Making its predators tremble: Multiple defenses act synergistically in aspen

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If plants did not defend themselves in some way, they would certainly be gobbled up by a whole suite of voracious predators ranging from little insects to large mammalian herbivores. Indeed, not only do plants defend themselves, they typically have more than one kind of defense. When a plant has several options, how does it choose? Does it allocate multiple defenses to the same tissues or defend different tissues in different ways?

Diane Wagner and colleagues from the University of Alaska, Fairbanks, examined how two defenses—phenolic glycosides (a direct chemical defense) and extrafloral nectaries (an indirect defense)—were distributed among leaves of a plant in the trembling aspen (Populus tremuloides) in Alaska. They found unique findings contradicting all expectations and published them in the April issue of the American Journal of Botany.

Diane Wagner has had a long-standing interest in extrafloral nectaries, or EFNs, which in general serve as an indirect plant defense. EFNs are found on the petiole at the base of a leaf and serve to attract insect predators who consume both the nectar produced by the plant and herbivorous insects that attack the plant.

"After noticing EFNs on aspen leaves about 7 years ago, I was surprised to find that very few biologists had studied their function in aspen," Wagner noted. Trembling aspen is common and widespread in North America and is a species of considerable aesthetic and ecological

importance. So Wagner joined forces with Pat Doak, an insect population ecologist, to look at the functional significance of EFNs in trembling aspen. The study was funded by the National Science Foundation.

"The expression of EFNs in aspen is unusually variable," Wagner notes. "Some leaves within a plant express nectaries but others do not, and the frequency with which EFNs are expressed varies both within and among aspen stands. That variation was intriguing to us in several respects." On the other hand, as with many plants, trembling aspen direct more phenolic glycosides, a direct chemical defense, to the younger, more vulnerable leaves, and as they age and grow, fewer of the compounds are allocated to these ramets.

The authors reasoned that aspen leaves that possessed high concentrations of phenolic glycosides might not need extrafloral nectaries if the chemicals directly deterred the herbivores or if these secondary compounds were also present in the nectary and had a negative effect on the very insects the plant was trying to attract. To see if this might be the case, they assessed the presence of EFNs and phenolic compounds on leaves from different shoot positions from short and tall ramets across multiple sites.

"What we found was the opposite of what we expected," said Wagner. "Instead of segregating the two defenses, aspen plants tended to express both in the same set of leaves. Other leaves on the plant were relatively poorly defended, with no EFNs and concentrations of phenolic glycosides too low to be effective against the major herbivore in our study." Indeed, while shorter ramets and younger leaves had higher levels of phenolic gylcosides, the presence of EFNs was correlated unexpectedly with higher phenolic glycoside levels when other factors (i.e., leaf position) were controlled, and damage from leaf mining insects was not related to presence of EFNs.

The authors hypothesize that leaves with EFNs might need higher levels of chemical defenses because they might attract nectar-drinking herbivores who may also lay their eggs on the leaves. However, EFNs may provide a diffuse form of indirect defense that extends to all the leaves by attracting predators of herbivores onto the aspen ramet in general.

"Our study shows that the expression of biotic defenses such as EFNs can covary with expression of other types of defense, at least within individuals," Wagner concludes. "I think the most important take-home message of the study is that natural correlations between EFN expression and herbivory could be influenced by correlated defensive traits. Experimental approaches are necessary to disentangle the effects of these correlated characters."

More information: http://www.amjbot.org/cgi/content/full/97/4/601

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