

Research paper

Plant–plant signalling reduces herbivore damage in two *Arabidopsis thaliana* populations with contrasting life historiesRodrigo R. Granjel^{a,*}, Lucía Martín-Cacheda^{b,c}, Gregory Röder^d, Iago Izquierdo-Ferreiro^e, Andrea Martín-Díaz^f, F. Xavier Picó^f^a Basque Centre for Climate Change (BC3), Leioa, 48940, Spain^b Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, SE, 10691, Sweden^c Misión Biológica de Galicia (MBG-CSIC), Apartado de correos 28, Pontevedra, Galicia, 36080, Spain^d Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, Neuchâtel, 2000, Switzerland^e Centro Oceanográfico de Vigo, Instituto Español de Oceanografía (IEO, CSIC), Subida a Radio Faro 50, Vigo, 36390, Spain^f Departamento de Ecología y Evolución, Estación Biológica de Doñana (EBD), Consejo Superior de Investigaciones Científicas (CSIC), Sevilla, 41092, Spain

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ABSTRACT

Volatile organic compounds (VOCs) mediate plant–plant signalling and may contribute to phenotypic differentiation among populations. However, how signalling responses and VOC–life-history associations vary among locally adapted populations remains poorly understood. We conducted a greenhouse experiment using two genetically and phenologically divergent (i.e. rapid and slow cyclers) Iberian populations of *Arabidopsis thaliana*. We exposed emitter plants to *Spodoptera exigua* herbivory and quantified VOC emissions, subsequent herbivore damage in neighbouring conspecific receivers, and associations between VOC emissions and life-history traits. We detected no overall population difference in measured VOC profiles. Herbivory explained little variation in VOC profiles, and evidence for a treatment-induced shift in mean emission profiles was inconclusive. In the rapid cyler population, later-flowering maternal lines had higher constitutive emissions of several VOCs and higher total emissions, but these associations were not detected in herbivore-induced plants. Exposure to herbivore-induced emitters reduced receiver damage in both populations, with no detectable population difference in the treatment response. These findings indicate that plant–plant signalling increases resistance to herbivory in both populations despite their contrasting life histories. Furthermore, they suggest that herbivory may reshape associations between VOC emissions and life-history traits, such as flowering phenology, differently among populations.

1. Introduction

Chemical traits play a central role in plant–herbivore interactions. Among these, volatile organic compounds (VOCs) are of particular interest because they mediate both within-plant defence responses and information transfer among neighbouring individuals. Plants subjected to herbivory emit characteristic blends of VOCs that can be perceived by conspecific and heterospecific neighbours, enabling plant–plant signalling (Heil and Karban, 2010; Karban et al., 2014b). In response, neighbouring plants may prime or induce defensive pathways (Martínez-Medina et al., 2016; Karban, 2021), increasing resistance to herbivores and potentially affecting survival and reproductive success (Karbon et al., 2016; Aratani et al., 2023). Consequently, variation in

VOC emission and VOC-mediated signalling may influence ecological performance and contribute to phenotypic differentiation within and among populations.

Despite their potential adaptive importance, linking chemical traits to plant fitness remains challenging because it requires quantifying how variation in VOC traits affects survival and reproduction (Karbon and Maron, 2002). Nevertheless, growing evidence indicates that VOC traits can vary substantially within and among populations, a prerequisite for VOC trait evolution. For example, some plant species exhibit different chemotypes, characterised by pronounced within- or among-population differences in VOC production and emission (Karbon et al., 2016, 2024; Clancy et al., 2020; Eckert et al., 2023), which likely reflect divergent microevolutionary trajectories. Researchers have also

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attempted to relate variation in VOC emission and VOC-mediated signalling to selective pressures such as environmental gradients and local environmental heterogeneity. However, results have been inconsistent across systems (Wason et al., 2013; Karban et al., 2016; Aartsma et al., 2019).

One way to better understand VOC trait variation and its evolutionary implications is to examine VOC traits in broader genetic and phenotypic contexts. However, studies investigating genetic variation in VOC emissions and VOC-mediated signalling have yielded contrasting results. Although genetic differentiation in VOC traits is commonly detected, the extent to which this variation translates into differences in VOC-mediated plant–plant communication varies among systems (Karbon and Shiojiri, 2009; Karban et al., 2014a; Moreira et al., 2016; Martín-Cacheda et al., 2023). These findings suggest that VOC traits may form part of broader integrated phenotypes alongside morphological and life-history traits. Correlations among traits may arise through shared genetic architecture and selection acting on multiple aspects of the phenotype (Jiang and Zhang, 2023). Under this framework, selection acting on major fitness-related traits may indirectly shape variation in herbivore-induced VOC emission and VOC-mediated signalling. Nevertheless, signalling outcomes remain strongly context-dependent, as cue perception can vary with environmental conditions, developmental stage, and the simultaneous detection of multiple chemical cues (Karbon and Maron, 2002; Holopainen and Gershenzon, 2010; Karban, 2021).

The primary objective of this study was to quantify variation between populations in VOC emissions and VOC-mediated signalling effects between neighbouring conspecifics. To achieve this goal, while accounting for shared maternal-line origin, we focused on two wild, well-characterised Iberian populations of the annual mustard *Arabidopsis thaliana* locally adapted to contrasting environments: one from a low-elevation, warm site, and the other from a high-elevation, cold site (de la Mata et al., 2024). These populations differ strongly in life-cycle phenology, with individuals from the low-elevation population predominantly exhibiting a spring-cycling strategy characterised by high seed dormancy and early flowering (i.e. rapid cycler), whereas individuals from the high-elevation population mainly display facultative winter-cycling with variable seed dormancy and delayed flowering (i.e. slow cycler). Such contrasting phenological strategies underlie seasonal adaptation in *A. thaliana* at regional and global scales (Debieu et al., 2013; Vidigal et al., 2016; Marcer et al., 2018; Exposito-Alonso M., 2020; Martínez-Berdeja et al., 2020). Because adaptation acts on integrated phenotypes rather than on isolated traits (Adams and Collyer, 2019), strong divergence in life-history strategies may also be associated with differentiation in other complex traits, including herbivore-induced VOC emission and VOC-mediated signalling. Under this framework, genetic variation in VOC traits may covary with major fitness-related traits as a consequence of trait correlations shaping phenotypes in populations adapted to contrasting environmental conditions.

To examine population variation in VOC emission and VOC-mediated signalling, and associations between VOC emissions and life-history traits, we conducted a greenhouse experiment in which individuals from two locally adapted *A. thaliana* populations were exposed to leaf herbivory by larvae of the generalist insect *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae). We quantified herbivore-induced VOC emissions and VOC-mediated signalling between neighbouring conspecifics using multiple maternal lines per population, allowing us to evaluate population-level differentiation while accounting for underlying intraspecific genetic variation. In addition, we characterised the chemical composition of emitted VOCs to examine patterns of variation in VOC profiles between populations and herbivory treatments. Finally, we tested whether VOC traits covaried with major fitness-related traits associated with local adaptation, namely germination rate (inversely related to seed dormancy) and flowering time. Specifically, we predicted that VOC traits would covary with these life-history traits as part of

broader integrated phenotypes shaped by adaptation to contrasting environments. For VOC-mediated signalling, however, we did not formulate a directional prediction because previous studies have reported inconsistent patterns of genetic variation in plant–plant communication; we therefore treated population differences in signalling responses as an open question. Together, this approach allowed us to assess how local adaptation, life-history divergence, and genetic variation are associated with herbivore-induced VOC emission and VOC-mediated plant–plant signalling in *A. thaliana*, and to shed light on how VOC trait evolution may be intertwined with life-history evolution in plants.

2. Materials and methods

2.1. Study system

2.1.1. Source populations

We selected two populations from the Iberian collection of *Arabidopsis thaliana* natural populations (Picó et al., 2008; Méndez-Vigo et al., 2011; Castilla et al., 2020; de la Mata et al., 2024) that differ markedly in their geographical, environmental, and ecological attributes (Fig. 1). The first population, Bonanza (Bon; 36.88 °N, 6.29 °W, 2 m a.s.l., Cádiz province), occurs in a coastal stone pine (*Pinus pinea* L.) forest on sandy soils, whereas the second population, Canencia (Cai; 40.87 °N, 3.76 °W, 1520 m a.s.l., Madrid province), is located in a montane Scots pine (*Pinus sylvestris* L.) forest (Fig. 1b,c). Although forest cover is similar at both sites (66–68%; de la Mata et al., 2024), they experience contrasting climates, with Bon being warmer and drier than Cai (mean minimum and maximum annual temperatures: 12.3 and 24.1 °C vs. 2.4 and 14.9 °C; total annual precipitation: 563.7 vs. 735.6 mm; Fig. 1d).

These climatic contrasts are reflected in population-specific ecological niches. At both sites, *A. thaliana* exhibits a strong preference for forest openings, but plants at Bon occupy shadier and cooler microsites (Fig. 1b), whereas plants at Cai thrive in more exposed and warmer spots (Fig. 1c). Thus, despite sharing a similar forest context, the two populations experience opposite microclimatic optima shaped by their local environments.

Bon and Cai were originally sampled in 2017 as part of a broader study to estimate adaptive life-history variation in Iberian *A. thaliana* (de la Mata et al., 2024) and represent the lowest and highest elevations in that dataset. They differ strongly in life-history strategies. At Bon, seeds germinate in mid-winter and plants flower in late winter, shedding seeds in March, consistent with a spring-cycling strategy and prolonged seed-bank dormancy. At Cai, germination spans autumn to late winter, but flowering and seed set occur later in the spring (June), reflecting a mix of winter and spring annual cycles typical of many Iberian natural populations (Montesinos et al., 2009; Picó FX., 2012).

We collected seeds from 50 to 60 individuals per population and propagated them by single-seed descent in 2018 in a glasshouse at the Centro Nacional de Biotecnología (CNB-CSIC, Madrid, Spain) to minimise maternal and environmental effects. For the experiment, we selected 15 maternal lines per population to maximise spatial and genomic diversity. Mean ($\pm$ SE) pairwise geographic distances were 74.25 ± 5.65 m at Bon (range: 4.12–146.32 m) and 140.79 ± 8.43 m at Cai (range: 17.00–291.76 m), and mean ($\pm$ SE) genomic distances (based on allele-difference proportions across 2.7 million non-singleton SNPs) were 0.0227 ± 0.0023 at Bon (range: 0.0002–0.0412) and 0.0593 ± 0.0032 (range: 0.0002–0.1029) at Cai. During propagation before the greenhouse experiment (see below), four Bon lines yielded too few viable plants and were discarded, leaving 11 Bon and 15 Cai lines.

Both populations belong to the Iberian relict genetic cluster, an early-diverging lineage associated with long-term climatic stability since the Last Glacial Maximum (Brennan et al., 2014; Durvasula et al., 2017; Castilla et al., 2020; Toledo et al., 2020). Despite this shared evolutionary background, Bon and Cai are strongly genetically differentiated and form distinct genetic groups with internal structure (Fig. 1e). Taken

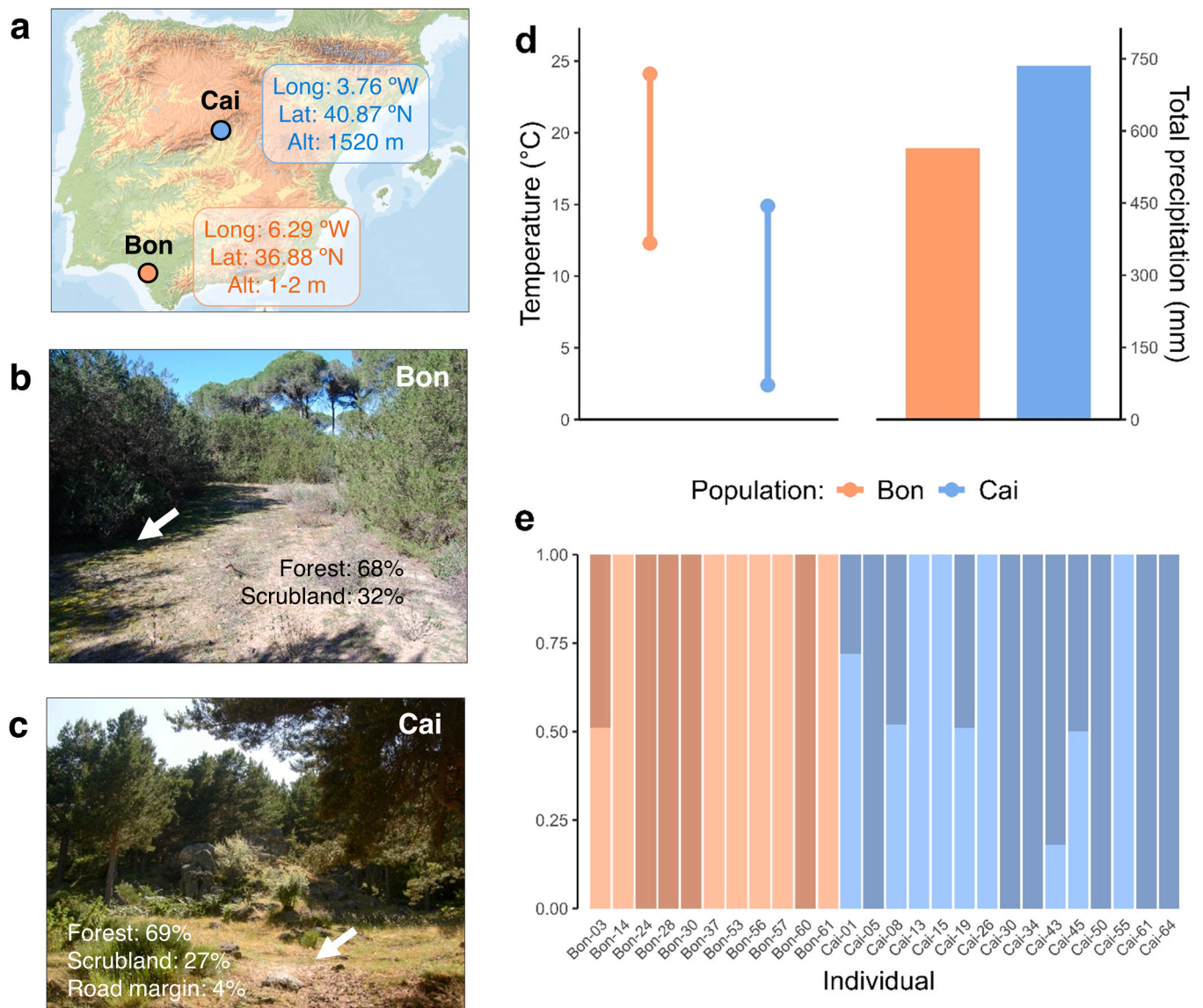


Fig. 1. Characterisation of the two *Arabidopsis thaliana* study populations. (a) Geographical location of Bonanza (Bon) and Canencia (Cai) in the Iberian Peninsula, with coordinates and elevation. (b–c) Photographs of the Bon and Cai sites showing dominant vegetation types and the particular micro-environments where *A. thaliana* occurs within each population (white arrows). (d) Climate records for each site, including the average temperature range and the total annual precipitation. (e) Genetic cluster membership of individuals from Bon and Cai. Each population comprises two genetic clusters, represented by varying shades of orange (Bon) or blue (Cai).

together, these differences motivate the use of Bon and Cai as contrasting locally adapted populations for analysing variation in VOC emissions and neighbour-induced responses.

2.1.2. Genetic structure

To characterise genetic differentiation between the two study populations, we used a VCF file containing 2798,036 non-singleton nuclear SNPs from a previous study including 298 maternal lines from six *A. thaliana* populations (de la Mata et al., 2024). From this dataset, we extracted the 26 maternal lines used here (11 from Bon and 15 from Cai), yielding 470,456 SNPs. SNP filtering was performed with VCFtools v1.16 (Danecek et al., 2011) and PLINK v2.00a3 (Chang et al., 2015), retaining loci with < 10% missing data and minor allele frequency > 5%. We inferred genetic structure using ADMIXTURE v1.3.0 (Alexander et al., 2009), which estimates ancestry proportions from SNP genotype data. We used cross-validation and explored $K = 1-5$ ancestral populations with 20 replicate runs using different random seeds. We selected $K = 4$, which minimised the cross-validation error (0.43), and

used the resulting ancestry coefficients to visualise genetic structure within and between the two focal populations (Fig. 1e).

2.1.3. Herbivore species

We used the generalist chewing herbivore *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae) to induce leaf damage in *A. thaliana*. *Spodoptera exigua* is a highly polyphagous insect that readily feeds on Brassicaceae and is widely used in plant–insect interaction studies (Greenberg et al., 2001; Cipollini et al., 2004). Furthermore, previous work has shown that leaf damage by *S. exigua* induces strong defensive and volatile responses across a wide range of plant species (Schmelz et al., 2003; Danner et al., 2018; Martín-Cacheda et al., 2023). On this basis, we expected *S. exigua* feeding to induce VOC production and volatile-mediated signalling in *A. thaliana*.

2.2. VOC induction and herbivory experiment

The experiment was conducted at the facilities of the Misión

Biológica de Galicia (MBG-CSIC; Salcedo, Pontevedra, Spain). In September 2021, we placed seeds from each maternal line in Petri dishes containing filter paper soaked with deionised water and stratified at 4 °C in complete darkness for four days, followed by five days at 22 °C under continuous light in a FitoClima-10.000-EH growth chamber (ARALAB, Rio de Mouro, Portugal) to promote germination. Germinated seedlings were transplanted with a fine brush into plastic seed trays (104 wells of 40 × 40 × 50 mm³ each) filled with a peat-based substrate (Gramoflor GmbH & Co. KG) pre-saturated with water. For each maternal line, we transplanted 48 seedlings to ensure a sufficient number of plants for the experiment.

We maintained trays in a greenhouse under controlled conditions (10/25 °C night/day, with a minimum photoperiod of 10 h). During the first week, we irrigated cells from above every two days and also kept them in shallow water to prevent desiccation; thereafter, we irrigated only from above at the same interval. After four weeks, an average of 27 ± 7 plants per line (57% ± 18% of the original 48 seedlings) reached a rosette diameter of at least 4 cm.

We then separated individual wells from the seed tray and established six pairs of similar-sized plants per maternal line. In each pair, one plant was randomly designated as the emitter and the other as the receiver (Fig. 2). Each emitter–receiver pair was enclosed in a transparent rectangular plastic container (100 × 100 × 220 mm³) fitted with a lid and closing flaps to limit airborne exchange between containers while allowing passive venting through small gaps, resulting in a total of 156 containers. Containers belonging to the same replicate number (1–3) were spatially grouped, with each replicate group containing plants from both populations and treatments. Within each maternal line, treatment allocation was random, with three pairs assigned to the control treatment (no herbivory on emitters) and three to the herbivore-induced treatment (*S. exigua* larvae feeding on emitters). Under the herbivore-induced treatment, one third-instar *S. exigua* larva was placed on each emitter plant, and a nylon mesh was attached to the top of the plant's well to prevent larval escape. *S. exigua* eggs were provided by the Control Biotecnológico de Plagas research group at the University of Valencia, and larvae were reared at the ECO-EVO laboratory of the Misión Biológica de Galicia (MBG-CSIC).

Five hours after larval placement, we removed the *S. exigua* larvae from emitter plants and collected aboveground VOCs from all emitters following Rasmann et al. (2011). VOC sampling was conducted over five consecutive days in November 2021. Larvae were placed in the morning and VOCs were collected 5 h later in the afternoon. To accommodate the small size of *A. thaliana*, we enclosed each emitter plant together with its individual soil-filled tray well in a 2 L Nalophan bag. We trapped VOCs on a charcoal filter (SKC sorbent tube filled with Anasorb CSC coconut-shell charcoal) for 1.5 h using Sidekick 224–52MTX pumps (SKC Ltd, United Kingdom) operated in a pull-only configuration at 0.25 L min⁻¹, drawing ambient greenhouse air through the bag and charcoal filter. No purified or synthetic air was supplied. After sampling, charcoal traps were sealed and stored at –80 °C until chemical analysis.

We eluted traps with 150 µL dichloromethane (CAS#75–09–2, Merck, Dietikon, Switzerland) to which we had previously added one internal standard (naphthalene, CAS#91–20–3, 200 ng in 10 µL dichloromethane). We then injected 1.5 µL of the extract for each sample into an Agilent 7890B gas chromatograph (GC) coupled with an Agilent 5977B mass selective detector (Agilent Technologies, Santa Clara, CA, USA) fitted with a 30 m × 0.25 mm × 0.25 µm film thickness HP-5MS ultra inert fused silica column (Agilent Technologies, Santa Clara, CA, USA). We operated the injection into the GC in pulsed splitless mode (250 °C, injection pressure 15 psi) with helium as the carrier gas. The GC oven temperature programme was: 3.5 min hold at 40 °C, 5 °C min⁻¹ ramp to 230 °C, then a 3 min hold at 250 °C post run (constant helium flow rate 0.9 mL min⁻¹). The transfer line was set at 280 °C. In the MS detector (EI mode, 70 eV), a 33–350 (*m/z*) mass scan range was used with the MS source and the quadrupole set at 230 °C and 150 °C, respectively. We identified volatile compounds using either commercial

pure standards or mass spectrum comparisons with the NIST library. For compounds identified by mass spectrum comparison, Kováts indices were calculated relative to the retention times of a series of n-alkanes (C8–C20; Sigma-Aldrich, Merck KGaA, Darmstadt, Germany) analysed under the same chromatographic conditions and compared with values reported in the literature. Although our Kováts indices matched well with previously reported values, compounds not confirmed using commercial standards should be considered putatively identified (Table 1).

VOC amounts collected during the 1.5-h trapping period were estimated semiquantitatively by multiplying each compound's peak-area ratio to the naphthalene internal standard by the 200 ng of standard added at elution (Abdala-Roberts et al., 2022). Values are expressed as naphthalene-equivalent ng per sample and provide approximate collected amounts rather than compound-specific absolute emission rates (Table 1; Fig. S2). To characterise background VOC signals associated with the experimental system (Fig. S3), four blank samples consisting of soil-filled containers without plants were collected using the same procedure as for plant samples. For each compound, we used the maximum value recorded across the four blanks as an empirical background threshold, and compound amounts at or below this threshold were coded as zero in subsequent analyses. Across compounds, 59.49 ± 13.27% of measurements were above the background threshold (mean ± SD; Fig. S4). Total VOC amount was calculated by summing the background-filtered naphthalene-equivalent amounts across compounds and represents an approximate index of collected abundance because compound-specific MS response factors were not determined. For class-level summaries, individual VOCs were grouped according to chemical structure and predominant biosynthetic origin (Rosenkranz and Schnitzler, 2016; Bouwmeester et al., 2019), distinguishing terpenoids, which derive mainly from the MEP (2-C-methyl-D-erythritol 4-phosphate) biosynthesis pathway, non-terpenoid aliphatic VOCs, which derive mainly from lipid-derived pathways including LOX (lipoxygenase), and aromatic compounds, which derive from the shikimate/phenylpropanoid pathway (Grechkin, 1998; Maeda and Dudareva, 2012; Vranová et al., 2013; Liu et al., 2023). An elution issue prevented VOC quantification in seven samples, leaving 149 measured profiles (74 control and 75 herbivore-induced). Moreover, 18 profiles contained only zero values after background screening, while the remaining 131 retained non-zero VOC measurements. Emitter plants were returned to their containers after VOC collection and left overnight (approximately 15 h) with their paired receivers.

To evaluate whether exposure to VOCs from damaged emitters enhanced resistance to herbivory, and whether this effect differed between populations, the following morning we placed one third-instar *S. exigua* larva on each receiver plant using the same procedure applied to emitter plants. Larvae were allowed to feed for 5 h before herbivore damage was scored. Using a Canon EOS 750D and a 55 mm lens (Canon Inc., Tokyo, Japan), we took top-view photographs of all emitter and receiver plants immediately before larval placement and after the 5-h feeding period to visually estimate the percentage of damage (0–100%). To account for potential differences in plant and herbivore size across populations and treatments, we used the pre-herbivory photographs to estimate plant size on a categorical scale from 1 (smallest) to 4 (largest), and we weighed each *S. exigua* larva to the nearest 0.0001 g using an analytical scale (ABS 120–4 N; Kern & Sohn GmbH, Balingen, Germany) before placement on the plants. Photographs of the experimental setup, larval preparation, VOC collection and plant imaging are provided in Fig. S1.

2.3. Life-history traits

To assess the relationship between life-history traits and VOC emission under control and herbivore-induced treatments in *A. thaliana* populations, we focused on three traits with high adaptive value: seed weight, seed germination, and flowering time. In a separate assay conducted at the experimental facilities of the Estación Biológica de Doñana

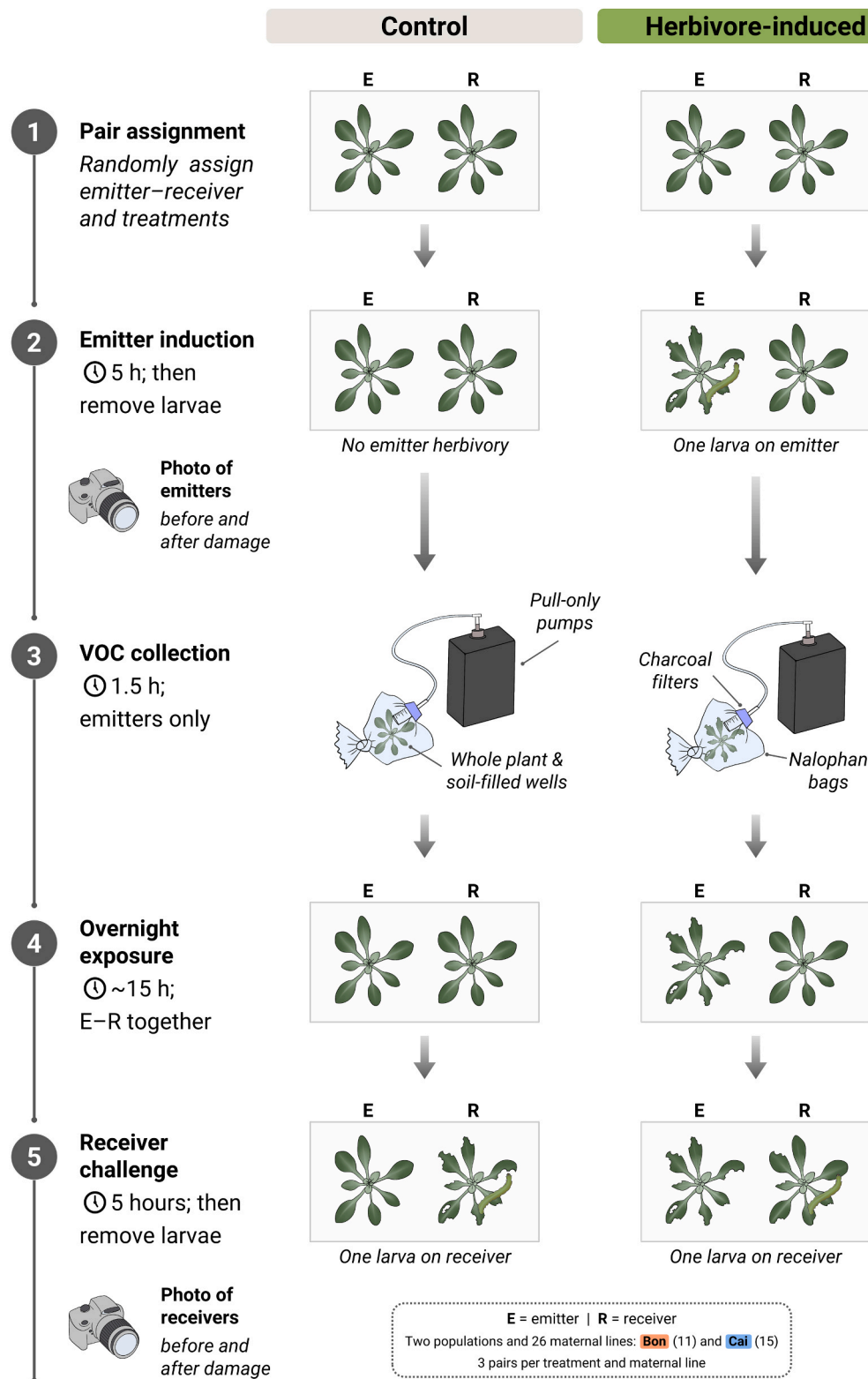


Fig. 2. Experimental sequence used to assess herbivore-induced plant–plant signalling. The experiment included 11 maternal lines from Bonanza (Bon) and 15 from Canencia (Cai), with three emitter–receiver pairs per treatment and maternal line (156 pairs in total). Grey and green headers indicate control and herbivore-induced treatments, respectively. 1) Plants from the same maternal line were paired, with emitter (E) and receiver (R) roles and treatments randomly assigned within maternal lines. Each pair shared a container, with plants occupying separate soil-filled wells. 2) Induced emitters received one *Spodoptera exigua* larva for 5 h, while control emitters remained undamaged; receivers remained alongside their emitters during this period. Larvae were then removed. 3) Volatile organic compounds (VOCs) were collected for 1.5 h from emitters in both treatments. Each emitter and its soil-filled well were enclosed in a Nalophan bag connected to a charcoal filter and a pull-only sampling pump. 4) Emitters were returned to their paired receivers for approximately 15 h of overnight exposure. 5) Receivers in both treatments were challenged with one larva for 5 h. Emitters and receivers were photographed before and after their respective feeding periods to quantify plant size and herbivore damage. Photographs of the experimental setup and procedures are provided in Fig. S1. Illustrations by Rheann Earnest.

Table 1

Identification and collected amounts of volatile organic compounds (VOCs). Mean naphthalene-equivalent amounts (ng) collected during the 1.5-h trapping period from *Arabidopsis thaliana* emitter plants across populations and treatments. Parentheses indicate the 5th–95th percentiles (P5–P95); values coded as zero after background screening were excluded from these summaries. Compounds are grouped by chemical class (italic rows). Class summaries pool non-zero compound measurements within each class. Mass spectral searches were performed using NIST MS Search v2.3. Daggers (†) indicate compounds confirmed using commercial standards; unmarked compounds were putatively identified using mass spectrum comparisons and Kováts indices.

VOCs	Mean amount (P5–P95)	Retention time (min)	Molecular formula	CAS number
<i>Aromatic ketones</i>	2.88 (1.03–6.02)			
Acetophenone†	2.88 (1.03–6.02)	12.76	C ₈ H ₈ O	98–86–2
<i>Esters</i>	4.14 (0.96–11.57)			
Butanoic acid, methyl ester	4.14 (0.96–11.57)	11.06	C ₅ H ₁₀ O ₂	623–42–7
<i>Long-chain aldehydes and alkanes</i>	15.62 (1.24–54.24)			
Decanal†	24.06 (9.96–70.25)	15.82	C ₁₀ H ₂₀ O	112–31–2
Dodecanal	27.61 (9.02–68.58)	19.82	C ₁₂ H ₂₄ O	112–54–9
Dodecane†	12.08 (4.03–28.74)	15.67	C ₁₂ H ₂₆	112–40–3
Nonanal†	50.16 (17.69–131.03)	13.61	C ₉ H ₁₈ O	124–19–6
Tetradecanal	6.79 (2.29–17.35)	23.36	C ₁₄ H ₂₈ O	124–25–4
Tetradecane†	14.35 (3.36–36.33)	19.62	C ₁₄ H ₃₀	629–59–4
Tridecane†	8.91 (2.59–24.79)	17.71	C ₁₃ H ₂₈	629–50–5
cis-2-Nonenal	2.72 (0.73–7.20)	14.84	C ₉ H ₁₆ O	60784–31–8
<i>Short-chain oxygenated VOCs</i>	15.06 (2.03–41.68)			
(E)-2-Methyl-2-butenal	14.10 (5.07–33.32)	4.85	C ₅ H ₈ O	497–03–0
2-Ethyl-1-hexanol†	5.54 (1.55–14.20)	11.84	C ₈ H ₁₈ O	104–76–7
5-Methyl-2-heptanone	8.75 (3.90–18.30)	10.78	C ₈ H ₁₆ O	18217–12–4
6-Methyl-5-hepten-2-one†	38.03 (13.27–112.14)	10.85	C ₈ H ₁₄ O	110–93–0
<i>Terpenoids</i>	9.54 (1.19–36.46)			
trans-geranylacetone†	16.66 (4.52–59.62)	20.63	C ₁₃ H ₂₂ O	3796–70–1
α-Pinene†	9.59 (1.63–34.47)	9.48	C ₁₀ H ₁₆	80–56–8
β-Pinene†	3.36 (0.95–9.21)	10.57	C ₁₀ H ₁₆	127–91–3

(EBD-CSIC, Sevilla, Spain) and the Centro Nacional de Biotecnología (CNB-CSIC, Madrid, Spain), we estimated seed weight per maternal line by weighing three batches of 60 filled seeds each, to the nearest 0.1 mg, using a Sartorius BP61S balance (Sartorius AG, Göttingen, Germany). The same three batches were used to estimate the mean seed germination rate per maternal line. Seeds were placed in Petri dishes containing filter paper soaked with deionised water and stratified at 4 °C in complete darkness for four days, followed by five days at 22 °C under continuous light in a FitoClima-10.000-EH growth chamber (ARALAB, Rio de Mouro, Portugal). Germination was scored under a Stemi-2000-C stereomicroscope (Carl Zeiss Optical, Inc., Chester, VA, USA) when the root tip protruded through the seed coat. Finally, in a different experiment, seeds from each maternal line were germinated in a growth chamber as mentioned above. Seedlings were then transplanted into 28-well plastic trays (50 × 50 × 70 mm per well) filled with a 3:1 soil:vermiculite mixture in the greenhouse. Flowering time was estimated as the number of days from seedling transplantation to the opening of the first flower, averaging up to 12 full-sibs per maternal line under a 16-hour photoperiod at 22 °C.

2.4. Statistical analyses

All statistical analyses were conducted in R (R Core Team, 2025). A full list of the software used, generated with grateful v. 0.3.0 (Rodríguez-Sánchez and Jackson, 2025), can be found in the [Supporting Information](#).

2.4.1. Constitutive resistance to herbivory

To test whether constitutive resistance to *S. exigua* differed between populations, we analysed herbivory damage in emitter plants subjected to herbivory (i.e. the herbivore-induced treatment). Herbivory damage was square-root transformed to improve model assumptions and analysed using a linear model with emitter population (Bon vs. Cai) as the explanatory variable. We evaluated whether larval mass, emitter plant size, and maternal line nested within population improved model fit by comparing models using AIC; however, none of these terms improved the model and were therefore excluded.

2.4.2. Effects of population and herbivory on VOC emissions

We analysed total VOC emission as a function of population (Bon vs. Cai), emitter herbivory treatment (control vs. herbivore-induced), and their interaction. We fitted generalised linear mixed-effects models with a Tweedie error distribution and log link, including maternal line nested within population as a random intercept. We evaluated larval mass and emitter plant size as covariates by comparing models using AIC; however, neither improved model fit, and they were not retained in the final model. For each VOC class, we analysed individual compound amounts using Tweedie generalised linear mixed-effects models with a log link, including population, herbivory treatment and their interaction as fixed effects, and maternal line nested within population as a random intercept. For classes containing several compounds, we additionally included compound identity as a fixed effect and plant identity as a random intercept to account for repeated measurements within plants. These models estimated a shared proportional treatment response across compounds within each population. Covariates were evaluated using the same AIC procedure described above. Estimated marginal means were averaged equally across compounds on the log scale and back-transformed to the response scale; treatment contrasts were expressed as control/herbivore-induced ratios.

We analysed VOC emission profiles using PERMANOVA based on Bray–Curtis dissimilarities of background-filtered emission amounts (Bray and Curtis, 1957; Anderson, 2001). All-zero profiles were excluded, leaving 131 plants for the distance-based treatment analyses. Population comparisons used treatment-balanced profiles from 25 maternal lines (10 Bon, 15 Cai), giving equal weight to control and herbivore-induced means within each line. Treatment analyses conditioned on maternal line within population and evaluated the joint treatment response, population × treatment interaction, and treatment responses within each population. The interaction test additionally conditioned on the common treatment term. Separate whole-model tests used hypothesis-specific sums of squares adjusted for the specified conditioning terms. We used 10,000 permutations, unrestricted among line profiles for population comparisons, and reduced-model residual permutations within maternal-line blocks for treatment comparisons, with no additional plot level. PERMANOVA effect sizes were expressed as R^2 , calculated as the sum of squares for each tested hypothesis divided

by total inertia, including variation associated with the conditioning terms.

We tested multivariate dispersion using distances to group spatial medians with small-sample bias adjustment (Anderson, 2006), following the observational units and permutation restrictions of the corresponding PERMANOVAs. We additionally tested treatment responses and their interaction with population using the heterogeneity-robust modified ANOVA-type statistic (MATS; Friedrich and Pauly, 2018). This analysis used paired control and herbivore-induced mean profiles from 25 maternal lines (129 plants) and 10,000 zero-mean Gaussian bootstrap replicates generated using population-specific covariance matrices, preserving covariance among compounds and between treatments within lines. Holm adjustment was applied across the two population-specific treatment tests separately for PERMANOVA, dispersion, and MATS.

Population patterns were visualised using PCoA of treatment-balanced maternal-line profiles, and treatment patterns using a pooled partial PCoA conditioned on maternal line within population (Legendre and Anderson, 1999). Axis percentages refer to positive inertia, or positive residual inertia for the partial ordination. Compound vectors were fitted descriptively to the first two axes using envfit without permutation tests, and vectors with $R^2 \geq 0.8$ were displayed.

2.4.3. Correlations between VOCs and life-history traits

We estimated Pearson's correlation coefficients between individual and total VOC emissions and seed weight, seed germination, and flowering time, separately for each population and treatment. VOC emissions were averaged within maternal line and treatment using available measurements, including zero emissions, and matched to the corresponding maternal line trait values (11 Bon and 15 Cai lines). Two-sided p -values were adjusted using the Benjamini–Hochberg false discovery rate procedure (Benjamini and Hochberg, 1995), jointly across correlations involving individual VOCs and total VOC emissions within each population $\times$ treatment $\times$ trait combination. We calculated pointwise 95% confidence intervals for each correlation coefficient using Fisher's z transformation.

2.4.4. Signalling effects on receiver plants

To test for signalling effects on receiver resistance, we analysed the percentage of leaf area consumed by *S. exigua* using linear mixed-effects models. Leaf damage was square-root transformed to improve residual normality and modelled as a function of emitter treatment (control or

herbivore-induced), population (Bon or Cai), and their interaction, with maternal line nested within population included as a random intercept. We evaluated larval mass and receiver plant size as covariates by comparing models using AIC; only larval mass improved model fit and was therefore retained in the final model. The treatment $\times$ population interaction was of special interest, as it tested whether signalling effects in response to herbivory were contingent on population. Fixed effects were evaluated using Type III F-tests with Satterthwaite-approximated degrees of freedom. We additionally estimated treatment contrasts within each population using estimated marginal means. All 156 receiver plants were included in this analysis.

3. Results

We detected 17 VOCs in the headspace of *A. thaliana* plants across the experiment and grouped them into five major classes, which in descending order of mean emission were long-chain aldehydes and alkanes, short-chain oxygenated VOCs, terpenoids, esters, and aromatic ketones (Table 1).

3.1. Constitutive resistance and VOC emissions across populations

Constitutive resistance to herbivory by *S. exigua* differed between populations (Fig. 3a). Under the herbivore-induced treatment, emitter plants from Bon experienced significantly higher leaf damage than those from Cai ($t_{76} = 3.33$, $p < 0.01$; Table S1), indicating lower constitutive resistance in the low-elevation population. In contrast, we detected no population difference in overall VOC emission profiles when treatment-balanced maternal-line profiles were compared (PERMANOVA: pseudo- $F_{1,23} = 0.43$, $R^2 = 0.019$, $p = 0.776$; Table S2a). Multivariate dispersion did not differ detectably between populations (PERMDISP: $F_{1,23} = 0.09$, $p = 0.761$; Table S2b). The population PCoA showed substantial overlap between Bon and Cai, with the first two axes accounting for 55.2% and 15.9% of positive inertia, respectively (Fig. 3b). Five compounds were strongly associated with the displayed ordination axes: 5-methyl-2-heptanone, dodecanal, tridecane, dodecanol, and tetradecanal. Their vectors describe variation among maternal-line profiles rather than compounds demonstrated to distinguish the populations.

3.2. Effects of herbivory on VOC emissions

The joint PERMANOVA detected a treatment-associated difference in

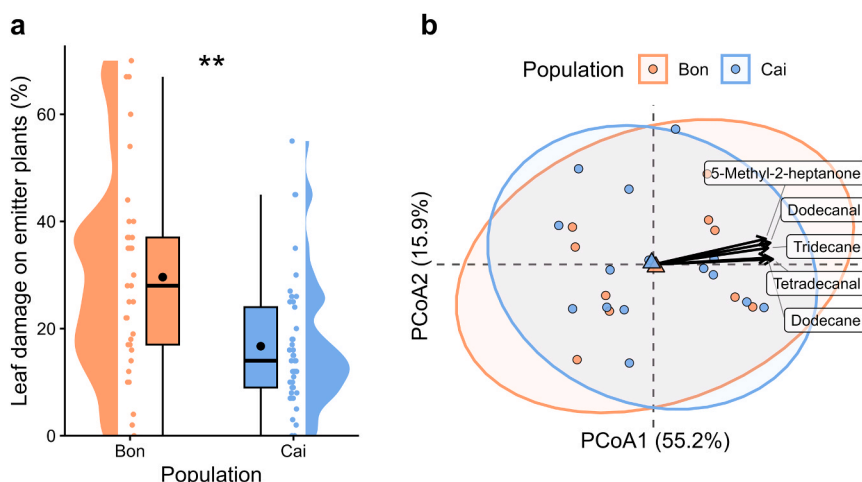


Fig. 3. Population-level differences in herbivore damage and volatile organic compound (VOC) emission profiles from emitter plants. (a) Percentage of leaf damage caused by *Spodoptera exigua* on emitter plants from two *Arabidopsis thaliana* populations (Bon and Cai). Violin plots show data distribution; boxplots indicate median and interquartile range; dots represent individual observations; black dots indicate means; and asterisks denote statistical significance (** $p < 0.01$). (b) Principal coordinates analysis of Bray–Curtis dissimilarities among treatment-balanced maternal-line VOC profiles, comprising 10 Bon and 15 Cai lines. Arrows show descriptive compound vectors with $R^2 \geq 0.8$. Triangles mark population centroids, and ellipses show 95% data ellipses.

VOC emission profiles after accounting for maternal line (pseudo- $F_{2103} = 2.04$, $R^2 = 0.023$, $p = 0.021$; Table S2a). The population $\times$ treatment interaction was not significant (pseudo- $F_{1103} = 1.90$, $R^2 = 0.011$, $p = 0.075$). Treatment responses within individual populations were also non-significant after Holm adjustment (Bon: pseudo- $F_{1,42} = 2.32$, $R^2 = 0.031$, adjusted $p = 0.068$; Cai: pseudo- $F_{1,61} = 1.78$, $R^2 = 0.018$, adjusted $p = 0.093$).

However, multivariate dispersion differed between treatments in Bon (PERMDISP: $F_{1,52} = 5.34$, Holm-adjusted $p = 0.019$), but not detectably in Cai ($F_{1,75} = 0.06$, Holm-adjusted $p = 0.800$; Table S2b). The complementary MATS analysis of paired maternal-line means detected neither a joint treatment response (MATS = 7.25, bootstrap $p = 0.574$) nor a population $\times$ treatment interaction (MATS = 3.85, bootstrap $p = 0.465$; Table S2c). Population-specific MATS tests were also non-significant after Holm adjustment (Bon: $p = 0.708$; Cai: $p = 0.618$). The pooled partial PCoA showed substantial overlap between treatments, with the first two axes accounting for 26.5% and 16.6% of positive residual inertia, respectively (Fig. S5). Together, these analyses provided limited evidence for an overall treatment-induced shift in mean VOC emission profiles.

Class-level analyses detected higher amounts per compound of long-chain aldehydes and alkanes following herbivory in Bon ($z = -2.81$, $p = 0.005$), whereas the corresponding treatment contrast was not significant in Cai ($z = -0.25$, $p = 0.804$; Fig. 4; Table S3). No significant treatment effects were detected for aromatic ketones, esters, short-chain oxygenated VOCs, or terpenoids in either population. Total VOC emissions overlapped broadly between control and herbivore-induced treatments in both populations, with no consistent increase under herbivory (Fig. S6; Table S4). Accordingly, herbivory did not significantly affect total collected VOC amounts in either population (Bon: $z = -1.12$, $p = 0.263$; Cai: $z = -0.76$, $p = 0.445$).

3.3. Correlations between VOCs and life-history traits

Maternal lines with later flowering tended to have higher constitutive VOC emissions in Bon, whereas those with lower seed germination tended to emit more VOCs in Cai under both treatments (Tables 2 and S5). In Bon controls, flowering time was positively correlated with emissions of 12 individual VOCs ($r = 0.60$ – 0.83 ; unadjusted $p < 0.05$) and with total VOC emissions ($r = 0.67$; 95% CI: 0.11–0.91). In Cai, seed germination was negatively correlated with several individual VOCs in both treatments ($r = -0.66$ to -0.51 ; unadjusted $p < 0.05$), as well as total emissions (control: $r = -0.59$; herbivore-induced: $r = -0.57$).

After adjusting for multiple comparisons, the positive associations with flowering time in Bon controls remained significant for nine individual VOCs and total emissions (adjusted $p = 0.028$ – 0.048). None of the negative germination associations in Cai remained significant after correction (adjusted $p \geq 0.086$). No significant flowering-time associations were detected in Bon under herbivory or in Cai under either treatment, even before correction. Likewise, no significant associations were detected for seed germination in Bon or for seed weight in either population or treatment.

3.4. Signalling effects on receiver plants

Exposure to herbivore-induced emitters significantly reduced leaf damage on receiver plants (Fig. 5; Table S6; $F_{1127.3} = 18.36$, $p < 0.001$). We found no statistical evidence that this reduction differed between populations, as indicated by the non-significant emitter treatment $\times$ population interaction ($F_{1126.9} = 0.37$, $p = 0.546$). In Bon, estimated

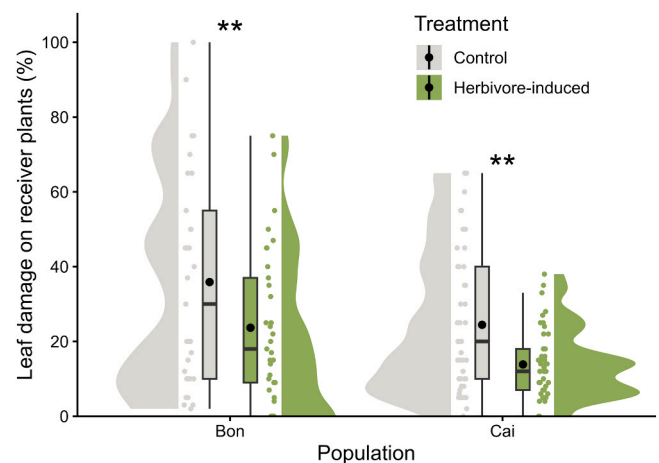


Fig. 5. Effects of emitter plant treatment on herbivore damage in receiver plants. Percentage leaf damage caused by *Spodoptera exigua* on receiver plants exposed to control or herbivore-induced emitter plants, shown separately for each *Arabidopsis thaliana* population (Bon and Cai). Violin plots show data distribution; boxplots indicate median and interquartile range; dots represent individual observations; black dots indicate means; and asterisks denote statistical significance (** $p < 0.01$).

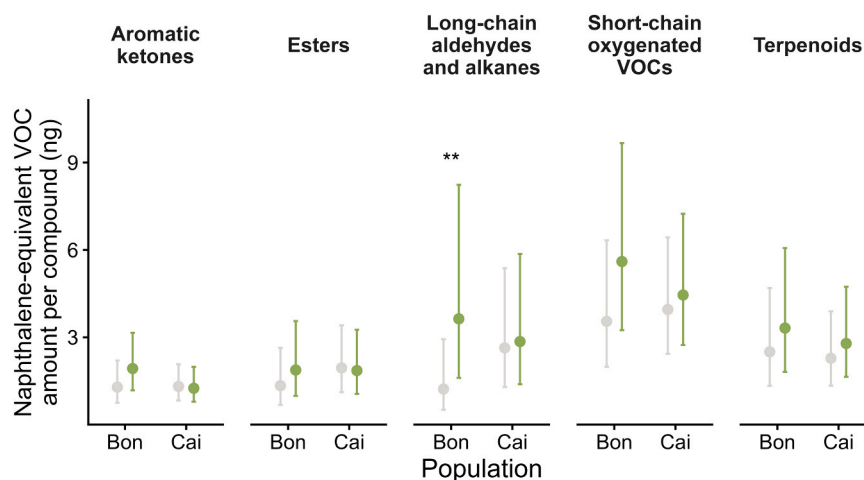


Fig. 4. Effects of herbivory on five classes of volatile organic compounds (VOCs). Naphthalene-equivalent VOC amounts per compound (ng) collected from *Arabidopsis thaliana* emitter plants in the Bon and Cai populations. Grey and green indicate control and herbivore-induced plants, respectively. Points show back-transformed estimated marginal means, averaged equally across compounds within each class on the log scale; whiskers indicate 95% confidence intervals. Asterisks denote significant treatment contrasts within each population and VOC class (** $p < 0.01$); unmarked contrasts are non-significant.

receiver damage decreased from $29.05 \pm 5.49\%$ (estimated marginal means $\pm$ SE) after exposure to control emitters to $17.87 \pm 4.30\%$ after exposure to herbivore-induced emitters, corresponding to a 38.5% reduction ($t_{127.06} = 3.29$, $p = 0.001$). Similarly, in Cai, estimated receiver damage decreased from $19.94 \pm 3.90\%$ to $12.86 \pm 3.14\%$, corresponding to a 35.5% reduction ($t_{127.57} = 2.82$, $p = 0.006$).

4. Discussion

Herbivore-induced VOCs are important mediators of plant defence and plant–plant communication, yet the extent to which VOC-mediated signalling varies across locally adapted populations remains poorly understood. Because adaptation acts on integrated phenotypes, population divergence in life-history strategies and other fitness-related traits may also influence patterns of VOC emission and VOC-mediated signalling. To investigate these relationships, we used two genetically and phenologically divergent *Arabidopsis thaliana* populations adapted to contrasting environments (Fig. 1) and quantified herbivore-induced VOC emissions, VOC-mediated signalling, and their associations with fitness-related traits. This approach allowed us to examine whether effective plant–plant signalling occurs in populations with contrasting life histories, and how volatile production covaries with life-history variation within them.

4.1. VOC-mediated signalling is effective in two locally adapted populations

Emitter plants from Bon sustained greater leaf damage by *Spodoptera exigua* than those from Cai (Fig. 3a), suggesting a difference in susceptibility or palatability between populations. More importantly, receiver plants from both populations experienced lower herbivore damage after exposure to herbivore-induced emitters (Fig. 5), indicating that VOC-mediated signalling was functional and effective in both populations. Defensive responses to damaged neighbours have been documented across species (Karban et al., 2014b), including *A. thaliana*, where exposure to mechanically damaged neighbours can increase or decrease receiver attractiveness to snails depending on genotype (Estarague et al., 2023). However, much of the work on volatile-mediated responses in this species has focused on within-plant induced defence responses (Cipollini et al., 2004), pathogen-mediated interactions (Riedlmeier et al., 2017), and floral scents (Huang et al., 2012). Our experiment extends this previous work by demonstrating a defensive benefit of exposure to herbivore-induced neighbours in two natural populations with contrasting genetic backgrounds, life-history strategies, and susceptibility to herbivory. These differences can therefore coexist with effective plant–plant signalling, allowing receivers in both populations to benefit from exposure to herbivore-induced neighbours.

Our findings provide little support for a simple correspondence between population divergence in life-history traits and differentiation in overall VOC emission profiles (Fig. 3b). Herbivory explained 2.3% of multivariate variation, while treatment-related dispersion in Bon and the robust mean-profile tests left evidence for a shift in mean emission profiles inconclusive (Table S2). Nevertheless, comparisons of whole-blend profiles may not fully capture the chemical changes relevant to signalling. Changes in particular compounds, their relative abundance or the timing of emission could contribute to receiver responses without producing a readily detectable shift in the multivariate mean. The increase in long-chain aldehyde and alkane emissions in Bon identifies one component of the chemical response to herbivory (Fig. 4). The occurrence of these chemical classes is consistent with previous reports of aldehydes and alkanes in *A. thaliana* volatile profiles, including dodecanal in a study of plant–whitefly interactions (Rohloff and Bones, 2005; Zhang et al., 2013).

Recent evidence further strengthens the biological relevance of this chemical pattern. Kinoshita et al. (2026) showed that herbivore-damaged *A. thaliana* Col-0, a laboratory accession that

produces no detectable green leaf volatiles, elicited calcium signalling and activation of the defence marker VSP1 in neighbouring plants. Herbivory also increased acetophenone and alkanes, including dodecane and tridecane, in their headspace samples, providing a direct chemical overlap with our study. Evidence for defensive functions of hydrocarbons also comes from other plants, such as maize, where synthetic compounds identified in herbivore-induced blends reduced *Spodoptera frugiperda* feeding and growth when incorporated into larval diets (Murali-Baskaran et al., 2026). Together, these studies identify plausible chemical candidates for further testing, although functional assays are still needed to establish which compounds elicit receiver defence. Our evidence of reduced receiver damage complements this mechanistic work by demonstrating a defensive benefit in two natural populations with contrasting life histories. Whether Bon and Cai achieve this response through the same emitted compounds and perception mechanisms remains unresolved.

Bon and Cai differed in their susceptibility to herbivory despite their overlapping VOC profiles, which highlights the importance of considering VOCs alongside other defence traits. Previous studies have documented substantial natural variation in herbivore-induced VOC blends among *A. thaliana* accessions (Huang et al., 2010; Snoeren et al., 2010), including differences in terpene emissions associated with allelic variation in terpene synthase genes (Huang et al., 2010). This variation extends beyond what plants emit to how their neighbours respond. For example, Estarague et al. (2023) found that changes in receiver attractiveness to snails were associated with variation in genes involved in stress response and jasmonate signalling. Yet volatile production and perception represent only part of the chemical defences that shape plant–herbivore interactions. Glucosinolates, for example, exhibit strong geographic structuring and differentiated chemotypes across European *A. thaliana* populations (Katz et al., 2021), including contrasting glucosinolate chemotypes in southwestern and central Iberia, where Bon and Cai are located, respectively. Although not measured here, such differences in non-volatile defences could contribute to the contrasting susceptibility of Bon and Cai. Population divergence may therefore be expressed differently in baseline resistance, volatile production and responses to neighbouring plants.

4.2. Herbivory may modify how VOCs relate to life-history traits across populations

Despite the limited differentiation in VOC profiles between populations, the correlations suggest that volatile production may be integrated with different aspects of their life histories. In Bon, later-flowering maternal lines had higher constitutive emissions of several VOCs and higher total emissions, whereas in Cai, maternal lines with stronger seed dormancy (i.e. lower germination rates) tended to emit more VOCs under both treatments (Table 2). The flowering associations in Bon remained significant after multiple-testing correction, whereas the germination relationships in Cai did not. With correlations estimated from 15 maternal lines in Cai, sample size may have constrained our ability to detect associations after accounting for multiple comparisons. Nevertheless, the recurring negative direction across treatments identifies an exploratory pattern worth examining in a larger set of maternal lines. These patterns point to different potential axes of covariation between volatile production and life-history in the two populations.

The flowering–VOC associations are of particular evolutionary interest because previous common-garden studies have documented selection on flowering time in *A. thaliana* (Méndez-Vigo et al., 2022; de la Mata et al., 2024). Specifically, a study of within- and among-population variation in Iberian *A. thaliana*, including Bon and Cai, found selection favouring early flowering across populations in one common-garden experiment, and selection related to recruitment in Cai in another (de la Mata et al., 2024). More generally, covariation among dormancy, growth, and flowering varies geographically and contributes to contrasting life-history strategies in *A. thaliana* (Debieu et al., 2013; Marcer

Table 2

Correlation between VOCs and life-history traits. Pearson's correlation coefficients (r) are shown for individual VOCs and total emissions in relation to seed germination and flowering time in two *Arabidopsis thaliana* populations (Bon and Cai), separately for control and herbivore-induced treatments. VOCs are grouped by chemical class (italic headings). Correlations used maternal-line means, with 11 Bon and 15 Cai lines per treatment. Asterisks indicate significance before multiple-testing correction (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Bold values indicate associations remaining significant after Benjamini–Hochberg false discovery rate correction within each population $\times$ treatment $\times$ trait combination (adjusted $p < 0.05$). Complete results are provided in Table S5. Daggers (†) indicate compounds confirmed using commercial standards; unmarked compounds were putatively identified using mass spectrum comparisons and Kováts indices.

VOCs	Germination rate				Flowering time			
	Control		Herbivore-induced		Control		Herbivore-induced	
	Bon	Cai	Bon	Cai	Bon	Cai	Bon	Cai
<i>Aromatic ketones</i>								
Acetophenone†	0.33	-0.54 *	0.20	-0.56 *	0.76 **	0.24	0.40	0.26
<i>Esters</i>								
Butanoic acid, methyl ester	0.26	-0.48	0.18	-0.51 *	0.60	0.02	0.39	0.23
<i>Long-chain aldehydes and alkanes</i>								
Decanal†	0.21	-0.66 **	0.20	-0.52 *	0.51	0.25	0.43	0.10
Dodecanal	0.26	-0.51	0.12	-0.48	0.68 *	0.10	0.48	-0.08
Dodecane†	0.37	-0.43	0.22	-0.52 *	0.79 **	0.10	0.36	0.15
Nonanal†	0.20	-0.63 *	0.30	-0.62 *	0.44	0.23	0.32	0.23
Tetradecanal	0.27	-0.52 *	0.20	-0.52 *	0.69 *	0.19	0.43	-0.12
Tetradecane†	0.29	-0.49	0.19	-0.39	0.66 *	0.11	0.50	-0.14
Tridecane†	0.32	-0.27	0.15	-0.30	0.71 *	-0.08	0.40	-0.11
cis-2-Nonenal	0.16	-0.36	-0.02	-0.39	0.63 *	0.14	0.30	0.20
<i>Short-chain oxygenated VOCs</i>								
(E)-2-Methyl-2-butenal	0.21	-0.42	0.02	-0.47	0.83 **	0.05	0.46	-0.01
2-Ethyl-1-hexanol†	0.15	-0.32	-0.09	-0.51	0.68 *	0.08	0.34	0.13
5-Methyl-2-heptanone	0.29	-0.27	0.08	-0.20	0.70 *	-0.06	0.39	-0.26
6-Methyl-5-hepten-2-one†	0.25	-0.60 *	0.23	-0.60 *	0.51	0.25	0.31	0.19
<i>Terpenoids</i>								
trans-geranylacetone†	0.25	-0.45	0.18	-0.57 *	0.48	0.03	0.21	0.14
α -Pinene†	0.08	-0.50	-0.03	-0.52 *	0.60 *	0.16	0.38	0.14
β -Pinene†	0.04	-0.47	-0.15	-0.49	0.61 *	0.17	0.38	0.14
Total VOCs	0.26	-0.59 *	0.19	-0.57 *	0.67 *	0.18	0.52	0.08

et al., 2018). Our results raise the possibility that selection acting on recruitment and reproductive schedules could also shape correlated VOC traits as part of broader integrated phenotypes. In Bon, for example, the positive association between flowering time and constitutive emissions provides a potential link through which selection on developmental timing might indirectly influence volatile production.

Herbivory may further modify these relationships in ways that depend on population background. The flowering–VOC associations detected in control Bon plants were not detected in herbivore-induced plants, whereas the negative germination–VOC pattern in Cai occurred under both treatments (Table 2). One possible interpretation concerns the different allocation contexts associated with their life-cycle dynamics. Plants from Bon develop and flower rapidly, whereas plants from Cai generally show slower development and delayed reproduction. In Bon, rapid life cycles (approximately two months between seed germination and seed shedding; F. X. Picó, pers. obs.) may favour maintenance of developmental schedules following herbivore attack, while induced defence responses introduce additional physiological demands that weaken the correspondence between flowering time and volatile production. In Cai, slower developmental dynamics, which may span several months from autumn to spring (F. X. Picó, pers. obs.), could allow a different balance between growth and defence, potentially permitting more consistent associations between chemical traits and traits linked to recruitment and dormancy. This interpretation remains a hypothesis about how contrasting developmental strategies could influence trait integration under herbivory. More broadly, shared genetic control of vegetative development and flowering initiation (Méndez-Vigo et al., 2010), together with pleiotropic effects of flowering-time genes on other developmental and ecological traits (Hanemian et al., 2020), provides a framework for investigating how developmental schedules relate to volatile production. Together, these patterns suggest that herbivory may influence not only volatile emissions themselves, but also their coordination with life-history strategies. Testing changes in the strength of these associations across populations

and treatments would help establish how such coordination contributes to the ecological and evolutionary roles of VOCs.

4.3. Perspectives and conclusions

A few aspects of our experimental design should be considered when interpreting these results. Although we used two contrasting, locally adapted populations, comparisons across additional populations are needed to establish how widespread the responses observed here are in *A. thaliana*. Because experiments were conducted under greenhouse conditions using a single herbivore species and a single induction period, patterns of VOC emission and VOC-mediated signalling may differ under more complex natural conditions, where plants experience greater environmental variability and interact with multiple herbivores and other trophic levels (Turlings and Erb, 2018). Within our experimental context, the timing of VOC collection is especially relevant because VOC production is known to vary temporally. VOC emissions can vary between the day and night (De Moraes et al., 2001), while green leaf volatiles can be formed and metabolised rapidly after tissue damage in *A. thaliana* (Matsui et al., 2012). Terpenoid emissions can develop over longer periods. For example, Herde et al. (2008) found that emissions under most induction treatments in *A. thaliana* were highest during the second light period, 21–30 h after treatment began. Our 1.5-hour collection following five hours of herbivore exposure therefore captured one part of the longer period of receiver exposure and may have missed both early green leaf volatile bursts and stronger later emissions of some terpenoids. While this temporal perspective could help explain the composition of the measured volatile profiles, the presence of receiver defence activation without detectable green leaf volatiles has also been demonstrated (Kinoshita et al., 2026).

Our experiment focused exclusively on rosette-stage plants, whereas flowering *A. thaliana* individuals emit distinct floral volatiles (Huang et al., 2012) that could further modify plant–plant interactions and signalling outcomes. Also, although we quantified inducible VOCs,

additional measurements of constitutive chemical defences and molecular markers of defence activation would provide further insight into the observed differences in herbivore resistance between populations. To account for potential emissions from the pot and soil enclosed during collection, we also used four blanks to characterise the background and conservatively coded compound amounts at or below the maximum blank value for each compound as zero. Building on this approach, future studies combining more detailed background measurements (Armbruster and Pry, 2008) with compound-specific bioassays and measurements of receiver defences could identify the chemical cues and mechanisms underlying these signalling benefits.

At the same time, an important strength of our approach is that we incorporated multiple maternal lines per population, allowing us to represent within-population variation while accounting for shared maternal-line origin. Expanding this framework to additional populations, environmental contexts, developmental stages, and temporal scales may help clarify whether the relationships observed here between VOC emissions and fitness-related traits represent stable components of locally adapted phenotypes or vary according to ecological context and herbivory pressure. Identifying the specific compounds, genes, and molecular pathways underlying VOC-mediated receiver responses remains an important challenge. Experiments with individual compounds and reconstructed blends can connect chemical structure to defence induction (Heil et al., 2008), while recent work demonstrating volatile-triggered calcium signalling in *A. thaliana* provides a route towards understanding early perception responses (Aratani et al., 2023). Future studies could also evaluate the relative importance of VOC-mediated changes in receiver resistance and indirect defence mechanisms involving the attraction of natural enemies of herbivores (Turlings and Erb, 2018). Finally, integrating aboveground and belowground interactions, including volatile-mediated signalling and root exudates, may provide a more complete understanding of plant chemical responses across heterogeneous environments. The emerging evidence for belowground communication (Guerrieri and Rasmann, 2024), together with natural variation in root exudate composition among Iberian *A. thaliana* accessions (Subrahmaniam et al., 2025), makes this a promising extension of the population-based approach used here.

Our study shows that herbivore-induced plant–plant signalling increased receiver resistance in both Bon and Cai, reducing subsequent herbivore damage by 38.5% and 35.5%, respectively. These defensive benefits occurred despite pronounced differences between populations in life-history strategies, genetic structure, and baseline susceptibility to herbivory, indicating that such divergence does not preclude effective signalling between neighbouring conspecifics. In Bon, constitutive VOC emissions were positively associated with flowering time, whereas no such association was detected in herbivore-induced plants. This pattern suggests that volatile production may be integrated with life-history traits in ways that vary with herbivory and population background.

CRedit authorship contribution statement

Rodrigo R. Granjel: Writing – review & editing, Writing – original draft, Visualization, Project administration, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Lucía Martín-Cacheda:** Writing – review & editing, Writing – original draft, Resources, Methodology, Formal analysis. **Gregory Röder:** Writing – review & editing, Resources, Methodology, Investigation. **Iago Izquierdo-Ferreiro:** Methodology, Investigation. **Andrea Martín-Díaz:** Writing – original draft, Methodology, Formal analysis. **F. Xavier Picó:** Writing – review & editing, Writing – original draft, Resources, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Rodrigo R. Granjel reports equipment, drugs, or supplies was provided by Biological Mission of Galicia. Lucía Martín-Cacheda reports equipment, drugs, or supplies was provided by University of Valencia. F. Xavier Pico reports equipment, drugs, or supplies was provided by National Centre for Biotechnology. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.envexpbot.2026.106472](https://doi.org/10.1016/j.envexpbot.2026.106472).

Data availability

The data and code supporting the findings of this study are openly available in Zenodo (Granjel et al., 2026), at <https://doi.org/10.5281/zenodo.23210290>.

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