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COMMENTARY

New Synthesis—Trade-offs in Chemical Ecology

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Although many chemical ecologists may not consider themselves evolutionary biologists first and foremost, evolutionary thinking pervades much of our science. Indeed, the concept of trade-offs is central to nearly all arguments about adaptation—what else would limit organisms from being perfectly adapted to all predators, changing climates, and sundry other life challenges? And such trade-offs (aka costs) often are held as a holy grail for those trying to explain variation in investment in traits, including chemical compounds, assumed to be adaptive. Nonetheless, we still lack a taxonomy for the causes and types of trade-offs. Trade-offs in chemical ecology may be caused by resource limitation, direct chemical interference, suppression of genes or biosynthetic pathways, or even divergent natural selection on a single trait. New papers, discussed below, contribute to the discourse working towards this needed taxonomy.

Because chemical compounds intertwine within organisms and biosynthetic pathways intersect during expression, there is great potential for trade-offs in chemical ecology. Recently, Ballhorn (2011) and Ballhorn et al. (2010) demonstrated the *direct chemical interference* of one plant defense by another and its ecological consequence. Using cultivated and wild lima bean (*Phaseolus lunatus*), they first report a pattern: insect resistant, high cyanide (HCN) bean accessions were susceptible to a fungal pathogen. Indeed, this pattern also was reported for clover by Rodolfo Dirzo in the early 1980s. But what is the mechanism? Ballhorn et al. (2010) show that HCN directly disrupts the enzymatic activity of polyphenol oxidase (PPO), a likely mechanism of resistance to fungi. Thus, a direct chemical trade-off results in a dilemma for plants: to resist insects or pathogens? A similar ecological pattern could, however, occur via an *ecological trade-off*. In this case, a single compound may be deterrent to some herbivores and attractive to others, as has been well-documented for cucurbitacins and some glucosinolates.

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Of course, historically, and even predating Darwin, *resource-based trade-offs* were presumed to be the rule—that is, resources allocated to one trait simply cannot be allocated to another trait. Although resource-limitation clearly is important at the level of the whole organism, resource-based trade-offs are unlikely to be the direct drivers of most negative correlations between two traits. In fact, we realize now that some negative associations between traits may be *adaptive negative correlations*. Take, for example, the oft cited trade-off between chemical resistance and tolerance. Tolerance is the ability of plants to withstand and regrow following herbivory. Theory and some evidence has suggested that highly resistant plants, need not tolerate damage (and *vice versa*, highly tolerant plants do not experience selection for resistance to herbivory). If these traits are, indeed, ecologically redundant and even a little energetically costly, then a "trade-off" may occur because selection has favored it. Current mechanistic work is showing how tolerance mechanisms can be induced following herbivory. Nonetheless, we know little about the mechanistic basis of variation in tolerance, and its relation to chemical resistance among plant genotypes or species.

Finally, neither the mechanistic nor evolutionary basis of some trade-offs may be known, even if quite general. *Negative hormonal cross-talk* between jasmonate and salicylate in plant defense signaling appears to be nearly ubiquitous. Is this a resource-based trade-off? Or does it make sense for plants—when one is employed the other is not needed? It seems unlikely to be direct chemical interference. Whatever the case, all sorts of organisms manipulate these pathways to their benefit and perhaps to the decrement of plants. The latest case is the induction of salicylate by insect eggs, which reduces jasmonate-induction following egg hatch, and thereby benefits caterpillars (Bruessow et al., 2010). Isn't chemical ecology wonderful!

But remember, nearly all trade-offs can be overcome by natural selection—they just have to be important enough. Thus, an important next step is understanding the evolutionary context of trade-offs among compounds that mediate ecological interactions.

References

Ballhorn, D. J. 2011. Constraints of simultaneous resistance to a fungal pathogen and an insect herbivore in lima bean (*Phaseolus lunatus* L.). *J. Chem. Ecol*. 37:141–144.

Ballhorn, D. J., Pietrowski, A., and Lieberei R. 2010. Direct trade-off between cyanogenesis and resistance to a fungal pathogen in lima bean (*Phaseolus lunatus* L.). *J. Ecol.* 98:226–236.

Bruessow, F., Gouhier-Darimont, C., Buchala, A., Metraux, J. P., and Reymond, P. 2010. Insect eggs suppress plant defence against chewing herbivores. *Plant J.* 62:876–885.