ECOLOGY

Fear No Weevil?

Donald R. Strong

Control of pests by biological means is rationalized by the simplest food chain: herbivores suppress plant populations, and carnivores that suppress herbivores protect plants. This tic-tac-toe of one move blocked by another implies that introduced species grow to pestiferous numbers just because they lack natural enemies to consume them, and with introduction of the enemies, the problems can be solved. The bright side has been that the simple model sometimes works, and the spectacular successes—substantial suppression of truly noxious introduced species such as scale insects and ragwort, cactus, and rabbits in Australia (*1*)—sustain optimism through the disappointments of the duds. Because the enemies reproduce on their own, classical biological control can provide great economic benefit for modest investment (*2*), and by supplanting pesticides, biological control can be safer to humans than chemical pest control. Environmental benefits can accrue from diminished pesticides and from reduced competition and predation upon the native fauna that derive from the reduced alien species.

The dark side of biological control has been viewed mainly in economic terms, and problems caused by the introduced enemies have been discounted relative to the target pest damage that they would prevent (*3*). However, more recently, judicious accounting with an ecological perspective suggests a less rosy picture (*4*). The contention that little evidence exists for negative impacts of alien enemies (*3*) has been challenged; the absence of evidence is not evidence of absence (*5*). The clean-kill image of the simple model is certainly wrong for parasitoids, which are the major agents released against herbivorous insect pests. For example, 32% of the 115 parasitoids introduced into Hawaii have been recorded to attack insects other than the intended target species (*6*), and 16% of 313 species introduced into North America have attacked native species (*7*). The effects of this spillover are unclear because few resources have been directed to the ecological issues of biological control, but these analyses suggest that the appropriate model is a reticulate web of species interactions rather than a simple unbranched food chain.

Recent, startling news of a mainstream biocontrol project gone haywire is reported by Louda *et al.* on page 1088 of this issue (*8*). The Eurasian weevil *Rhinocyllus conicus*, released widely by Canadian, U.S., and state agencies since 1968 for control of introduced thistles, has been found attacking five native thistle species in U.S. National Parks and Nature Conservancy preserves. Larvae kill many of the immature seeds within developing flower heads (see diagram). Reductions of seed up to 86% are associated with attack by the alien weevil in the Platte thistle, *Cirsium canescens*, of the Sandhill Prairie Preserve of Nebraska. Hundreds of kilometers away in Mesa Verde National Park, Colorado, wavyleaf thistle, *Cirsium undulatum*, infested with *R. conicus* averaged a 72% reduction in viable seed compared with noninfested flower heads.

Flower head of the Platte thistle, *Cirsium canescens*. [Photo: courtesy of S. Louda]

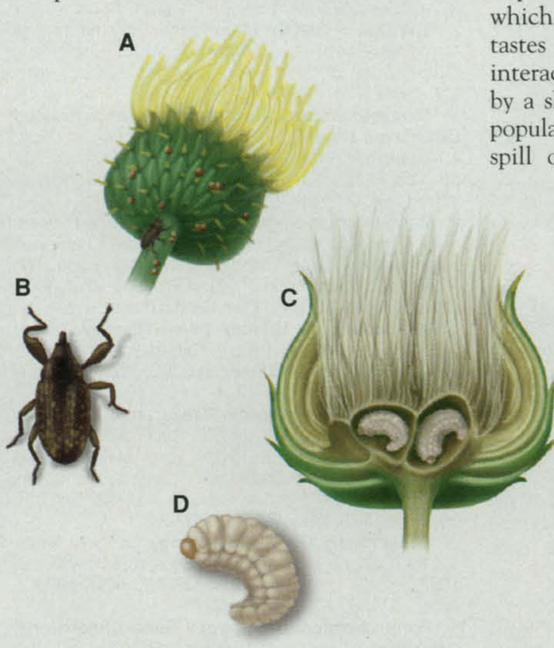

ILLUSTRATION: K. SUTLIFF

Inflorescence of *Cirsium canescens* showing (**A**) the adult *R. conicus* on the stem and eggs beneath the flower. (**B**) Adult *R. conicus*. (**C**) A pair of *R. conicus* larva inside the flower head, having consumed developing seeds of *C. canescens*. (**D**) Larva of *R. conicus*.

The first of these weevils appeared in the native Sandhill Prairie thistles in 1992, two decades after their first release in the region. Populations are up sharply in all sites sampled in 1992 and 1996. This weevil also menaces Pitcher's thistle, *Cirsium pitcheri*, a rare plant that lives on Great Lakes dunes. Not yet attacked, this federally listed threatened species could be the next victim of *R. conicus*.

Actually, the attack of native thistles by *R. conicus* comes as no surprise; early on it was clear that its host range includes *Cirsium* species (*9*). The early studies also detected a set of host races of the weevil over southern Europe, indicating its propensity to evolve. Yet, since introduction, governmental and private groups have continued to spread it around with little consideration or study of the ecological effects (*10*).

The complex relationships among *R. conicus* and thistles illustrate the inadequacies of a simple food chain model for biological control, which ignores the other species that are inevitably involved directly and indirectly in food webs (*11*). Louda and her colleagues found that native picture-winged flies feeding in the flower heads have declined precipitously in both Platte and wavyleaf thistle where the weevil attack rates are high; this implies interspecific competition (*12*), in which the native flies lose. The catholic tastes of the weevil predispose an indirect interaction, termed "apparent competition by a shared enemy" (*13*), in which weevil populations that build up on alien thistles spill over to attack and suppress native thistles. Even if the weevil preferences were not as great for native as for alien thistles [a justification for the introduction of "oligophagous" insects (*9*)], the result of this indirect interaction could readily be curtains for the native plant. With increasing attention to mechanisms, the best science in the biological control field has shifted to the ecological arena in the last decade. Understanding of food web reticulations, such as interspecific competition among plants, the soil seed bank, and evolution of weeds in alien environments (*14*), has shed light on why biological control actually works when it does and why it does not work much of the time (*15*). Although biological control is predicated on short unbranched food

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chains, many introduced species become involved in more complex natural food webs, with species interactions more reminiscent of chess than tic-tac-toe.

The touchstone of every biological control project should be an extremely narrow host range for any species considered for introduction. The questions asked at the outset should include: Is the target organism really a substantial public problem? What are the alternatives to introduction of an alien species for controlling the pest? What kinds of mischief, both direct and indirect, could the proposed introductions cause? What is the balance of benefits and costs, ecological as well as economic, from the introduction (*5*)? Biological control is an important arrow in the quiver of pest management, perhaps the only arrow in some cases of pests of grave environmental concern. However, willy nilly biological control without regard for environmental costs could result in societal resistance so great as to prevent even the sensible application of biological control. The troubling case of *R. conicus* in North America highlights the need for ecology to be at the heart of both science and application of biological control.

References

1. P. B. McEvoy, N. T. Rudd, C. S. Cox, M. Huso, *Ecol. Appl.* **1**, 55 (1993); P. A. Thomas and P. M. Room, *Nature* **320**, 581 (1986);. L. E. Caltigerone, *Annu. Rev. Entomol.* **26**, 213 (1981).
2. P. DeBach and D. Rosen, *Biological Control by Natural Enemies* (Cambridge Univ. Press, ed. 2, Cambridge, 1991).
3. R. S. Soper, in *Regulations and Guidelines: Critical Issues in Biological Control*, R. Charudattan and H. W. Browning, Eds. [U.S. Department of Agriculture (USDA), Cooperative State Research Service, Washington, DC, 1992], pp. 49–52.
4. C. E. Turner, in *Proceedings of the Sixth International Symposium on Biological Control Weeds*, University of British Columbia, Vancouver, BC, 19 to 25 August 1984; E. S. Delfosse, Ed. (Agriculture Canada, Ottawa, 1985), pp. 203–225; F. G. Howarth, *Annu. Rev. Entomol.* **36**, 485 (1991).
5. J. A. Lockwood, *Environ. Entomol.* **22**, 904 (1993).
6. G. Y. Funasaki, P. O Lai, L. M. Nakahara, J. W. Beardsley, A. K. Ota, *Proc. Hawaii Entomol. Soc.* **28**, 105 (1988).
7. B. A. Hawkins and P. C. Marino, *Oecologia*, in press.
8. S. M. Louda, D. Kendall, J. Connor, D. Simberloff, *Science* **277**, 1088 (1997).
9. Z. Zwolfer, P. I. Harris, A. Angew, *Entomology* **97**, 36 (1984); D. Schroeder, *Biocontrol New Inf.* **1**, 9 (1980).
10. P. E. Boldt and J. A. Jackman, *Southwest. Entomol.* **18**, 173 (1993); G. D. Buntin, R. D. Hudson, T. R. Murphy, *J. Entomol. Sci.* **28**, 213 (1993); N. E. Rees, *Biological Control of Weeds in the West* (Western Society of Weed Science in Cooperation with USDA Agricultural Research Service, Montana Department of Agriculture and Montana State University, Bozeman, MT, 1996).
11. P. A. Abrams, *Oecologia* **73**, 272 (1987); B. A. Menge, *Ecol. Monogr.* **65**, 21 (1995).
12. D. R. Strong, *Ecology* **73**, 747 (1992); G. A. Polis and D. R. Strong, *Am. Nat.* **147**, 813 (1996).
13. S. M. Louda, K. H. Keeler, R. D. Holt, in *Perspectives on Plant Competition*, J. B. Grace and D. Tilman, Eds. (Academic Press, New York, 1990), pp. 413–437.
14. P. B. McEvoy, *Ecol. Monogr.* **63**, 55 (1993); B. Blossey and R. Notzold, *J. Ecol.* **83**, 887 (1995).
15. P. Stiling, *Am. Entomol.* **39**, 31 (1993).

POLYMER LUMINESCENCE

Those Blinking Single Molecules

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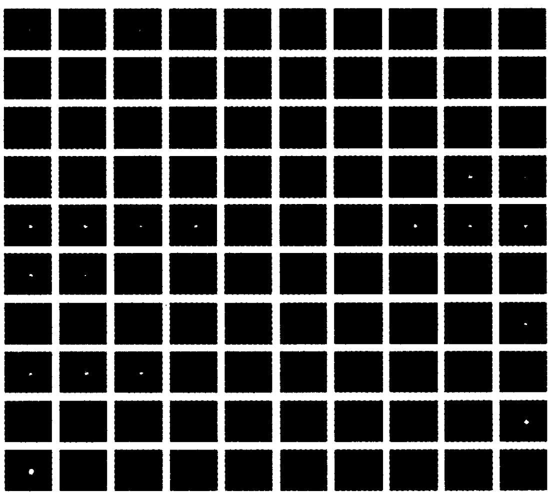
A dramatic revolution has occurred in the study of matter on a nanometer scale. In the past few years, a variety of optical experiments have reached the regime of detecting and measuring the properties of an individual molecule in a condensed matter sample (*1*). To observe only one molecule, researchers typically use extremely small sample volumes (<1 μm^3), work at extremely low concentrations (<10^{-9} mol/liter), and rigorously optimize the collection of the single-molecule emission while rejecting background signals. This field of study can appropriately be called "single-molecule nanophotonics" because exactly one molecule is optically pumped at a time, providing an exquisitely sensitive probe of the structure and dynamics of the molecule itself and of the immediate local environment. As they report on page 1074 of this issue, Vanden Bout *et al.* (*2*) have used such methods to probe a new system: a single conjugated polymer molecule.

Why is it useful to study individual molecules, each of which may be marching to a different drummer? Indeed, single-molecule measurements completely remove the normal ensemble averaging that occurs when a large number of molecules are probed at the same time. It is important to remember that workers in this field never measure only one single molecule, but many single molecules, one by one. This process allows direct observation of the true distribution of behavior, rather than just the average (mean) value of an experimental parameter. To illustrate by analogy, consider the problem of characterizing the houses in which people live: One could judge the quality of housing by noting the average square footage, the average number of rooms, and so on, or one could observe in detail many houses, one by one, and build up a comprehensive distribution of features (*3*). Clearly, the distribution contains more information than the average alone.



A sequence of 100 images of the emission from a single green fluorescent protein mutant molecule trapped in a gel. Each frame corresponds to a 100-ms exposure with a 488-nm–wavelength laser in a total–internal-reflection geometry. [Figure courtesy of R. M. Dickson; see (*6*) for details]

Surprisingly, almost all single-molecule systems studied to date have shown some form of fluctuating, flickering, or stochastic behavior. For example, in the initial work on single molecules of the aromatic hydrocarbon pentacene in a *p*-terphenyl crystal at liquid-helium temperatures (*4*), spectral shifts of the resonance frequency were observed, attributable to phonon-driven fluctuations in the local environment. This behavior has been termed "spectral diffusion," and it has also been observed for single molecules in polymers at low temperatures (*1*) and for single molecules on surfaces at room temperature (*5*). If a fixed-frequency laser is used to probe a spectrally diffusing molecule, the shifting of the absorption in and out of resonance generates amplitude

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