

hydrolysis would be small, so it is still possible to estimate preindustrial CCl_4 levels accurately from measurements in slowly renewed deep waters (1).

In contrast, loss of CH_3CCl_3 would be considerable even in cold waters over a period of only 40 years (that is, since CH_3CCl_3 was introduced into the environment), and it has an input function that is not dramatically different in nature from those of F-11 and F-12 (1). We thus reiterate that no great advantage will be gained from its use as an additional tracer.

We recommend that CCl_4 be measured together with F-11, F-12, and F-113 during future oceanographic sampling expeditions. We also encourage our colleagues to perform hydrolysis rate measurements for these compounds and the chlorofluorocarbons in seawater: data concerning the latter class of

compounds, and measurements in seawater in general, are notably lacking in the literature.

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Caterpillars and Polymorphisms

Greene reports (1) that two seasonal morphs of the herbivore *Nemoria arizonaria* are adapted for feeding and hiding on their respective substrates, oak catkins and leaves. While we do not dispute the occurrence of this polymorphism, the striking resemblance of each to its substrate, or its purported adaptiveness, we contend that the proposed mechanism for its induction, dietary tannin, is unlikely.

Greene's conclusion that the "developmental polymorphism is triggered by the dietary concentration of defensive compounds [tannins]" is based on two lines of evidence. First, he observed that caterpillars eating spring catkins remain as catkin morphs while those feeding on summer foliage of four Arizona oak species develop into twig-like morphs. He assumes that catkins are low in tannins relative to leaves on the basis of citations (1, note 16) that do not deal explicitly with catkin phytochemistry. We examined this assumption by analyzing tannin content of catkins of *Quercus emoryi*, one of the host plants of *N. arizonaria* (2). Condensed tannin content of catkins is relatively low [three trees, 0.59% (± 0.05), 0.39% (± 0.01), 0.29% (± 0.10)] but comparable to that of mature leaves (2). Hydrolyzable tannin content, however, is relatively high [three trees, 15.08% (± 2.28), 18.50% (± 0.82), 17.65% (± 2.66) (2)]. Clearly, low tannin content is not a common feature of catkins, weakening Greene's contention that dietary tannin level is the mechanism for the polymorphism.

Second, Greene found that diets of catkins plus the tannin quebracho, of catkins

plus leaves, or of only leaves induced the twig morph. The latter two artificial diets included new, spring leaves (3), but in nature the twig morphs feed on mature, summer leaves. Something common to mature leaves and artificial diet plus new leaves or quebracho must induce the twig morph; Greene proposes it is either specific tannin compounds or tannin concentrations, but neither are likely to be shared among the three diets. *Quercus emoryi* and *Q. arizonica*, two hosts of *N. arizonaria*, vary seasonally in tannin types and concentrations (4). New and mature leaves differ in condensed tannin content (new, <1% dry mass; mature, $\approx 5\%$ dry mass) and hydrolyzable tannin content (new, 25% dry mass; mature, 10 to 12% dry mass), as well as in other phenolic compounds (4). Quebracho is mostly condensed tannins, yet it triggers the same response as new leaves with little condensed tannin. Further, condensed tannins are unlikely to be the inducing factor since they are typically bound indissolubly to plant tissues (5) and are too large to pass through the peritrophic membrane of insects (6). Finally, Greene presents no evidence, and we are not aware of any, for the existence of tannin "receptors" in insects.

A more parsimonious explanation for Greene's results is that the twig morph is simply induced by a low protein diet. Low protein is a shared feature of the twig morph's natural and artificial diets. New and mature oak leaves are low in protein (for example, *Q. emoryi*, 2 to 5% dry mass; *Q. arizonica*, 2 to 6% dry mass). Adding quebracho or ground leaves that contain pheno-

lic compounds to an artificial diet would lower relative protein, since tannins bind to plant proteins in agar media (7). Higher protein levels in catkins could inhibit development of twig morphs.

Low dietary protein triggers polymorphisms in other insects (8) and in vertebrates (9). Low protein is also consistent with slow development and decreased mass and fecundity of the twig morph (10). Toughness (fiber content) of leaves could also induce the twig morph. Consumption of hard tissues can induce morphological changes in insects (11) and in vertebrates (9). Greene's dietary experiments do not distinguish among increased tannins, reduced protein, or increased toughness as the inducing mechanism because tannins interfere with protein availability and fiber content was not controlled. Dietary experiments with varying levels of protein without tannins or fiber could resolve this issue.

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2. Catkins were collected from three trees of *Q. emoryi* at Oak Flat, Pinal County, AZ, on 2 April 1989 and immediately frozen on dry ice. Catkins were lyophilized, ground into a fine powder, extracted, and analyzed for condensed and hydrolyzable tannin content according to methods reported elsewhere [S. H. Faeth, *Ecology* **67**, 479 (1986)]. Values reported are means (% dry mass) and standard deviations of subsamples analyzed in triplicate from each tree.
3. Leaves used in diet experiments were collected within 2 weeks of budbreak (E. Greene, personal communication).
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12. We thank J. Howard and R. Rooney for comments. Supported by NSF grant BSR 8715743.

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Response: Faeth and Hammon are correct in pointing out that the feeding experiments with *Nemoria arizonaria* (1) do not establish what differences between catkin and leaf diets are responsible for inducing the development of the two morphs. Polyphenolic compounds may trigger the development of