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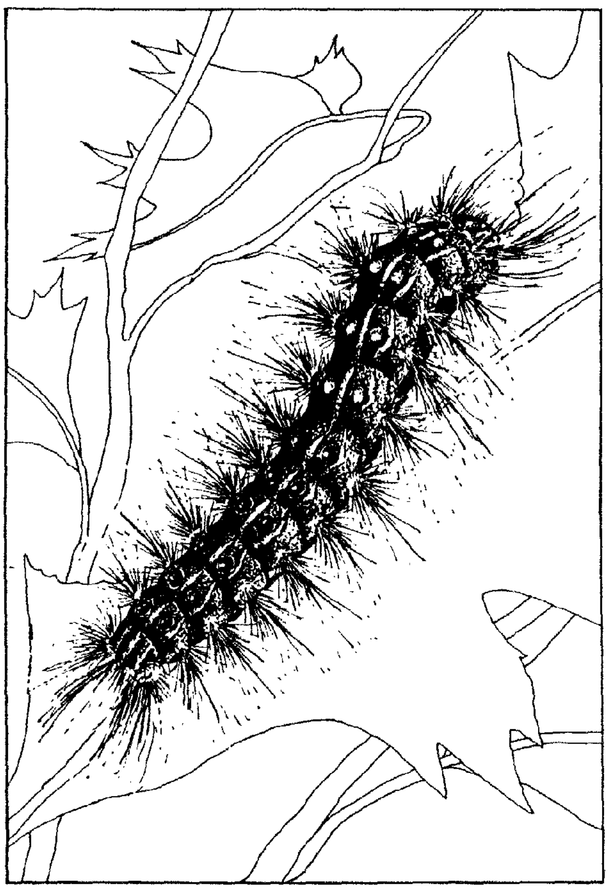
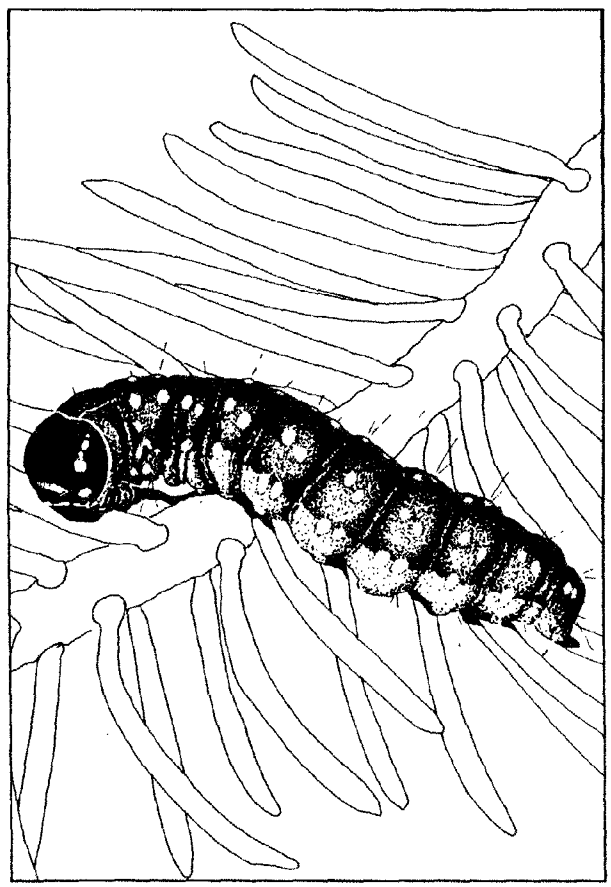
Forest Defoliator - Host Interactions: A Comparison between Gypsy Moth and Spruce Budworms





FOREWORD

The Canada/U.S. Spruce Budworms Program in cooperation with the Center for Biological Control of Northeastern Forest Insects and Diseases of the Northeastern Forest Experiment Station co-sponsored this Forest Defoliator-Host Interaction Workshop. This invitational workshop was limited to investigators of the spruce budworms and gypsy moth in the Forest Service, Canadian Forestry Service, and the University sector. The primary purpose of this workshop was to foster communication between researchers having a mutual interest and active research projects designed to understand the relationships between the host plant and forest defoliator feeding behavior, growth, and reproduction.

This Workshop was a follow-up to two previous meetings on host-insect interaction. In 1980, Dr. W. Mattson hosted a CANUSA-sponsored meeting at the North Central Forest Experiment Station, St. Paul, MN. This informal gathering brought together CANUSA Program investigators from the US and Canada for the purpose of sharing preliminary information and data on host-insect interactions. The second meeting took place in the fall of 1982. CANUSA(E) sponsored a Symposium on Spruce Budworm-Host Interaction at the Eastern Branch Meeting of the Entomological Society of America, Hartford, CT. The current Workshop developed from this Symposium. We found that participants were raising question concerning the similarity or differences between the spruce budworm and gypsy moth host interaction systems.

These Proceedings resulted from a three-day Workshop held in April 1983 at the Park Plaza Hotel, New Haven, CT. The structure of the Workshop allowed each participant a period for a presentation followed by lengthy discussion. These discussions were lively, friendly technical exchanges clarifying or elaborating on points raised by the speaker. Frequently, these exchanges were thought-provoking and often provided avenues for further detailed discussions and in some cases, future cooperative efforts.

The papers that make up these Proceedings were submitted at the Workshop as camera-ready copy. As a result, the participants did not have the benefit of reappraising their work in light of the discussions that followed their presentations or other ideas that developed at the Workshop.

Since the Workshop was planned late in the life of the CANUSA Program, we asked each investigator to be especially aware of the implications of these interactions on population dynamics of the insect in relation to forest management potential. When possible, we also asked that future research needs and direction be mentioned.

As technical coordinators for this Proceedings, it was our task to arrange and more effectively focus material so that papers provide a smooth transition of ideas and research activities on insect-host interactions for the spruce budworms and gypsy moth.

Lastly, we would like to acknowledge the support and confidence expressed by the following:

Denver P. Burns, Director, Northeastern Forest Experiment Station

Melvin E. McKnight, Program Leader, CANUSA

William E. Wallner, Director's Representative, Hamden, CT

August 1983 Robert L. Talerico, Broomall, PA

COVER SKETCH

Left, gypsy moth larva; right, spruce budworm larva.

PROCEEDINGS,

forest defoliator--host interactions:

A comparison between gypsy moth and spruce budworms

New Haven, Connecticut, April 5-7, 1983

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CONTENTS

WESTERN SPRUCE BUDWORM CONSUMPTION - EFFECTS OF HOST SPECIES AND FOLIAGE CHEMISTRY

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Feeding efficiencies and growth rates of western spruce budworm larvae varied among hosts tested. Pupae attained normal size regardless of host species. Candidate defensive compounds (tannins and phenols) varied only slightly with the vigor of the host. The relationship between these defensive compounds and measures of larvae growth were not entirely consistent with current theories on the role of secondary plant compounds.

Introduction

Within a population of host plants, the intensity of insect attack and subsequent damage may vary considerably. It is not uncommon for two Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco, trees near each other to have quite different populations of western spruce budworm, *Choristoneura occidentalis* Freeman (McDonald 1981). Western spruce budworm (WSBW) frequently exhibits this preferential habit within and among its hosts in the Southwest.

Numerous explanations for preferential attack by insects have been suggested including differences in nutritional values, phenology, foliage toughness, host vigor, and plant defensive compounds. Foliage chemicals have been implicated as specific factors in the resistance-susceptibility characteristics of Douglas-fir (McMurray 1980). Literature on the important plant defensive compounds has been adequately reviewed by the following authors: tannins (Swain 1979), phenols (Levin 1971, Swain 1977), and nitrogen (Mattson 1980).

In this paper we present some preliminary results on differences in feeding by WSBW among the important hosts in the Southwest. We also report on correlations between WSBW feeding and concentrations of phenols, tannins, and proteins in white fir, *Abies concolor* (Gord. and Glend.) Lindl. ex Hildebr., and Douglas-fir foliage.

Methods

Tree Selection

Four hosts of WSBW occurring in northern Arizona were selected for the feeding experiments: Douglas-fir, white fir, corkbark fir, *Abies lasiocarpa* var. *arizonica* (Merriam) Lemm.; and Engelmann spruce, *Picea engelmannii* Parry ex Engelm. Trees were selected from mixed conifer stands approximately 16 km north of Flagstaff, Arizona, stand elevation approximately 2,440 meters. These stands had no recent history of WSBW outbreaks.

Trees suitable for site index determination were rated for vigor according to Waring et al. (1980). This technique uses the ratios of the basal area growth for one-year and five-year increments to total sapwood area. To obtain average measurements, four increment cores were taken at 90° angles from each of 25 trees of each host species. The increment cores were then stained with potassium iodide-iodine to aid in distinguishing the sapwood from the heartwood (Kutscha and Sachs 1962). Total radius, sapwood radius, and one- and five-year increment radii were measured. The ratios were calculated using this formula:

$$\frac{BA_x}{SA} = \frac{R^2\pi - (R - r_x)^2\pi}{R^2\pi - (R - r_s)^2\pi}$$

BA_x: basal area of growth increment for period x

SA : sapwood area

R : total radius

r_x : radius of increment growth

r_s : radius of sapwood

Fifteen trees were selected from the 25 which were cored for each species (five trees in each of three vigor categories). The five trees with the highest ratios were classified as high vigor trees, the five trees with the lowest ratios were classified as low vigor trees, and the five trees closest to the mean were classified as medium vigor trees. The theoretical range of BA/SA ratio is 1.00 to 0.00. The actual range of BA_5/SA observed for the four species was: Douglas-fir 0.49 to 0.14, white fir 0.59 to 0.20, corkbark fir 0.63 to 0.24, and Engelmann spruce 0.60 to 0.13.

Selection of Larvae

Second and third instar larvae were collected in early May from an ongoing WSBW outbreak within the Kaibab Naitonal Forest, Arizona. Budworm infested branch tips were collected from the four host species used in this study. Larvae were carefully segregated according to host species; this allowed the larvae to be fed foliage from the same host species from which they were collected. The branch tips were laced in Aquapics® to maintain freshness and transported to the laboratory.

The field collected larvae were stored at 2-4°C to slow development until five to seven days before the experiments were to begin. The larvae were then placed at room temperature until they advanced to the fourth instar. Larvae were determined to be in the fourth stadium by head capsule measurements. Bean and Blatzer (1957) and Wagg (1958) were used as guidelines.

Foliage Collection

To standardize the host phenological stage, feeding experiments were begun when the host foliage was determined to be at the "brush" stage (bud cap gone, needles even but no shoot growt : so needles appear to arise from one spot) (Shepard unpublished).

We collected paired foliage samples from the midcrown of the host trees at the four cardinal directions. Paired twigs were selected for uniformity in size and phenology. One twig was fed to a budworm, the other twig was used to estimate the average dry weight per needle of the feeding twig. This average dry weight was later used to estimate the dry weight of the foliage consumed by the budworm larva.

Feeding Procedure

The paired twigs were saturated in a 100% relative humidity environment overnight. The following morning the mature foliage was trimmed from the feeding twig. While being held under water, the twig was excised and placed in a water-filled Aquapic®. The prepared foliage was then placed in a paper-lined 150 x 25 mm petri dish.

Fourth instar larvae were weighed fresh and placed on the prepared foliage to feed. Initial dry weight of each larva was estimated using an average percent dry weight of fourth instar larvae. The petri dishes were placed in controlled environmental chambers for the duration of the experiments. Temperature in the chambers ranged from 24 to 26°C; the photoperiod was 16 hours of light and 8 hours of darkness, as recommended by Robertson (1979).

Following each 72 hour feeding period the feeding twigs were removed and replaced with fresh foliage. The number of damaged needles was recorded and the damaged needles still attached to the twig and wasted needles were collected and oven dried at 60°C until no further weight loss occurred. Both wasted and remaining foliage were then weighed on a balance accurate to 0.1 mg. The amount of foliage ingested by each larva was estimated using the following formula:

$$I = (DW \times N) - (W + R)$$

I : foliage ingested

DW: mean dry weight per needle

N : number of needles damaged

W : foliage wasted (clipped but not consumed)

R : foliage remains (damaged but not clipped from the twig)

Each replicate was terminated within 24 hours of pupation. Total foliage ingested was calculated; pupae were sexed and weighed fresh. Feces and pupae were then oven dried at 60°C and weighed.

Nutritional indices were calculated on a dry weight basis according to Waldbauer (1968). The following nutritional indices are used in this study: foliage ingested (I), relative consumption rate (RCR), relative growth rate (RGR), approximate digestibility (AD), and efficiency of conversion of ingested food to body weight (ECI).

Chemical Analysis

Foliage used in the chemical analyses was clipped from the host trees selected for the feeding experiment and immediately frozen for 18 hours at -20°C. Samples were then freeze-dried at -50°C and 50 millitorr in a freeze dryer. Samples were stored at -20°C under dessication until analyzed.

Proteins were analyzed using the Coomassie Brilliant Blue Dye technique (Bradford 1976). Total phenols were determined using the Folin-Denis technique according to Swain and Hillis (1959) and Ribereau-Gayon (1972). Tannins were analyzed using the vanillin reaction assay (Price et al. 1978) as modified by Zucker (unpublished).

Results and Discussion

Comparison of Rearing Methods

The effect of three commonly used rearing procedures on fresh and dry pupal weights was determined for WSBW feeding on Douglas-fir and corkbark fir. Fresh pupal weights were significantly different among rearing methods for corkbark fir but not for Douglas-fir (Table 1). For corkbark fir, fresh pupal weights were significantly higher for insects bagged on foliage in the field than for insects fed excised foliage in the lab. Excised foliage and bagged foliage tests were conducted on the same trees and crown positions. Fresh pupal weights were not significantly different between insects reared on excised foliage and insects that developed under normal field conditions for either host species. Dry weights of pupae were not significantly different between rearing methods (Table 2).

Table 1. Fresh pupal weights of female western spruce budworm by rearing method and host species. a/

REARING METHOD	DOUGLAS-FIR	CORKBARK FIR
EXCISED FOLIAGE	70.6 (5) b/	69.0 (5) A c/
FIELD BAGGED	91.6 (4)	83.6 (6) B
FIELD COLLECTED	70.5 (77)	59.8 (51) A
F-PROB.	0.1390	0.0014

a/ weights in milligrams.
b/ numbers in parentheses are number of cases.
c/ oneway ANOVA, LSD multiple range test, $\alpha = 0.10$, values followed by different letters are significantly different.

Table 2. Oven-dry pupal weights of female western spruce budworm by rearing method and host species. a/

REARING METHOD	DOUGLAS-FIR	CORKBARK FIR
EXCISED FOLIAGE	20.8 (5) b/	19.2 (5)
FIELD BAGGED	16.4 (4)	18.7 (6)
FIELD COLLECTED	———	———
F-PROB.	0.4705	0.8974

a/ oneway ANOVA, $\alpha = 0.10$, LSD multiple range test, values followed by different letters are significantly different.
b/ numbers in parentheses are number of cases.

The technique of excising foliage for feeding experiments may lead to misleading results if inducible defensive mechanisms exist, because excised branches may not be able to respond to insect feeding by increasing concentrations of defensive compounds as would a normal branch. However, our study shows that feeding on excised foliage in the laboratory is probably a good approximation of feeding as it occurs under natural conditions. Bagging of insects on trees (white muslin bags) tends to increase pupal weights, probably as a result of reduced harassment from predators and parasites and possibly because of a modified microclimate.

Influence of Host Species

A commonly held belief among foresters is that some host species are more resistant to both WSBW and eastern spruce budworm, *Choristoneura fumiferana* Clemens, than are other hosts. We compared the relative suitability of three of the important hosts in Arizona (Table 3). Pupal weights were not significantly different among the three hosts, which indicates that all hosts are a suitable substrate for insect development. Feeding efficiency (ECI) and growth rate (RGR) were significantly higher on Douglas-fir than on either white fir or corkbark fir. However, budworm larvae can apparently compensate for the lower quality of the foliage, as reflected in low ECI and RGR, by increasing their consumption rate (I) and probably the duration of the feeding period. This ability of insects to compensate for lower food quality by increasing consumption is often overlooked in studies of host plant-herbivore interaction. Too few replicates of Engelmann spruce were available to include in this analysis; however, qualitatively it appeared as if WSBW did quite well on spruce foliage when the host growth and the herbivore requirements were synchronized.

Table 3. Nutritional indices and pupal weights for western spruce budworm reared on three host species in Arizona.

HOST	N	I (mg)	RCR	RGR	ECI	PUPAL WT. a/ (mg)
DOUGLAS-FIR	13	185.	1.7	0.12 A b/	7.8 A	58.6
WHITE FIR	20	226.	2.0	0.10 B	5.4 B	60.6
CORKBARK FIR	10	223.	1.7	0.09 B	5.8 B	60.0
F-PROB.		0.341	0.163	0.012	0.003	0.957

a/ pupal weight on fresh basis, all other values based on oven-dry weights.
b/ values followed by different letters are statistically significant, oneway ANOVA, LSD multiple range test, $\alpha = 0.10$.

Chemical Content of WSBW Host Foliage

Current year's foliage of selected host trees was collected seven to 10 days after the beginning of the feeding studies. Foliage was collected from the same trees and crown position as those used in the feeding studies. Tannin concentration did not vary significantly between host vigor categories for any of the species tested (Table 4). Engelmann spruce had approximately twice the tannin content of any other host. Total phenols were not different among vigor categories for Douglas-fir and white fir (Table 5). However, medium vigor corkbark fir trees had lower total phenols than did the high or low vigor trees. Low vigor Engelmann spruce trees had lower total phenols than high and medium vigor trees. Protein content of foliage tended to decrease with host vigor for all host species tested (Table 6). However, this trend was statistically significant only for Engelmann spruce.

efficiency. It is difficult to explain these apparently opposite results, except that tannins and proteins are intercorrelated in Douglas-fir which may result in a random correlation. Clearly we know little about the role of foliage tannins in larval feeding and growth in the WSBW.

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