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HIPVS ENHANCE PHOTOSYNTHESIS WHILE INCREASING HERBIVORE RESISTANCE IN *BRASSICA RAPA*.

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Key Words: *Brassica*, Volatile Organic Compounds, Photosynthesis, Induced Defences, Priming, Plant-Plant Interactions, *Plutella Xylostella*.

Abstract: Herbivore-induced plant volatiles (HIPVs) mediate plant–plant communication and can induce or prime responses in neighbouring plants. However, their effects on primary physiological processes and whether these responses are consistent across wild and cultivated varieties remain poorly understood. We investigated how exposure to HIPVs influences photosynthesis, stomatal conductance, volatile emissions, and resistance to the herbivore *Plutella xylostella* in two wild and two cultivated varieties of *Brassica rapa*. Receiver plants exposed to HIPVs increased net photosynthesis and stomatal conductance compared with plants exposed to constitutive volatiles. HIPV exposure also altered plant–herbivore interactions. In oviposition assays, *P. xylostella* females laid fewer eggs on HIPV-exposed plants, and larval feeding resulted in reduced leaf consumption and lower larval weight gain relative to controls. Multivariate analyses revealed qualitative shifts in volatile blend composition in cultivated varieties but not in wild populations. Together, these findings demonstrate that perception of HIPVs can enhance primary physiological activity while increasing resistance to herbivores, highlighting a link between volatile signalling and plant physiological responses.

INTRODUCTION

Airborne volatile organic compounds (VOCs) mediate ecological interactions among plants, herbivores, and their natural enemies (Brosset and Blande 2021). Herbivore-induced plant volatiles (HIPVs), released by damaged plants, can be perceived by neighbouring plants and are known to induce or prime defensive responses, thereby enhancing resistance to herbivores (Kost and Heil, 2006). Receiver plants exposed to HIPVs often exhibit enhanced resistance to herbivores through increased expression of defence-related genes, accumulation of secondary metabolites, or emission of defensive volatiles that deter herbivores or attract their natural enemies (Arimura et al. 2000; Heil et al. 2007; Kessler et al. 2006; Kost and Heil 2006). In primed plants, defences are not necessarily expressed immediately but are activated more rapidly or more strongly following damage (Conrath 2011; Frost et al. 2008). For example, maize plants exposed to volatile cues emitted by herbivore-infested neighbours respond more rapidly to subsequent herbivory by enhancing induction of defence genes and this priming correlated with reduced caterpillar feeding and development (Ton et al. 2007). Such priming mechanisms are thought to represent an efficient defensive strategy because they allow plants to maintain readiness for attack while limiting the metabolic costs associated with constitutive defence expression (Waterman et al. 2024).

While the defensive effects of HIPVs are well established, their influence on primary physiological processes remains less understood (Brosset and Blande 2022). Photosynthesis provides plants with a source of energy; they harvest sunlight to produce ATP and NADPH involved in various biological processes, sustaining growth, defence, and reproduction (Züst and Agrawal 2017). Yet few studies have examined whether HIPV exposure directly alters these functions (Brosset and Blande 2022). Understanding how plants integrate volatile signals with primary metabolism is essential for clarifying the broader consequences of plant–plant communication. Previous work on *B. rapa* has shown that exposure to HIPVs can enhance photosynthetic activity and accelerate flowering, suggesting a potential link between VOC perception and primary functions (Brosset et al. 2023).

In addition, domestication has profoundly altered plant traits through selection for yield, palatability, and storage, often reducing genetic and phenotypic diversity (Meyer et al. 2012). Selection has also

57 modified plant defence traits, particularly by reducing toxic or unpalatable phytochemicals such as
58 glucosinolates in Brassica crops (Chaudhary 2013). In many wild species, higher constitutive defence
59 levels are maintained under natural selection, whereas cultivated plants often exhibit reduced
60 constitutive resistance (Paudel et al. 2019). However, several studies have shown that cultivated
61 plants can display stronger induced defensive responses following herbivore attack than their wild
62 relatives, including increased emission of HIPVs (Rodriguez-Saona et al. 2009; Tamiru et al. 2017;
63 Paudel et al. 2019; Brosset et al. 2020).

64 In contrast, the influence of domestication on plant responses to HIPVs emitted by neighbouring
65 plants remains poorly understood. Because wild species have evolved under natural selection without
66 intensive breeding for productivity-related traits, they may retain stronger responsiveness to these
67 volatile cues than cultivated species. To our knowledge, this question has received little direct
68 experimental attention, particularly in comparisons between cultivated and wild relatives. Therefore,
69 in this study we examined whether HIPV exposure enhances photosynthesis and resistance to
70 herbivores in *Brassica rapa*, and whether responses differ between wild and cultivated varieties.

71 **MATERIALS AND METHODS**

72 ***Plants and Insects:*** Seeds of wild *B. rapa* (W_N) were obtained from a natural population in the
73 Netherlands (provided by E. Poelman, Wageningen University) and from a Moroccan population
74 (W_M) supplied by Kew Gardens, London, UK. Seeds of cultivated *B. rapa* ssp. oleifera var.
75 Cordelia (C_C) and var. Valo (C_V) were obtained from Boreal Plant Breeding Ltd (Jokioinen,
76 Finland). Varieties Cordelia and Valo are of particular interest as they are widely cultivated in
77 Sweden and Finland.

78 Seeds were sown in a peat:mull:sand mixture (3:1:1) in 0.8 L pots and grown in climate chambers
79 (Weiss Technik, Lindenstruth, Germany) under control conditions (16L:8D photoperiod, 21/16°C
80 day/night, 60–80% RH).

81 *Plutella xylostella* was reared on *Brassica oleracea* var. italica (broccoli) in polycarbonate cages (33 ×
82 33 × 60 cm) in mesh cages (33 × 33 × 60 cm) under a 16L:8D photoperiod at 22 ± 0.5°C. Adults were

provided with 30% honey solution and allowed to oviposit on host plants, maintaining a continuous colony.

Exposure of Plants to HIPVs: Plants were arranged in growth chambers under the same conditions as above. Within each chamber, emitter and receiver trays (five plants each) were positioned 20 cm apart, with airflow directed from emitters to receivers. The trays were separated by a thin layer of water to prevent larval movement between plants. Airflow was directed from the emitter to the receiver tray. Emitters were either infested with 15 second- or third-instar larvae (I_VOC) or left undamaged (C_VOC). Receiver plants were exposed for four days to volatiles from emitters of the same variety.

Each batch included five receiver plants per treatment and variety, and the experiment was repeated to obtain sufficient replication.

Measurement phase

Immediately after exposure, induction responses were assessed.

Gas Exchange Measurements: Net photosynthesis and stomatal conductance were measured using a portable photosynthesis system (LI-6400 XT; LI-COR Inc., Lincoln, NE, USA) under saturating light (1000 μmol m^{-2} s^{-1} PAR), 400 μL L^{-1} CO_2, and 25°C.

Oviposition Assays: Paired receiver plants (C_VOC and I_VOC) were placed in polycarbonate cages (33 × 33 × 60 cm; 20°C, 16L:8D), and 20 adult moths (1:1 sex ratio) were released per cage (Figure 2). Eggs were counted after 28 h (as preliminary trials indicated some females required more than 24 h to lay eggs).

Collection and Analyses of Volatile Organic Compounds: Volatile emissions from a subset of receiver plants (C_VOC and I_VOC) were collected immediately after exposure to assess direct induction, following the dynamic headspace sampling protocol described in Brosset et al. (2022). Samples in adsorbent tubes (Tenax TA and Carbopack B), were desorbed thermally were desorbed with a thermal desorption unit (TD-100, 250°C for 10 min; Markes International Ltd, Llantrisant,

UK), cryofocused at −10°C and injected in splitless mode onto an HP-5 capillary column (60 m, 250 µm x 0.25 µm; Agilent). The oven temperature programme from 40°C for 4 minutes, then ramped 5°C min^{-1} to 210°C and further ramped at 20°C min^{-1} to 280°C and held for 6.5 minutes. Helium was used as carrier gas, and MS detection (300°C) was performed at 70 eV with scan range 35–430 m/z. Compounds were identified using analytical standards and the Wiley 275 library. Emission rates (ER) were calculated from Total Ion Chromatograms relative to standards, with blank subtraction, and expressed as ng gDW^{-1} h^{-1} (Brosset et al. 2021).

Larval Feeding and Taken Weight: Following exposure, five larvae were placed on each receiver plant and allowed to feed for 24 h. Larval weight gain was quantified (microbalance, BP211D Analytical Balance, Sartorius AG, Göttingen, Germany; accuracy ±1 µg). Volatiles were then collected using the protocol previously described, and plant biomass was determined after drying. The leaf area consumed by the larvae was quantified by photographing leaves placed on A4 paper and analysing images using the LeafAreaAnalyzer software (https://github.com/EmilStalvinge/LeafAreaAnalyser; emilstalvinge@gmail.com).

Gas exchange, oviposition, and initial VOC measurements were conducted on one plant cohort, whereas feeding assays and post-feeding VOC collections were performed on a separate cohort.

Statistical Analyses: Data were analysed using SPSS 25 (IBM Corp., Armonk, USA) and R v.3.4.3. Net photosynthesis, stomatal conductance, fed area, and larval weight were analysed using two-way ANOVA to test the main and interactive effects of treatment and variety. Stomatal conductance, fed area, and larval weight data were log-transformed to meet assumptions of normality and homogeneity of variance. Significant interactions were examined using simple main effects with Bonferroni correction.

Oviposition data were analysed with paired t-tests to compare egg-laying on treated versus control plants. To improve normality of the differences, pairs in which adults laid fewer than 10 eggs were excluded. Exclusion of these data ensures that statistical tests reflect meaningful differences in oviposition behaviour rather than artifacts of very low or uninformative egg counts.

Volatile emission rates were log transformed and auto-scaled (mean-centered and divided by the standard deviation of each variable) before Partial Least Squares–Discriminant Analysis (PLS-DA) in R software (v. 3.4.3; package vegan and RVAideMemoire), with cross-validation based on 50 submodels (5-fold outer loop and 4-fold inner loop). A pairwise test was performed, based on PLS-DA with 999 permutations, to highlight the differences between treatments.

RESULTS

Gas Exchange Measurements:

Two-way ANOVA revealed that exposure to HIPVs enhanced net photosynthesis rate (Fig. 1a) and stomatal conductance in receiver plants (Fig. 1b) with a significant main effect of treatment on net photosynthesis rate ($F_{1,98} = 4.31$, $P = 0.041$), and stomatal conductance ($F_{1,98} = 7.98$, $P = 0.006$). In addition, the significant interaction between treatment and variety ($F_{3,98} = 2.35$, $P = 0.077$) indicating that the response to HIPVs differed among varieties (Fig. 1b). Post hoc tests (Table S1) for the interaction effects showed that stomatal conductance was significantly enhanced in the cultivated variety Cordelia (C_C; difference in means = −0.087, F_1,df = 10.732, p = 0.001), while no significant effect of treatment was detected in the wild Moroccan population (W_M; difference in means = −0.073, F_1,df = 1.403, p = 0.239), the wild population W_N (difference in means = 0.003, F_1,df = 0.073, p = 0.788), or the cultivated variety C_V (difference in means = −0.048, F_1,df = 1.525, p = 0.220).

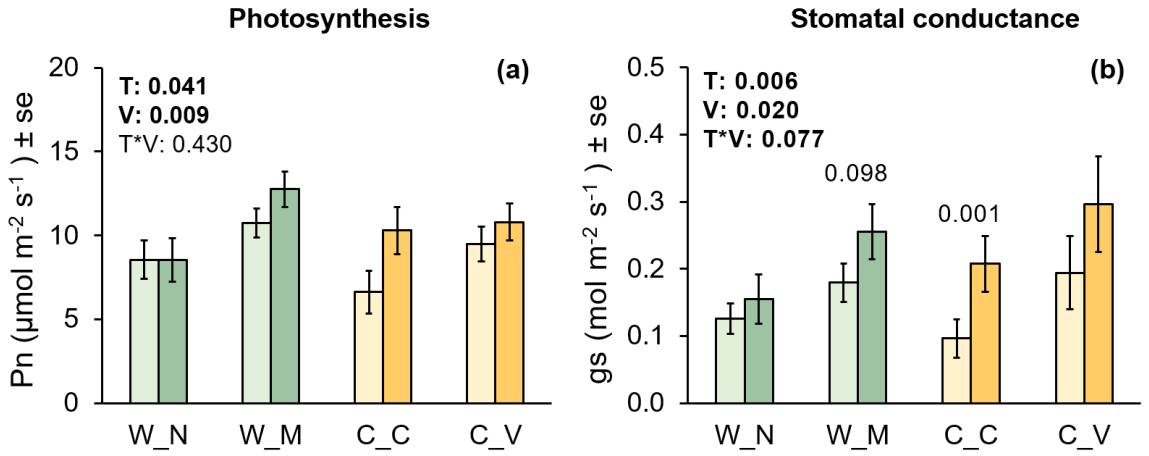
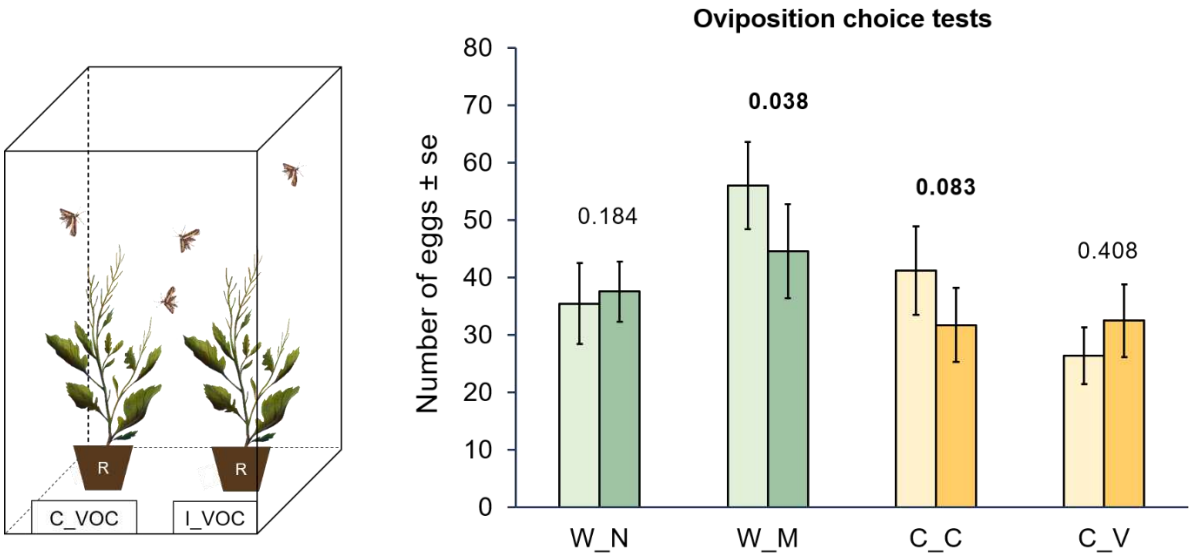


Fig. 1. Mean of net photosynthesis (a), and stomatal conductance (b) in the different varieties. Wild varieties are in green and cultivated varieties in yellow. Light green and yellow for receivers exposed to control VOCs (C_VOC), and dark colours for receivers exposed to HIPVs (I_VOC). Results of post hoc tests are given in the main text and table S1.

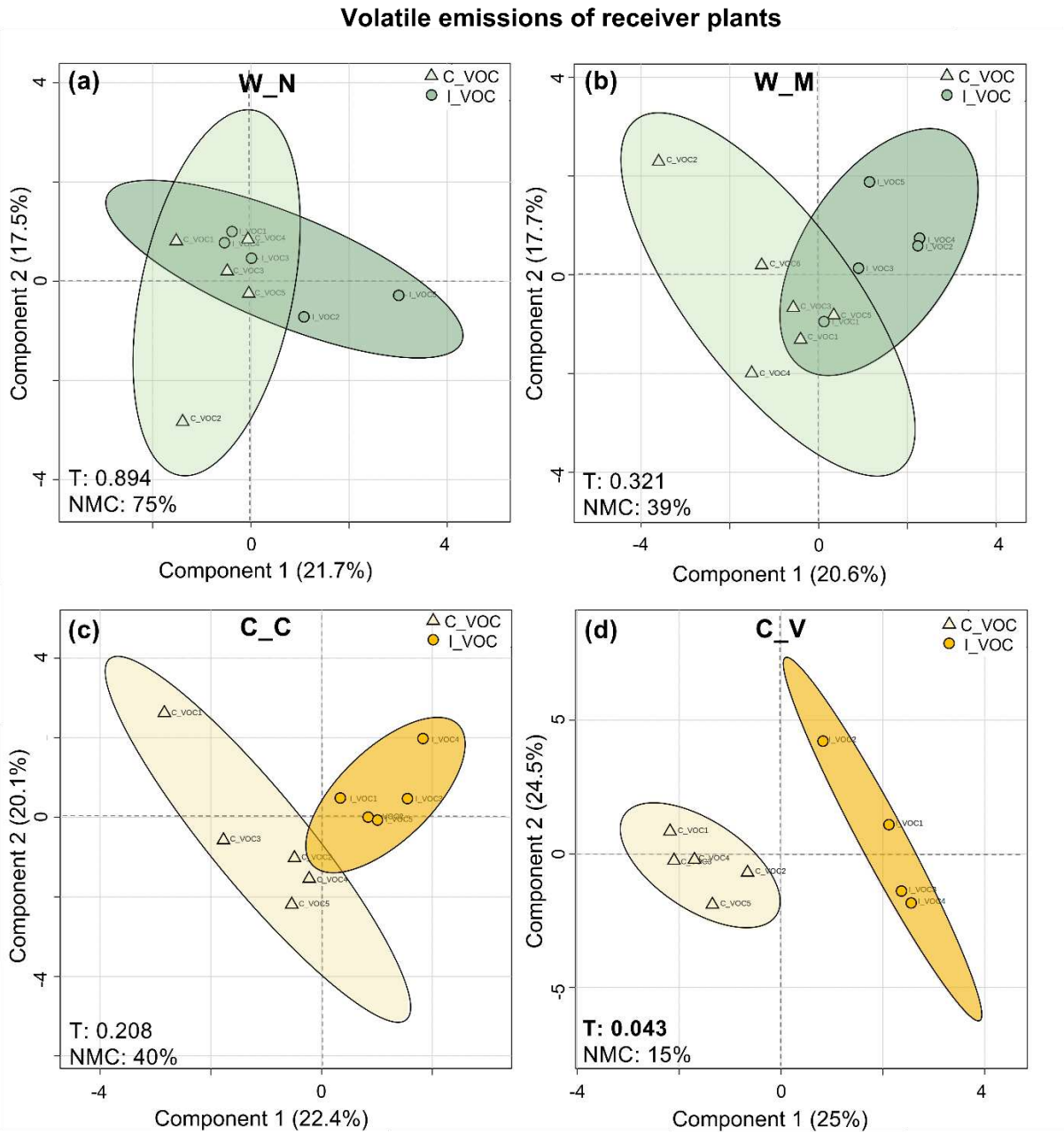
Oviposition Tests: Among wild populations, W_M did not exhibit a significant difference between control and HIPV conditions (mean difference = −0.103; t_{18} = −1.383; 95% CI [−0.261, 0.053]; p = 0.184), whereas W_N showed a significant effect of treatment, with higher values under control conditions relative to HIPV exposure (mean difference = 0.132; t_{16} = 2.255; 95% CI [0.007, 0.257]; p = 0.038). In cultivated varieties, C_C showed a non-significant trend toward higher values under control conditions compared with HIPV exposure (mean difference = 0.177; t_{21} = 1.822; 95% CI [−0.025, 0.380]; p = 0.083), while C_V exhibited no significant effect of treatment (mean difference = −0.067; t_{16} = −0.849; 95% CI [−0.234, 0.1]; p = 0.408).



165

166 **Fig. 2.** Representation of an oviposition choice test in polycarbonate cages, and mean number of eggs
167 deposited on receiver plants exposed to differently treated emitter plants. Wild varieties are in green
168 and cultivated varieties in yellow. Light green and yellow colours indicate receivers exposed to
169 control VOC (C_VOC), and dark colours indicate receivers exposed to HIPVs (I_VOC).

170 ***Volatile Emissions:*** Partial least-squares regression (PLSR) conducted on the complete volatile
171 blends of all plants provided further insights into differences in volatile composition between
172 treatments for each variety. No differences in volatile blends were observed for the wild varieties (Fig.
173 3a, b). However, ellipse s with 95% confidence intervals showed a separation in the blend of volatile
174 emissions between plants exposed to HIPVs and non-exposed plants for the cultivated varieties C_C
175 and C_V (Fig. 3c, d). Further statistical tests indicated that volatile blends from receivers exposed to
176 HIPVs significantly differed from control receivers for C_V plants (Fig. 3d).



177

178 **Fig. 3.** Partial least-squares – Discriminant Analysis (PLS-DA) regressions performed on the volatile
179 emission rates with 95% confidence interval ellipses of each variety: (a) Wild *B. rapa*, Netherlands,
180 (b) Wild *B. rapa*, Morocco, (c) *B. rapa* spp. oleifera var: Cordelia, (d) *B. rapa* spp. oleifera var: Valo.
181 Wild varieties are in green and cultivated varieties in yellow. Light coloured ellipses represent the
182 95% confidence interval for receivers exposed to control VOCs (C_VOC), and darker ellipses
183 represent the 95% confidence interval for receivers exposed to HIPVs (I_VOC). Significant
184 differences from pairwise tests based on PLS-DA are in bold (n=4 to 6 per treatment). NMC, the

percentages of misclassification. Graphics were produced in MetaboAnalyst (https://www.metaboanalyst.ca/).

Larval Performance: Following larval feeding, receiver plants exposed to HIPVs from damaged emitters exhibited a lower leaf area consumed compared to plants exposed to undamaged emitters ($F_{1,39} = 15.809$, $p < 0.001$, Fig. 4a). Larvae had similar initial weights across treatments, but after feeding, weight gain was lower on plants previously exposed to HIPVs from damaged emitters ($F_{1,54} = 46.445$, $p < 0.001$, Fig. 4b). There was a significant main effect of variety ($F_{2,39} = 4.844$, $p = 0.013$) on the fed area, and larval weight ($F_{2,54} = 84.465$, $p < 0.001$). However, there was no significant interaction between variety and treatment ($F_{2,54} = 0.476$, $p = 0.624$).

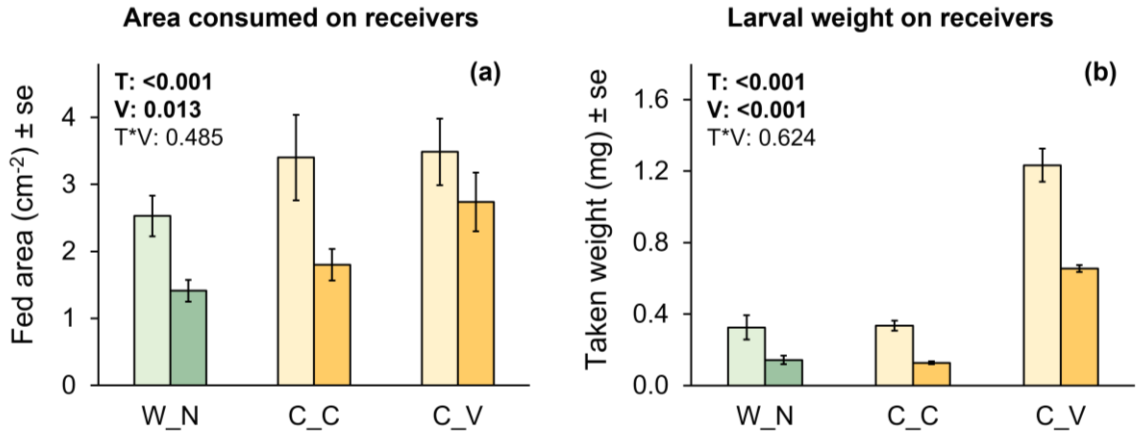


Fig. 4. Mean of fed area (a), and larval weight (b) in the different varieties in priming experiments. Wild varieties are in green and cultivated varieties in yellow. Light green and yellow for receivers exposed to control VOCs (C_VOC), and dark colours for receivers exposed to HIPVs (I_VOC). Significant results from two-way ANOVA assessing main and interactive effects of treatment (T) and variety (V) are indicated in bold.

DISCUSSION

Herbivore-induced plant volatiles are increasingly recognised as important mediators of plant–plant information, and recent studies indicate that HIPVs can have consequences for primary physiology. In this paper, we found that exposure to HIPVs simultaneously altered primary physiological function and resistance to herbivores in *B. rapa*. Receiver plants exposed to HIPVs exhibited increased net

photosynthesis and stomatal conductance and showed enhanced resistance to herbivory compared with plants exposed to constitutive volatiles. These findings provide evidence that volatile-mediated plant communication may influence not only defensive traits but also core physiological processes associated with carbon acquisition.

Changes in primary physiological functions following HIPV exposure remain relatively poorly documented (Brosset and Blande 2022). In the present study, HIPV-exposed plants displayed enhanced photosynthetic activity and stomatal conductance, suggesting that perception of airborne cues can modify gas-exchange processes. Similar responses have been observed in other plant species, including *Pinus sylvestris*, (Yu et al. 2022, Yu et al. 2024) and *B. rapa* (Brosset et al. 2023) indicating that modulation of primary metabolism may represent a more widespread component of plant responses to volatile signals.

The increase in stomatal conductance is particularly noteworthy because stomata play a central role in the exchange of gases and volatile compounds between plants and the atmosphere (Jiang et al. 2020; Maleki et al. 2024; Wang and Erb 2022). Increased conductance in HIPV-exposed plants could therefore facilitate the perception and transport of volatile signals within leaf tissues, potentially enhancing the efficiency of interplant communication.

Enhanced photosynthetic activity may also have important implications for plant defence strategies. The production of defensive compounds, including both volatile and non-volatile metabolites, requires substantial metabolic resources (Zrimec et al. 2025). Increased carbon assimilation following HIPV exposure may therefore provide additional resources supporting defence induction or priming (Brosset and Blande 2022). Consistent with this interpretation, plants exposed to HIPVs in our study had an enhanced resistance reflected by reduced herbivore damage and supported lower larval weight gain compared with control plants, as well as a shift in VOC blends emitted upon feeding in two varieties.

HIPV exposure also influenced herbivore behaviour. In oviposition assays, *Plutella xylostella* females laid fewer eggs on some HIPV-exposed plants. Herbivorous insects often rely on plant volatiles as

cues for host selection, and even subtle changes in volatile blend composition can influence oviposition decisions (Li et al. 2016). Our multivariate analyses revealed qualitative shifts in volatile blends in the cultivated varieties following HIPV exposure, which may have contributed to the observed differences in oviposition behaviour.

Our comparison of wild and cultivated varieties further suggests that responsiveness to HIPVs is maintained across diverse *B. rapa* lineages. However, the magnitude of responses varied among varieties. For example, stomatal conductance increased most strongly in the cultivated variety Cordelia, while oviposition responses were most pronounced in the wild Moroccan population. These differences may reflect variation in both signal perception and the composition of emitted cues. The variability in responsiveness could reflect differences in both perception (receptor or signalling pathways) and the chemical composition of emitted cues, emphasizing the complexity of plant–plant interactions in genetically diverse systems (Glinwood et al. 2009; Ninkovic et al. 2021).

In our experimental design, receiver plants were exposed to volatiles emitted by damaged plants of the same variety. Consequently, each variety was exposed to a distinct volatile signal. Future experiments using standardized HIPV blends or cross-exposure among varieties would help disentangle whether variation in responses is driven primarily by differences in receiver sensitivity or differences in emitter volatile composition.

In conclusion, our findings highlight that volatile-mediated plant communication can influence both primary metabolism and defensive outcomes. By enhancing photosynthetic activity and resistance to herbivores simultaneously, HIPVs may play a broader ecological role than previously appreciated. Understanding how plants integrate airborne cues into their physiological and defensive strategies will be important for clarifying the ecological significance of plant–plant signalling in natural and agricultural systems.

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Statements and Declarations

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AUTHOR CONTRIBUTIONS

J.B. and A.B designed the research. A.B., F.S., H.Y. conducted the experiments. A.B. analysed the data. A.B. wrote the original draft; and all authors contributed to revising and editing the draft.

CONFLICT OF INTEREST

The authors declare no competing interests.