Communication between plants: this time it's real

Of course, neighboring plants in natural communities interact: we usually think of plants competing for sunlight and soil nutrients. Few topics in plant ecology have inspired so much excitement and controversy, however, as communication between plants. The idea, simply put, is that rooted and immobile plants might act to increase their levels of defense by responding to cues from neighbors that are being attacked by herbivores or pathogens. As some authors have suggested, perhaps 'listening trees' is a better descriptor than 'talking trees', but, in either case, the interaction holds unquestionably fascinating natural history. Communication is so prevalent and important among animals that its presence in plant communities could be revolutionary. In addition, if the phenomenon is real, it poses important questions about community evolution, including altruism (although the interaction might only benefit the listener). Unfortunately, the first demonstrations of these phenomena were trashed and disregarded by ecologists because of methodological inadequacies and the lack of realism in the experimental designs. Recent interest in volatile compounds produced by plants, such as jasmonate (known as the 'queen of aroma' in the perfume industry) and salicylate, has provided potential mechanisms for interplant communication. Three recent papers resurrect interplant communication by conducting rigorous and far-reaching studies spanning gene expression, physiology and field ecology.

Dolch and Tscharntke[1] show that defoliation of single trees at ten sites in Germany caused natural herbivory to increase with distance from the defoliated tree. This result was confirmed in laboratory experiments reducing the possibility of associational resistance causing the field result. This effect might be due to airborne or soilborne cues. Karban *et al.*[2] demonstrated, over several years, that damaged sagebrush plants cause neighboring native tobacco plants to be more resistant to herbivores than tobacco plants next to undamaged sagebrush. This interaction is correlated with induced production of volatile methyl jasmonate in the sagebrush and increased polyphenol oxidase (a putative defense) in the tobacco. The communication was not mitigated by removing soil contact between plants, but was mitigated by bagging the damaged sagebrush plants. Arimura *et al.*[3] examine specific signals released by bean leaves attacked by herbivores and the activation of five putative defense genes. Indeed, at least three volatile terpenoids induced by herbivory, not by mechanical wounding, caused neighboring leaves to induce these genes and the induction was similar to that caused by exposure to jasmonate.

Critics are going to love these studies: two of them used artificial clipping to damage the emitter plants and the other was conducted entirely with cut leaves in the laboratory. Those of us studying plant responses to herbivory know that neighboring plants in greenhouses do not always communicate, at least to a level that it obscures finding differences between treated plants and controls. But, there is still an emerging synthesis here. These systems, which show coordinated and sophisticated responses to cues from neighboring plants, might lead us to understand where and why such positive interactions are important in nature. Plants out there are listening and responding.

Anurag A. Agrawal
agrawal@botany.utoronto.ca

References

1 Dolch, R. and Tscharntke, T. Defoliation of alders (*Alnus glutinosa*) affects herbivory by leaf beetles on undamaged neighbours. *Oecologia* (in press)

2 Karban, R. *et al.* Communication between plants: induced resistance in wild tobacco plants following clipping of neighboring sagebrush. *Oecologia* (in press)

3 Arimura, G. *et al.* (2000) Herbivory-induced volatiles elicit defence genes in lima bean leaves. *Nature* 406, 512–515

A not-quite-so inordinate fondness for beetles

When asked what insights his study of biology had given him into the nature of a Creator, J.B.S. Haldane replied with his now-legendary quip about beetles. Theological questions aside, the fact that Coleoptera are among the most speciose of orders has important ramifications for a deceptively basic question in conservation biology: how many species are there on earth?

Although recent informed guesses span orders of magnitude that are a lesson in scientific humility (from around 1.8 million species currently named, up to perhaps 100 million in total), the answer to this question is crucial for quantifying biodiversity. Of the diverse chains of reasoning available for tackling the how-many-species problem, more than a few rest on the number of tropical beetle species there might be. As pointed out by Terry Erwin in his initial attempt to provide an estimate, the number of tropical beetles itself might rest on other unknown quantities, such as the number of tree species in a typical forest, the degree to which beetles found on those trees are specialized to them, the degree to which canopy beetles are representative of beetles as a whole, and so on.

A research note by Ødegaard *et al.*[1] provides data that are designed specifically to address the question of specialization in tropical beetles. Over the course of a year, they hand-collected 35 479 adult individuals from 1167 phytophagous beetle species. Their sample covered 24 tree and 26 liana species from an 8000-m^2 area in a dry forest in the Parque Natural Metropolitano, Panama, which they accessed with a canopy tower crane. This produced 2561 observations of host–beetle associations. Using nonparametric subsampling of these data, they calculated ~30% effective specialization on the 50 plant species examined. However, effective specialization decays as host species richness increases; a sample including just one plant species will necessarily find 100% specialization, whereas sampling two host species will find somewhat less than 100%, because some beetle species will be found on both hosts. Therefore, Ødegaard *et al.* use a parametric model to extrapolate beyond the spatial scale of their study, estimating that, in a typical tropical dry forest with 300 higher plant species, effective specialization would hover around 10%. Thus, host specialization appears to be closer to half of the 20% that was previously thought.

Because this information brings down estimates of the number of tropical beetle species, it also brings down estimates of total biodiversity; the number of species on earth might be closer to 5–15 million, rather than the 30 million or more that some have estimated. However, the work of Ødegaard *et al.* only addresses one of the links in the chain of reasoning that leads to larger estimates of global species richness. Other questions, such as the ratio of canopy to ground-dwelling arthropod richness or the proportion of all canopy arthropods that are beetles, remain largely unanswered.

Kathryn M. Rodríguez-Clark
kmclark@princeton.edu

Jon Paul Rodríguez
jon@princeton.edu

Reference

1 Ødegaard, F. *et al.* (2000) The magnitude of local host specificity for phytophagous insects and its implications for estimates of global species richness. *Conserv. Biol.* 14, 1182–1186

Erratum

The final paragraph of the Journal Club article by M.E. Hochberg [Hochberg, M.E. (2000) Displaced characters get some space. *Trends Ecol. Evol.* 15, 355–356] was inadvertently altered after the proof stage. The paragraph should read:

"The phenomenon of character displacement – that species evolve divergent biologies in areas of sympatry to lessen the costs of competition – is subjected to mathematical modelling by two promising approaches that take spatial environmental variation of resources into the equation."

We apologize to the author and our readers for this error.

  PII: S0169-5347(00)01986-8