-5-heptene-2-one	SS	0.13[a] (0.10, 0.16)	0.12[a] (0.09, 0.16)	0.12[a] (0.09, 0.16)	0.14[a] (0.10, 0.18)
2-undecanone	SS	0.52[a] (0.38, 0.67)	0.43[a] (0.30, 0.58)	0.41[a] (0.29, 0.55)	0.59[a] (0.43, 0.78)

Table 1 (continued)

Compound	ID[1]	Fallow		Cover	
		− WSS	+ WSS	− WSS	+ WSS
2-tridecanone	SS	2.58[a] (1.95, 3.41)	2.32[a] (1.72, 3.13)	2.16[a] (1.64, 2.86)	3.13[a] (2.30, 4.26)
2-pentadecanone	SS	1.00[a] (0.75, 1.27)	0.83[a] (0.59, 1.11)	0.85[a] (0.63, 1.11)	1.28[b] (0.97, 1.64)
Hexahydrofarnesyl acetone	SS	2.63[a] (1.83, 3.58)	2.50[a] (1.67, 3.50)	2.37[a] (1.61, 3.26)	3.21[a] (2.23, 4.35)
Aldehydes		1.11[a] (0.85, 1.44)	1.12[a] (0.84, 1.47)	1.06[a] (0.81, 1.38)	1.34[a] (1.01, 1.77)
Nonanal	SS	0.66[a] (0.51, 0.87)	0.71[ab] (0.54, 0.95)	0.63[a] (0.48, 0.83)	0.85[b] (0.64, 1.13)
Decanal	SS	0.44[a] (0.34, 0.57)	0.40[a] (0.30, 0.52)	0.42[a] (0.33, 0.54)	0.48[a] (0.37, 0.63)
Green leaf volatiles (GLV)		0.21[a] (0.14, 0.31)	0.21[a] (0.14, 0.32)	0.21[a] (0.14, 0.31)	0.23[a] (0.15, 0.35)
Z-3-hexenyl acetate	SS	0.21[a] (0.14, 0.31)	0.21[a] (0.14, 0.32)	0.21[a] (0.14, 0.31)	0.23[a] (0.15, 0.35)
Irregular terpenes		0.10[a] (0.07, 0.14)	0.09[a] (0.06, 0.13)	0.09[a] (0.06, 0.13)	0.13[a] (0.09, 0.18)
Geranyl acetone	SS	0.10[a] (0.07, 0.14)	0.09[a] (0.06, 0.13)	0.09[a] (0.06, 0.13)	0.13[a] (0.09, 0.18)

Differences in lower case letters represent significant differences in emissions between treatments ($\alpha < 0.05$)

[1] Identification (ID) of compounds based upon comparison of retention time and mass spectra with synthetic standards (SS) or comparison of mass spectra using NIST Mass Spectral Search Program (NIST)

[2] MT = unidentified monoterpene

[3] ST = unidentified sesquiterpene

[4] ALK = unidentified alkane

vary for plants grown in fallow inoculum after feeding ($t_{213} = 1.01$, $P = 0.744$), and plants emitted the same amounts of total and individual VOCs whether infested with larvae or not (Fig. 2; Table 1). Plants grown in cover crop inoculum, however, emitted 28% more total volatiles (3.17 ng gFW^{-1} h^{-1}) when fed upon by larvae compared to constitutive levels ($t_{212} = -2.38$, $P = 0.084$) and 34% more total volatiles than infested plants grown in fallow inoculum ($t_{211} = -2.66$, $P = 0.041$).

Six of the 26 compounds differed in response to either soil inoculum, larval feeding (infestation), or their interaction. Plants grown in cover crop inoculum emitted 35% more nonanal when infested than when not infested (Fig. 3; $t_{210} = -2.87$, $P = 0.024$). We also observed treatment effects on the emissions of 2-pentadecanone (Fig. 4; Soil x Infestation: $F_{1, 217.0} = 6.44$, $P = 0.012$) and four alkane compounds including unknown alkane 2 (Fig. 5a; Soil: $F_{1, 208.8} = 10.16$, $P = 0.002$), tridecane (Fig. 5b; Soil:

$F_{1, 208.8} = 16.72$, $P < 0.001$), tetradecane (Fig. 5c; Soil: $F_{1, 208.7} = 8.74$, $P = 0.003$), and unknown alkane 3 (Fig. 5d; Soil: $F_{1, 208.8} = 13.94$, $P < 0.001$). Under larval feeding, these compounds were emitted at higher rates from plants grown in cover crop inoculum than those grown in fallow inoculum (Table 1; 2-pentadecanone: $t_{214} = -2.51$, $P = 0.013$; unknown alkane 2: $t_{211} = -2.85$, $P = 0.025$; tridecane: $t_{211} = -3.09$, $P = 0.012$; tetradecane: $t_{211} = -2.68$, $P = 0.039$; unknown alkane 3: $t_{211} = -2.59$, $P = 0.050$). Finally, we found that infested plants grown in cover crop inoculum emitted ∼35% more total alkanes compared to those grown in fallow (Table 1; $t_{211} = -3.06$, $P = 0.013$).

Soil inoculum also influenced plant biomass (Fig. 6; Soil: $F_{1, 209.7} = 3.93$, $P = 0.049$) with a 5.4% mean increase in biomass (0.424 g ± 0.216) for plants grown in cover crop inoculum. While three weeks post-infestation plants only trended towards lower biomass
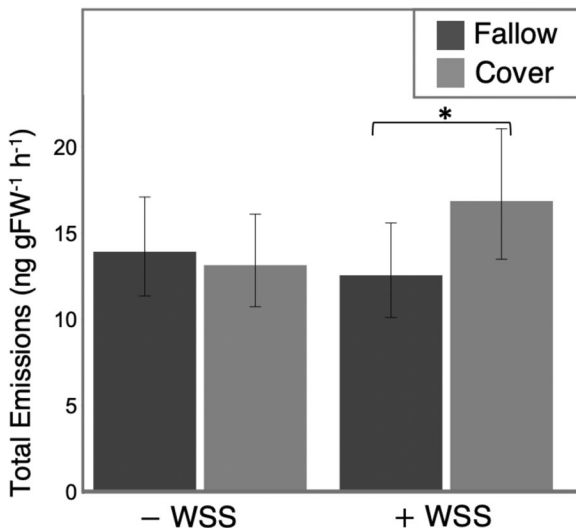
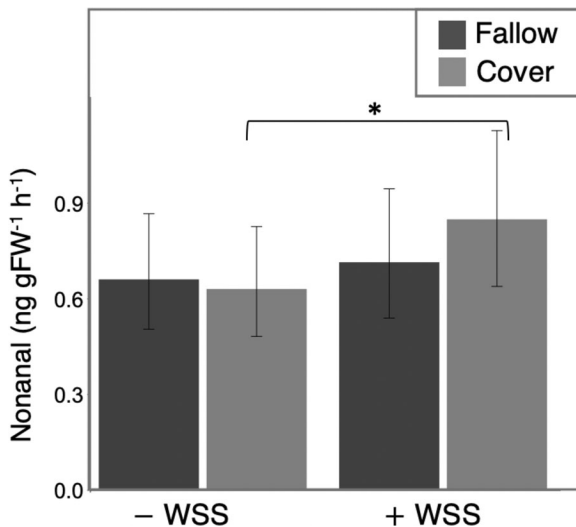**Fig. 2** Total VOC (ng nonyl acetate equivalents $gFW^{-1}\,h^{-1}$) as a function of soil inoculum and larval feeding (Soil x Infestation: $F_{1,\,211.8} = 5.78$, $P = 0.017$). Soil inoculum originated from either a wheat-fallow rotation (Fallow) or wheat-cover crop rotation where the cover crops were terminated by grazing cattle (Cover). Individual wheat plants were infested with wheat stem sawfly larvae (+ WSS) or remained uninfested (-WSS) to assess induced and constitutive VOCs, respectively ($n_{Fallow/Uninfested} = 66$, $n_{Fallow/Infested} = 51$, $n_{Cover/Uninfested} = 68$, $n_{Cover/Infested} = 46$). Means ± SEM are shown. (*) denotes a significance level < 0.05

compared to non-infested plants (Infestation: $F_{1,\,214.1} = 3.20$, $P = 0.075$), it is likely that this trend would have become more prominent had larval feeding progressed further into plant development. The soil inoculum did not influence the proportion of stem bored by larvae ($t_{153} = -0.02$, $P = 0.98$, mean = 0.15), the proportion of internodes bored ($t_{153} = -0.61$, $P = 0.54$, mean = 0.39), or larval weight ($t_{153} = 1.01$, $P = 0.32$, mean = 0.014 g).

Discussion

Despite the important role of the soil physical-chemical and biological characteristics in agroecosystem functioning (Brussaard et al. 2007), we still have limited knowledge of its role in mediating crop-insect interactions through modification of plant VOCs. In this study, we found that inoculation of plants with soil from two different cropping systems did not alter constitutive emissions of VOCs but did influence their emissions following larval feeding. Wheat VOCs from plants grown in fallow inoculum were not induced by WSS larval feeding. In contrast, wheat grown in cover crop inoculum produced more total volatiles in response to


Fig. 3 Emissions (ng nonyl acetate equivalents $gFW^{-1}\,h^{-1}$) of nonanal as a function of soil and larval feeding (Infestation: $F_{1,\,210.2} = 6.65$, $P = 0.011$). Soil inoculum originated from either a wheat-fallow rotation (Fallow) or wheat-cover crop rotation where the cover crops were terminated by grazing cattle (Cover). Individual wheat plants were infested with wheat stem sawfly larvae (+ WSS) or remained uninfested (-WSS). Means ± SEM are shown. (*) denotes a significance level < 0.05
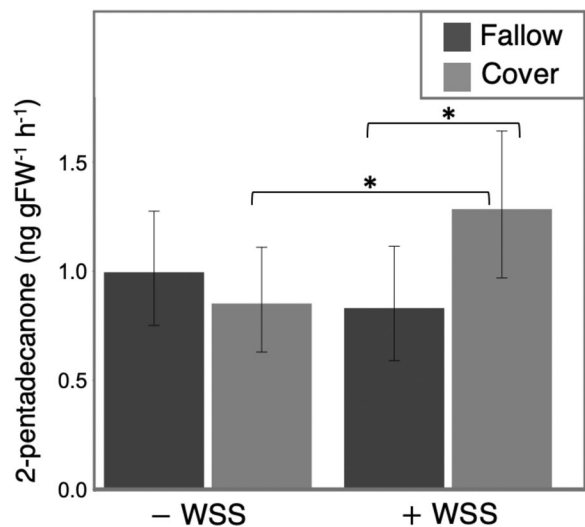
Fig. 4 Emissions (ng nonyl acetate equivalents $gFW^{-1}\,h^{-1}$) of 2-pentadecanone as a function of soil and larval feeding (Soil x Infestation: $F_{1,\,217.0} = 6.44$, $P = 0.012$). Soil inoculum originated from either a wheat-fallow rotation (Fallow) or wheat-cover crop rotation where the cover crops were terminated by grazing cattle (Cover). Individual wheat plants were infested with wheat stem sawfly larvae (+ WSS) or remained uninfested (-WSS). Means ± SEM are shown. (*) denotes a significance level < 0.05

Fig. 5 Emissions (ng nonyl acetate equivalents gFW^{-1} h^{-1}) of unknown alkane 2 (panel a; Soil: $F_{1,\,208.8} = 10.16$, $P = 0.002$), tridecane (panel b; Soil: $F_{1,\,208.8} = 16.72$, $P < 0.001$), tetradecane (panel c; Soil: $F_{1,\,208.7} = 8.74$, $P = 0.003$), and unknown alkane 3 (panel d; Soil: $F_{1,\,208.8} = 13.94$, $P < 0.001$) as a function of soil and larval feeding. Soil inoculum originated from either a wheat-fallow rotation (Fallow) or wheat-cover crop rotation where the cover crops were terminated by grazing cattle (Cover). Individual wheat plants were infested with wheat stem sawfly larvae (+ WSS) or remained uninfested (-WSS). Means ± SEM are shown. (*) denotes a significance level < 0.05
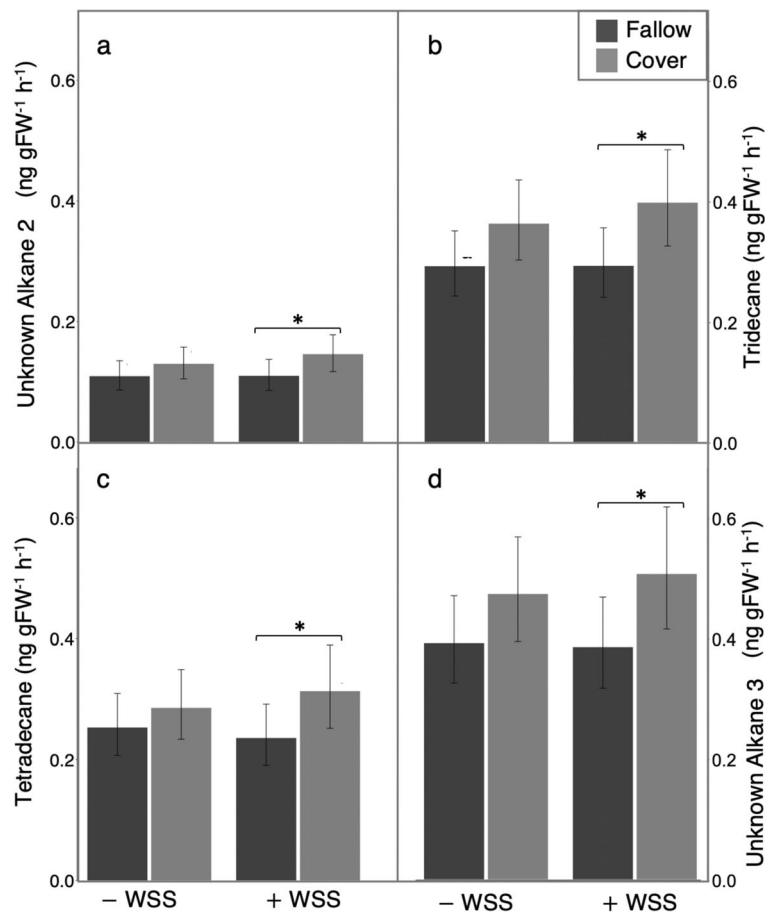
larval feeding, including increased emissions of key compounds known to repel insect pests and attract natural enemies. Our findings indicate that soil from different agricultural practices have the potential to influence pest-resistance of crops through altered HIPVs, leading to enhanced direct defense through repellence of pests and enhanced indirect defense through attraction of their natural enemies.

Contrary to our hypothesis, we found that soil from two different cropping systems had no effect on the quantity or quality of constitutive VOCs emitted by plants. Alternatively, VOC emissions did vary among soil inoculum when plants were infested with larvae. Wheat grown in soil with inoculum from the cover crop rotation exhibited elevated emissions of VOCs in response to infestation while VOCs of wheat grown in soil with inoculum from wheat-fallow rotation were unaffected by herbivory. These results are consistent with a previous study measuring the effect of soil type and herbivory on foliar plant defenses: following insect
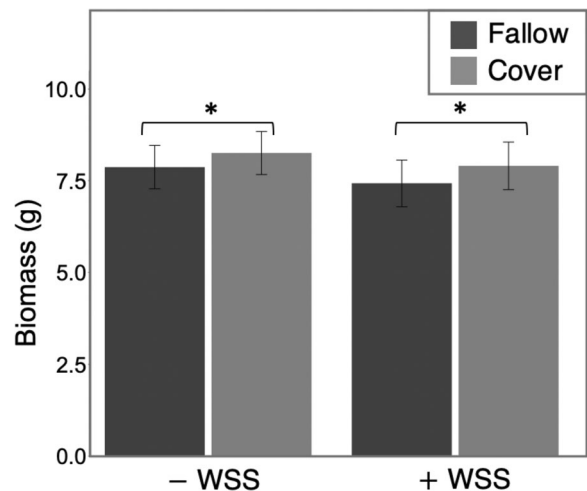
Fig. 6 Plant biomass (g) as a function of soil inoculum and larval feeding (Soil: $F_{1,\,209.7} = 3.93$, $P = 0.049$). Soil inoculum originated from either a wheat-fallow rotation (Fallow) or wheat-cover crop rotation where the cover crops were terminated by grazing cattle (Cover). Individual wheat plants were infested with wheat stem sawfly larvae (+ WSS) or remained uninfested (-WSS). Means ± SEM are shown. (*) denotes a significance level < 0.05

feeding, some soil treatments showed no induced response to herbivory, even at the transcriptional level, whereas other soil treatments showed robust herbivore-induced upregulation of defense-related genes (Zhu et al. 2018). Because many soil legacy effects are mediated by microbes in the soil (Huang et al. 2013; Wang et al. 2019), the patterns we observed may be due to priming mechanisms where microbes present in the cover crop inoculum, but not the fallow inoculum, induced systemic resistance in the plants (Conrath et al. 2006; Pozo and Azcón-Aguilar 2007). Compared to fallow systems, cover crops increase microbe abundance and diversity (Kim et al. 2020), minimizing the accumulation of soil-borne pathogens and leading to proliferation of beneficial microbes in the rhizosphere (Vukicevich et al. 2016). Beneficial microbes, upon colonization of roots, can cause the induction of a unique physiological state within the plant known as "priming". Primed plants display faster and stronger activation of defense pathways following attack by herbivores (Conrath et al. 2006), including altered emissions of VOCs. Indeed, studies have observed microbially-driven differences in VOC emissions that were significant only after herbivore feeding (Pangesti et al. 2015; Pineda et al. 2013), suggesting that soil microbes present in cover crop soils primed plant defenses, altering HIPVs but not constitutive volatiles.

Alternatively, it is possible that the differences in induced VOCs by soil type were due to other soil properties affecting plant vigor, including nutrient availability and the accumulation of autotoxins (Gouinguené and Turlings 2002; Huang et al. 2013). Plants grown in cover crop soils had ~5% greater biomass than those grown in fallow soil. While we tried to minimize any effects of inherent nutrient differences between soil inoculums by fertilizing all plants at a constant rate, it is possible that the soil inoculations altered nutrient availability for plant growth among treatments. Cover crop inoculums having higher nutrient availability than fallow inoculums could be a direct effect of the farming practice (e.g. manure inputs from grazing cattle) or indirect effect (e.g. beneficial plant-microbe interactions that increase plant nutrient acquisition) (Koricheva et al. 2009; Rasmann et al. 2017). Finally, it is possible that other feedback mechanisms, such as accumulation of autotoxic compounds, may have hindered plant growth in fallow soil inoculums. Wheat straw residues—such as those found in fallow fields—are a source of autotoxins, including ferulic and p-coumaric acids. In fallow rotations,

autotoxin may accumulate in the soil and exert negative plant-soil feedbacks on wheat, hindering photosynthesis and overall carbon acquisition (Huang et al. 2013; Lodhi et al. 1987). Thus, the greater inducibility of wheat grown in cover crop plants may be due to greater carbon availability for investment in VOC metabolism upon herbivory, which is ultimately mediated by soil legacy effects that vary between cropping systems.

Biological control of pests offers an effective strategy for managing damaging species without the use of pesticides (Runyon et al. 2002; Rand et al. 2016). Given that natural enemies of herbivores rely on induced volatile cues for effective host-foraging (Arimura et al. 2009; Bruce et al. 2005; De Moraes et al. 1998; Heil 2014), biological control is often dependent on effective volatile signaling by herbivore-attacked crops. While plants commonly alter VOCs in response to herbivory (Heil 2014), lack of induction or modification to VOC blends has been shown to reduce recruitment of natural enemies (Megali et al. 2015; Pineda et al. 2013), which may lead to increased pest abundance. The absence of HIPVs observed in our study by wheat grown in fallow inoculum suggests that these crop rotations may be less effective at recruiting natural enemies for biological control of pests through reduced host-searching efficacy. As such, biological control efforts may be less effective when used in tandem with agricultural practices and crop rotations that diminish the crops' ability to induce indirect VOC defenses.

In addition to increasing emissions of total VOCs, we found that wheat grown in soils from cover crops emitted more nonanal and 2-pentdadecanone when infested by larvae. Nonanal is known to serve as an attractant to natural enemy insects (Yu et al. 2008) but can also have synergistic properties for insect herbivores (Dickens 2006). Nonanal has also been shown be important in plant-plant communication in lima bean (*Phaseolus lunatus*), triggering resistance expression against a bacterial pathogen in uninfected lima bean plants (Yi and Heil 2009), however this role for nonanal has not been demonstrated in cereal crops. 2-pentadecanone has been shown to repel insect herbivores, including a major pest of wheat, the grain aphid (*Sitobion avenae*) (Drakulic et al. 2015; Sun et al. 2016). Clearly, altered emissions of nonanal and 2-pentadecanone has the potential to alter multitrophic plant-insect interactions, and these should be further studied to better understand how cropping systems can influence pest resistance in agroecosystems.

Finally, it is worth noting that HIPVs by wheat grown in cover crop inoculum consisted of significantly more alkane compounds, especially the lower alkane species (C_{11}-C_{13}). Higher alkanes (C_{21}-C_{35}) found in cuticular waxes (Lavergne et al. 2018) are often used by phytophagous insects to determine whether plants are suitable for feeding and laying eggs (Eigenbrode and Espelie, 1995; Müller and Riederer 2005). However, less is known about how lower alkanes are metabolically regulated in plants and their role in mediating plant-insect interactions. Lower alkanes are known to be produced by insects and help to mediate intraspecific insect interactions (Blum et al. 1960; Lenz et al. 2013). Many common insect VOC signals, including a number of lower alkanes, are also produced by plants, suggesting that plants and insects can converge in patterns of volatile production, both for attraction and defense (Schiestl et al. 2014). As such, plants producing greater amounts of lower alkanes may do so to mimic signals displayed by insects; however, while a number of studies report plant emissions of lower alkanes (Kigathi et al. 2009; Pierre et al. 2011), they have not been shown to influence insect behavior (Weissteiner and Schütz, 2006; Pierre et al. 2011). For insects such as the WSS and its braconid parasitoids that employ GLVs, terpenes, and ketones to locate appropriate plant (Piesik et al. 2008; Weaver et al. 2009) and insect hosts (Pérez, 2009), respectively, whether altered alkane emissions are synergistic or antagonistic remains unknown and should be tested with insect bioassays.

This study demonstrates the effect of system-level farming practices, such as the use of cover crops and animal grazing, on plant VOCs. These effects were likely driven by the interaction of multiple soil properties, including soil microbe community, nutrient availability, and chemistry. Unraveling the primary drivers of such system-level responses will enhance our mechanistic understanding of soil-plant interactions influencing crop VOCs. While the interactions observed in this greenhouse study were made in isolation of a number of other environmental factors known to impact emission profiles, they allowed us to test specific hypotheses on the impact of soil legacy effects from cover crops on constitutive and herbivore-induced volatile emissions. Our results are characteristic of agricultural practices at one point in the growing season, and we recognize that many soil features experience temporal shifts independent of agricultural practice in response to seasonality and crop phenology (Ishaq et al. 2020).

Thus, more work is needed to elucidate specific mechanisms and temporal trends in soil-mediated pest resistance, and future research should investigate how soil legacy effects of agricultural practices modify crop VOCs over a range of abiotic and biotic conditions including climate, crop variety, and plant development.

Here, we provide evidence that the soil legacy effects of diversified agricultural systems can be important drivers for insect-plant interactions in agroecosystems via their influence on HIPVs of crops. Our findings indicate that cropping system diversification may have substantial effects on multitrophic interactions and differentially influence recruitment of natural enemies of pests through altered herbivore-induced VOC signaling.

Authors' contributions D.K.W., T.F.S., F.D.M., and A.M.T., conceived the project; S.C.M. conducted the experiments with assistance from M.L.H.; S.C.M. analyzed the data with assistance from T.F.S.; S.C.M. drafted the initial manuscript, and all co-authors revised, read, and approved the final manuscript.

Data availability The datasets generated and analyzed during the current study are available in the Dryad repository, https://doi.org/10.5061/dryad.2jm63xskm.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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