

Smells like trouble: β -ocimene primes plant defenses through chromatin remodeling

Guadalupe L. Fernández-Milmanda  1,2

- 1 Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura (IFEVA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad de Buenos Aires, Buenos Aires, Argentina
- 2 Max Planck Institute for Chemical Ecology, Jena, Germany

In response to herbivore attack, plants emit blends of volatile organic compounds (VOCs) that can be sensed by both plants and insects. Exposure of undamaged plants (the receivers) to VOCs from plants under herbivory (the emitters) can prepare the receivers for future threats, even if no defense response is detected in the receivers at the time of exposure. However, when the receivers find themselves under attack, the defense response will be faster and stronger, a phenomenon known as priming (Engelberth et al., 2004; Heil, 2014). Enhanced resistance to herbivory by VOCs is widespread (Karban et al., 2014) and can take place even if the receivers and emitters are not from the same species (Sukegawa et al., 2018). However, little is known about VOCs signaling and the molecular control of priming.

In this issue of *Plant Physiology*, Onosato et al. (2022) uncover how β -ocimene, one of the most common VOCs, can prime *Arabidopsis* (*Arabidopsis thaliana*) defenses by changing chromatin structure. The authors exposed plants to β -ocimene for 6 days before challenging them with larvae of tobacco cutworm (*Spodoptera litura*). Although the *Arabidopsis* Col-0 ecotype does not produce a considerable amount of this VOC, plants were still able to recognize and respond to β -ocimene, as treated plants were less susceptible to herbivory than control ones. This observation confirms that plants can react to VOCs regardless of their capacity for emission. The authors also noted that the protective effect of β -ocimene-enhanced resistance lasts up to five days after exposure (referred to in the paper as “memory”).

As VOCs prime rather than induce defenses, they usually do not cause huge transcriptomic alterations (Heil, 2014), although they have been linked with epigenetic changes, such as histone acetylation (Sukegawa et al., 2018). Acetylation lowers the affinity of histones for DNA, which makes DNA

more accessible for the transcription machinery (Hsieh and Fischer, 2005). To see if β -ocimene affects chromatin status, the authors performed ChIP-seq with an anti-acetylated-histone antibody. From this analysis, they identified a set of defense-related genes as well as transcription factors belonging to the AP2/ERF family. The authors further showed that histone acetylation and transcription of *ERF8* and *ERF104* coincided with the protective effect of β -ocimene.

Finally, the authors aimed to identify the single histone acetylases (HATs) involved in β -ocimene priming. Taking advantage of the availability of knockout lines, they showed that plants lacking *HAC1*, *HAC5*, and *HAM1* did not show enhanced *ERF8* or *ERF104* histone acetylation or expression, nor did they show enhanced resistance to cutworms after β -ocimene treatment.

When it comes to VOCs receptors and signaling, we still have many open questions. Onosato and collaborators combined the ability of plants to sense VOCs emitted by others with the flexibility of *Arabidopsis* as a genetic tool to pinpoint single genes involved with the β -ocimene priming effect. When plants perceive β -ocimene, HATs acetylate histones associated with *ERF8* and *ERF104* coding regions, which upregulates their transcription. *ERFs* expression dynamics coincided with enhanced resistance to chewing insects (Figure 1). Their results represent one of the most detailed molecular mechanisms in response to VOCs. Definitely, a paper worth keeping in memory.

Conflict of interest statement. None declared.

References

- Bethke G, Unthan T, Uhrig JF, Pöschl Y, Gust AA, Scheel D, Lee J (2009) Flg22 regulates the release of an ethylene response factor

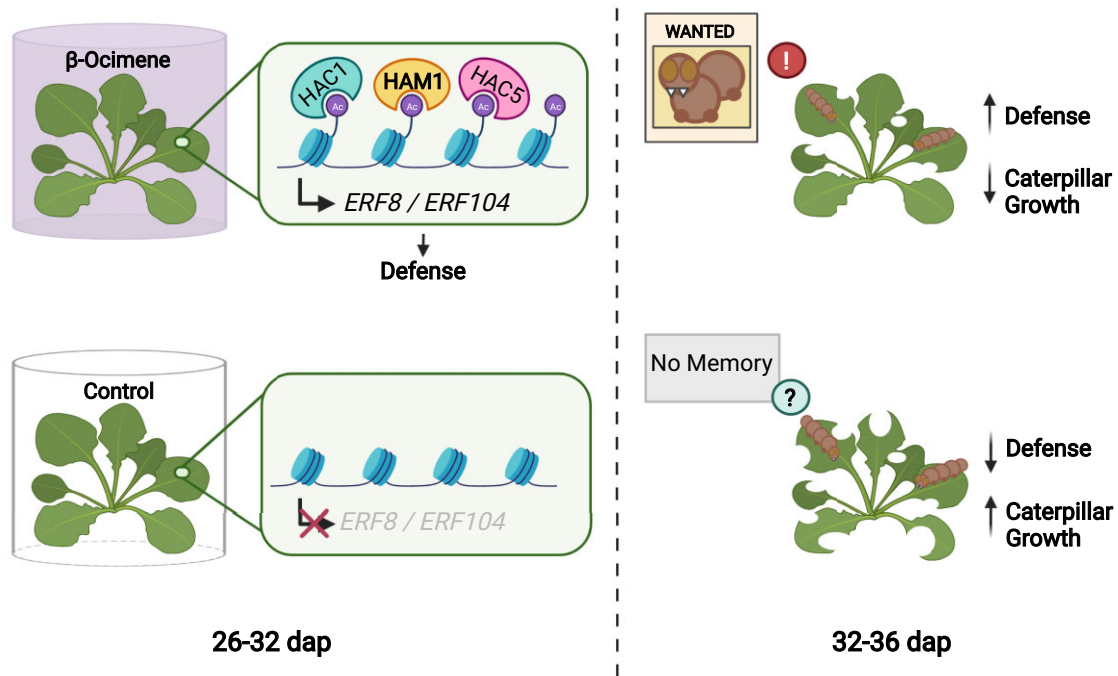


Figure 1 β -Ocimene primes plant defenses through chromatin remodeling. When plants are exposed to β -ocimene, HAC1, HAC5, and HAM1 acetylate histones at *ERF8* and *ERF104*, genes encoding transcription factors related to defense (Bethke et al., 2009; Cao et al., 2018, 2019). The histone acetylation of *ERF8* and *ERF104* enhances their transcription and primes plants up to five days after exposure. Dap = days after planting. Created with BioRender.com.

substrate from MAP kinase 6 in *Arabidopsis thaliana* via ethylene signaling. *Proc Natl Acad Sci USA* **106**: 8067–8072

Cao FY, DeFalco TA, Moeder W, Li B, Gong Y, Liu X-M, Taniguchi M, Lumba S, Toh S, Shan L, et al. (2018) *Arabidopsis* ETHYLENE RESPONSE FACTOR 8 (*ERF8*) has dual functions in ABA signaling and immunity. *BMC Plant Biol* **18**: 211

Cao FY, Khan M, Taniguchi M, Mirmiran A, Moeder W, Lumba S, Yoshioka K, Desveaux D (2019) A host–pathogen interactome uncovers phytopathogenic strategies to manipulate plant ABA responses. *Plant J* **100**: 187–198

Engelberth J, Alborn HT, Schmelz EA, Tumlinson JH (2004) Airborne signals prime plants against insect herbivore attack. *Proc Natl Acad Sci USA* **101**: 1781–1785

Heil M (2014) Herbivore-induced plant volatiles: Targets, perception and unanswered questions. *New Phytol* **204**: 297–306

Hsieh T-F, Fischer RL (2005) Biology of chromatin dynamics. *Annu Rev Plant Biol* **56**: 327–351

Karban R, Yang LH, Edwards KF (2014) Volatile communication between plants that affects herbivory: a meta-analysis. *Ecol Lett* **17**: 44–52

Onosato H, Fujimoto G, Higami T, Sakamoto T, Yamada A, Suzuki T, Ozawa R, Matsunaga S, Seki M, Ueda M, et al. (2022) Sustained defense response via volatile signaling and its epigenetic transcriptional regulation. *Plant Physiol* **189**: 922–933

Sukegawa S, Shiojiri K, Higami T, Suzuki S, Arimura G (2018) Pest management using mint volatiles to elicit resistance in soy: mechanism and application potential. *Plant J* **96**: 910–920