

1 **IN BRIEF**2 **Secrets of the Forest: Volatiles First Discovered in Pine Trees Propagate Defense**  
3 **Signals Within and Between Plants**

4  
5 Systemic acquired resistance (SAR)—a plant-wide heightened state of defense following  
6 localized exposure to a pathogen—is characterized by increased salicylic acid (SA) and ROS  
7 levels and elevated expression of pathogenesis-related genes. SAR depends on ENHANCED  
8 DISEASE SUSCEPTIBILITY1 (EDS1), which both generates the SAR signal at the primary infection  
9 site and perceives it in distal, uninfected tissues (Breitenbach et al., 2014). Various vascular  
10 mobile signals function within SAR, including methyl salicylate (Park et al., 2007), the non-  
11 proteogenic amino acid pipecolic acid (Návarová et al., 2012), and the dicarboxylic acid azelaic  
12 acid (Jung et al., 2009).

13  
14 In a new study, Riedlmeier et al. (2017) examined the role of volatile organic compounds (VOCs)  
15 in SAR. Using gas chromatography/mass spectrometry, they compared the emissions released  
16 by wild-type *Arabidopsis* plants and SAR-deficient *eds1-2* mutants several hours after induction  
17 of SAR. Whereas the wild-type plants released substantial amounts of the bicyclic  
18 monoterpenes  $\alpha$ -pinene and  $\beta$ -pinene—volatiles best known for giving pine forests their  
19 enchanting scent—the mutants with compromised SAR released almost undetectable levels of  
20 these VOCs.

21  
22 Based on these findings, the authors hypothesized that  $\alpha$ -pinene and  $\beta$ -pinene induce SAR. To  
23 test this possibility, they exposed wild-type plants to a mixture of  $\alpha$ -pinene and  $\beta$ -pinene or to  
24 the VOC solvent control for 3 days and then challenged the plants with the pathogenic  
25 bacterium *Pseudomonas syringae* pv tomato strain DC3000 (*Pst*). They found that bacterial  
26 growth was ~10-fold less in the leaves of plants that had been exposed to the monoterpenes,  
27 and that the effect depended on pinene concentration. Bacterial growth was not limited in the  
28 *non-expressor of PR genes1-1* (*npr1-1*) mutant, which has defects in signaling downstream of  
29 SA, or in the *sa induction deficient2-1* (*sid2-1*) mutant, which has defects in SA biosynthesis,  
30 after 3 days of monoterpene exposure. Furthermore, ROS  $O_2^{\bullet-}$  accumulated in the leaves of  
31 plants treated with pinenes, but not in those of control plants. Microarray analysis showed that  
32 pinene treatment directly influenced key regulatory genes in SA biosynthesis and SAR (e.g., the  
33 gene encoding the lipid transfer protein AZELAIC ACID INDUCED1). Therefore, pinenes appear  
34 to induce SAR, in a manner that depends on SA signaling.

35  
36 As monoterpenes are highly volatile, the authors directly tested whether these VOCs could  
37 function as mobile plant-to-plant defense signals. Wild-type receiver plants enclosed in a  
38 vacuum dessicator for three days with SAR-induced (i.e., monoterpene-emitting) sender plants  
39 were indeed more resistant to *Pst* infection than were receiver plants enclosed with control  
40 plants.

41

42 Thus, in addition to functioning in SAR signaling within the plant,  $\alpha$ -pinene and  $\beta$ -pinene act as  
43 airborne signals that prime neighboring plants for impending danger (see figure). This exciting  
44 finding suggests that the aroma of a pine forest has an important function.

45

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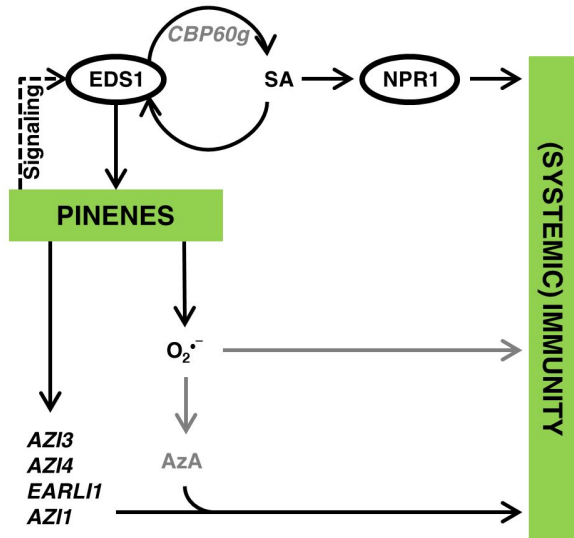
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52

53 **Figure legend:**

54

55 Model explaining the contribution of  $\alpha$ -pinene and  $\beta$ -pinene to systemic immunity. Pinenes  
56 induce immunity via EDS1, SA biosynthesis (possibly via *CBP60g*), and NPR1, and upregulate the  
57 expression of AZI1. In addition, pinenes trigger the production of ROS, which in turn cause SAR-  
58 promoting AZA to accumulate [*Adapted from Riedlmeier et al. (2017), Figure 11.*]



## Parsed Citations

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