







RESEARCH ARTICLE

Effect of water availability on volatile-mediated communication between potato plants in response to insect herbivory

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Abstract

1. Airborne plant communication is a widespread phenomenon in which volatile organic compounds (VOCs) from damaged plants boost herbivore resistance in neighbouring, undamaged plants. Although this form of plant signalling has been reported in more than 30 plant species, there is still a considerable knowledge gap on how abiotic factors (e.g. water availability) alter its outcomes.
2. We performed a greenhouse experiment to test for communication between potato plants *Solanum tuberosum* in response to herbivory by the generalist insect *Spodoptera exigua* and whether communication was affected by water availability. We paired emitter and receiver potato plants, with half of the emitters damaged by *S. exigua* larvae and half serving as undamaged controls. Both emitter and receiver plants were factorially subjected to one of two watering treatments: high (i.e. well-watered) vs. low (i.e. reduced watering) availability, thus effectively teasing apart water availability effects on the emission and reception components of signalling. After 4 days of herbivore feeding, we collected emitter VOCs and receivers were subjected to feeding by *S. exigua* to test for effects of signalling on induced resistance.
3. Herbivory by *S. exigua* led to increased VOCs emissions as well as changes in VOCs composition in emitter plants. Furthermore, emitters subjected to low water availability exhibited a weaker induction of VOCs in response to herbivory relative to well-watered emitters. Results from the feeding bioassay indicated that receivers exposed to VOCs from herbivore-induced emitters showed lower *S. exigua* damage (i.e. induced resistance) compared to receivers exposed to undamaged emitters. However, we did not observe a significant effect of water availability in either emitters or receivers on plant signalling effects on receiver resistance.
4. Overall, our study contributes to understanding how the abiotic context affects plant communication by providing evidence of water availability effects on the

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induction of VOCs that act as airborne signals between plants. The observed changes in induced VOCs due to the water treatment had no detectable consequences for plant communication. Accordingly, the induction of key compounds mediating communication was apparently not compromised by our experimental conditions.

KEYWORDS

drought, plant–plant signalling, *Solanum tuberosum*, *Spodoptera exigua*, volatile organic compounds, water availability

1 | INTRODUCTION

Research has shown that plants can perceive and respond to complex blends of above- and below-ground volatile organic compounds ('VOCs' hereafter) emitted by conspecific or heterospecific neighbours, a phenomenon termed 'plant communication' (Heil & Karban, 2010; Karban et al., 2014). This form of plant–plant signalling frequently involves either priming or induction of defences in undamaged 'receiver' plants when exposed to VOCs released by herbivore-induced neighbours ('emitters'), which results in increased induced resistance against herbivory in receiver plants (Karbon, 2015). Several non-mutually exclusive hypotheses have been proposed to explain the ecological and evolutionary role of plant communication. Among those, kin selection has been proposed as a key mechanism driving the origin and maintenance of plant communication among conspecifics (Karbon et al., 2013; Karban & Shiojiri, 2009). Namely, communication between unrelated individuals would come at high costs for the emitter plants, as they would increase competitors' fitness at the expense of their own fitness (Heil & Karban, 2010; Heil & Ton, 2008). Another hypothesis argues that inter-plant signalling arose as a by-product of plants using volatiles for efficient intra-plant signalling (Frost et al., 2007; Heil & Silva Bueno, 2007). That said, and while these explanations provide a useful framework for understanding the evolutionary relevance of plant communication, we still lack mechanistic data for understanding ecological variation in plant communication. Thus, while VOCs emissions have been amply shown to drive this phenomena, how biotic and abiotic factors interact with VOCs induction and perception to drive variation in communication needs to be elucidated (Bouwmeester et al., 2019; Turlings & Erb, 2018).

Recent advances point to several key factors that determine the strength of plant–plant signalling through VOCs (Moreira & Abdala-Roberts, 2019). Notably, the total amount of volatiles emitted as well as the blends of compounds and the abundance of individual compounds present in emissions depend on multiple biotic and abiotic factors, leading to specificity and context dependency in plant communication (Moreira & Abdala-Roberts, 2019). For example, recent work has shown that communication is strongly contingent upon the identity of the attacking herbivore, whereby resistance in receivers is only boosted when emitters and receivers are attacked by the same insect (Moreira et al., 2018). In addition, though much less

studied, plant communication is likely contingent on abiotic factors such as soil nutrients, salinity or water availability, as these often affect plant defence induction in response to herbivory, including VOCs (Gouinguéné & Turlings, 2002; Moreira et al., 2015; Quijano-Medina et al., 2021; Sampedro et al., 2011; Suárez-Vidal et al., 2019). There are at least two non-exclusive mechanisms by which abiotic conditions could affect plant communication. First, abiotic factors can modulate the inducibility of VOCs in response to herbivory in emitter plants (Gouinguéné & Turlings, 2002; Holopainen & Gershenzon, 2010; Scott et al., 2019; Vallat et al., 2005). Second, these factors can shape receiver responses to emitter VOCs such as the physiological priming of defences and subsequent induced resistance in response to damage (Martinez-Medina et al., 2016; Ton et al., 2007; Wilkinson et al., 2019). Accordingly, studies that simultaneously address abiotic effects on emitters and receivers are needed to advance our understanding of the mechanisms that underlie context dependency of plant communication in response to herbivory.

Despite research on water availability effects on plant defences in both natural and cultivated species, including VOCs, its effects on plant–plant signalling are poorly understood. To date, only two studies have evaluated the effects of water availability on plant communication (Catola et al., 2018; Pezzola et al., 2017). First, Catola et al. (2018) investigated the individual and combined effects of emitter water stress and aphid feeding on the emission of VOCs in tomato *Solanum lycopersicum* and whether reception of VOCs from stressed emitters increased the attraction of parasitic wasps (i.e. indirect resistance by natural enemies) in receiver plants. They found that both factors (aphid feeding and water stress), individually or in combination, significantly induced VOCs emission. Correspondingly, receivers exposed to VOCs from stressed emitters exhibited increased indirect resistance by parasitic wasps, independently of whether abiotic (water availability) or biotic (aphid feeding) effects on emitters were considered individually or in combination. Second, Pezzola et al. (2017) similarly found that VOCs from damage-induced sagebrush *Artemisia tridentata* plants boosted receiver resistance to generalist grasshoppers but this effect was not contingent on the level of water availability, which in this case was manipulated for receiver plants. These studies together suggest that signalling is resilient to effects of water availability in both systems. However, more studies are needed to understand the commonness

and abiotic context-dependency in plant signalling, particularly in cases where abiotic stress impairs VOCs induction. In particular, manipulations of water availability for both emitters and receivers (i.e. emission vs reception components) coupled with detailed assessments of quantitative vs. qualitative changes in VOCs are needed to unveil the mechanisms of abiotic effects on signalling.

In this study, we investigated whether VOC-mediated airborne communication in potato *Solanum tuberosum* plants in response to leaf herbivory by the generalist insect *Spodoptera exigua* was contingent on water availability effects on both emitter and receiver plants (interactive effects of emitter herbivory and water availability in the emitter and receiver), and evaluated qualitative and quantitative changes in emitter VOCs emissions to gain insight on the mechanism behind such effects. For this, we carried out a greenhouse experiment where we paired potato plants (i.e. emitters and receivers) and induced half of the emitters with *S. exigua* larvae. We subjected emitter and receiver plants to one of two water availability treatments: high (i.e. well-watered) vs. low (i.e. reduced watering) water availability. We measured total emission and composition of VOCs in emitter plants and then conducted a caterpillar bioassay on receiver plants to test for effects on the amount of leaf area consumed by *S. exigua* (i.e. induced resistance). We hypothesized that low water availability in emitters would hamper the inducibility of VOCs in response to herbivory, resulting in weaker (or null) airborne signalling effects on receiver resistance. Similarly, we hypothesized that low water availability in receivers would hamper the physiological priming and subsequent induced resistance boosted by perception of VOCs from herbivore-induced emitters. Our work provides insights into the effects of water availability on both the emission and reception of herbivore-induced VOCs and their implications for plant communication. This knowledge may not only inform and optimize sustainable methods that make use of plant volatiles to boost crop resistance (Pickett & Khan, 2016; Stenberg et al., 2015; Turlings & Erb, 2018), but also contribute to mechanistic research on the multiplicity of ecological roles of plant VOCs. We do so first, by investigating the mechanisms that underlie plant communication and second, by investigating the abiotic context dependency and potential effects of reduced water availability on induced resistance in plants via VOCs.

2 | MATERIALS AND METHODS

2.1 | Study system

Solanum tuberosum L. (Solanaceae) is an herbaceous perennial plant that grows up to 60 cm high and propagates via seeds and tubers. It was domesticated c. 8,000 years ago in the Central Andes region (Peru-Bolivia) and introduced to Europe during the second half of the 16th century (Hijmans & Spooner, 2001). There are more than 4,000 edible varieties of potato which together represent the world's fourth largest food crop after maize, wheat and rice (FAOSAT, 2017). A previous meta-analysis reported stronger plant-plant signalling in

response to herbivory and concurrent induced resistance in crops than natural species (Karban et al., 2014). Thus, agricultural species represent valuable model systems to evaluate abiotic modulation of plant communication. In turn, insights gained from crop species such as potato can be transferred to natural systems, contributing to understand how environmental variation in natural ecosystems (e.g. in climate conditions) may affect induced responses and plant-plant signalling in a broad ecological sense. In addition, the role of volatile emissions in plant-plant signalling affecting induced resistance has not been investigated for potato plants and thus represents both a timely and potentially important research avenue for improving potato resistance to pests in the context of integrated pest management.

2.2 | Experimental design

In April 2021, we sowed 168 tubers from three different *S. tuberosum* varieties (cv. Baraka, cv. Desiree and cv. Monalisa) in 4-L pots containing potting soil and peat (Gramoflor GmbH & Co. KG Produktion). We grew plants in a glasshouse under controlled light (minimum 10 hr per day, photosynthetically active radiation = $725 \pm 19 \mu\text{mol m}^{-2} \text{s}^{-1}$) and temperature (10°C night, 25°C day), and watered them twice a week up to field capacity. Five weeks after germination, we assigned half of the plants to one of two water availability treatments: high (i.e. well-watered) vs. low (i.e. reduced watering) water availability (Figure 1). We watered plants in the high water availability treatment every 3 days to replenish the 100% of their water demand, whereas for plants in the low water availability treatment watering was reduced to meet the 25% of the total water demand (Li et al., 2019). We estimated water demand gravimetrically. To corroborate that plants in the low water availability treatment were under stronger physiological stress than well-watered plants, 2 weeks after the start of the treatments (right before applying the herbivory treatment, see below) we used a subset of 24 plants (half high and half low water availability; four of each potato variety) to measure stomatal conductance and photosynthesis (Gilbert & Medina, 2016). We measured stomatal conductance and net photosynthetic rate on a leaflet of a young, fully expanded leaf from 11:30 to 12:30 am at an irradiance of $1,500 \mu\text{mol m}^{-2} \text{s}^{-1}$ and CO_2 concentration of $400 \mu\text{mol mol}^{-1}$ with a portable photosynthesis system Li-6400XT (Li-Cor Inc.). Plants in the low water availability treatment exhibited significantly lower stomatal conductance ($F_{1,22} = 22.1, p < 0.001$) and photosynthetic rates ($F_{1,22} = 31.5, p < 0.001$) compared to well-watered plants. Specifically, reduced watering resulted in a 90% and an 80% decrease in stomatal conductance (high water availability: $0.073 \pm 0.01 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$; low water availability: $0.008 \pm 0.01 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and photosynthesis rates (high water availability: $9.31 \pm 0.94 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; low water availability: $1.88 \pm 0.94 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), respectively (Figure S1a,b).

Seven weeks after germination (2 weeks after establishing the water availability treatments), we paired the remaining 144 potato plants in $37.5 \times 37.5 \times 96.5$ cm plastic cages to

Communication under four water availability treatments

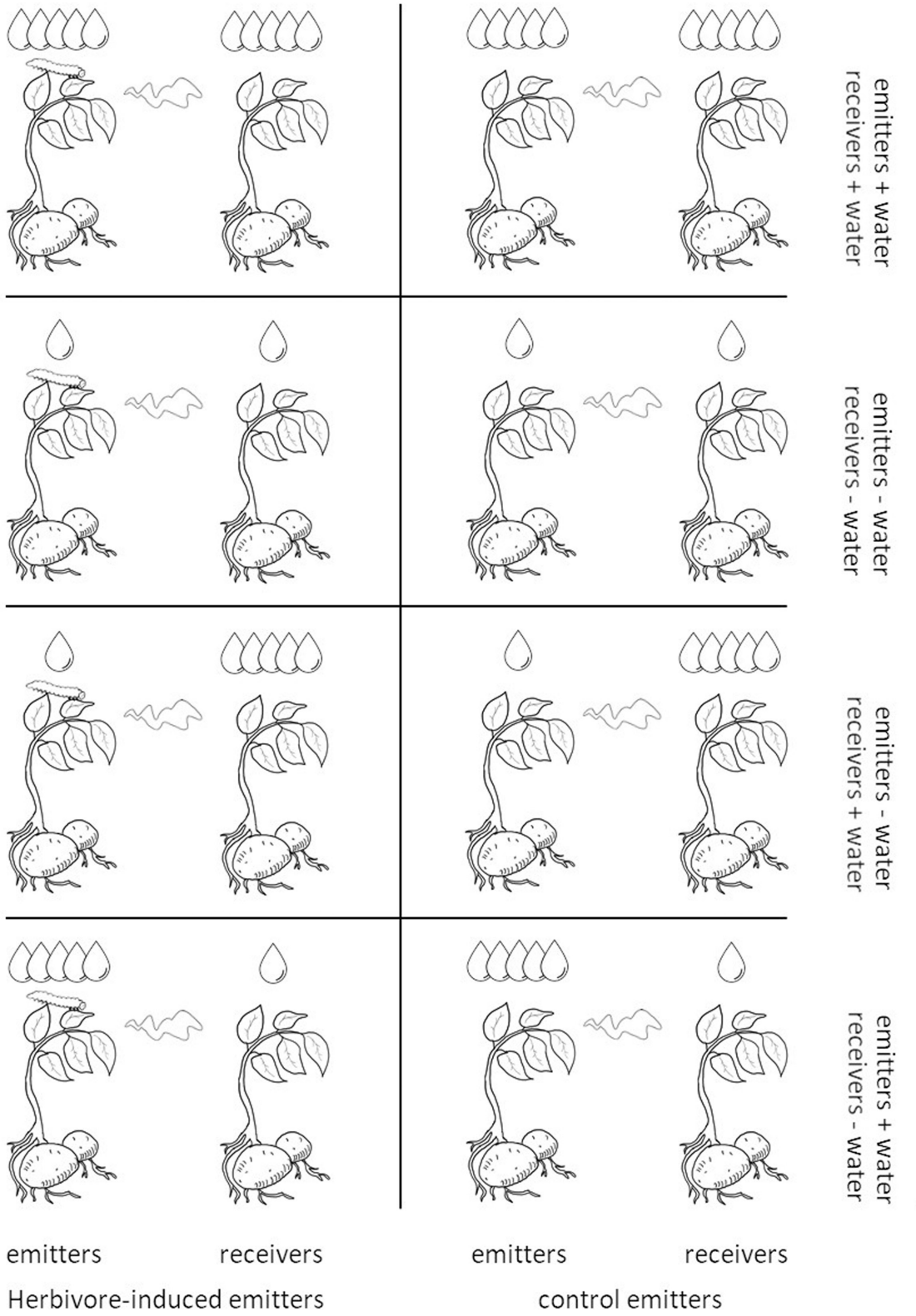


FIGURE 1 Experimental design to test for effects of water availability on communication between potato plants ($N = 72$). We paired potato plants designated as emitters and receivers, with half of the emitters receiving damage by *Spodoptera exigua* larvae (i.e. herbivore-induced plants) and half serving as undamaged controls. Both emitter and receiver plants were also subject to one of two water availability treatments: high (i.e. well-watered) vs. low (i.e. reduced watering).

prevent VOCs cross-contamination between replicates. One plant of each pair (i.e. replicate) acted as the emitter (average height $\pm SE = 51.17 \pm 0.64$ cm) and the other served as the receiver (48.52 ± 0.70 cm). Within each cage, emitter and receiver plants were placed 20 cm apart so that they did not touch each other. Plants in each water stress treatment were randomly selected as either receiver or emitter plants resulting in a factorial design consisting on four combinations of water availability treatment in the emitter (two levels; high vs. low) and water availability treatment in the receiver (two levels; high vs. low) (Figure 1). In addition, we randomly assigned emitter plants within each cage to one of the following herbivory treatments: (a) subjected to *S. exigua* feeding ('herbivore-induced plants' hereafter) or (b) control (intact; no herbivory) plants (Figure 1). Overall, the experiment consisted in 72 replicate cages, namely 36 for the herbivore-induced treatment (nine per emitter vs. receiver water availability combination) vs. 36 for the control (nine per emitter vs. receiver water availability combination). Emitter and receiver plants were always of the same variety and varieties were similarly distributed across treatment combinations. For herbivore-induced emitters, we placed two third-instar larvae of *S. exigua* on each of three fully expanded leaves per plant using a fine paintbrush and covered these leaves with a nylon bag to prevent herbivore dispersal. For control plants, we covered three fully expanded leaves with a nylon bag but without adding the larvae to control for a possible bagging effect. After 4 days of herbivore feeding, we removed all emitter plants from cages and collected VOCs from each emitter (see below). After VOCs sampling, we collected leaves subjected to larvae feeding and photographed them with a Samsung Galaxy A30s (25 effective megapixels, 4x digital zoom). We estimated the percentage of leaf area consumed using the mobile application BioLeaf—Foliar Analysis™ (Brandoli Machado et al., 2016). Average percentage leaf area consumed by *S. exigua* for herbivore-induced emitters was 77.58% (± 3.72) and was homogeneously distributed among plants in the high ($80.46\% \pm 3.50$) vs. low ($73.63\% \pm 4.25$) water availability treatments ($F_{1,33} = 0.7$; $p = 0.399$).

We collected above-ground VOCs produced by emitter plants following Rasmann et al. (2011). Briefly, we bagged plants with a 2-L Nalophan bag and trapped VOCs on a charcoal filter (SKC sorbent tube filled with anascorb CSC coconut-shell charcoal) for 2 hr at a rate of 0.25 L/min. We eluted traps with 150 μ l dichloromethane (CAS#75-09-2; Merck) to which we had previously added one internal standard (tetralin [CAS#119-64-2], 200 ng in 10 μ l dichloromethane). We then injected 1.5 μ l of the extract for each sample into an Agilent 7890B gas chromatograph (GC) coupled with a 5977B mass selective detector (MSD) fitted with a 30 m \times 0.25 mm \times 0.25 μ m film thickness HP-5MS fused silica column (Agilent). We operated the GC in pulsed splitless mode

(250°C, injection pressure 15 psi) with helium as the carrier gas (constant flow rate 0.9 ml/min). The GC oven temperature programme was: 3.5 min hold at 40°C, 5°C/min ramp to 230°C, then a 3 min hold at 250°C post-run. Transfer line was set at 280°C. In the MS detector (EI mode), a 33–350 (m/z) mass scan range was used with MS source and quadrupole set at 230 and 150°C, respectively. We identified volatile terpenes using the NIST MS Search Program v.2.3 and by comparison with the terpenes reference database developed at the University of Neuchâtel and based on pure standards. We quantified total emission of individual VOCs using normalized peak areas and expressed it as nanograms per hour (ng/hr). We obtained the normalized peak area of each individual compound by dividing their integrated peak area by the integrated peak area of the internal standard (Abdala-Roberts et al., 2022). The total emission of VOCs was then calculated as the sum of individual VOCs.

The same day after collecting VOCs in emitters, we set up an herbivore bioassay on receivers to test whether prior exposure to VOCs from herbivore-induced emitters increased herbivore resistance. For this, we placed one third-instar *S. exigua* larvae on each of two fully expanded leaves per plant following the same procedure described above for emitter induction. We kept larvae on receivers for 3 days and then estimated the percentage of leaf area consumed by *S. exigua* ('leaf damage' hereafter) using the same procedure described above for emitter plants.

2.3 | Statistical analyses

First, we used general linear mixed models to test the effect of emitter herbivory treatment (two levels: control vs. herbivore-induced), water availability treatment in emitters (two levels: high vs. low), and their interaction (all fixed factors) on total VOCs emission by emitter plants. We included potato variety as a random factor. We also included the height of emitter plants as a covariate to account for differences in plant size which may affect volatile emissions. We square-root-transformed total VOCs emission to achieve normality of model residuals.

Second, we ran a permutational multivariate analysis of variance (PERMANOVA) based on 10,000 permutations to test the effects of herbivory and water availability (and their interaction) in emitter plants on VOC composition (using abundances of each individual compound), also controlling for variation among potato varieties. To visualize these results, we conducted a principal coordinate analysis based on Bray–Curtis pairwise dissimilarities, and graphed the centroids of each herbivory and water availability treatment effect (Moreira et al., 2021). We also identified influential VOCs defined as those having strong associations with the first two ordination axes

($R^2 > 0.40$), and displayed these relationships using biplot arrows with the length scaled to R^2 values.

Third, to test the effects on receiver-induced resistance, we ran a general linear mixed model with leaf damage as the response variable. We treated the main effects of herbivory in the emitter plant (two levels: control vs. herbivore-induced), water availability in the emitter plant (two levels: high vs. low), water availability in the receiver plant (two levels: high vs. low) as fixed factors. We also included all two- and three-way interactions as fixed factors to test for the effects of emitter and receiver water availability on induced resistance in receivers as boosted by VOCs emitted by herbivore-induced emitters (i.e. abiotic modulation of plant communication). We included individual plant as a random factor to control for non-independence of each pair of leaves analysed per receiver. We also included plant height as a covariate to account for differences in size which could affect induced responses. We square-root-transformed mean leaf damage to achieve normality of model residuals.

Statistical analyses were run in R software version 3.06.0 (R Core Team, 2013). Linear mixed models were implemented using the *lmer* function from the *LMERTEST* package (Kuznetsova et al., 2017). Least-squared means and standard errors from these models were obtained using the *lsmeans* function from the *LSMEANS* package (Lenth, 2016). PERMANOVA and ordination methods were implemented using the *adonis* and *capscale* functions, respectively, both from the *VEGAN* package (Oksanen et al., 2010). All graphs were built using *ggplot* (Wickham, 2016).

3 | RESULTS

We identified a total of 40 relevant VOCs emitted by *S. tuberosum* plants (Table S1). The herbivory and water availability treatments both significantly increased the total emission of VOCs released by emitter plants (Table 1). In particular, total emission of VOCs was on average a 186.8% higher for herbivore-induced (226.88 ± 25.69 ng/hr) than for undamaged control (79.11 ± 15.00 ng/hr) plants, and

114.4% higher under the low (202.65 ± 24.05 ng/hr) vs. high (94.51 ± 16.30 ng/hr) water availability treatment. We also found a significant interaction between treatments on total emission of VOCs (Table 1), whereby low water availability weakened the induction of VOCs in response to herbivory (difference between control and herbivore-induced plants; Figure 2). Specifically, plants with low water availability showed an 84.5% increase in the emission of VOCs in response to herbivory (control: 145.75 ± 26.05 ng/hr; herbivore-induced plants: 263.9 ± 35.49 ng/hr), compared to a 476.6% increase in plants with high water availability (control: 32.68 ± 12.07 ng/hr; herbivore-induced plants: 188.42 ± 20.48 ng/hr) (Figure 2).

The PERMANOVA analysis showed that VOCs composition was also affected by herbivory (Table 1, Figure 3a) and water availability (Table 1, Figure 3b). The herbivory treatment explained a 14% of the variation, with the first two axes of the ordination combined accounting for 35.2% of the variation in VOCs due to this treatment (23.3% and 12.9%, respectively, Figure 3a). Variation in VOCs composition in this case was mainly associated with variation in the relative amount of β -farnesene ($R^2 = 0.42$, $p < 0.05$). On the other hand, the water availability treatment explained 7% of the variation, with the first two axes together accounting for 33% of the variation in VOCs due to this treatment (19.7% and 13.3% respectively, Figure 3b). Variation in VOCs composition in this case was mainly associated with variation in the relative amount of ledol ($R^2 = 0.54$, $p < 0.05$), β -farnesene ($R^2 = 0.45$, $p < 0.05$), cis-nerolidol ($R^2 = 0.44$, $p < 0.05$), germacrene D ($R^2 = 0.41$, $p < 0.05$), β -cubenene ($R^2 = 0.41$, $p < 0.05$) and β -caryophyllene ($R^2 = 0.44$, $p < 0.05$). We also detected a significant interaction between treatments (Table 1), indicating that changes in VOC composition in response to herbivory were contingent on water availability.

The emitter herbivory treatment significantly affected leaf damage on receiver plants (Table 1). Specifically, mean leaf damage was a 62.7% lower for receiver plants exposed to VOCs from herbivore-induced emitters ($2.29 \pm 1.13\%$) compared to receiver plants exposed to VOCs from control emitters ($6.14 \pm 1.86\%$) (Figure 4a). In addition, the emitter water availability treatment also affected leaf

TABLE 1 Effects of herbivory (two levels; control vs. herbivory by *Spodoptera exigua*) and water availability (two levels; high vs. low) treatments and their interaction on (a) total emission of volatile organic compounds (VOCs) and (b) VOCs composition in emitter potato *Solanum tuberosum* plants. (c) Effects of emitter herbivory treatment, water availability treatments on both the emitter and receiver (W_E and W_R , respectively), and their two- and three-way interactions (all fixed factors) on the percentage leaf area damage by *S. exigua* on receiver plants. *F*-values/pseudo-*F* for each factor, degrees of freedom and associated *p*-values as obtained from the corresponding linear mixed models are reported. Significant *p*-values are highlighted in bold

	(a) Emitter total VOCs emission		(b) Emitter VOCs composition		(c) Receiver leaf damage	
	<i>F</i> _(1,65)	<i>p</i>	Pseudo- <i>F</i> _(1,68)	<i>p</i>	<i>F</i> _(1,61)	<i>p</i>
Herbivory	42.6	<0.001	12.8	<0.001	4.2	0.044
W_E	23.5	<0.001	6.8	<0.001	4.1	0.048
Herbivory \times W_E	4.0	0.049	5.2	<0.001	0.2	0.641
W_R	–	–	–	–	0.0	0.871
Herbivory \times W_R	–	–	–	–	0.1	0.773
Herbivory \times $W_E \times W_R$	–	–	–	–	0.3	0.866

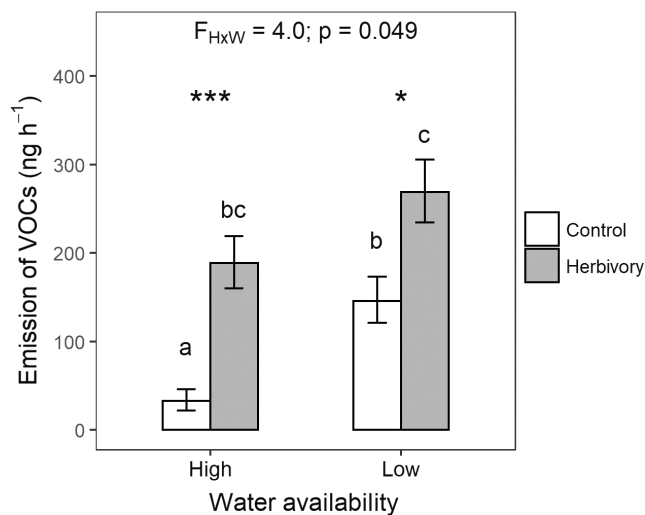


FIGURE 2 Total emission of volatile organic compounds (VOCs; measured as normalized peak areas in nanograms per hour) across herbivory treatment levels (two levels; control vs. herbivory by *Spodoptera exigua*) in emitter potato *Solanum tuberosum* plants with high vs. low water availability. Bars are back-transformed least-square means \pm SE obtained from a linear mixed model ($N = 72$; Table 1). Same letters on the top of bar indicate non-significant differences between means. Asterisks indicate significant differences between control and herbivore-induced plants within each water availability treatment (* p -value < 0.05 ; *** p -value < 0.001). F -value and associated p -value for the interaction term are also shown.

damage in receivers (Table 1), with a 164% higher mean leaf damage for receivers paired to low water availability emitters ($6.10 \pm 1.85\%$) compared with those paired to high water availability emitters ($2.31 \pm 1.14\%$). In contrast, water availability on receivers did not affect leaf damage on receivers (Table 1). Finally, there were no significant two-way or three-way interactions between the herbivory treatment and the emitter or receiver water availability treatments (Table 1; Figure 4b,c), that is plant communication was not contingent on the water treatment on the emitter or the receiver.

4 | DISCUSSION

Both *S. exigua* damage and water availability produced qualitative and quantitative changes in VOCs released by emitter plants, and herbivory-induced changes in VOCs emissions were contingent on emitter water availability treatment. Specifically, emitters subjected to low water availability showed a weaker induction (difference between control and herbivore-induced plants) of VOCs in response to herbivory. Results from the receiver feeding bioassay indicated that herbivore-induced VOCs boosted receiver induced resistance as receiver plants exposed to herbivore-induced emitters were less consumed by *S. exigua*. Nonetheless, and despite the hampering effect of water availability on the induction of VOCs, we failed to detect a significant effect of water availability on either emitter or receiver plants on signalling (i.e. difference in degree of induced resistance in

receivers among water treatment levels). Therefore, contrary to expectations, airborne plant-plant signalling appears to be consistent across different regimes of water availability affecting both emitter and receiver plants, at least under the specific experimental conditions tested here. These results can be transferred to natural systems to inform potential effects of environmental variation (e.g. in climate conditions) on plant-plant signalling and induced resistance to insect herbivores.

We found that herbivore-induced emitters released greater amounts of total VOCs with a different composition compared to control (undamaged) emitters. Inducibility of VOCs in response to herbivory has been widely documented in both wild and crop species, including potato plants (Dicke et al., 2009; Gosset et al., 2009; Heil, 2014; Paré & Tumlinson, 1997; Zhang et al., 2009). This finding contrasts with a previous study which did not find evidence of induced emission of VOCs in potato in response to leaf herbivory by the specialist insect *Leptinotarsa decemlineata* (Abdala-Roberts et al., 2022). However, the amount of leaf damage imposed to emitters in such study was considerably lower compared to the present study ($\sim 25\%$ vs. $\sim 78\%$ defoliation, respectively), which may have resulted in a weaker induction of plant volatiles. In addition, and probably more importantly, the herbivore species used in that study was different and specialist herbivores have been shown to inhibit the induction of plant defences (Sarmiento et al., 2011), potentially explaining the non-significant effect. The induction of VOCs in potato plants could therefore be herbivore specific, as demonstrated for other plant species (Moreira et al., 2018; Robert et al., 2012). Further work comparing induced responses to feeding by specialist and generalist herbivores, while controlling for different levels of damage, would allow to test for herbivore diet breadth-mediated specificity in VOC-induced responses in potato.

Water availability also triggered qualitative and quantitative changes in VOCs emissions in potato plants. We found that emitters with low water availability released greater amounts of total VOCs as well as a different blend compared to emitters subjected to high water availability. Plant defence theory predicts that lower resource availability promotes the production of defences when growth, but not photosynthesis, is constrained (Herms & Mattson, 1992). However, this does not seem to be the case, since lower water availability significantly reduced photosynthetic rates in our experimental plants (see Methods section). Alternatively, induced emissions of VOCs under low water availability conditions may be the result of physiological responses to abiotic stresses as already reported elsewhere (Holopainen & Gershenson, 2010; Vallat et al., 2005). We further found that low water availability resulted in a weaker induction of plant volatiles in response to *S. exigua* damage. This result is in agreement with our expectations and also supports a previous study reporting that low water availability prevented the induction of VOCs by *Camellia sinensis* in response to exogenous application of methyl-jasmonate (Scott et al., 2019). Relatedly, Quijano-Medina et al. (2021) found that soil salinization hampered the induction of phenolic compounds as well as a similar trend for some VOCs in wild cotton *Gossypium hirsutum* plants. Such effects of abiotic stress on

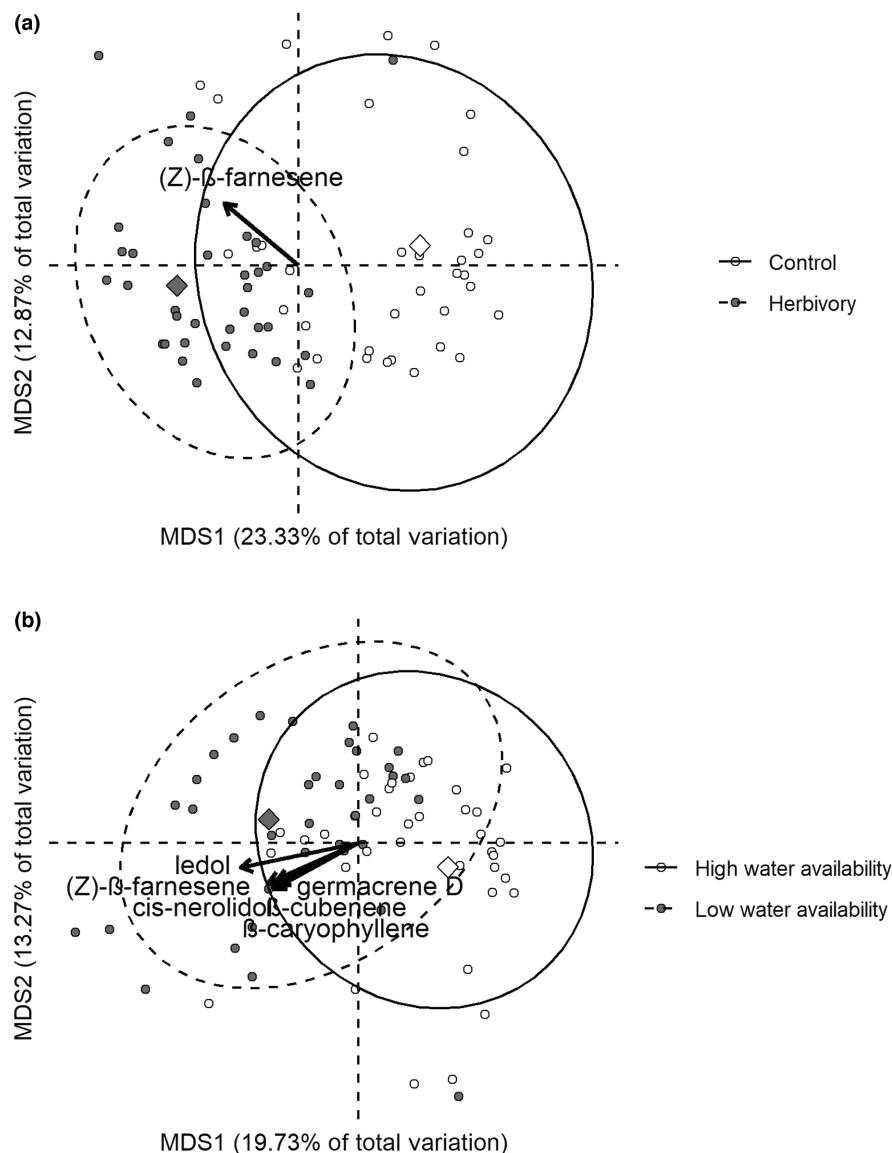


FIGURE 3 Unconstrained ordination (principal coordinate analysis [PCoA]) showing the effects of emitter (a) herbivory (two levels; control vs. herbivory by *Spodoptera exigua*) and (b) water availability (two levels; high vs. low) on the composition of volatile organic compounds (VOCs) emitted by potato *Solanum tuberosum* plants. Biplot arrows represent linear associations with selected volatiles based on R^2 values ($R^2 > 0.4$, $p < 0.001$), scaled to reflect relative magnitude of effects. Diamonds represent the centroids for each herbivory or water availability treatment and associated 95% ellipses. The first two axes together accounted for 35.2% and 33% of total variation in volatile composition due to herbivory and water availability, respectively.

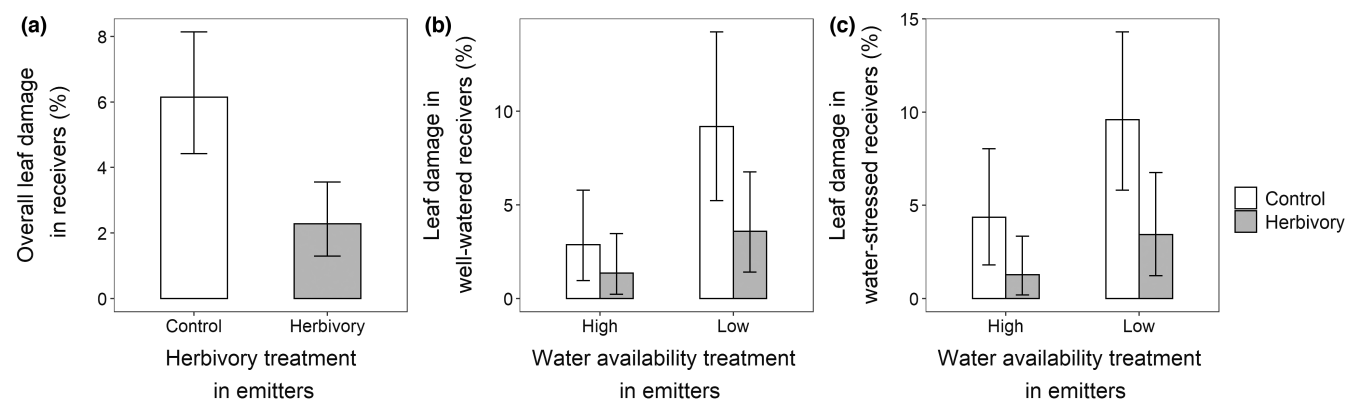


FIGURE 4 Percentage of leaf area consumed by *Spodoptera exigua* on control (white bars) and herbivore-induced (grey bars) receiver potato *Solanum tuberosum* plants. Values are back-transformed least square means \pm SE obtained from the corresponding linear mixed model ($N = 72$; Table 1). (a) Main effect of emitter herbivory treatment on receiver resistance. (b) Results for receivers with high water availability when emitters were under either high or low water availability. (c) Results for receivers with low water availability when emitters were under either high or low water availability.

the induction of VOCs can be explained by allocation costs associated with the synthesis and transport of plant secondary metabolites (Wilkinson et al., 2019). The physiological effects of abiotic forcing and associated costs of defence expression likely increase under unfavourable conditions, constraining the ability of plants to respond to biotic challenges (Sampedro et al., 2011) and vice versa.

Consistent with the herbivore-induced increase in VOCs emissions and changes in VOCs blends in emitter plants, receiver plants exposed to herbivore-induced emitters exhibited greater resistance to *S. exigua* (i.e. lower percentage of leaf damage) compared to receivers exposed to undamaged emitters. Interestingly, previous work by our group testing VOCs-mediated communication in potato in response to herbivory by the specialist *L. decemlineata* (Abdala-Roberts et al., 2022) and infection by the generalist fungal pathogen *Sclerotinia sclerotiorum* (Moreira et al., 2021) showed no evidence of changes in VOCs emissions, and, correspondingly, no effects on receiver resistance. These results again suggest that VOCs-mediated signalling in potato plants is attacker specific, whereby defence induction of receiver plants is contingent on the type (e.g. feeding mode, associated plant signalling pathways) or species of attacker, as has been found in other systems (Moreira et al., 2018).

Receivers exposed to emitters subjected to low water availability exhibited lower resistance, this despite increased VOCs release by emitters exposed to low water availability. Recent research has demonstrated that abiotic stresses shape VOCs released by plants and that these can trigger plastic responses in neighbouring conspecifics. For instance, Zhao et al. (2020) reported that tea plants *Camellia sinensis* exposed to VOCs from cold-stressed neighbours were more tolerant to cold stress. Similarly, Caparrotta et al. (2018) showed that unstressed faba bean *Vicia faba* plants responded to cues emitted from salt-stressed neighbours and became more tolerant to further salinity stress. Accordingly, although speculative, it may have been the case that VOCs released by emitters subjected to low water availability increased abiotic resistance to drought in receivers compromising biotic resistance to herbivory due to involvement of trade-offs in abiotic vs. biotic responses (Berens et al., 2019). Finally, the fact that receiver resistance increased in response to herbivore-induced VOCs but decreased in response to VOCs from emitters with low water availability suggests that different VOCs blends and underlying compounds drive contrasting outcomes of signalling between potato plants.

Unexpectedly, and despite the dampening effect of low water availability on VOCs inducibility in emitter plants, we did not find evidence of effects of low water availability for either emitter or receiver plants on the strength of plant communication (i.e. difference in resistance of receivers exposed to herbivore-induced vs. control emitters). This result is in agreement with a previous study on tomato *S. lycopersicum* reporting that patterns of indirect defence by parasitoids wasps in receivers exposed to VOCs from herbivore-induced emitters were similar to those observed when herbivore-induced emitters were subjected under low water availability (Catola et al., 2018). In our case, it is possible that the difference in total VOCs (or their composition) between control and herbivore-induced

emitters was not large enough to produce differences in induced resistance on receivers. It is also worth noting that total VOCs in herbivore-induced plants, on average, did not differ between water availability treatments (see Figure 2) which could help explain similar levels of induced resistance in receivers exposed to emitters with low vs. high water availability. This raises the question of whether the relative difference between emitter control vs. induced VOCs levels (i.e. inducibility) and/or absolute induced levels matter for predicting effects of abiotic stress on plant communication. Relatedly, abiotic conditions may in some cases influence constitutive (i.e. background) VOC levels, as observed here for undamaged emitters under high vs. low water availability (see Figure 2), therefore influencing the difference between control and herbivore-induced emitters. It is also important to note that water availability in receivers did not affect plant communication, suggesting that VOCs reception was similarly not contingent on this abiotic factor. In agreement with our results, Pezzola et al. (2017) found that sagebrush plants exposed to VOCs from induced emitters increased resistance against defoliators but did not observe additive effects of water availability in the receiver plant. Our own results and those reported by Pezzola et al. (2017) thus suggest that effects of signalling on induced resistance in receiver plants remain consistent despite heterogeneity in water availability. It may be the case, however, that larger differences in water availability would lead to different outcomes, and that water availability may have stronger effects at limiting plant communication under specific physiological conditions that promote plant communication, for instance, when plants are actively growing (Shiojiri & Karban, 2006). Finally, we must not discard that the observed hampering effect of low water availability on induction of VOCs may have further implications for plant communication at the population level (rather than among pairs of emitters and receivers) by affecting features such as the distance volatiles travel in natural ecosystems (Hagiwara et al., 2021).

Overall, our results provide evidence of VOCs-mediated airborne plant-plant signalling in response to insect herbivory in potato plants, resulting in enhanced resistance to a generalist herbivore. Surprisingly and against expectations, we did not find evidence that volatile communication was affected by changes in water availability in both the emitter and the receiver, despite the observed reduction in VOCs induction under low water availability. These results suggest that changes in VOCs profiles were not strong enough to produce concomitant changes in plant-plant signalling or that emissions of core compounds or groups of compounds that matter for signalling remained relatively unchanged. We must acknowledge, however, that different outcomes may have been obtained under different experimental conditions. For instance, further work testing long-term and more contrasted regimes of water availability under field conditions are warranted. Importantly, other abiotic factors (e.g. soil nutrients, light, soil salinity) could also influence the outcomes of signalling in plants and interact with water availability. Testing multiple sources of abiotic variation on volatile communication would provide a more integrated approach to understanding the effects of abiotic forcing on

VOC-mediated plant signalling in response to herbivory. Insights gained from this study build towards a deeper understanding of the sources of variation that modulate induced responses in defences and biotic resistance in plants and can potentially inform the development of applied methods for pest control based on the artificial application of VOCs as a function of varying regimes of water availability.

AUTHOR CONTRIBUTIONS

Xoaquín Moreira and Carla Vázquez-González obtained the funding. Xoaquín Moreira, Luis Abdala-Roberts and Carla Vázquez-González conceived the study and designed the experiment; Carla Vázquez-González, Xoaquín Moreira and Laura Pombo-Salinas performed the experiment. Lucía Martín-Cacheda measured stomatal conductance and photosynthetic rates. Sergio Rasmann and Gregory Röder performed the chemical analysis. Carla Vázquez-González performed the statistical analysis and wrote the first version of the manuscript. Xoaquín Moreira, Luis Abdala-Roberts, Kailen A. Mooney, Sergio Rasmann and Gregory Röder contributed significantly to the revision of the manuscript and the interpretation of the results.

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CONFLICT OF INTEREST

K.A.M. and S.R. are Associate Editors of Functional Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.kkwh70s78> (Vázquez-González et al., 2022).

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