ORIGINAL ARTICLE

Test of communication between potato plants in response to herbivory by the Colorado potato beetle

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Funding information
Ramón y Cajal Research Programme, Grant/Award Number: RYC-2013-13230; Spanish Ministry of Science, Innovation and Universities, Grant/Award Number: RTI2018-099322-B-I00

Abstract

1. Plant communication via airborne volatile organic compounds is a widespread phenomenon by which volatile organic compounds from damaged plants boost herbivore resistance in receiver plants. This phenomenon has been studied only in a handful of crop species.

2. We tested for communication between potato (*Solanum tuberosum*) plants in response to herbivory by the Colorado potato beetle, *Leptinotarsa decemlineata*. For this, we performed a greenhouse experiment with 15 potato varieties for which we caged pairs of plants (i.e., emitters and receivers) of the same variety. Half of the emitter plants were subjected to leaf damage by beetle larvae and the other half remained intact. We collected volatile organic compounds from emitter plants and estimated *L. decemlineata* damage on receivers.

3. We found no evidence of quantitative (total production) or qualitative (compound composition) changes in volatile organic compound emissions due to beetle herbivory. In addition, the leaf damage treatment on emitters had no significant effect on receiver herbivore resistance, suggesting no communication between infested and non-infested potato plants in response to Colorado potato beetle damage.

4. Overall, this study provides baseline information on airborne signalling (or the lack of thereof) in potato plants which can inform subsequent work that identifies airborne volatiles with potentially strong effects on priming or defence induction.

KEYWORDS
herbivory, *Leptinotarsa decemlineata*, plant–plant signalling, *Solanum tuberosum*, volatile organic compounds

INTRODUCTION

Plants perceive and respond to complex blends of above- or belowground VOCs emitted by conspecific or heterospecific neighbouring plants, resulting in so-called "plant communication" (Heil & Karban, 2010; Karban et al., 2014). Specifically, studies have found full induction or priming of defences by "receiver" plants when exposed to incoming VOCs released by attacked neighbours ("emitters"), thus boosting their resistance against herbivory (reviewed by Karban, 2015). To date, plant communication has been documented in over 30 plant species, including several agricultural crops and tree species (Heil & Karban, 2010; Karban et al., 2014), and is now a well-accepted form of airborne signalling influencing plant-induced defences. Moreover, its use in pest management (e.g., exogenous application of VOCs to induce resistance) has been proposed to boost plant protection and reduce pesticide use (Pickett & Khan, 2016; Stenberg et al., 2015; Turlings & Erb, 2018).

Research on plant communication has gained increased awareness of the importance of considering more robust design features and assessing the molecular and chemical basis of plant signalling

(Bouwmeester et al., 2019; Turlings & Erb, 2018). One of these features is the consideration of broad sample of plant genotypes to adequately control or test for intra-specific variation (or genetically-based specificity) in plant communication, ultimately increasing realism and inference from the obtained results (Moreira & Abdala-Roberts, 2019). This is particularly important in the case of domesticated species for which genotypes (varieties, landraces, etc.) can vary greatly in physical and chemical traits, and potentially also vary in induced responses and VOCs emissions (Stenberg et al., 2015). In addition, an essential feature of studies on plant–plant interactions is the assessment of the qualitative and quantitative changes in VOCs emissions, which are the signals mediating plant communication (Bouwmeester et al., 2019; Ninkovic et al., 2019). Ultimately, these assessments are aimed at identifying compounds or mixtures mainly responsible for plant communication.

Solanum tuberosum L. (Solanaceae) is an herbaceous perennial plant that can grow up to 60 cm high and propagates via seeds and tubers. It was first domesticated in modern-day southern Peru and north-western Bolivia between 8000 and 5000 BC (Hijmans & Spooner, 2001), and was introduced to Europe from the Americas during the second half of the 16th century. At present, there are more than 4000 edible varieties of potato, and this species is the world's fourth-largest food crop after maize, wheat, and rice (FAOSTAT, 2017). Due to the intensification of agriculture, potato plantations in both the Old and New World have faced many challenges in the last decades, including elevated threat of insect pests and diseases (Alyokhin et al., 2013). Notably, the specialist Colorado potato beetle (*Leptinotarsa decemlineata* L., Coleoptera: Chrysomelidae) is one of the most economically important pests on potato and is highly resistant to insecticides (Radcliffe & Lagnaoui, 2007). Both adults and larvae of *L. decemlineata* beetles feed on leaves of the plants, in turn causing a dramatic decrease in potato tuber production (Maharijaya & Vosman, 2015).

In this study, we investigated whether airborne communication occurs between potato (*S. tuberosum*) plants in response to leaf herbivory by *L. decemlineata*. Several species of Solanaceae have been shown to communicate through VOCs in response to herbivory (e.g., Farmer & Ryan, 1990; Karban et al., 2000; Meents et al., 2019). For instance, it was recently shown that sweet potato (*Ipomoea batata*) plants attacked by the defoliator *Spodoptera littoralis* markedly increased the emission of (E)-4,8–dimethyl–1,3,7-nonatriene (DMNT) which in turn induced the production of jasmonic acid-related defences on neighbouring plants (Meents et al., 2019). Here we used 15 commercial potato cultivars commonly cultivated worldwide, and measured the amount of leaf damage (i.e., a proxy of induced resistance) for "receiver" plants exposed to VOCs released by "emitter" plants damaged by *L. decemlineata* versus intact (control) emitters. In addition, we tested for beetle herbivory effects on the total emission and composition of VOCs to address changes in emissions potentially associated with any such plant communication. Results from this study provide baseline information on airborne signalling in potato plants which can inform environmentally-friendly methods for pest control in this crop.

MATERIALS AND METHODS

Experimental design

In June 2019, we individually sowed tubers from 15 varieties of *S. tuberosum* in 4-L pots containing potting soil with peat. Plants were grown in a glasshouse at the Mision Biológica de Galicia (Spain) under controlled light (minimum 12 h per day, photosynthetically active radiation = 725 ± 19 μmol/m^2/s) and temperature (10°C night, 25°C day), and were watered twice a week. We collected first-instar *L. decemlineata* larvae from surrounding potato plantations and reared them on potato plants of all varieties. Three weeks after sowing, we randomly assigned pairs of potato plants of the same variety to a $37.5 \times 37.5 \times 96.5$-cm plastic cage. Having pairs of plants in individual cages prevented cross-contamination of VOCs among cages (Moreira, Nell, Meza-Lopez, et al., 2018). One plant of each pair acted as the emitter and the other served as the receiver (emitter height [mean $\pm$ SE]: 44.45 ± 0.86 cm, receiver height: 44.34 ± 0.82 cm). Plants had on average 20 leaves at the time of the experiment. Within each cage, we separated emitter and receiver plants by 20 cm to avoid plant contact. We assigned half of the emitter plants to one of the two treatments: (1) subjected to *L. decemlineata* feeding (i.e., herbivore-induced plants) or (2) control (untreated plants). In total, there were 90 cages (45 per treatment) for a total of 90 receiver and 90 emitter plants, with potato varieties represented approximately equally across treatments (three replicate cages per variety by treatment level combination). In all cases, we paired emitters and receivers of the same variety. For the herbivore-induced treatment, we added one third-instar larva of *L. decemlineata* to each of two medium-sized leaves using a fine paintbrush and covered these leaves with a nylon bag in order to prevent herbivore dispersal. This level of infestation is similar to that found on young potato plants in surrounding field sites (X. Moreira, personal observation). For control plants, we also covered two medium-sized leaves with a nylon bag but did not add the larvae to control for any effect of bagging. After 3 days of herbivore exposure, we removed emitter plants from each cage whereas receivers remained inside the cages for a bioassay of induced resistance (see ahead). For the emitter plants, we collected all leaves for which we placed caterpillars, photographed them with a Nikon COOLPIX P100 digital camera (10.3 effective megapixels, $26\times$ zoom NIKKOR) and estimated the percentage of leaf area consumed by the herbivore using ImageJ software (version 1.52a; LOCI, University of Wisconsin, USA). The resulting mean percentage of leaf area removed by caterpillars for emitters subjected to the herbivore-induced treatment was $24.05 \pm 2.27\%$.

Prior to collecting emitter leaves for herbivory assessments, for a subset of randomly chosen emitter plants ($N = 25$ for each treatment, 1–3 plants per variety in each treatment), we collected aboveground VOCs following Rasmann et al. (2011). Briefly, we bagged plants with a 2-L Nalophan bag, and we trapped VOCs on a charcoal filter (SKC sorbent tube filled with Anasorb CSC coconut-shell charcoal) for 90 min at a rate of 0.25 L/min. We eluted traps with 150 μL dichloromethane (CAS#75-09-2, Merck, Dietikon, Switzerland) to which we had previously added two internal standards (n-octane

[CAS#111-65-9] and nonyl acetate [CAS#143-13-5], 200 ng of each in 10 μL dichloromethane). We subsequently injected 1.5 μL of each sample onto an Agilent 7890B Gas Chromatograph coupled with a 5977B Mass Selective Detector fitted with a 30 m × 0.25 mm × 0.25 μm film thickness HP-5MS fused silica column (Agilent, Santa Clara, CA, USA). We operated the GC in splitless mode with helium as the carrier gas (flow rate 1 mL/min). The GC oven temperature programme was: 3.5 min hold at 40°C, 5°C/min ramp to 250°C, and 1 min hold at 250°C. We identified volatile terpenes using the library NIST Standard Reference Database 1A v17 and by comparison with commercial standards when available. We measured total emission of individual VOCs by using normalized peak areas per fresh weight. We obtained the normalized peak area per fresh weight of each compound by dividing their integrated peak area by the integrated peak area of the internal standard and then dividing this value by the leaf fresh weight (Moreira et al., 2019).

The same day after collecting emitter VOCs, we set up a bioassay to test whether exposure to VOCs from emitters boosted herbivore resistance in receiver plants. For this, we used all receiver plants and exposed two newly developed leaves per plant to larvae of *L. decemlineata* following the same procedure described above for the induction of emitter plants. After 3 days, we collected all leaves subjected to larval feeding, photographed them and estimated the percentage of leaf area consumed as described earlier for emitter plants.

Statistical analyses

Treatment effect on emitter VOCs

We analysed the effect of the induction treatment (control vs. leaf herbivory by *L. decemlineata*) and potato variety (fixed factors) on total VOCs emission by emitter plants by using a linear mixed model with PROC MIXED in SAS (SAS 9.4 System, SAS, Cary, NC, USA) (Littell et al., 2006). We also included the height of emitter plants as a covariate to account for differences in plant size which may affect volatile emissions. We did not test for genetic variation in the inducibility of VOCs (i.e., induction treatment × potato variety) due to insufficient replication. We log-transformed total VOC emission to achieve normality of residuals. In addition, we ran a permutational multivariate analysis of variance (PERMANOVA) model with the same predictor variables testing for an effect of induction treatment on VOC composition (using abundances of each compound). This analysis was based on 10,000 permutations using the *vegan* package in R version 4.0.2 software (Oksanen et al., 2016). To visualize these results, we conducted a principal coordinates analysis based on Bray–Curtis pairwise dissimilarities, and graphed the centroids of each induction treatment effect (Moreira et al., 2021). We also identified influential VOCs as those having strong associations ($R^2 > 0.50$) for with the first two ordination axes (using *envfit* function in *vegan* package; Oksanen et al., 2016), and displayed these relationships using biplot arrows with length scaled to R^2 values.

TABLE 1 Total emission (measured as normalized peak areas per fresh weight) of volatile organic compounds for control and herbivore (*Leptinotarsa decemlineata*)-induced emitter potato (*Solanum tuberosum*) plants

Compound	Control	Herbivory
(E)-2-hexenal	—	—
3-hexen-1-ol	—	—
1-methylpropyl-2-cyclopentene	0.286 ± 0.059	0.306 ± 0.051
1,2,3,3,4-pentamethyl-1-cyclopentene	0.358 ± 0.125	0.557 ± 0.142
1R-α-pinene	0.093 ± 0.053	0.150 ± 0.051
Cyclohexane, 1-methyl-2-propyl-	0.076 ± 0.030	0.255 ± 0.078
Cumene	0.029 ± 0.011	0.109 ± 0.019
Tridecane	0.076 ± 0.028	0.080 ± 0.030
Elixene	0.087 ± 0.028	0.113 ± 0.039
α-cubebene	0.441 ± 0.127	0.128 ± 0.046
Copaene	—	0.022 ± 0.011
β-bourbonene	—	0.716 ± 0.187
β-elemene	0.303 ± 0.023	0.354 ± 0.020
Tetradecane	0.272 ± 0.080	0.251 ± 0.081
α-gurjunene	9.781 ± 2.369	7.293 ± 1.460
β-caryophyllene	0.086 ± 0.023	0.084 ± 0.030
β-cubebene	0.175 ± 0.064	0.129 ± 0.044
α-bergamotene	0.245 ± 0.106	0.356 ± 0.126
β-sesquiphellandrene	0.127 ± 0.050	0.434 ± 0.175
Germacrene-D	1.712 ± 0.430	2.584 ± 0.947
10-methylnonadecane	0.154 ± 0.031	0.132 ± 0.029
(Z)-β-farnesene	0.181 ± 0.043	0.177 ± 0.053
Nonadecane	1.260 ± 0.286	1.750 ± 0.541
2,6,10-trimethyltetradecane	0.548 ± 0.142	0.467 ± 0.093
α-cubebene	0.490 ± 0.144	—
β-eudesmene	0.154 ± 0.043	0.201 ± 0.050
Zingiberene	0.733 ± 0.090	0.735 ± 0.092
Elixene	0.072 ± 0.030	0.139 ± 0.041
β-bisabolene	0.643 ± 0.180	0.727 ± 0.202
Nerolidol	0.044 ± 0.026	0.051 ± 0.026
β-sesquiphellandrene	0.115 ± 0.045	0.065 ± 0.024
Carotol	0.021 ± 0.011	0.044 ± 0.018
2-hexyl-1-octanol	—	—
Unknown 1	0.971 ± 0.202	1.376 ± 0.398
Unknown 2	0.129 ± 0.069	0.041 ± 0.017
Unknown 3	0.342 ± 0.028	0.295 ± 0.026
Caryophyllene oxide	0.095 ± 0.034	0.147 ± 0.051
Ledol	0.064 ± 0.017	0.046 ± 0.013
Unknown 4	0.137 ± 0.038	0.126 ± 0.053

*Note*: Least-square means ± SE are shown. —, present in less than three samples.

Treatment effect on receiver resistance

To investigate whether the exposure to emiter VOCs boosted resistance against herbivory in receiver plants, we tested for the effect of induction treatment (control vs. leaf herbivory by *L. decemlineata*) and

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TABLE 2 Results from linear models testing for the effect of herbivore induction treatment (control vs. leaf herbivory by *Leptinotarsa decemlineata*) and plant variety (fixed effects) on the total amount and composition of volatile organic compounds (VOCs) released by emitter potato (*Solanum tuberosum*) plants and the percentage of leaf damaged area by herbivore feeding on receiver potato plants

	Treatment			Plant variety			Plant height		
Response	d.f.$_{num,den}$	F/Pseudo-F/χ^2	p	d.f.$_{num,den}$	F/Pseudo-F/χ^2	p	d.f.$_{num,den}$	F/pseudo-F/χ^2	p
VOC emission	1, 34	0.40	0.533	14, 34	2.38	**0.019**	1, 34	2.93	0.096
VOC composition	1, 34	1.41	0.197	14, 34	1.84	**0.003**	1, 34	0.82	0.493
Leaf area consumed	1, 87	1.43	0.231	14, 87	12.28	0.584	1, 87	0.01	0.948

Note: For VOCs composition, we used a permutational multivariate analysis of variance (PERMANOVA) model. Plant height (of emitters for VOCs and of receivers for leaf damage) was included as a covariate to control for differences in plant size. Statistical descriptor (F-values for VOC emission, pseudo-F values for VOC composition and chi-square values [χ^2] for leaf area consumed), degrees of freedom and associated significance levels (p) are shown. Significant effects (p < 0.05) are in bold.
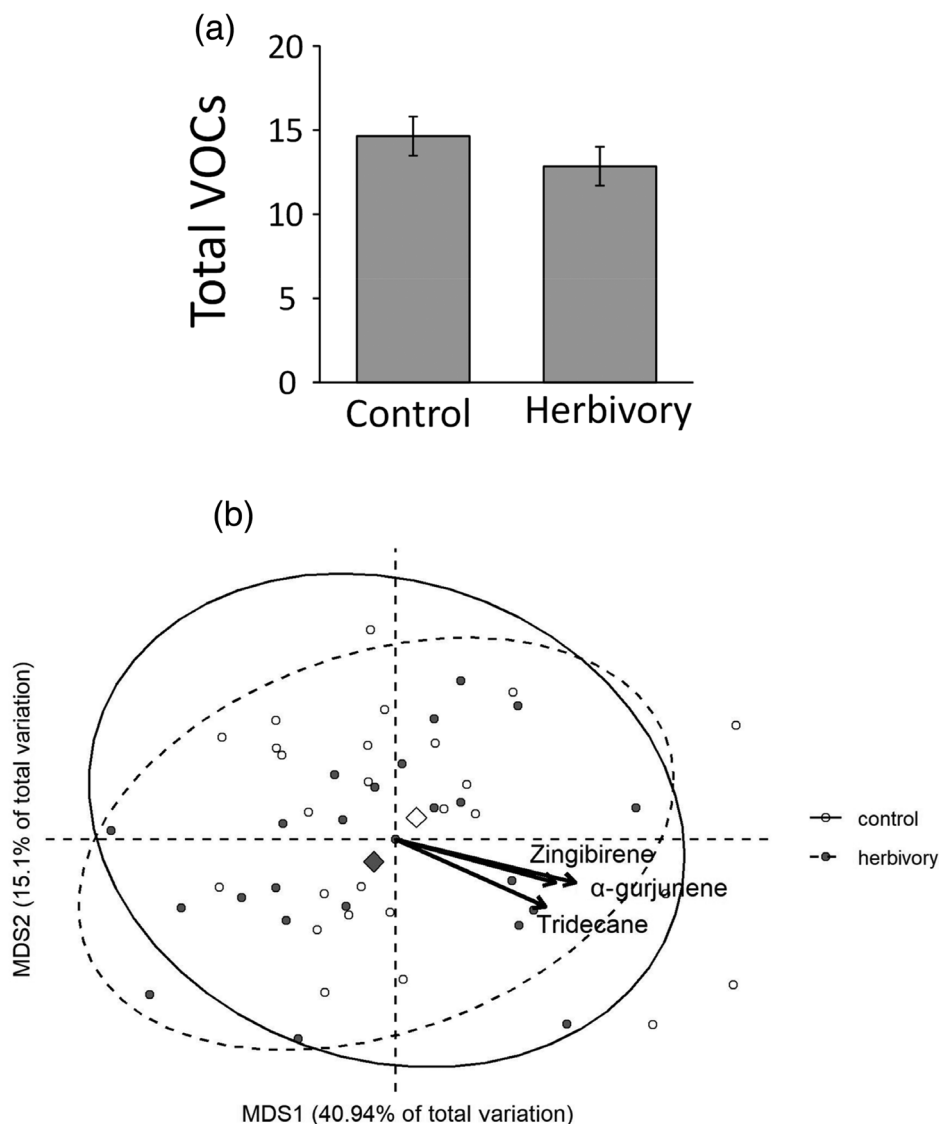
FIGURE 1 (a) Effects of herbivore induction treatment (control vs. leaf herbivory by *Leptinotarsa decemlineata*) on the total amount of volatile organic compounds (VOCs; measured as normalized peak areas per fresh weight) released by emitter potato (*Solanum tuberosum*) plants. Bars are back-transformed least-square means ± SE obtained from the statistical model (N = 25; see Table 2). (b) Unconstrained ordinations showing the effects of emitter induction treatment on log-transformed composition of VOCs released by emitter plants. Biplot arrows show associated linear trends with volatiles, scaled to reflect relative magnitude of effects based on R^2 values (R^2 > 0.50, p < 0.001). The emitter induction treatment ordination displays control and pathogen-induced centroids (represented as diamonds) and 95% ellipses. The first two axes of this ordination accounted for ca. 56% of the treatment effect in volatile composition (41% and 15%, respectively). Control and herbivore-induced plants are depicted as closed and open circles, respectively. See Table 2 for permutational analysis of variance (PERMANOVA) test on VOCs composition related to this ordination
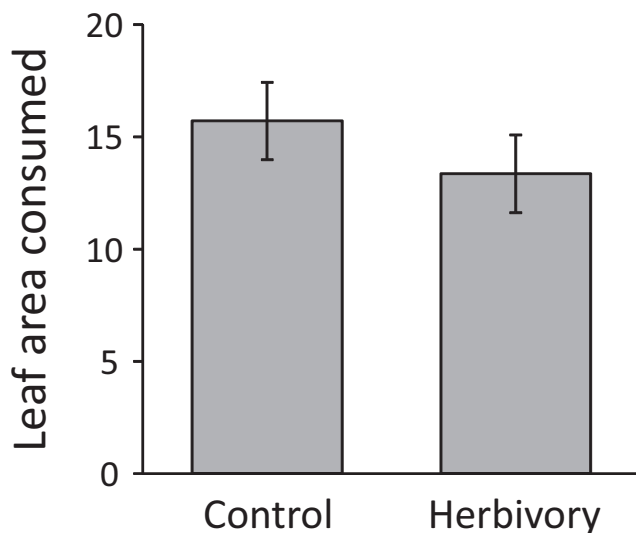
FIGURE 2 Effects of emitter herbivore induction treatment (control vs. leaf herbivory by *Leptinotarsa decemlineata*) on the percentage of leaf area consumed by *L. decemlineata* on receiver potato (*Solanum tuberosum*) plants. Bars are back-transformed least-square means $\pm$ SE obtained from the statistical model ($N = 45$; see Table 2)

potato variety (fixed factors) on the percentage of leaf area consumed of receivers using a generalized linear mixed model with a beta distribution (*gamlss* function in the *gam* package in R; Stasinopoulos & Rigby, 2007). In addition, we included the effect of individual plant as a random factor to control for non-independence of each pair of leaves analysed per receiver (see above). We again included the height of receiver plants as a covariate to account for differences in size which could affect induced responses. Likewise, we did not test for genetic variation in neighbouring plant resistance (i.e., induction treatment × potato variety) due to insufficient replication.

RESULTS

We detected a total of 39 VOCs in the headspace of emitter potato plants, of which 32 were positively identified (Table 1). Contrary to expectations, the induction treatment (control vs. *L. decemlineata* damage) did not significantly affect the total emission (Table 2, Figures 1a and S1A) or composition (PERMANOVA: Table 2, Figure 1b) of VOCs released by emitter plants. We found significant variation among potato varieties in the total emission and composition of VOCs released by emitter plants (Table 2). Total emission of VOCs varied up to 11-fold among varieties (3.68–41.23 normalized peak area per fresh weight; Figure S2A).

Analyses indicated that neither the emitter induction treatment nor potato variety had significant effects on the percentage of herbivore-damaged leaf area of receiver plants (Table 2, Figures 2, S1B, and S2B).

DISCUSSION

Overall, we found no evidence of quantitative (total production) or qualitative (compound composition) changes in potato VOC emissions by *L. decemlineata* herbivory across 15 potato varieties. Accordingly, the leaf damage treatment on emitters did not result in a significant change in herbivory levels on receiver plants, as there was no effect on VOCs emissions to mediate any such plant communication due to beetle attack. This study provides the first assessment of *L. decemlineata* effects on induced volatile emissions by potato and its effects on the resistance of neighbouring plants. Although no effects were found, results call for subsequent work addressing plant communication in this crop. We next discuss potential interpretations of the obtained results, methodological considerations, as well as other features to be considered in future investigations.

The amount of herbivory inflicted by beetle larvae on emitter plants was close to 25% of leaf area removed. Although outbreak levels of this pest can result in complete defoliation of plants (Maharijaya & Vosman, 2015), the inflicted levels of damage on emitter leaves presumably have substantial impacts on young potato plants and therefore strongly drive induced responses at this stage. Having said this, higher damage levels might be needed to elicit stronger changes in VOCs emissions. Alternatively, it is also possible that this specialist insect manipulates potato defences and inhibits their induction, as shown for other plant species attacked by specialist (and generalist) herbivores (Moreira, Abdala-Roberts, Galmán, et al., 2018; Robert et al., 2012; Sarmento et al., 2011). By contrast, recent work by our group showed communication among potato plants in response to leaf damage by the generalist *Spodoptera exigua* (Martín-Cacheda et al., unpublished data), another common insect pest on potato, suggesting that plant–plant signalling is herbivore-specific. In addition, in another study we found that the pathogen *Sclerotinia sclerotiorum* apparently prevented the induction of VOCs emissions in potato plants, as shown by down-regulation of genes coding for VOC precursors of terpene synthase genes (Moreira et al., 2021). By contrast, genes associated with the salicylic acid pathway and synthesis of phenolics were up-regulated. This suggests that these compounds play a role in resistance against this pathogen, and potentially also insect herbivores. In summary, further work assessing molecular changes (e.g., gene expression, precursors of end products) and secondary metabolite levels in potato plants after beetle damage, as well as bioassays for induced resistance (control vs. plants previously damaged by beetle) are needed. In addition, testing for multiple levels of herbivory (including higher levels than those used here) would be desirable to assess thresholds and differences in the magnitude of induction in emitter plants potentially affecting communication. Likewise, although we used VOCs exposure times similar to other species for which communication has been found (e.g., Heil & Silva Bueno, 2007; Karban et al., 2016; Moreira, Nell, Katsanis, et al., 2018), a longer induction period could help strengthen conclusions about the presence as well as magnitude of potato communication in response to *L. decemlineata* herbivory.

An important consideration in plant communication studies is to test for actual changes in receiver plant defences as well as priming

after VOCs exposure (Ton et al., 2007). For several plant species, it has been shown that incoming VOCs from damaged emitters may not elicit full induction of receiver defences, but rather trigger metabolic changes which result in a stronger response only after herbivory has taken place (i.e., a priming effect) (Heil & Kost, 2006; Martinez-Medina et al., 2016). Thus, although the lack of treatment effect on receiver leaf damage suggests that there was no evidence of either initial (full) induction or priming, it is worthwhile considering future designs that separate and test for these two stages or types of response to emitter VOCs. To this end, work is needed which measures receiver defences after VOCs exposure, and, subsequently, also on damaged receivers to assess effects of VOC-mediated priming on defence induction. Doing so can uncover the nature of receiver-induced responses as well as develop work aimed at testing for ecologically relevant scenarios of plant–plant signalling in potato.

As a closing comment, we note that there has been a pressing need for the development of environmentally-friendly methods for pest management that involve reduced pesticide use and alternative biocontrol strategies. Although our results provide no evidence of communication and boosted resistance to a specialist beetle in potato plants, we call for continued work to devise sustainable and less resource-intensive methods for pest control in potato. Further tests under different conditions (including field trials), exploring alternative experimental design features (exposure time, damage levels) and mechanisms (e.g., molecular) can help to better understand plant-plant signalling and the potential use of VOCs for pest management in this crop.

CONFLICT OF INTEREST
The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT
The data used in this study will be archived at the Dryad Digital Repository.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Figure S1 Boxplots showing the effects of induction treatment (control vs. leaf herbivory by *Leptinotarsa decemlineata*) on (A) the total amount of volatile organic compounds (VOCs, measured as normalized peak areas per fresh weight) released by emitter potato (*Solanum tuberosum*) plants and (B) percentage of leaf area consumed by *Leptinotarsa decemlineata* on receiver plants.

Figure S2. Variation among 15 varieties of potato (*Solanum tuberosum*) in (A) total amount of volatile organic compounds (VOCs, measured as normalized peak areas per fresh weight) released by emitter plants and (B) percentage of leaf area consumed by *Leptinotarsa decemlineata* on receiver plants. Bars are least-square means $\pm$ SE ($N = 3$–6).