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Cropping systems alter plant volatile emissions in the field through soil legacy effects

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Abstract

Crops emit a variety of volatile organic compounds (VOCs) that serve as attractants or repellents for pests and their natural enemies. Crop rotations, off-farm chemical inputs, and mechanical and cultural tactics – collectively called cropping systems – alter soil nutrients, moisture content, and microbial communities, all of which have the potential to alter crop VOC emissions. Soil legacy effects of diversified cropping systems have been shown to enhance crop VOC emissions in greenhouse studies, but how they influence emissions under field conditions remains virtually unknown. To determine the effect of cropping systems on plant VOC emissions in the field, air samples were collected from the headspace of wheat (*Triticum aestivum* L. Judee) grown in simplified wheat-fallow rotations or diversified wheat-cover crop rotations where cover crops were terminated by grazing cattle. Across two growing seasons, wheat grown in rotation with fallow emitted greater amounts of *Z*-3-hexenyl acetate and β-ocimene, key attractants for wheat stem sawfly (*Cephus cinctus* Norton), a major pest of wheat. While overall VOC blends were relatively similar among cropping system during the first growing season, emissions varied substantially in the second year of this study where wheat grown in rotation with cover crops emitted substantially greater quantities of volatile compounds characteristic of abiotic stress. Below-average precipitation in the second growing season, in addition to reduced soil water content in cover crop rotations, suggests that cropping system effects on wheat VOCs may have been driven primarily by water availability, a major factor limiting crop growth in dryland agriculture. While the specific mechanisms driving changes in VOC emissions were not explicitly tested, this work shows that agricultural practices applied in one growing season can differentially influence crop VOC emissions in the next through soil legacy effects, illustrating additional avenues through which cropping systems may be leveraged to enhance pest management.

Introduction

Plants produce an array of volatile organic compounds (VOCs) that mediate a variety of plant-insect interactions (Metcalf and Metcalf, 1992) including the attraction or repulsion of pollinators, pests and predators (Kessler and Kalske, 2018; Bouwmeester *et al.*, 2019). Plant volatile emissions are affected by a suite of soil abiotic and biotic properties such as temperature, moisture, nutrients, allelochemicals, and microbes (Gouinguené and Turlings, 2002; Pineda *et al.*, 2010; Sharifi *et al.*, 2018), all of which can result in the altered attraction of pests and their natural enemies (Pineda *et al.*, 2013; Pangesti *et al.*, 2015; Mariotte *et al.*, 2018). Agricultural practices alter many – if not all – of the aforementioned soil properties known to alter crop VOC emissions, and as such, may result in unintended consequences for crop pest management.

By developing soils that yield more favorable crop VOC blends, producers could leverage agricultural practices to increase pest management efficiency (Shrivastava *et al.*, 2010; Kaplan *et al.*, 2018). It is well-established that crop rotation complexity reduces insect pest and pathogen incidence by disrupting their life cycles (Wang *et al.*, 2002; Huang *et al.*, 2013); however, crop rotation complexity can also confer pest resistance indirectly through soil effects that alter plant defense metabolism (Hu *et al.*, 2018; Pineda *et al.*, 2020; Davidson-Lowe *et al.*, 2021). Studies have shown that the soil legacy effects of organic systems and cover crop rotations increase foliar defenses important for pest resistance (Murrell *et al.*, 2019; Blundell *et al.*, 2020), and these responses are driven by changes in soil nutrients and microbial communities. Not only can diversified agricultural practices enhance foliar defense, they can also alter crop VOC emissions. Compared to monocultures, crops grown in polyculture with a companion crop emit altered VOCs and experience reduced herbivory (Mutyambai *et al.*, 2019), and in greenhouse studies, plants grown in soil from diversified crop rotations emit altered constitutive and herbivore-induced VOC emissions (Malone *et al.*, 2020; Davidson-Lowe *et al.*, 2021). Still, the extent to which cropping system diversification through the inclusion of cover crops influences *in situ* VOCs emissions is virtually unknown.

Abiotic and biotic soil properties can alter VOC synthesis and emission (Gouinguené and Turlings, 2002; Pineda *et al.*, 2010; Sharifi *et al.*, 2018). For example, greater nutrient availability and soil water content tend to increase VOC emissions (Gouinguené and Turlings, 2002; Timmusk *et al.*, 2014), while microbial colonization of plants may increase (Fontana *et al.*, 2009) or decrease (Babikova *et al.*, 2014) emissions of VOCs, which can enhance (Ballhorn *et al.*, 2013; Babikova *et al.*, 2014) or reduce (Brock *et al.*, 2018) their attraction to herbivores. While many studies have demonstrated effects of individual soil properties and biological variables on the emissions of volatiles, how these properties interact in field conditions is less clear, limiting our ability to understand the practical implications of soil-modified VOC emissions in agricultural settings (Brilli *et al.*, 2019).

Crop rotations, off-farm chemical inputs, and mechanical and cultural tactics – collectively called cropping systems – drive biotic and abiotic soil properties (Navarro-Noya *et al.*, 2013; Lapsansky *et al.*, 2016; Ishaq *et al.*, 2020), and thus, may influence VOC emissions indirectly through soil legacy effects (Kaplan *et al.*, 2018). Compared to fallowing practices, cover crops enhance soil organic matter enrichment and nutrient availability, while reducing soil compaction and species-specific autotoxins (Fageria *et al.*, 2005; Huang *et al.*, 2013). Cover crops also increase the abundance and diversity of soil microbes important to plant growth and productivity (Fageria *et al.*, 2005; Kim *et al.*, 2020). However, cover crops may pose trade-offs, particularly in dryland agroecosystems where water is a primary driver of crop productivity. Cover crops may deplete deep-soil water stores and reduce cash crop growth in the following season (Robinson and Nielsen, 2015; Ghimire *et al.*, 2018; Bourgault *et al.*, 2021).

Crop production in the semi-arid Northern Great Plains (NGP) is dominated by monocultures of drought-resistant crops, especially wheat (*Triticum aestivum* L.), that are grown in rotation with a fallow growing season, a period when the land is left unsown to replenish soil moisture (Padbury *et al.*, 2002). In this region, wheat production is largely limited by low precipitation and a highly specialized pest complex that includes the wheat stem sawfly (WSS; *Cephus cinctus* Norton), which is the most economically important insect pest of wheat (Beres *et al.*, 2011). Female WSS use volatile cues from wheat, including (*Z*)-3-hexenyl acetate and β-ocimene, to locate appropriate hosts for oviposition (Weaver *et al.*, 2009; Buteler and Weaver, 2012). Other insect pests and beneficial species, including wheat grain aphid (*Sitobion avenae*), cereal leaf beetle (*Oulema melanopus*), and two species of braconid parasitoids (*Bracon cephi and B. lissogaster*) (Pérez, 2009; Delaney *et al.*, 2013; Drakulic *et al.*, 2015) also exhibit preferential attraction to wheat plants based on the composition and quantity of the volatile compounds they emit.

Given the importance of VOCs in mediating wheat–pest–parasitoid interactions, it is possible that wheat plants emitting unattractive, unrecognizable, or reduced amounts of VOC blends could experience enhanced pest resistance directly or indirectly by altering the attraction of pests or their natural enemies, respectively. To assess whether cropping systems might be leveraged to increase resistance of crops through shifts in their volatile emissions, we measured wheat VOCs across two growing seasons from wheat grown in rotation with fallow and paired with wheat grown in rotation with a seven-species cover crop mixture that was terminated by grazing cattle.

Materials and methods

Study site and cropping systems

The study was conducted at the Montana State University (MSU) Northern Agriculture Research Center located south of Havre, MT (48°29′48.8″N, 109°48′10.4″W). The site is a representative water-limited agroecosystem of the 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). The present study is part of a larger long-term study established in 2012 to assess cover crops in the NGP (Bourgault *et al.*, 2021). Using a randomized complete block design, two replicate fields (40 × 360 m each) were divided into 8 × 14 m plots to which cropping systems were assigned in replicates of three (Fig. 1). The location of each cropping system was randomized in 2012 and has been maintained through time. For a comprehensive description of crop rotations and management methods, see Bourgault *et al.* (2021).

VOCs were collected from wheat grown in two cropping systems: (1) wheat rotated with a fallow season, hereafter called ‘fallow’, and (2) wheat rotated with a seven-species mixture of cover crops that was terminated with grazing cattle, hereafter called ‘cover crop’. Species in the cover crop mixture included radish (*Raphanus raphanistrum* L.), lentil (*Lens culinaris* Medikus), field pea (*Pisum sativum* L.*)*, oat (*Avena sativa* L.), turnip (*Brassica rapa* L.), sorghum-sudangrass (*Sorghum* × *drummondii* (Steud.) Millsp. & Chase), and soybean (*Glycine max* (L.) Merr.). Species were selected based on United States Department of Agriculture-Agricultural Research Service (USDA-ARS) recommendations for the NGP and represent a range of functional groups with potential for the provision of various ecosystem services. Cover crops were planted on 14 May 2018, and 9 May 2019. At peak development, cover crop was dominated by oat which represented ~70% of the total biomass (Dupre *et al.*, 2021). Termination by targeted cattle grazing, an ecologically based management approach used to enhance the economic and environmental sustainability of farm diversification (McKenzie *et al.*, 2017), occurred from 26 to 28 July 2018, and from 14 to 16 August 2019. Cropping systems were treated with a glyphosate application prior to planting, and fallow plots were treated with an additional application of glyphosate during the season to control weeds. Wheat was visually monitored for pathogens and herbivores throughout the course of the study and no notable pest or pathogen damage was observed. Specifically, stem cutting by mature wheat stem sawfly larvae was less than <5% during the experiment. Total precipitation was 343 and 287 mm in 2018 and 2019, respectively, and mean annual temperatures were 4.6 and 4.7°C (Table 1).

Volatile organic compound (VOC) collections

To characterize the effect of cropping systems on VOC emissions, wheat VOCs were collected during two days over two growing

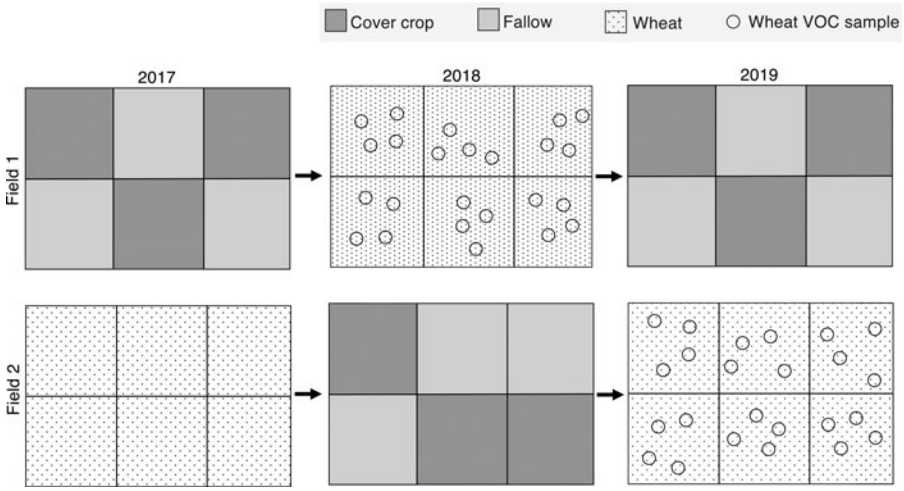

Fig. 1. Sample design used to determine the effect of diversified cropping systems on VOC emissions through soil legacy effects. Two replicate fields divided into 8 × 14 m plots were randomly assigned cropping systems in replicates of three. VOCs were measured from wheat grown in wheat-fallow and wheat-cover crop rotations where the cover crops were terminated by grazing cattle. VOC emissions were collected twice each season in 2018 and 2019. For each collection period, four VOCs samples were collected and averaged within a plot ($n_{\text{fallow}} = 3$, $n_{\text{cover}} = 3$).

Table 1. Summary of climatic data for crop years 2018 and 2019 at the Northern Agricultural Research center in Harve, MT (Northern Agricultural Research Center, 2019)

Crop year	Total annual precipitation (mm)	Mean annual temp (°C)
2018	342.9 (+27.9)	4.6 (−1.5)
2019	286.7 (−19.8)	4.7 (−1.3)

Crop year 2018 and 2019 include September 2017–August 2018 September 2018–August 2019, respectively. Deviation from the historical averages (1916-current year) are in parentheses.

seasons: 2018 (20 June and 4 July) and 2019 (11 June and 25 June). These sample dates overlap with the host searching periods of WSS adults (June) and of their natural enemy parasitoids (July). The average developmental stage of plants at the time of sampling was Zadoks 75, 86, 55 and 77, respectively (Zadoks *et al*., 1974). VOCs were collected from four ∼10 cm sections of a row within each plot and the four samples were averaged to determine the mean emission rate within each plot ($n_{\text{cover}} = 3$, $n_{\text{fallow}} = 3$). We used a push-pull sampling technique in which VOCs were collected from the headspace of chambers constructed from Teflon bags (48.26 × 54.61 cm; ClearBags, El Dorado Hills, CA) placed over the row and secured at the base of the plants with twist ties. VOC-free air was delivered into the chamber at 225 ml min^{-1} for at least 10 min prior to sample collection to flush ambient air from the chamber. Sample air including wheat VOCs was then collected over single HayeSep Q solid-phase adsorbent traps (Sigma Scientific, Gainesville, FL) at a flow rate of 225 ml min^{-1}. Wheat VOC emissions were collected for 2 to 3.5 h between the hours of 9:00 and 14:00 on mostly sunny days to avoid excessive afternoon heat and correspond to times when WSS and their natural enemies are most actively ovipositing (Beres *et al*., 2011).

After collection of VOCs, sampled wheat plants were immediately harvested to standardize the emission rate by aboveground fresh weight. Adsorbent traps were wrapped in aluminum foil and stored on ice for transport and eluted within 24 h. Identities and relative amounts of VOCs were determined using GC-MS and are reported as nonyl acetate equivalents (Text S1). To account for day-to-day variability of temperature and light, chamber temperature and PAR were measured (Text S2) and used to calculate basal VOC emission rates standardized to 30°C according to Guenther (1997). Basal emission rates are reported as emissions standardized by aboveground fresh weight and for the number of hours collected (ng nonyl acetate equivalents g^{-1} h^{-1}).

Biomass and volumetric water content

To assess variation in plant growth among rotation and season, we quantified the end-of-season wheat biomass by harvesting aboveground tissue from one quadrat (0.75 × 0.75 m) within each plot from which we had collected VOC emissions earlier in the growing season. End-of-season biomass was sampled immediately before wheat harvest in mid-July. Plants were cut at the soil surface and dried at 50°C for 48 h before being weighed.

Volumetric soil water content was measured during the 2018 growing season from field 2 only when the field was planted with cover crops or laid follow (see Fig. 1). Because these rotations preceded the wheat from which we sampled VOCs in 2019, 2018 soil water content measurements serve as a proxy for understanding how the cropping system may have influenced the soil water stores available to wheat crops subsequently planted. We measured volumetric soil water content (%) at six depths – 10, 20, 30, 40, 60 and 100 cm – using a PR2/6 Profile Probe (Delta-T Devices Ltd, Burwell, Cambridge, UK) on 25 May, 4 June, 20 June and 2 July. Probes were removed prior to grazing.

Data analysis

To determine the effect of cropping system and year on the composition of VOCs, we calculated dissimilarity in VOC composition using the Bray-Curtis metric and by applying the 'vegdist' function in the 'vegan' package (Oksanen *et al*., 2019). We used the permutational multivariate ANOVA (perMANOVA) and the 'adonis' algorithm to evaluate whether a significant proportion of the variation in VOC composition was accounted for by cropping system, year, and their interaction; however, the interaction term was insignificant and not included in the final model (Anderson, 2014). To visualize differences in VOC composition across cropping system and year, we used 'metaMDS' to perform non-metric multidimensional scaling (NMDS) analysis and we plotted the first two axes.

To compare the effect of cropping system on the quantity of VOC emissions for individual compounds, families of compounds (ketones, aldehydes, etc.), and the sum of all measured compounds, hereafter called 'total', we fit linear mixed models using the 'lmer' function in the 'lm4' package (Bates *et al.*, 2015). Measures of individual, family, or total VOCs were the dependent variables, cropping system, year, and their interaction were the fixed effects, and sample day was the random effect. When the interaction term was not significant for a given family or compound, it was not included in the model. Prior to the analysis, response variables were log-transformed to meet assumptions of normality and homoscedasticity, except when volatile compounds were not detected (i.e., when emission rates for a given compound were zero), in which case, square root transformations were used. To assess whether cropping system, year, and their interaction accounted for variation in VOCs, we performed Type III ANOVA using the 'Anova' function in the 'lmerTest' package (Kuznetsova *et al.*, 2017) and when the interaction term was not included in the final model, we used Type II ANOVA. To assess post hoc pairwise comparisons among treatments, we used Tukey's HSD test using the 'emmeans' package.

We modeled the effect of cropping system on end-of-season biomass by fitting a linear model with cropping system and year as the predictors. To determine the relationship between cropping system and soil water content, we fit linear mixed models with soil water content as the response variable, cropping system, depth, and their interaction as fixed effects and sample day as the random effect. We performed all analyses in R version 3.5.2 (R Core Team, 2018).

Results

VOC emissions

A total of 33 volatile compounds were quantified from wheat plants grown in rotation with fallow or cover crops including five ketones, nine aldehydes, seven terpenes, eleven alkanes/alkenes and one green leaf volatile (Table S1). Wheat VOC composition varied in response to cropping system and year (Fig. 2; cropping system: $F_{1,23} = 3.13$, $P = 0.03$, year: $F_{1,23} = 19.87$, $P < 0.0001$), with year explaining considerably more variation in VOC composition ($R^2 = 0.45$) than cropping system ($R^2 = 0.07$). The total VOC emission rate varied in response to the interaction of cropping system and year (cropping system × year: $F_{1,18} = 14.65$, $P = 0.001$). In 2018, wheat grown in rotation with fallow emitted VOCs at rates 1.6 times greater than wheat grown in rotation with cover crops ($P = 0.02$; Fig. 3 and Table S1). However, in 2019, the opposite was observed: wheat grown in rotation with cover crops emitted VOCs at rates 1.7 times greater than wheat grown in rotation with fallow ($P = 0.01$). VOC emissions showed day-to-day variability (Fig. 3) with the interaction of cropping system and year explaining 11% of the variation while sample day – a random effect in our model – explained an additional 88%. Though sample day impacted the magnitude of emissions, likely due to plant ontogeny and seasonality, the overall pattern of VOC emissions remained consistent among sample days within a growing season (Fig. 3).

Across both growing seasons, wheat grown in rotation with fallow emitted more terpenes, alkanes and alkenes, and GLVs (Fig. 3 and Table S1). In 2019, however, wheat grown in rotation with cover crops emitted more 4.7 more ketone and 3.2 more aldehyde compounds (Fig. 3 and Table S1) than wheat grown in rotation with fallow, and these compound families drove the observed increase in total VOC emissions by cover crop rotations in 2019. Across both growing seasons, wheat grown in rotation with fallow emitted greater amounts of compounds known to attract WSS adults: β-ocimene and Z-3-hexenyl acetate were emitted at rates 3.9 and 2.6 times greater compared to wheat grown in rotation with cover crops (Table S1).

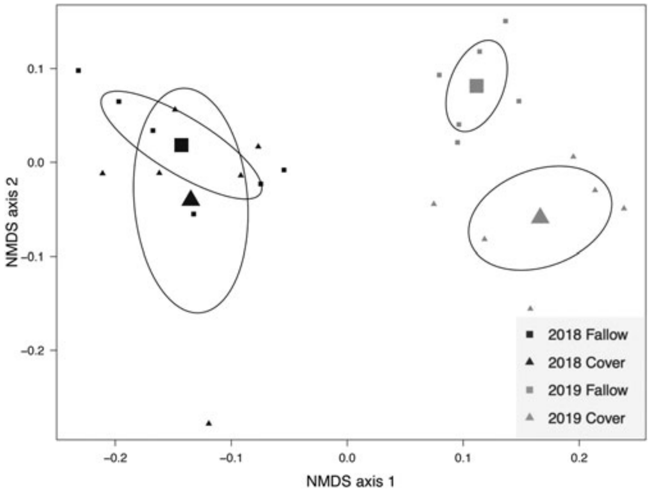

Fig. 2. Variation of VOC composition in response to cropping system and year. Large symbols represent the centroid of each grouping.

Biomass and volumetric water content

End-of-season biomass varied by cropping system (Fig. 4; $F_{1,9} = 5.13$, $P = 0.05$). Wheat grown in rotation with cover crops had reduced biomass, particularly in 2019 when the total annual precipitation was ~20 mm below average (Table 1). Soil water content in 2018 varied in response to the interaction of rotation and depth (Fig. 5; $F_5 = 9.52$, $P < 0.0001$), and there was minimal variation among sample day ($R^2_{marginal} = 0.51$, $R^2_{conditional} = 0.52$). Fallow plots exhibited higher percentages of soil water content at 30, 40 and 60 cm (Fig. 5), though soil water content was greater in cover crop rotations at 100 cm.

Discussion

Understanding whether cropping systems influence crop volatile emissions through soil legacy effects can provide critical insights into how and when to implement best management practices aimed at enhancing pest resistance. Using a two-year field study, we demonstrated that cropping systems influence the quantity and quality VOCs via soil legacy effects. Specifically, we showed that wheat crops emit varied VOCs depending on the rotation and management practices that proceed their growth. Importantly, we demonstrate strong interannual effects of cropping system on VOC emission, suggesting that annual climatic variation may dictate the extent to which cropping systems could influence crop pest-resistance.

In agroecosystems, shifts in crop VOC emissions can alter pest attraction and crop resistance (Shrivastava *et al.*, 2010; Mutyambai *et al.*, 2019). In 2018, VOC emission rates were greater from wheat grown in rotation with fallow, even though VOC composition was relatively similar among cropping systems. In contrast, during 2019, VOC emission rates were greater from wheat grown in rotation with cover crops, and the composition of VOCs varied markedly among cropping systems. Though we did not measure insect

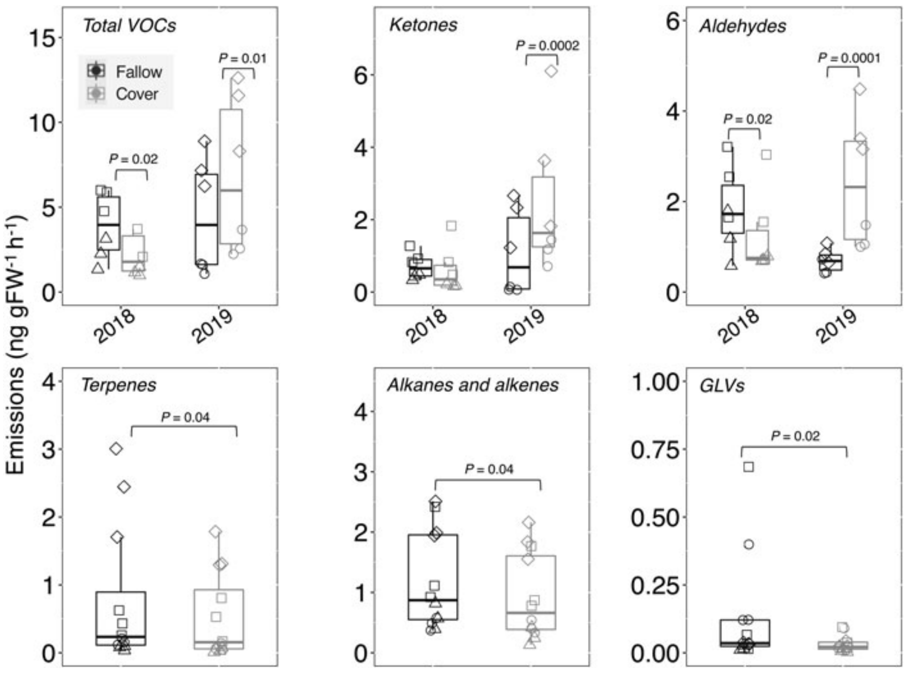

Fig. 3. VOC emissions by wheat grown in wheat-fallow (Fallow) or wheat-cover crop (Cover) rotations. Year is shown when emissions varied by sampling year. 'Total VOCs' represents the sum of all families of compounds (ketones, aldehydes, terpenes, alkanes and alkenes, and green leaf volatiles (GVLs)). Shapes represent individual sampling day.

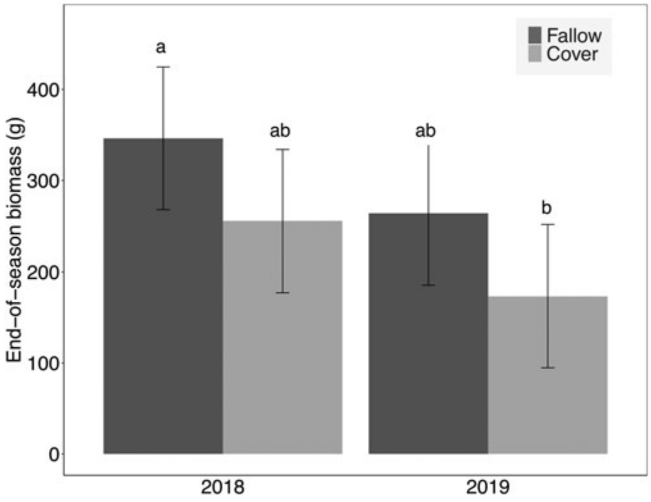

Fig. 4. Mean wheat aboveground biomass in response to cropping system and year. Significance between treatments is expressed using different lower-case letters (95% CI).

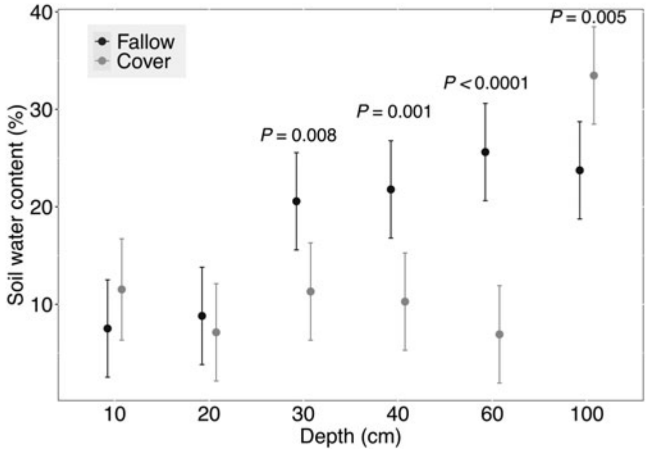

Fig. 5. Mean water content (%) (95% CI) of soil during fallow and cover crop rotations at six soil depths: 10, 20, 30, 40, 60 and 100 cm. Water content was measured during the 2018 growing season on 25 May, 4 June, 20 June and 2 July when the plots were fallow or planted with cover crops.

behavior in the present study, the observed VOC differences among cropping systems suggest that cropping systems may differentially attract or repel insect pests and their natural enemies. For example, across both growing seasons wheat-cover crop rotations emitted lower amounts of terpene compounds. Greater terpene emissions by wheat have been shown to effectively repel adult cereal leaf beetles (Delaney *et al.*, 2013), suggesting that wheat-cover crop rotations may be less resistant to herbivore damage by cereal leaf beetles. However, in the case of WSS, wheat grown in rotation with cover crops may be less conspicuous to host-searching females. Wheat grown in rotation with cover crops emitted lower amounts of β-ocimene and *Z*-3-hexenyl acetate, both of which have been shown to act as important host-location cues for ovipositing WSS females (Weaver *et al.*, 2009; Buteler and Weaver, 2012). Additionally, smaller wheat plants, like those observed in the cover crop rotation, are less attractive to ovipositing WSS (Perez-Mendoza *et al.*, 2006; Buteler and Weaver, 2012), suggesting that wheat grown in rotation with cover crops may experience reduced WSS herbivore pressure through olfactory and visual modalities. Given these observations, future research is required to determine whether the observed shifts in VOCs emissions translate to the altered attraction of pests and natural enemies. Finally, it is important to note that significant reductions in wheat yields were detected in wheat-cover crop rotations in 2019 (Bourgault *et al.*, 2021). While cropping systems may improve pest resistance through altered volatile emissions, reductions in crop biomass and yield will likely be the key factors that drive cropping management decisions.

We observed interannual variability in VOC emissions among cropping systems. While our experimental design precludes us from testing specific mechanisms driving the observed emissions, we posit that annual differences in VOC emissions were driven by the interaction of cropping system and annual precipitation. Total precipitation was nearly 30 mm above average in 2018, but ~20 mm below average in 2019 when we observed lower wheat biomass. Given that cover crops can reduce water stores (Fageria *et al.*, 2005; Robinson and Nielsen, 2015), timely cover crop termination is vital to maintain subsequent cash crop productivity, especially in dryland agriculture where precipitation is the primary constraint of wheat production (Padbury *et al.*, 2002; Bourgault *et al.*, 2021). In 2018, we observed reduced soil water content in cover crop plots compared to those that remained fallow, which – compounded by below-average precipitation in 2019 – may have created drought-like conditions for wheat grown in rotation with cover crops during 2019. Indeed, these plants emitted unusually high amounts of C9-C14 aldehydes, natural oxidation products of lipid peroxides (Shahidi, 2001) that occur concomitantly with environmental stressors such as drought (Wildt *et al.*, 2003; Giron-Calva *et al.*, 2017). To understand how cropping systems will impact crop emissions in a given growing season, future research should seek to understand the mechanisms driving crop emissions in the field where multiple abiotic and biotic factors are likely to interact in contrasting ways to influence net VOC emissions (Gadhave *et al.*, 2018; Heinen *et al.*, 2018).

Our work explored the role of cropping system on plant VOCs through soil legacy effects. While our study suggests that soil water availability is vitally important in predicting shifts in VOC emissions, our goal was not to identify specific mechanisms, and future studies should work towards disentangling the abiotic and biotic drivers responsible for the observations made here. Our results indicate that crop management strategies have the potential to modify plant volatile emissions of cash crops through soil legacy effects, illustrating the importance of considering the temporal role of cropping systems and soils on pest resistance.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S174217052200014X

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

Data availability. Data available from the Dryad Digital Repository.

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