

# Does Previous Defoliation Affect Ovipositional Choice of the Western Tent Caterpillar?

WILLIAM P. WEAVER, Jr.  
Department of Biology  
University of California  
Los Angeles, California 90024-1606

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## Abstract

Egg masses of the Western Tent Caterpillar were censused on 100 individuals of each of three host plant species at one site in the eastern Sierra Nevada as part of an investigation of ovipositional choice by *Malacosoma californicum fragile* Stretch (Lepidoptera: Lasiocampidae). Highly significant differences ( $P < 0.001$ ) between consecutive years were found for all three of the host species. Although current plant-herbivore theory can explain these results, it does so in a nonpredictive manner. More attention should be given to the herbivores in modifying current theory.

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## Introduction

Induced defenses in plants are chemical or structural responses to herbivory, fungal attack, or mechanical damage. Rapidly induced defenses are allelochemicals that increase in concentration locally soon after herbivore attack [Greene and Ryan, 1972; Green and Ryan, 1973; Carroll and Hoffman, 1980; Edwards and Wratten, 1982; Haukioja, 1982; Baldwin and Schultz, 1983; Karban and Carey, 1984; Raupp and Denno, 1984; Haukioja and Hanhimaki, 1985; Tallamy, 1985]. Bioassays and chemical analyses have shown that the response may peak anywhere from 20 minutes to several days later, gradually diminishing with time if no further damage is incurred [Greene and Ryan, 1972; Carroll and Hoffman, 1980].

The extent and significance of induced defenses in plants is controversial [Benz, 1977; Rhoades, 1979, 1983b, 1985; Ryan, 1979; Tuomi *et al.*, 1984; Edwards and Wratten, 1985; Fowler and Lawton, 1985; Neuvonen and Haukioja, 1985]. Some workers have suggested that these chemical changes are purely a physiological response to the wound; however, the detrimental effects on herbivores argue against this. Another controversy concerns conflicting results obtained in two separate lines of research. Rhoades [1983a] found induced defenses in *Alnus rubra* (Red Alder), while Myers and Williams [1984] did not. Similarly, several researchers reported induced defenses in *Betula pubescens* (White Birch) [Haukioja and Niemela, 1977; 1979; Niemela *et al.*, 1979; Haukioja, 1982; Edwards and Wratten, 1982, 1983,

## Ovipositional Choice of the Western Tent Caterpillar

1985; Wraten *et al.*, 1984; Neuvonen and Haukioja, 1985; however, Fowler and Lawton did not report any in their [1985] study.

This might not be as anomalous as it seems. For instance, plants undergoing nitrogen stress may not have the resources to spare for this method of defense, or perhaps certain induced defenses are only present during particular stages of leaf development (*e.g.*, some extrafloral nectaries are functional only in expanding leaves). Most studies of induced defenses show "small" effects on herbivore performance [Fowler and Lawton, 1985]; therefore, it has also been argued that even if the chemical changes are real, they might not affect herbivore behavior or population levels. However, other experiments [Bentley *et al.*, 1980; Louda, 1984; Crawley, 1985] have demonstrated that plants subject to low levels of defoliation (8-21 percent of the leaf area) by low-density herbivore populations, produced from 2.5 to 40 times less seed than individuals of the same population that were protected from damage. It is not known whether this substantial reduction in seed production actually leads to a reduction in recruitment, but does suggest that slight differences in the level of herbivory between plants can cause important differences in plant fitness.

Long-term induced changes in leaf tissue are well documented and probably a physiological response to defoliation and the availability of nutrients, especially nitrogen [Benz, 1974; Baltensweiler *et al.*, 1977; Haukioja and Niemela, 1977; Wallner and Walton, 1979; Werner, 1979; Haukioja, 1980, 1982; Schultz and Baldwin, 1982; McNaughton and Tarrant, 1983; Rhoades, 1983b; Valentine *et al.*, 1983; Neuvonen and

Haukioja, 1984; Tuomi *et al.*, 1984; Haukioja and Neuvonen, 1985; Haukioja *et al.*, 1985]. These changes occur after defoliation, with a second flush of leaves later in the season or produced the following year. The tissue of these leaves commonly has lower levels of nitrogen and water, higher amounts of lignin, fibers, and other sclerotic structures, and increased levels of carbon-based allelochemicals such as various phenolic compounds, all of which may be harmful to herbivores.

The investigation described in this paper was a pilot project assessing the feasibility of examining induced plant defenses which occurred in response to attack by the Western Tent Caterpillar, whose social larvae are capable of defoliating thousands of hectares. Assuming that the adult moths were responding to changes in host-plant quality induced by defoliation, the number of ovipositions on the same individual plants were compared in two consecutive years (1984 and 1985).

### Methods

This study was carried out during 1984 and 1985 in the eastern Sierra Nevada at an elevation of 2,070 meters along Bishop Creek, Inyo County, California. The vegetation at the study area is Great Basin Sagebrush Steppe, dominated by *Purshia tridentata* (Antelope Bitterbrush, 38 percent cover) and *Artemisia tridentata* (Big Sagebrush, 16 percent cover). The study site is situated on the canyon bottom alongside the riparian zone. This relatively flat area was chosen to reduce the effects of a slope, aspect, and moisture on the plants.

Three *Malacosoma* host species were present in the study area, viz. *Purshia tridentata*, *Prunus andersonii* (Desert Peach), and *Ribes velutinum* (Plateau Gooseberry). Tent caterpillars were extremely abundant both years, defoliating all the host plants at the study site. Each year, *P. tridentata* refoliated later in the season and eventually produced large numbers of flowers and fruits. During both years, *P. andersonii* and *R. velutinum* did not refoliate later in the season, nor did they produce any flowers or fruits.

In 1984 one hundred individuals of each species were randomly selected, tagged, measured for canopy volume (mean length x width x height), and censused for *M. californicum fragile* egg masses. During 1985 the same individuals were censused again for *Malacosoma* egg masses. The total number of egg masses for each host species was expressed as a percentage of the total number of egg masses counted that year. Changes in percent from 1984 to 1985 were analyzed using the *chi-square* test.

## Results

Changes in percent of the total number of *M. californicum fragile* egg masses from 1984 to 1985 were highly significant ( $P < 0.001$ ) for all three host species (Table 1). The overall *chi-square* test also gives  $P < 0.001$ . *P. tridentata* had the greatest change (more than double, from 14.6 to 32.2 percent). Relative ovipositions also increased on *P. andersonii*, but to a smaller degree (from 10.1 to 16.6 percent). Relative ovipositions on *R. velutinum* decreased by about one third (75.3 to 51.1 percent).

## Discussion

The results of this investigation suggest that *R. velutinum* might have long-term induced defenses in response to tent caterpillar defoliation. Since *R. velutinum* was leafless when the *Malacosoma* adults were flying, the moths may have had fewer cues to use for host identification and as a result did not oviposit on this species as frequently as they had in 1984. However, if this were the case, one would expect a smaller percentage

Table 1  
Year-stratified egg mass distribution over host species

Species	1984		1985		P-value*
	No.	Percent	No.	Percent	
<i>Purshia tridentata</i>	511	14.6	693	32.2	< 0.001
<i>Prunus andersonii</i>	353	10.1	359	16.7	< 0.001
<i>Ribes velutinum</i>	2630	73.5	1100	51.1	< 0.001
Totals	3494	100.0	2152	100.0	

\* Changes in percent from 1984 to 1985 using *chi-square* test.

## Ovipositional Choice of the Western Tent Caterpillar

of ovipositions in 1985 on *P. andersonii* since it, too, was leafless when the *M. californicum fragile* adults were present. Future studies of this system will include leaf-tissue analysis from year to year as well as laboratory feeding-performance tests using *M. californicum fragile* larvae.

The development of plant-herbivore theory over the past decade has focused on plant defenses, especially foliar allelochemicals. Too often the herbivores have been ignored. It is necessary to include the dynamic nature of herbivore host usage and responses to plant defenses in order to gain a more complete understanding of this interaction. More work needs to be done on the facets of herbivore behavior and population dynamics that are relevant. For example, different levels of folivorous insect populations may mean differences in ovipositional choice, survivorship, and fecundity. The general health of a phytophagous insect population influences their response to plant defenses, disease, predators, parasites, and weather. These are commonly synergistic effects and must be incorporated into future models of plant-herbivore interaction.

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William P. Weaver, Jr.

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