











Volatile-mediated oviposition preference for healthy over root-infested plants by the European corn borer

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Abstract

The selection of oviposition sites by female moths is crucial in shaping their progeny performance and survival, and consequently in determining insect fitness. Selecting suitable plants that promote the performance of the progeny is referred to as the Preference–Performance hypothesis (or ‘mother-knows-best’). While root infestation generally reduces the performance of leaf herbivores, little is known about its impact on female oviposition. We investigated whether maize root infestation by the Western corn rootworm (WCR) affects the oviposition preference and larval performance of the European corn borer (ECB). ECB females used leaf volatiles to select healthy plants over WCR-infested plants. Undecane, a compound absent from the volatile bouquet of healthy plants, was the sole compound to be upregulated upon root infestation and acted as a repellent for first oviposition. ECB larvae yet performed better on plants infested below-ground than on healthy plants, suggesting an example of ‘bad motherhood’. The increased ECB performance on WCR-infested plants was mirrored by an increased leaf consumption, and no changes in the plant primary or secondary metabolism were detected. Understanding plant-mediated interactions between above- and below-ground herbivores may help to predict oviposition decisions, and ultimately, to manage pest outbreaks in the field.

KEYWORDS

above- belowground interactions, herbivore-induced plant volatiles, maize, plant-mediated interactions, preference–performance hypothesis, Western corn rootworm

1 | INTRODUCTION

The selection of oviposition sites by herbivorous insects is a key determinant of their fitness, as the quality of the chosen plant modulates the progeny performance, fecundity and survival (Awmack & Leather, 2002).

The ‘Preference–Performance hypothesis’ (also known as the ‘mother-knows-best hypothesis’) predicts that females maximize their fitness by laying eggs on plants that are the most suitable for their progeny (Gripenberg et al., 2010; Jaenike, 1978; Mayhew, 1997; Thompson, 1988). The presence of a herbivore feeding on the plants may have a strong impact on the female’s decision to oviposit, as

simultaneous infestation by other herbivores can result in facilitation, neutral effects or competition/suppression on the female progeny (Martínez et al., 2013). These interactions can be direct, such as competition for limited resources, or indirect, mediated through changes in the host plant metabolism (Biere & Govers, 2016). The outcome of these plant-mediated interactions might depend on the feeding guild of the herbivores and has been widely reported for leaf-chewing herbivores versus piercing-sucking aphids (Agrawal, 2000; Li et al., 2014; Poelman et al., 2008; Rodriguez-Saona et al., 2005; Soler et al., 2012). For instance, females of the European corn borer (ECB), *Ostrinia nubilalis*, were shown to avoid plants infested with aphids for oviposition, a behaviour that benefits the performance of their progeny (Harmon et al., 2003). While plant-mediated interactions between leaf herbivores are well known, less information is available about plant-mediated interactions between root and leaf herbivores and how these interactions affect herbivore oviposition decisions (Erb et al., 2008; Pineda et al., 2015).

Root herbivory can trigger systemic changes in leaf defences and nutritive value (Arce et al., 2017; Bardgett & Wardle, 2003; Biere & Govers, 2016; Dam & Heil, 2011; van Geem et al., 2013; Putten, 2009). Root damage was reported to cause changes in water potential, terpenoid concentrations, carbon allocation patterns and volatile emissions (Danner et al., 2015; Erb et al., 2012; McKenzie et al., 2016). Such a drastic metabolic reconfiguration affects the performance and survival of leaf feeders and even of their natural enemies (Bardgett & Wardle, 2003; Bezemer & van Dam, 2005; Dam & Heil, 2011; Van Dam et al., 2005; Erb et al., 2008; Kaplan et al., 2008; Van der Putten et al., 2001; Rasmann & Turlings, 2007; Wäckers & Bezemer, 2003; Wardle et al., 2004). However, how root herbivory shapes oviposition decisions of aboveground females remains poorly understood (Dicke et al., 2003; van Geem et al., 2013; Soler et al., 2010). To date, only a few examples report that female moths can distinguish between healthy plants and plants attacked by root herbivores for oviposition. For instance, females of the African cotton leafworm, *Spodoptera littoralis*, preferentially lay their eggs on healthy cotton plants rather than on cotton plants infested belowground by wireworms (*Agriotes lineatus*) (Anderson et al., 2011). Similarly, two species of *Pieris* butterflies selectively lay eggs on healthy over root-infested mustard plants, although this phenomenon was reported to be dependent on the egg load of the female (Soler et al., 2010). Yet, the plant cues involved in assessing the root infestation status of a plant for oviposition site selection remain unknown.

Insect herbivores have evolved strategies to assess the suitability of a host plant for oviposition by exploiting multimodal sensory cues, including visual, tactile, gustative and olfactory signals (Cury et al., 2019). Herbivore-induced plant volatiles (HIPVs) are reliable indicators of the presence of a herbivore on a plant and were reported to be used by gravid females for oviposition site selection (Kessler & Baldwin, 2001; Martínez et al., 2013; De Moraes et al., 2001; Turlings & Erb, 2018; War et al., 2011). For example, HIPVs emitted by damaged tobacco plants are repellent to the female moths, *Heliothis virescens* (De Moraes et al., 2001). Despite their

potential importance in driving ecosystem processes, leaf volatile emissions upon root herbivory were rarely characterized. In turnip plants, root herbivory by *Delia radicum* drastically altered the leaf volatile bouquet (Pierre et al., 2011), suggesting that female moths may use the presence of compounds specifically induced by root herbivory to distinguish between healthy plants and plants infested belowground.

The ECB (*O. nubilalis*) and the Western corn rootworm (WCR, *Diabrotica virgifera virgifera*) are two of the most economically important maize pests of the Northern hemisphere. ECB feeds on maize leaves during early developmental stages, before migrating and feeding into the stems. WCR larvae, on the other hand, are specialist herbivores attacking maize roots. The two herbivores cooccur in nature, with WCR infestation preceding ECB oviposition (Meissle et al., 2011; Priesnitz et al., 2016). In the field, WCR-damaged maize plants showed lower ECB infestation, although the underlying mechanisms could not be investigated (Tanaskovic et al., 2018).

In this study, we investigated whether gravid ECB females distinguish between healthy and WCR-infested plants based on leaf volatile profiles and whether their oviposition decisions affect the performance of their progeny. We hypothesized that ECB females use volatile cues from WCR-infested plants to select healthy over infested plants. We expected that this behaviour would be consistent with the 'Preference-Performance hypothesis' and thus that ECB larvae would grow better on healthy plants rather than on WCR-infested plants. Understanding the drivers of ECB oviposition and identifying possible chemical cues involved would help to predict pest outbreaks and develop sustainable pest management strategies against ECB.

2 | MATERIALS AND METHODS

2.1 | Biological resources

Maize seeds (*Zea mays* var. NS640) were used in all experiments. NS640 is widely used as a forage maize variety in Eastern Europe, where both herbivore pests *O. nubilalis* and *D. virgifera* are present. Maize seedlings were grown in 1 L plastic pots under greenhouse conditions (24 ± 2°C, 14 h photoperiod, 55%–60% relative humidity). Oviposition assays were carried out under growth chamber conditions (26 ± 2°C, 14 h photoperiod, 60% relative humidity). Plants with four to five fully developed leaves were used for all experiments. The colony of the European Z-strain ECB was established from adults collected and annually refreshed from a maize field in Kéty town (46°26'41.2" N, 18°31'27.6" E), Hungary. The moth colony was maintained in the laboratory, on a semi-artificial diet (Nagy, 1970) at 25°C, 50% relative humidity under 18:6 h L:D light conditions. WCR eggs were kindly provided by Stefan Toepfer (CABI) and by Sharon Schneider and Chad Nielson (USDA-ARS). WCR larvae were reared on freshly germinated maize seedlings (var. Akku; Delley Semences et Plantes) until use.

2.2 | Oviposition preference

In a first oviposition assay, ECB females were given the choice between a healthy and a WCR-infested plant. WCR-infested plants were obtained by adding 100 WCR eggs in two 7-cm-deep holes in the soil on the day of sowing. Control plants were left intact. After 25 days, the plants were individually covered with an organza mesh (0.1 mm mesh size; Mathe Textil Ltd.). One plant of each treatment was placed in each cage (80 × 60 × 60 H × L × W cm, mesh size 0.23 × 0.33 mm, Mathe Textil Ltd, $n = 9$ cages). Five ECB gravid females were released in the centre of the choice arenas. The first oviposition was characterized on the following days (16 h later). Cages where eggs present on both plants rendered impossible to assess first event of oviposition and were excluded from the analysis ($n_{\text{first oviposition}} = 5$) but are presented in Supporting Information.

In a second oviposition assay, ECB females were allowed to oviposit on either a healthy or an undecane-complemented healthy plant. Because both plants were healthy, they were referred to as 'Control' and 'Undecane-complemented' plants thereafter. Undecane complementation was carried out by adding an undecane-releasing dispenser in the vicinity (on soil) of a healthy plant. The dispensers were prepared according to Erb et al. (2015). Briefly, 50 μL of 0.32 mM undecane (Sigma-Aldrich) in pure dimethyl sulfoxide (DMSO) were added in 1.5 mL glass vials ($\varnothing \times H$ 11.6 × 32 mm; VWR) containing ~100 mg glass wool. The vials were sealed with screw caps containing a rubber septum. The caps were then pierced with a 0.5 μL glass capillary (Drummond Scientific) and sealed with PTFE tape. All vials were wrapped with aluminium foil and equilibrated for >24 h before use. Control dispensers contained pure DMSO. Undecane-dispensers released 4.38 (± 0.94) ng/h (Supporting Information S1: 1), which is similar to the range emitted by maize plants. Four females were placed in cages (60 × 60 × 60 cm, BugDorm; Mega-view) containing a healthy and an undecane-complemented healthy plant ($n = 7$ cages). The number of batches and eggs on each plant were recorded 3 days later. Cages where egg batches were observed on both plants were removed from the analysis ($n_{\text{first oviposition}} = 3$) and are included in Supporting Information.

2.3 | Herbivore performance

First, ECB larval performance was recorded on healthy and WCR-infested plants. WCR-infested plants were obtained by adding five second-instar larvae into two 7-cm-deep holes in the soil. Control plants were not infested, but the two 7-cm-deep holes in the soil were similarly dug. Four days later, 10 ECB neonate larvae were placed on the leaves of control and WCR-infested plants. All plants were covered with PET bottles (1.5 L; Evian) to prevent the larvae from escaping. After 21 days, all ECB larvae were collected and weighed, and the leaf damage area was recorded. Leaf damage was recorded visually on each individual leaf by counting the number of

holes of different sizes using a printed sheet with holes of different diameters and lengths as described previously (Robert et al., 2013). Due to a high ECB mortality, the experiment was repeated twice ($n_{\text{Exp1}} = 12$, $n_{\text{Exp2}} = 11$ per treatment).

Second, ECB larval performance was measured on healthy and undecane-complemented plants. The volatile complementation was obtained using dispensers as described above. One pre-weighed second-instar ECB larva was added on each plant ($n = 20$ per treatment). All plants were covered with PET bottles as described above. After 4 days, the ECB larvae were collected and weighed.

Third, ECB larval performance was determined when feeding on artificial diet in the presence/absence of undecane. Pre-weighed second-instar ECB larvae were starved for 24 h and placed individually in Petri dishes (9 cm diameter) containing a 30 × 30 × 10 mm piece of artificial diet (Frontier Scientific) ($n = 11$ –12 per treatment). The Petri dish was placed into a 12 × 45 cm $\varnothing \times H$ transparent glass cylinder with a glass lid, and inlet and outlet ports. Either an undecane or a DMSO dispenser was placed within each cylinder (see above for dispenser specifications). A steady flow of 0.2 L/min of clean air was passed through each cylinder to prevent excess accumulation of undecane. The piece of artificial diet was changed daily to prevent desiccation. After 4 days, all larvae were collected and weighed.

2.4 | Plant volatile analysis

The volatile bouquets of control and WCR-infested plants were analysed by gas chromatography coupled to mass spectrometry (GC-MS). Briefly, maize leaves were wrapped in polyacetate bags (12 L; Alufix GmbH) 30 min before volatile collection. The plant volatiles from the headspace were collected using PorapakTM Q porous polymer adsorbent filled glass filters (80/100 mesh; Waters Corporation) over 10 min. The volatiles from a bagged empty pot were collected as blank. The adsorbed volatiles were eluted by washing the filters with 300 μL of *n*-hexane (purity $\geq 98\%$; Roth Ltd). The extracts were concentrated to 40 μL at room temperature in open-air. The headspace volatiles were analysed by GC-MS (5890 GC and 5975 MS; Agilent Technologies) with electron impact. The ionization mode was 70 eV, scanning m/z 29–400, at 2 scans. s^{-1} . The GC was equipped with an HP-5MS UI fused silica capillary column (30 m × 0.25 mm × 0.25 μm ; Agilent J&W Scientific). Helium was used as a carrier gas, with a flow rate of 35 $\text{cm}^3 \text{s}^{-1}$. An aliquot of 1 μL was injected in splitless mode. The oven temperature was held at 50°C for 1 min then increased 10°C min^{-1} to 230°C and held for 1 min. Headspace volatile compounds were identified based on their mass spectra, which were compared with the MS Library (NIST 17) using Agilent MSD Productivity ChemStation (MSD ChemStation F.01.03.2357-Agilent Technologies Inc.) software. The identification was verified by the calculated retention indices, based on available *n*-alkanes'

retention times. Calculated retention indices were compared with the published NIST Chemistry WebBook database (NIST).

2.5 | Electroantennography (EAG)

The electrophysiological responses of the female antennae were recorded using an EAG setup (Syntech Ockenfels). Antennae were excised and inserted into a glass capillary (ID 1.17 mm; Harvard Apparatus) filled with Ringer's solution (Beadle & Ephrussi, 1936) and attached to the reference silver/silver chloride electrode held in a micromanipulator. One or two segments from the distal end of the antennae were cut off and inserted into the recording glass electrode, which was also filled with Ringer's solution. The antennae were continuously under a charcoal-filtered, humidified air stream (1 L/min). One dose (100 ng/ μ L) of the synthetic compounds were diluted in mineral oil (CAS 8042-47-5; Sigma-Aldrich) and 10 μ L of the solutions were applied on a filter paper disk (12.7 mm \varnothing ; Schleicher & Schnell GmbH) and placed into a Pasteur pipette. Ten μ L of the mineral oil was used as a control stimulus. The 0.5 s stimuli (0.5 L/min) were delivered into the continuous air stream (1 L/min) using a stimulus controller (CS-55; Syntech Ockenfels). The compounds were tested in a random order and the mineral oil blank was applied before and after each series of odour stimuli. The antennal signal was pre-amplified by a factor of 10, converted to a digital signal by a high input impedance DC amplifier interface (IDAC-2; Syntech Ockenfels) and recorded with GcEad 2012 software (version 1.2.4.; Syntech Ockenfels). The antennal response was compared to the absolute response to the oil blank.

2.6 | Plant metabolite analyses

WCR-induced plant metabolic changes were evaluated by collecting maize stems and dividing them into three sections (basal, middle and upper sections). All samples were flash-frozen and ground to a fine powder in liquid nitrogen. Starch and sugars (glucose, fructose and sucrose) were extracted as previously described (Machado et al., 2015, 2017). Total soluble proteins were measured by performing a Bradford assay (Bradford, 1976; Machado et al., 2015). The extraction of benzoxazinoids was conducted as described in Robert et al. (2017). Briefly, 1 mL of 50:50:0.5 MeOH:H₂O:FA (Fisher Scientific UK Ltd) was added to 100 mg plant powder, vortexed rigorously and centrifuged for 10 min at 14 000 rpm. The supernatant was used for analyses. The analysis was conducted using High Performance Liquid Chromatography (HPLC) coupled to MS, using an Acquity HPLC system coupled to a G2-XS Quadrupole Time of Flight Mass Spectrometer (QTOF-MS) equipped with an electrospray source (Waters Waters Corp.). The separation was performed on an Acquity BEH C18 and the acquisition was realized in ESI-negative

mode over a mass (*m/z*) range of 100–1000 Da. Benzoxazinoids were identified based on their mass spectra and quantified using purified DIMBOA, DIMBOA-Glc, HDMBOA-Glc and synthetic MBOA (Merck KGaA).

2.7 | Statistical analyses

Data were analysed with R (R Statistical Software; Version 4.0.5; R Foundation for Statistical Computing), GraphPad online (Graphpad.com; GraphPad Software) and SigmaPlot (version 14.5; Systat Software Inc.). All data were tested for the heteroscedasticity and normality of the error variance using Brown–Forsythe and Shapiro–Wilk tests. Oviposition preferences were analysed with χ^2 tests on proportions against the assumption of a random preference of 50%–50%. Volatile bouquets were analysed using principal component analysis, linear discriminant analysis and powered partial least squares discriminant analysis (PLS-DA). Individual volatile emissions were first analysed using Student *t*-tests on arcsinh-transformed data followed by a Benjamini–Hochberg correction to correct for multiple tests. A Volcano plot was constructed by plotting the negative values of the log(*p*) against the log fold change in volatile emission. Individual volatile peak areas were further individually compared using Student *t*-tests and Mann–Whitney rank sum tests. The tests were conducted on arcsinh-transformed data and a Benjamini–Hochberg correction was applied for false discovery rate. Two experiments measuring ECB survival and performance on healthy and WCR-infested plants were pooled, as no experiment effect was detected. ECB survival, performance and tissue consumption were analysed with Student *t*-tests and Mann–Whitney rank sum tests. One plant was not fully assessed for leaf damage and was removed from the damage analysis. Antennal response was analysed by comparing the absolute response to a volatile to the response to the oil blank using Student *t*-tests. The effects of root herbivory and stem section on starch, sugar, protein and benzoxazinoid concentrations were analysed using two-way ANOVAs and two-way ANOVAs on ranks.

3 | RESULTS

3.1 | ECB females preferentially oviposit on healthy plants, while larvae perform better on WCR-infested plants

ECB females preferentially laid their first egg batches on healthy, WCR-free, plants (Figure 1a). Egg batches were only found on healthy plants after 16 h oviposition (Figure 1a). The effect was still present after 3 days, as 84% of all egg batches were found on healthy plants (Supporting Information S1: 2A–B). Although the survival of ECB larvae was similar in both treatments (Figure 1b), their performance was twofold higher on WCR-infested plants than on healthy plants (Figure 1c). The damage caused by the leaf herbivore was also higher on WCR-infested plants than on control plants (Figure 1d).

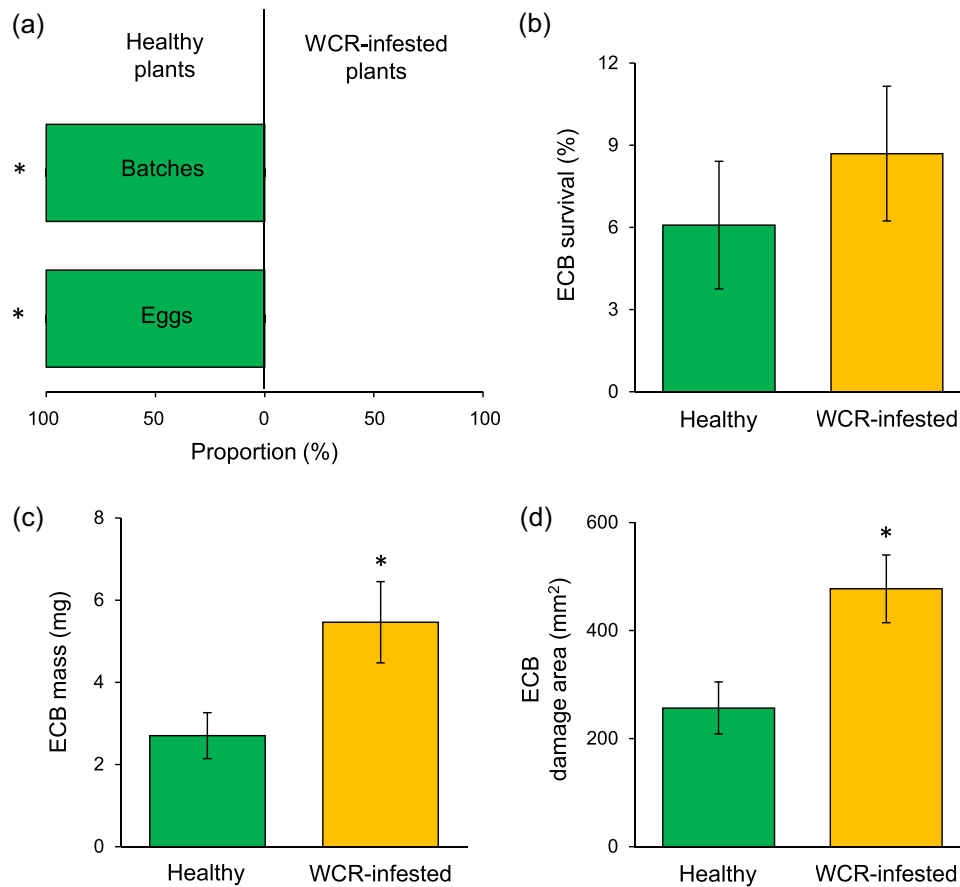


FIGURE 1 European corn borer (ECB) females preferentially oviposit on healthy plants that are suboptimal for their progeny performance. (a) Proportions (mean \pm SEM) of egg batches and eggs laid by ECB females, *Ostrinia nubilalis*, on healthy plants (green) and on plants infested belowground by the Western corn rootworm (WCR, 'WCR-infested plants', yellow), *Diabrotica virgifera*. ECB females laid 5.8 ± 2.1 batches (mean \pm SEM) and 39 ± 9 eggs (mean \pm SEM) on healthy plants, and no eggs on WCR-infested plants. (b) Survival rate of ECB larvae fed on healthy and WCR-infested plants for 21 days. (c) Performance of ECB larvae fed on healthy and WCR-infested plants. (d) Leaf damage by ECB larvae after feeding for 21 days on healthy and WCR-infested plants. Stars indicate significant differences: * $p < 0.05$, *** $p < 0.001$. [Color figure can be viewed at wileyonlinelibrary.com]

3.2 | Healthy and WCR-infested plants display different leaf volatile profiles

The aboveground volatile bouquets of healthy and WCR-infested plants were significantly different (999 permutations, Figure 2a). Out of 55 detected compounds, 23 were differentially emitted by control and WCR-infested plants (Figure 2b,c). Out of the 23 differentially emitted compounds, 22 showed a decreased emission rate under WCR infestation (Figure 2c). Undecane was the sole compound to be induced by WCR herbivory (Figure 2c). The higher release of volatiles by control plants was not related to differences in the size of control and infested plants, as plant biomass and height were similar (Supporting Information S1: 3). A list of all detected volatiles (including nonsignificantly affected volatiles) is available in Supporting Information S1: 4. Interestingly, the increased emission of undecane is likely to be line specific, as undecane was not detected in WCR-infested B73 plants (data not shown).

3.3 | ECB females respond to some WCR-modulated leaf volatiles

ECB female antennae responded to 3-hexanol, 7-methyl-3-methylideneocta-1,6-diene (β -myrcene), 3,7-dimethylocta-1,6-dien-3-ol (β -linalool), (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT), (3*Z*)-3,7-dimethylocta-1,3,6-triene (*cis*- β -ocimene), undecane and (*Z*)-3-hexenyl acetate (Figure 3). However, ECB antennae did not respond to butyl acetate, *o/p*-xylene, 3-carene, benzylacetate, dodecane, decanal and tridecane (Figure 3).

3.4 | Undecane drives ECB first oviposition choice

Strikingly, complementing healthy plants with undecane was sufficient to promote oviposition on control plants (Figure 4a). After 16 h oviposition, all females had laid eggs on control plants only (Figure 4a). Interestingly, the effect disappeared after 3 days

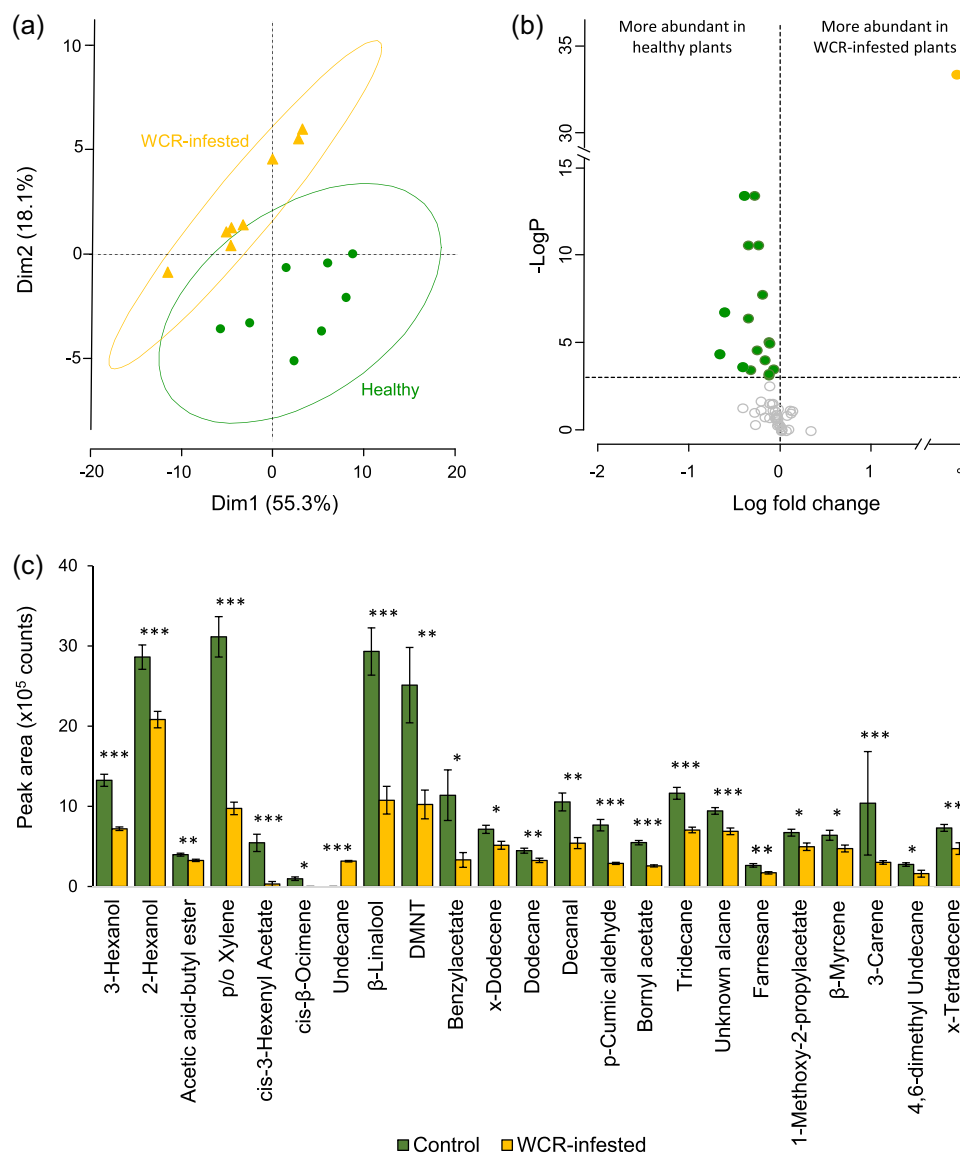


FIGURE 2 Root herbivory alters volatile emissions in leaves. (a) Principal component analysis (PCA) of the volatile bouquets emitted by healthy plants (green dots) and by plants infested by the Western corn rootworm (WCR, 'WCR-Infested', yellow triangles), *Diabrotica virgifera*, belowground. (b) Volcano plot showing the negative log₁₀-transformed *p*-values against the log ratios (log₁₀ fold change) of individual volatiles. Green dots represent volatiles being more abundant in healthy plants (on the left). Yellow dots represent volatiles being more abundant in WCR-infested plants (on the right). (c) Significantly different volatile emissions (mean ± SEM) of healthy (green bars) and WCR-infested plants (yellow bars). A list of all detected volatiles (including nonsignificantly affected volatiles) is available in Supporting Information S1: 4. Stars indicate significant differences **p* < 0.05, ***p* < 0.01, ****p* < 0.001. [Color figure can be viewed at wileyonlinelibrary.com]

oviposition, suggesting that the effect of undecane may be overridden by other cues related to the presence of conspecific eggs (Supporting Information S1: 2C-D).

3.5 | Undecane reduces ECB larval performance via plant-mediated effects

ECB larvae fed on undecane-complemented plants had a similar survival rate, but a lower performance, than ECB larvae fed on

control plants (Figure 4b,c). The difference was abolished when the ECB larvae fed on artificial diet in the absence/presence of undecane (Figure 4d,e), suggesting a plant-mediated effect of undecane. However, starch, sucrose, glucose, fructose, soluble protein and benzoxazinoid concentrations were similar in stems of control and WCR-infested plants (Figure 5). The levels of protein and benzoxazinoid concentrations differed in the different stem sections (Figure 5d,e). In particular, the basal stem sections had higher protein and individual benzoxazinoid concentrations than the middle and upper stem sections (Figure 5d,e).

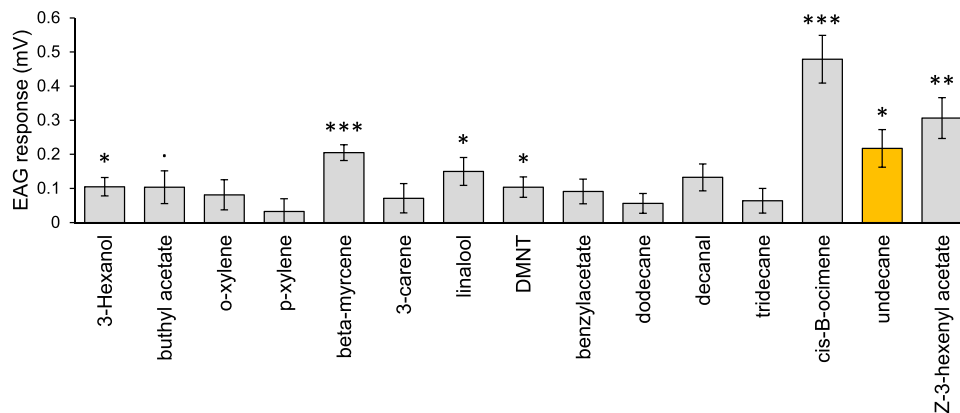


FIGURE 3 Electroantennographic (EAG) responses of European corn borer (ECB) females to maize volatiles. The EAG recordings were obtained by exposing the antennae of ECB females, *Ostrinia nubilalis*, to maize volatiles at a concentration of 100 ng. The amplitude of the EAG response was measured in millivolts (mV). The difference between the response to individual volatiles and corresponding blanks is shown. The response to undecane is highlighted in yellow. DMNT: (E)-4,8-dimethyl-1,3,7-nonatriene. Stars indicate significant differences. $p < 0.10$, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. [Color figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

This study reports a volatile-mediated oviposition preference for healthy over root-infested plants by a leaf herbivore. It identifies undecane as a leaf volatile cue specifically released under root herbivory and that acts as a repellent for oviposition. This work highlights a case of 'bad motherhood', as ECB females laid their eggs preferentially on plants that did not favour the growth of their progeny. We discuss the possible mechanisms and ecological relevance of our findings below.

The ECB females preferentially selected healthy plants over plants infested by WCR larvae belowground to oviposit. ECB females were previously found to be able to distinguish between healthy plants and plants infested with conspecifics or with heterospecific leaf feeders through plant volatile emissions (Binder et al., 1995; Harmon et al., 2003). It is further consistent with the fact that WCR-infested plants suffered lower ECB infestation in the field (Tanaskovic et al., 2018). In our study, the distinction of healthy plants from root-infested plants, was likely chemically-mediated, although possible visual cues cannot be fully excluded at this stage.

Overall, WCR infestation led to decreased volatile emissions, albeit no differences in plant development were observed. Identified volatiles that were differentially emitted by healthy and WCR-infested plants included terpenes, esters, alkanes, alkenes, aldehydes and aromatic compounds. It would be tempting to speculate that the increased odorant apparency of healthy plants was responsible for female attraction (Halitschke et al., 2008; Robert et al., 2013). Volatiles whose emissions were reduced included known oviposition attractants and repellents. For instance, the monoterpene linalool and the alcohol 2-hexanol were previously reported to be attractant and oviposition stimulants, while the sesquiterpene farnesene and the monoterpene (β)-myrcene were reported to act as a deterrent for gravid ECB females (Molnár et al., 2015; Solé et al., 2010).

Whether a decreased odorant apparency of WCR-infested plants explains the preference for healthy plants remains to be investigated.

Undecane was the sole compound to be induced in leaves of WCR-infested plants and was not detected in the odorant bouquet of healthy plants. Undecane elicited a response in ECB females' antennae and acted as repellent for the first oviposition event. The alkane was previously reported to be detected and involved in oviposition selection for other insects, such as the parasitic wasp *Anastatus japonicus* (Wang et al., 2017). Interestingly, we observed that the repellent effect of undecane disappeared once ECB eggs were present on control plants. This shift in behaviour suggests that egg visual, tactile or volatile cues overrid the undecane's effect. It was for instance previously reported that ECB eggs carries a pheromone which deters ECB females from ovipositing (Thiéry et al., 1991). Undecane is thus an important plant-derived driver of ECB oviposition that may shape pest population dynamics in the field.

According to the Preference–Performance hypothesis, females maximize their fitness by laying eggs on plants that are the most suitable for their progeny (Jaenike, 1978; Mayhew, 1997; Thompson, 1988). For instance, ECB females were shown to preferentially oviposit on healthy plants rather than on plants infested with aphids, thereafter favouring the growth and survival of their progeny (Harmon et al., 2003). Yet, in our study, the ECB larvae performed worse on the healthy plants selected by the females for oviposition than on root-infested plants. Such a phenomenon is referred to as 'Bad motherhood' and occurs when females select a plant that would increase their own longevity (García-Robledo & Horvitz, 2012; Mayhew, 2001). For example, if feeding preferences, longevity and oviposition preferences are correlated, females may lay their eggs on plants that increase their own longevity but that may be suboptimal for their progeny (Scheirs et al., 2000). In the case of ECB, healthy plants may promote a longer lifespan for females and remains to be investigated.

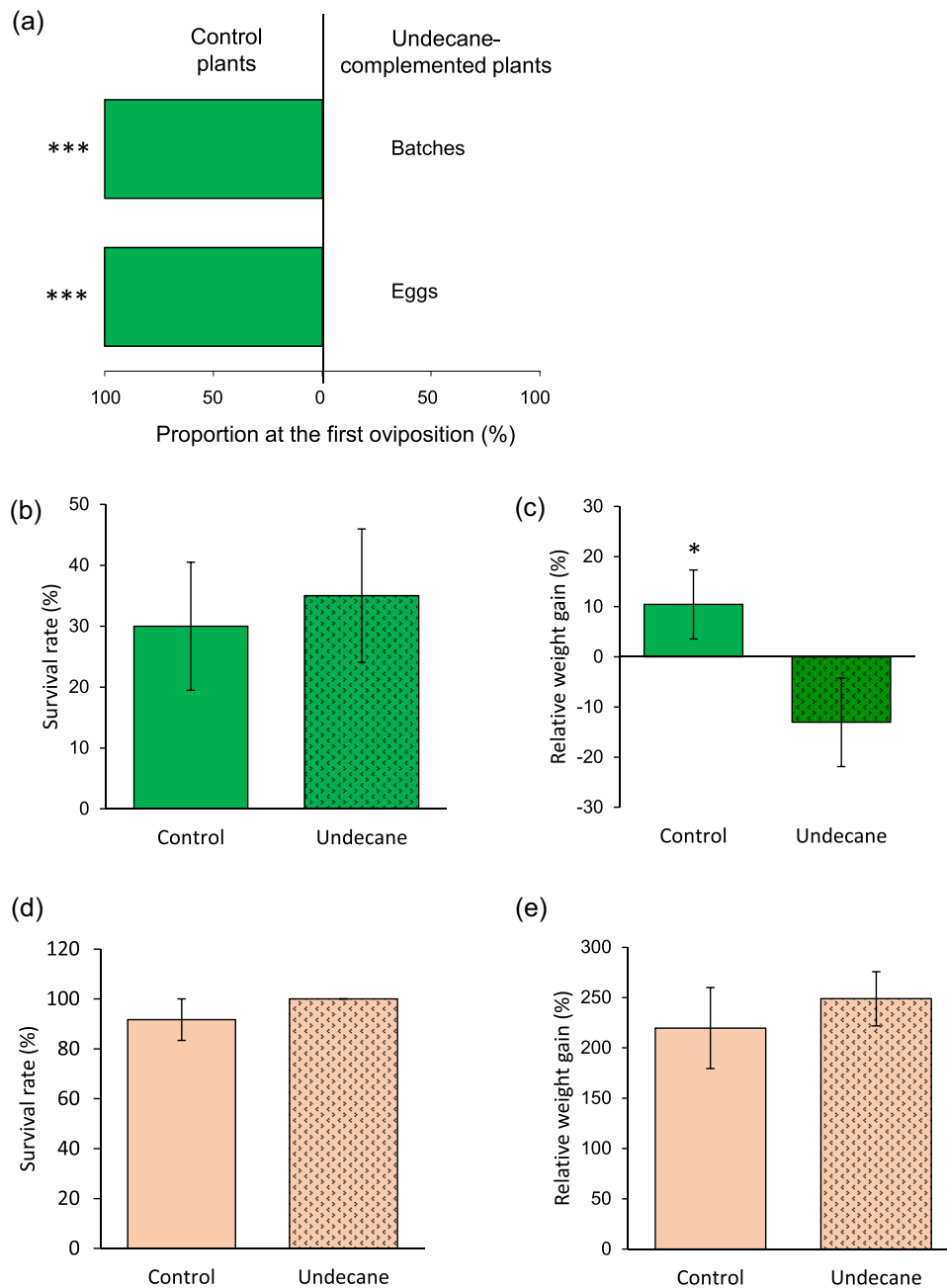


FIGURE 4 Undecane modulates oviposition decisions of European corn borer (ECB) females. (a) First oviposition decision made by ECB females, *Ostrinia nubilalis*. Proportions (mean \pm SEM) of egg batches and eggs laid by ECB on control plants (green) and on undecane-complemented plants. (b) Survival rate of ECB larvae fed for 4 days on control and undecane-complemented plants. (c) Performance of ECB larvae fed for 4 days on control and undecane-complemented plants. (a–c) Undecane complementation was obtained by placing a dispenser releasing 4 ng/h undecane on the soil. (d) Survival rate of ECB larvae fed for 4 days on diet in a control or undecane-complemented atmosphere. (e) Performance of ECB larvae fed for 4 days on a diet in a control or undecane-complemented atmosphere. (d, e) Undecane complementation was obtained by placing a dispenser releasing 4 ng/h undecane and ensuring an air flow of 0.2 L/min in the experimental cylinders. Stars indicate significant differences: * $p < 0.05$, *** $p < 0.001$. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pcce.14876)]

The fact that ECB larvae fed on healthy plants performed poorly compared to larvae fed on plants infested with WCR larvae belowground was unexpected, as WCR feeding was previously reported to trigger maize resistance to Lepidopteran leaf herbivores, including ECB (albeit not significant) in the field (Erb et al., 2009, 2011; Turlings, 2011). One possible explanation for this apparent

discrepancy may be that the observed field effect was due to lower oviposition of ECB females on WCR-infested plants. Furthermore, the observed lower performance of Lepidopteran herbivores on WCR-infested plants under laboratory conditions was pronounced at early caterpillar developmental stages (Turlings, 2011), and ECB larvae may have compensated for an early delay throughout the

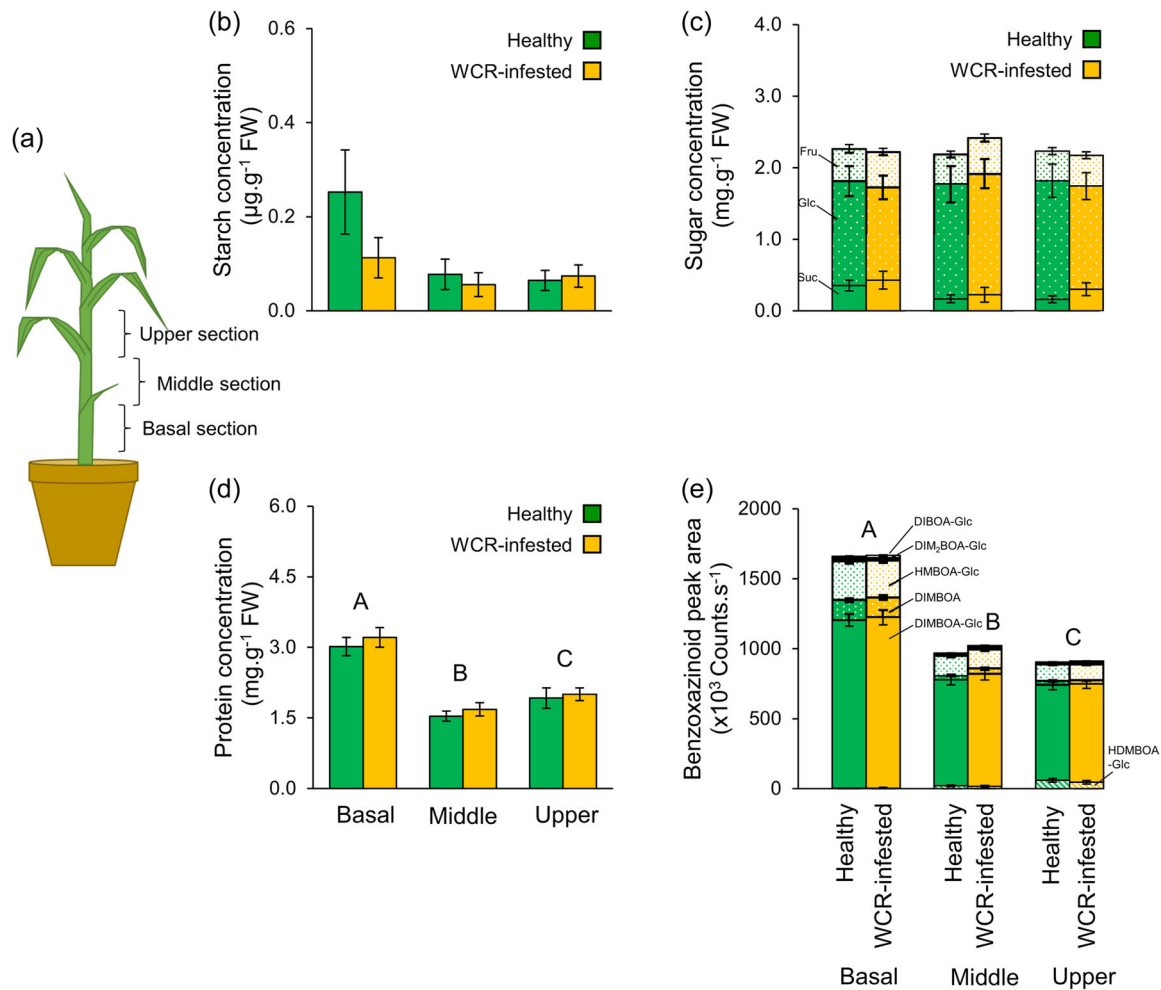


FIGURE 5 Healthy and WCR-infested plants have comparable levels of sugars, starch, proteins and benzoxazinoids in the stem. (a) Drawing of a maize plant indicating the three stem sections taken for analyses. (b) Starch concentrations (mean \pm SEM) in the three stem sections (basal, middle and upper section) of healthy plants (green) and of plants infested by the Western corn rootworm ('WCR-infested', yellow) below-ground. (c) Sucrose (Suc), glucose (Glc) and fructose (Fru) concentrations (mean \pm SEM) in the three stem sections (basal, middle and upper section) of healthy plants (green) and of 'WCR-infested' plants (yellow). (d) Soluble protein concentrations (mean \pm SEM) in the three stem sections (basal, middle and upper section) of healthy plants (green) and of 'WCR-infested' plants (yellow). (e) Benzoxazinoid concentrations (mean \pm SEM) in the three stem sections (basal, middle and upper section) of healthy plants (green) and of 'WCR-infested' plants (yellow). Capital letters indicate significant differences between the stem sections ($p < 0.05$). FW, fresh weight. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

experiment. Root herbivory by WCR larvae does not lead to a jasmonate burst in the leaves, but triggers water loss, abscisic acid induction and the expression of several marker genes encoding for defences, such as benzoxazinoids (Erb et al., 2009; Turlings, 2011). In the current work, we did not detect any differences in the measured markers of the plant primary and secondary metabolisms. Furthermore, no striking water loss symptom was observed, probably due to the fact that the maize plants were older when infested compared to previous studies and thus more likely to tolerate the water loss due to root herbivore damage. Interestingly, WCR feeding leads to resource reallocation and storage into the stem (Robert et al., 2014, 2015). It is therefore possible that ECB caterpillars may have benefitted from this WCR-induced nutrient storage, although the identity of the latter remains to be elucidated (Robert et al., 2014, 2015). Alternatively, it is conceivable that the better

performance of ECB larvae on WCR-infested plants was mediated through the reduction of anti-feedant volatile emissions. The detailed mechanisms underlying the increased performance of ECB larvae on WCR-infested plants remains to be elucidated.

Overall, we report an example of a plant volatile that mediates an herbivore oviposition behaviour in a context-dependent manner. Identifying volatiles involved in the oviposition site selection by ECB females can have outstanding potential for pest management strategies through push-pull strategies. For instance, spraying undecane early in the oviposition season may be sufficient to reduce ECB density in a field. Furthermore, understanding the mechanisms underlying plant-mediated above-ground interactions between herbivores may help to select resistant maize varieties for food production and to predict herbivore outbreaks in the field.

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DATA AVAILABILITY STATEMENT


The data that support the findings of this study are available from the corresponding author upon reasonable request.

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