

CHANGES IN TREE QUALITY IN RESPONSE TO

DEFOLIATION

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Abstract

Plant chemistry alone fails to explain why most trees escape defoliation most of the time. Chemical variation in space and time, acting to enhance the effectiveness of natural enemies, may be the key. Changes and increasing variation in direct response to insect attack ("induction") may be particularly important for irruptive pests.

Introduction

The search for an explanation for pest outbreaks and cycles has long been a focus of CANUSA and represents a multimillion dollar question. It is interesting to consider, however, that such outbreaks are actually rare. Few insect species exhibit them, and they are widely scattered in time (Schultz 1983a). Most insect species do not exhibit irruptive population dynamics, and exist at very low abundances almost all the time (Lawton and McNeil 1979). The occurrence of irruptions leads one to suspect that some regulatory factor has failed or been defeated. Since many things kill herbivorous insects and/or influence their feeding, growth, and fecundity, there is no shortage of possible explanations. Nonetheless, no successful generalization has emerged about these events; instead, individual investigators favor individual hypotheses (Schultz 1983a).

In our laboratory we emphasize the influence of host tree quality, especially defensive chemistry, on the performance of defoliating insects. The reason for this is that among those factors likely to be important to the insect, food quality is one which may influence all others, including the effectiveness of parasites, pathogens, and predators (Lawton and McNeil 1979, Schultz 1983a). Our major working hypothesis has two main parts: 1) tree chemistry has an impact on defoliating insects, but chemical variability is the key, and 2) the importance of host chemistry derives from its interaction with other mortality and morbidity factors.

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The reason for following this line of reasoning involves the observation that the relationship between insect and host plant is coevolutionary in nature (Ehrlich and Raven 1965). Each participant exerts natural selection on the other, resulting in an escalating "arms race". On the plant's part, chemicals may be produced which function as defenses against insects (Ehrlich and Raven 1965, Feeny 1970, Swain 1979). However, the presence of these chemicals selects for the ability to detoxify or avoid them on the part of the insect (e.g. Brattston 1979). If any plant or plant species were to defend itself with a uniform, singular chemical defense effective enough to keep insects as rare as they are most of the time, we would expect this strong selection to favor the evolution of insects immune to it (Maiorana 1981, Schultz 1983a). Exactly this result is common in agricultural systems, where humans apply the defense as artificial (or plant-derived) chemicals, or employ uniform, resistant cultivars (Lupton 1977). Since forest trees live many years (and many insect generations), something else must be important in defending them, because "super pests" do not continuously defoliate forests. We argue that "something else" necessarily involves variable plant chemistry.

Induced Variability

A form of variation we have been studying lately involves damage-induced changes in leaf chemistry in forest trees. A decrease in food value or increase in the concentrations of antiherbivore chemicals has now been observed in black oak (Wallner and Walton 1979), red oak (Schultz and Baldwin 1982), red alder and willows (Rhoades 1982), arctic birches (Haukioja and Niemela 1978, Bryant 1981), yellow birch, sugar maple, and poplars (Baldwin and Schultz 1983 and unpublished), to mention a few. It is becoming clear that tree leaf quality varies not only in space (e.g., Schultz et al. 1981, Whitham 1981, Zucker 1982) and seasonally (Feeny 1970, Schultz et al. 1981), but also rapidly in response to attack. We have found, for example, that phenolic concentrations are increased as much as 150% in undamaged leaves of partially (10%) defoliated sugar maples and poplars within 36 hours, apparently through de novo synthesis (Baldwin and Schultz 1983).

The potential significance of this form of leaf quality variability for understanding pest outbreaks takes several forms. First, the ongoing decline in food quality that results may help explain the conspicuous decline in insect population "quality" which occurs during irruptive episodes, including slowed caterpillar growth, reduced maximum size, and lowered fecundity (Wellington 1965, Wallner and Walton 1979, Rhoades 1979, Schultz and Baldwin 1982). Such declines often occur before available food is depleted, suggesting possible food quality reduction. Low food quality under induction alternating with high food quality under "relaxation" (and especially during periods of

plant stress) might generate the cyclic behavior some populations exhibit (Haukioja and Hakala 1975, Bryant 1981).

Second, increased effectiveness of predators, pathogens, and parasites as irruptions proceed could be due to or augmented by declining host plant quality (Schultz 1982). An estimated 26% increase in gypsy moth mortality due to tachinid fly infestation could result from the 3-4% reduction in caterpillar growth rates on "induced" foliage (Schultz 1983a). If lowered food quality influences searching behavior by larvae, so that more movement and tasting occur, contact rates with pathogens should increase (Schultz 1983a,b). Preliminary results in our laboratory suggest that gypsy moth larvae fed protein-deficient diets do indeed exhibit increased movement and searching behavior (Schultz, unpub. data).

A third potential consequence of the induction effect involves the role of spatial variability. More detailed chemical comparisons of oak leaves taken from trees being defoliated by gypsy moth larvae with those from unattacked trees growing nearby (see Schultz and Baldwin 1982 for sampling, extraction, and site descriptions) reveal differences in variability as well as total amounts of some phenolic compounds. Using capillary GLC methods for the quantitative analysis of two hydrolyzable tannins, gallic acid and ellagic acid (Arpino et al. 1977, Baldwin in prep.), we may plot the frequency distributions of leaves having various dry weight concentrations of these two astringent compounds. When we do this (Fig. 1), we find that undamaged leaves on "induced" trees exhibit significantly different frequency distributions (Chi² test, $p < .05$). Leaves from damaged trees have a significantly wider range of values than do leaves from unattacked trees.

Any insect which can perceive these chemical differences has a wider range of leaf values from which to select a preferred type. In an induced tree, fewer leaves fall into the lower hydrolyzable tannin content classes; hence an insect responding to gallic and ellagic acids as antifeedants must search farther and longer for suitable leaves. This could increase metabolic travelling costs, search time per consumption time, contact rates with pathogens and predators, and conspicuousness to predators and parasites (Schultz 1983a,b). Increased variability, together with overall lower leaf quality, should increase a variety of risks.

Some insects may not discriminate among leaves, but eat the broader range found in induced trees. Recent evidence suggests that switching from high to low quality or low to high quality leaves can result in even poorer growth performance than is attained on a diet consisting of only poor quality leaves (E. Haukioja, unpub. data). In either case, induced trees which also exhibit increased variance could become much poorer hosts than they were before they were attacked.

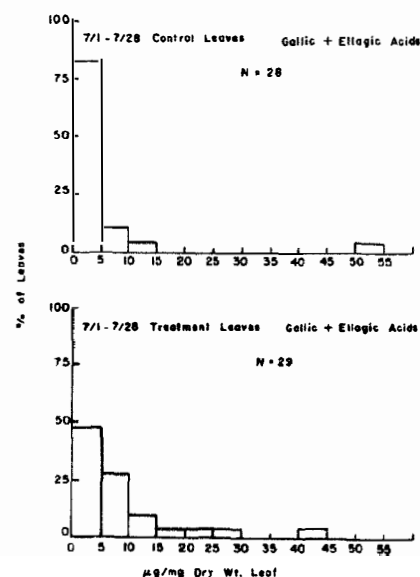


Figure 1. Frequency distributions of hydrolyzable tannin contents of leaves from red oak trees undamaged by gypsy moth larvae (top) and undamaged leaves from nearby trees defoliated 80-100% (bottom) during 1981.

Because the secondary chemistry of forest trees is often dominated by phenolics, especially tannins (Swain 1979), these are the compounds most studied in the context of induction. Recently, the importance of their biological activity as antiherbivore devices has been called into question (e.g., Bernays 1978, Martin and Martin 1983). Several investigators have found weak or nonexistent correlations between tannin contents and insect performance (e.g., Mattson, this volume, Wagner, this volume). There are at least two possible reasons for this. First, sampling for phenolics is made very difficult by the observation that tissue-to-tissue, leaf-to-leaf, and needle-to-needle variation is so great (Schultz et al. 1981). This means that we must know the phenolic/tannin content of the tissue actually consumed; it is not sufficient to sample similar, or even nearby tissues for correlative studies. The adjacent leaf may not represent or even resemble the chemical composition of the leaf an insect consumed. Second, both sampling and consumption can alter tissue chemistry. Hence, we have a catch-22: we must know what the chemical composition of a plant tissue was when the insect began to feed on it, but once the insect feeds on it, any remaining portion may be altered. In nature, insects may select low-phenolic tissues, but once partially eaten, our sampling and analysis may show them to be high-phenolic tissues.

Conclusions

This last point brings us to a point which is critical for understanding the role of tissue chemistry in the interaction between tree and insect. This observation is simply that because tissues vary tremendously in space and time, insects have a choice in selecting food. They may avoid tissues with one type of composition while seeking out tissues with other compositions, to which the insect may be physiologically adapted. As a result, understanding insect behavior and its sensory and ecological bases is central to explaining why certain insects eat certain tree species, move among individual trees, grow and reproduce better on some trees than others or at some times than others, or are more susceptible to natural enemies at certain times or in certain places. These issues, of course, are fundamental to answering the questions about population dynamics that interest us all. It is clear that studies of insect behavior, tree quality and tree chemistry are needed to understand insect population dynamics, but that we must pay as much attention to variances as to mean values.

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