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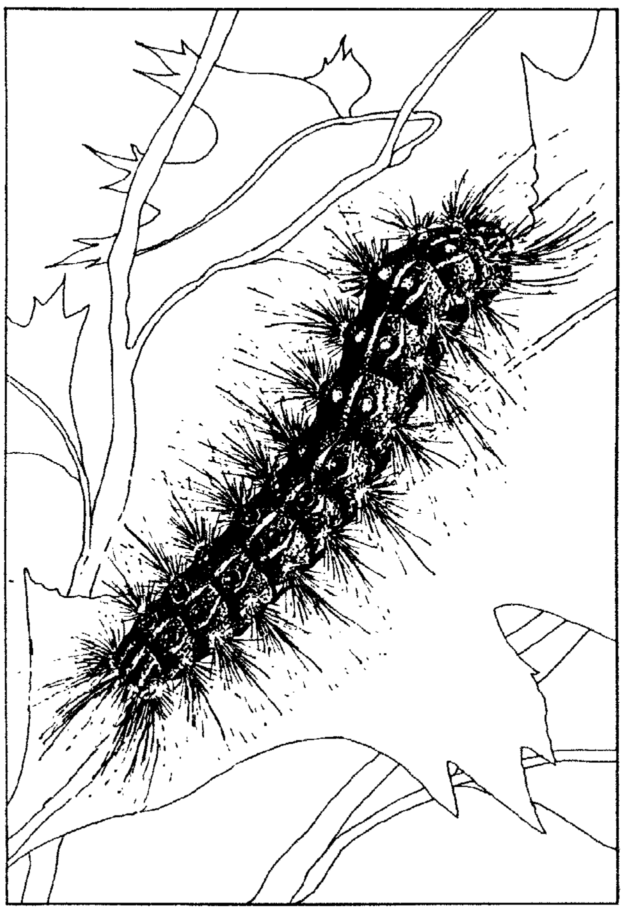
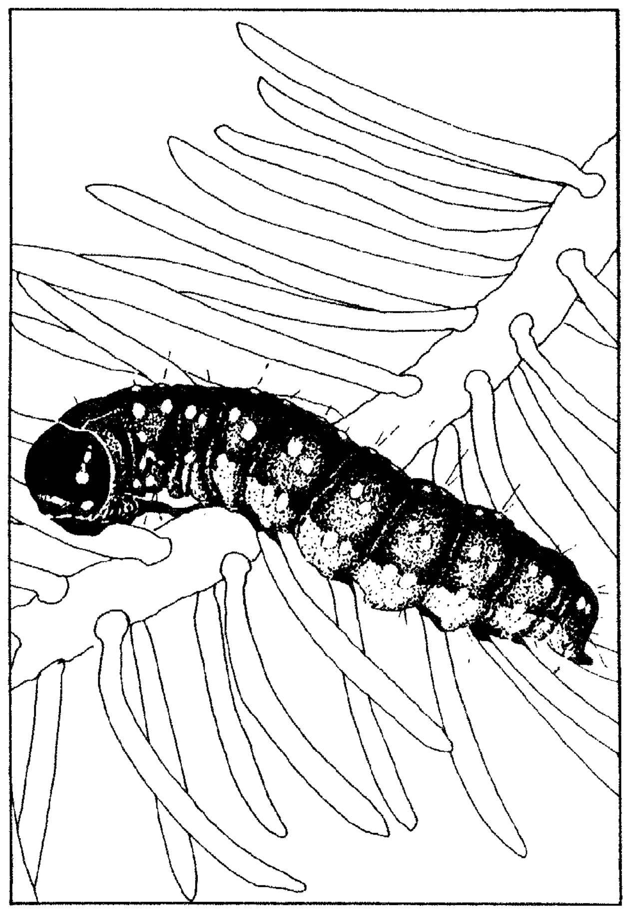
Forest Defoliator - Host Interactions: A Comparison between Gypsy Moth and Spruce Budworms





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

EFFECT OF FERTILIZATION ON WESTERN SPRUCE BUDWORM FEEDING IN YOUNG WESTERN LARCH STANDS

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This study evaluated effects of fertilization of young western larch stands on western spruce budworm feeding in Montana. Various combinations of nitrogen, phosphorus, and potassium resulted in nearly double the amount of feeding by western spruce budworm larvae, with nitrogen eliciting the most response. Larch growth response to fertilization can be negated by increases in budworm feeding.

Introduction

Forest fertilization is relatively new to the Northern Rockies and is primarily limited to experimental areas. Western spruce budworm (*Choristoneura occidentalis* Freeman), a defoliating insect native to the Northern Rockies, has persisted in epidemic proportions since the late 1940's. Although reported long before that, it was not considered a serious threat to forest management until about 1950. In the early 60's, we discovered and described the feeding behavior of western spruce budworm on young western larch (*Larix occidentalis* Nutt.) (Fellin and Schmidt 1967). Instead of foliage feeding only, budworm were found feeding on and severing the stems of new shoots of larch, jeopardizing the straight form and rapid juvenile height growth characteristic of this species. Subsequent evaluations of this unusual feeding habit showed that indeed height growth was reduced about 25 to 30 percent by these terminal and upper lateral stem severances and that there was at least a temporary reduction in form quality (Schmidt and Fellin 1973; Fellin and Schmidt 1973a).

Silvicultural attempts at dealing with forest pest problems have a long history, particularly with some of the beetles. One of these cultural methods--fertilization--has had only limited evaluation. In a review, Mustanoja and Leaf (1965) noted that "fertilizers have differential effects on insects, the effects being more or less similar within certain genetic groups." They note, however, that "the populations and attacks of all studied species of macrolepidoptera . . .," of which they list four, " . . . have been reduced with mineral fertilizers (especially N) and lime." They attribute the effect to increased larval mortality. In another review, Stark (1965) lists 28 fertilizer trials involving about a dozen species of forest insects in as many genera. In 21 of these trials, the treatment adversely affected the insects--including sawflies, shoot moths, aphids, and caterpillars--as reflected in reduction of cocoon or pupal density, increased larval mortality, decrease in female weight, and so forth. Six of the 28 trials showed no fertilizer effect and one showed increase in insect feeding.

In some specific examples, Merker (1958, 1961, 1963), studying 20- to 50-year-old spruce infested with *Pristiphora abietina*, found that he could significantly reduce pupal density and injury to shoots, sometimes in the same season, by applying NH_4NO_3, $CaCO_3$, or urea. Also, nitrogen applied as part of an NPK treatment to eastern white pine resulted in the least amount of damage by the white pine weevil, *Pissodes strobi* Peck, but the nitrogen treatment also resulted in the shortest trees (Xydias and Leaf 1964).

Conversely, there are documented cases where fertilizer increased the number of insects and/or stimulated feeding. For example, Xydias and Leaf (1964) found the greatest incidence of attack by the white pine weevil occurred with the same treatment of potash that resulted in the tallest trees. The treatment apparently made trees more palatable to the weevil. Also, Carrow (1967) found that the establishment rate of balsam woolly aphids (*Adelges picea* [Ratz.]) on Pacific silver fir (*Abies amabilis* [Dougl.] Forbes) grown on a humic, nitrogen-rich soil was 2.5 times as high as on host trees grown on a mineral nitrogen-poor soil. Increased pupal weights of spruce budworm (*Christonerua fumiferana* Clem.) were found on nitrogen fertilized balsam fir (*Abies balsamea* [L.] Mill.). These increased pupal weights were in turn positively correlated with increased numbers of larvae produced per female moth (Shaw and others 1978). Hughes and Jackson (1962) found fertilizer mixtures of either N, P_2O_5, or K_2O at the 100-lb/acre (112-k/ha) rate resulted in a highly significant increase in the incidence of attacks by a phloem insect, *Dioryctria amatella* (Hulst), to slash pine (*Pinus elliottii* Engelm. var. *elliottii*). Of the three components, incidence of attack was most closely associated with mixtures containing phosphorus. Even at the 50-lb/acre (56-k/ha) rate, phosphate in mixed fertilizers increased insect attacks fourfold over treatments containing no phosphate.

Soil type and/or host tree condition may be influential in the effect of some fertilizers on forest insects. In Sweden, poorly growing pine trees treated with phosphorus or nitrogen were little affected by attacks of the European pine shoot moth (*Rhyacionia buoliana* [Schiff.]). However, healthier trees treated with fertilizers affording phosphorus or nitrogen suffered heavy damage by the shoot moth (Eidmann and Ingestad 1963). Hughes and Jackson (1962) found *Dioryctria amatella* (Hulst) injury to slash pine most prevalent among fast growing trees; damage was negligible among slow growing trees of the same size in an adjoining plantation.

Insect predator-host relationships may also be involved in fertilizer responses. Thalenhorst (1964) warns against premature assumptions about the effects of fertilizers on insects. He describes a fertilizer trial in a spruce plantation where aphid species, mostly *Cinaropsis pilicornis*, infestations in May were heaviest on NPK and slightest on PK plots. However, since predator populations, particularly a lady beetle, *Coccinella septempunctata*, were also most numerous on these densely populated plots, the position was completely reversed a month later.

No general agreement exists on the mode of action in fertilizer interactions with insects. The physiology of the tree may be involved. Mustanoja and Leaf (1965) note that with some insects the sugar:protein ratio of the needles is important for nutrition of the larvae, and anything that decreases this ratio--water or mineral fertilizers, especially nitrogen--increases larval mortality. Carrow (1967) noted that an amino acid imbalance in the bark tissue of host trees was induced by fertilization with NH_4NO_3 and may have been responsible for a population decline of aphids. Also, nutrients may produce structural changes in host plant tissues that affect insect feeding. Lignification of plant tissues (Mustanoja and Leaf 1965), size of food (finely comminuted versus whole needles) (Merker 1961), and coarser bud scales or greater resin flow (Oldiges 1959) are all cited as possible effects of nutrient fertilization that in turn affected the feeding behavior of insects on the host trees.

Another hypothesis is that fertilizer elements are incorporated directly into various insect tissues, often with fatal or deleterious effects. Merker (1962) notes that the direct effects of absorbed fertilizers on forest pests are much more severe than any indirect effect upon the physiological condition of the tree. However, Carrow and Graham (1968) imply that treatment of host trees with ammonium nitrate reduces populations of the balsam woolly aphid primarily by inhibiting initial settling of larvae on the host trees.

Although there is apparently little consistency in the results of fertilizer trials--due in part at least to questionable observations on small plots, lack of knowledge of the nutritional and moisture relations of the soils, or impracticable methods--there does appear to be general agreement that fertilization affects the behavior of many insect populations (Stark 1965).

Neither the technical or economic aspects of forest fertilization are well understood, particularly in the Northern Rockies. Nevertheless, it is important that tree response to fertilization and interactions with other factors in the ecosystem be evaluated. With this in mind, we undertook the subject of this paper--the interaction of western spruce budworm with different combinations of fertilizers in young western larch forests of western Montana. This is the first report of the results of this exploratory study.

Methods

This western spruce budworm study was superimposed on a conventional fertilizer study that aimed primarily at determining the effect of different combinations of fertilizer on growth of young western larch forests. The original fertilizer/growth study established in 1966 consisted of 175 experimental plots at 13 locations in western Montana (Behan 1968). The basic design of the original fertilizer/growth study was a randomized block of six treatments replicated three times at each location. However, because of limited area or lack of sufficient homogeneity of the stands, it was not always possible to apply all six treatments. Hence, at each location, there were from two to six treatments, including controls of no fertilizer, but always three replications.

The fertilizer/budworm study reported here was established 2 years later in 1968 and was limited to four of the 13 locations of the original fertilizer/growth study. All four locations were within the budworm-infested areas of the Lolo and Flathead National Forests. The treatment combinations on these four plots are shown in Table 1, where the control had no fertilizer and the treatments were composed of various combinations of nitrogen, phosphorous, and potassium.

Table 1. Description of site, stand, and treatments used for this larch fertilizer/western spruce budworm study.

Location	Stand condition at time of treatment			Site index	Treatments
	Age	Height (feet)	Average density (trees/acre)	(50 yr)	
Upper Cottonwood	12	6 to 12	7,000	60	Control, NPK
Lower Cottonwood	12	4 to 8	300[a]	65	Control, NPK, N, NK, NP, PK
Rice Ridge	18	5 to 15	3,500	70	Control, NPK, N, NK, NP, PK
Barber Creek	11	4 to 10	3,600	80	Control, NPK, N

[a] thinned.

Nitrogen (N) was in the form of urea at the rate of 300 lb/acre (336 k/ha), phosphorus (P) was treble superphosphate at the rate of 200 lb/acre (224 k/ha) of P_2O_5 (phosphorus pentoxide), and potassium (K) was potassium chloride at the equivalent of 200 lb/acre (224 k/ha) of K_2O (potassium oxide). For example, the NPK treatment consisted of 300 lb nitrogen, 200 lb phosphorus, and 200 lb potassium per acre. Fertilizers were preweighed and applied separately with a hand spreader on the plots.

To sample the interaction of the budworm and the fertilizer treatments, five of the tallest trees per plot were randomly selected. Each tree was stratified vertically into six strata. In each stratum, beginning with the topmost stratum, we selected a branch or branches and examined the first 100 fascicles, beginning distally on the branch. Branches selected were in a helical pattern moving down the tree; i.e., the first branch selected on the south side of the tree, the next on the southwest, the next on the west, and so forth. Each branch was tagged for initial and subsequent measurements. On these 100 fascicles, we determined the number of larvae and the number of fascicles damaged during the larval feeding period. After the larval feeding was completed, we examined the same 100 fascicles to determine the number of damaged fascicles. Larvae counts were made the second year after fertilization on all four study areas. Observations, but no larval counts, were made in measurement years four and six.

In addition, on these same branches in each stratum, we determined the larval damage done to the lateral shoots in four categories: (a) no feeding; (b) needle feeding only; (c) external mining of the shoot; and (d) shoot severed (fig. 1). Damage to the terminal shoot of each tree was evaluated and classified into the same four damage categories listed for the lateral shoots.

Measurements of injuries caused by western spruce budworm larvae were taken in 1968, 1970, and 1972--2, 4, and 6 years after the fertilizers were applied in fall of 1966.

Results

Western spruce budworm larvae fed on the young western larch trees on these fertilizer study plots in much the same manner we described earlier (Fellin and Schmidt 1967, 1973a; Schmidt and Fellin 1973). However, budworm fed more heavily on larch in the fertilized plots than they did in the control plots. Overall, the effects of fertilizer treatment on budworm feeding were essentially the same on all four study areas. The absolute amount of budworm damage varied by area because of difference in budworm populations, but the ratios of larval damage in the fertilized and control plots were much the same. The following sections describe the types and amounts of budworm feeding as related to fertilizer treatment.

Fascicle Damage

The first noticeable budworm damage to la
in the spring was from larvae feeding on the l
fascicles. Fascicle needles started emerging
late March, well before the terminal and later
shoots started to elongate (Schmidt and Lotan
1980). Thus, the fascicle needles were the fi
readily available source of foliage for the
budworm on young larch.

Budworm fed on fascicles about one and a h
to twice as much on the fertilized plots as th
did on the control (not fertilized) plots (Tab
2). This was particularly apparent on any of t
plots where nitrogen was at least one of the
components of the fertilizer treatment. Effect
of PK treatment on budworm feeding were far le
pronounced than those treatments that included
nitrogen, but damage on the PK treatment excee
that on the control plots.

Table 2. Percent fascicles injured by western spruce budworm larvae 2 years after fertilization.

Treatment	Lower Cottonwood	Upper Cottonwood	Rice Ridge	Ba
		(percent)		
NP	25	--	28	-
N	28	--	23	
NK	22	--	26	-
Control	12	6	13	
PK	14	--	18	-
NPK	20	15	21	

Larvae fed on fascicles throughout the cr
but fed more heavily on those in upper strata c
the live tree crowns (Fig. 2). The number of
fascicles fed on was about three times heavier
the upper crown than in the lower crown. This
consistent with observations we had made earli
of budworm feeding behavior (Schmidt and Felli
1973).

Lateral Shoot Damage

Budworm larvae severed about one and a hal
to twice as many of the succulent new shoots o
lateral branches on fertilized plots as on the
control plots (Table 3). Over half of the late
shoots were severed by budworm larvae on the
fertilizer plots at Rice Ridge the second year
after fertilization compared to about one-fourt
of the lateral shoots on the control trees. Li
fascicle feeding, the PK treatment results fel
intermediate between those treatments that inc
nitrogen and the control. Since the above inj
coincided with a generally heavy budworm infest
tion in the area, practically none of the tree
escaped some type of budworm feeding, even tho
on the control plots. Only 8 percent of the t
in the control plots weren't fed on in some
manner.

Figure 1a. Types of western spruce budworm feeding on western larch--no feeding.

Figure 1b. Types of western spruce budworm feeding on western larch--needle feeding only.

Figure 1c. Types of western spruce budworm feeding on western larch--external mining of the shoot.

Figure 1d. Types of western spruce budworm feeding on western larch--shoot severed.

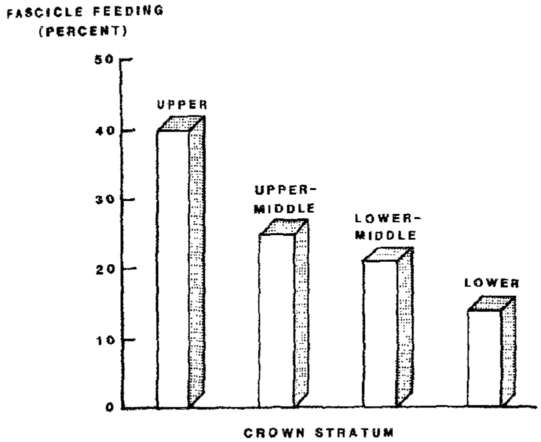

Figure 2. The percent of fascicles fed on by western spruce budworm larvae at four crown levels 2 years after fertilization (Lower Cottonwood). This includes only the upper four of the six crown strata. The lower two strata were in the receding portion of this shade-intolerant species and showed practically no budworm feeding.

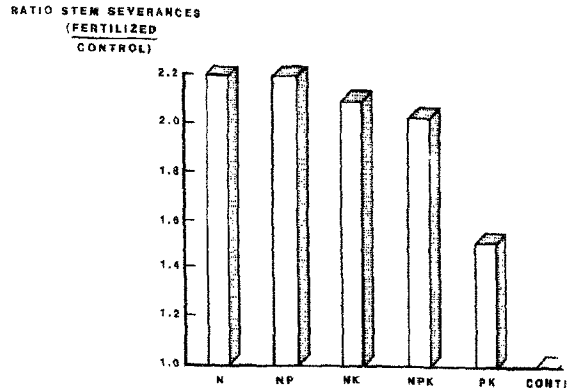

Figure 3. Budworm severance ratios on fertilized and control plots (fertilized/control) at Lower Cottonwood and Rice Ridge 2 years after fertilization.

Table 3. Percent lateral shoots of western larch severed by western spruce budworm at Rice Ridge and Lower Cottonwood 2 years after fertilization.

	Type of damage			
	Rice Ridge		Lower Cottonwood	
Treatment	None	Lateral shoots severed	None	Lateral shoots severed
	(percent)			
NP	1	56	10	65
N	1	53	6	68
NK	1	52	5	65
Control	8	23	21	34
PK	2	44	25	37
NPK	1	54	10	58

Table 4. Effect of NPK fertilizer on the percent of lateral shoots severed by western spruce budworm larvae on four study areas two years after fertilization.

Damage	Area	Control	NPK[a]
		--(percent)--	
Shoots severed	Lower Cottonwood	36	54
	Upper Cottonwood	34	58
	Rice Ridge	39	67
	Barber	7	10
None	Lower Cottonwood	21	10
	Upper Cottonwood	28	14
	Rice Ridge	1	1
	Barber	84	82

[a] The NPK and control treatments were the only treatments common to all four study areas.

We see little difference in percent lateral shoots severed between those four treatments that included nitrogen (Fig. 3). Budworm severed about twice as many of the lateral shoots on the nitrogen treated plots as on the controls. Lateral shoot severance ratios on the PK treated plots were intermediate to the controls and the plots with nitrogen.

The effect of fertilization on lateral shoot severance by western spruce budworm larvae was relatively consistent from area to area. The absolute amount of damage varied by area because of differences in budworm populations, but the ratios of damage on the NPK and control plots were much the same (Table 4). Lateral shoot severances were about one and a half to twice as great on NPK plots as on the controls.

The effect of budworm larval populations is most readily detected in the trees that had no damage (Table 4). For example, Rice Ridge had a high budworm population 2 years after fertilization and only 1 percent of the lateral shoots escaped both needle feeding and severance in both the NPK and control plots. Meanwhile, on the Barber area where budworm populations were light, over 80 percent escaped all types of damage.

Fertilization effects on budworm feeding, particularly in the most severe form of feeding (shoot severance), diminished rapidly (Table 5). The largest absolute differences in budworm feeding by fertilizer treatments occurred the second year after fertilization. This coincided with the year of greatest tree diameter growth response to fertilization (personal communication with Dr. Mark Behan, University of Montana, Missoula, 1982). Evaluations to determine treatment effects the fourth year after fertilization were confounded by a dramatic reduction in budworm

Table 5. Effect of NPK fertilizer on budworm shoot severances 2, 4, and 6 years after fertilization on four study areas.

Damage	Years since fertilization	Control	NPK
		(percent)	
Shoots severed	2	25	41
	4	8	8
	6	29	32
None	2	29	22
	4	83	84
	6	37	31

populations throughout much of western Montana in 1969, the third season after fertilization. An unseasonal cold-wet spell in June of that year reduced budworm populations about 90 percent and budworm injuries up to 70 percent the following season (Fellin and Schmidt 1973b). However, western spruce budworm populations resurged rapidly following their decimation by the frost--the number of shoots severed in the control plots in year 6 were back to, and had actually exceeded, what they were in year 2 (Table 5).

The data hint that there were small residual effects of fertilization on budworm feeding in year 6--the percent of lateral severances was slightly greater on the NPK treatment and also fewer totally undamaged trees than on the control.

Terminal Shoot Damage

Budworm feeding on terminal shoots was essentially the same as that on the lateral shoots and fascicles--damage was highest on the fertilizer treatments that included nitrogen, intermediate on the PK treatment, and lowest on the control plots (Table 6). Larvae severed about one and a half to twice as many of the terminal shoots on the fertilized plots as on the controls.

Table 6. Percent of terminal shoots severed by larvae 2 years after fertilization.

Treatment	Area: Lower Cottonwood	Area: Rice Ridge
	- - - - - (percent)	- - - - - -
NP	53	87
N	60	67
NK	53	67
Control	33	47
PK	40	73
NPK	60	67

We consider the severence of terminal shoots the most severe damage that budworm inflicts on western larch because it reduces both the rapid height growth and excellent bole form of western larch--two very desirable attributes of larch (Schmidt and Fellin 1973)(Fig. 4).

The incidence of damage was higher on the terminal shoots than on any other portions of the tree, a relationship that supports results of some of our earlier studies (Fellin and Schmidt 1973a; Schmidt and Fellin 1973). For example, at Rice Ridge, where budworm populations were high 2 years after fertilization, over three-fourths of the terminal shoots were severed on the fertilized plots compared to only about half of the lateral shoots.

Budworm Feeding Relationships

Certainly, fertilization did not deter any larval feeding on larch. Rather, all types of feeding were enhanced by fertilization, but the increases of the fertilized plots over that of the controls were least in needle feeding and greatest in the more severe form of feeding--the shoot mining and severances (Table 7). Using Lower Cottonwood as the example and a ratio of NPK/Control, the apparent increase in needle feeding due to NPK had a ratio of only about 1.14, 2 years after fertilization. At the same time, the ratio for lateral shoot mining was 1.78 and that for lateral shoot severance was 1.71.

Table 7. Effect of NPK fertilizer on type of budworm feeding, 2, 4, and 6 years after fertilization at Lower Cottonwood.

Damage	Control 2	Control 4	Control 6	NPK 2	NPK 4	NPK 6
	- - - - -		(percent)		- - - - -	
None	21	84	28	10	84	24
Needle feeding	79	16	72	90	16	76
Lateral shoots mined	37	5	38	66	7	45
Lateral shoots severed	34	4	35	58	5	41

Consistent with earlier studies (Schmidt and Fellin 1973), about 90 percent of those shoots mined were also severed--the budworm nearly always succeeded in severing the shoots.

Larval feeding damaged fascicles early in the season and was directly related to the number of lateral shoots severed later in the season (Fig. 5). There was a strong linear relationship of fascicle feeding to lateral shoot severances when data from all areas and years on both the NPK and control plots were combined. For example, if about 20 percent of the fascicles were fed on, about 50 percent of the lateral shoots could be expected to be severed a little later. There was no detectable difference in this relationship between the fertilized and control plots.

Figure 4a. Effects of western spruce budworm feeding on the form of the upper bole of western larch--no budworm feeding.

Figure 4b. Effects of western spruce budworm feeding on the form of the upper bole of western larch--repeated budworm feeding.

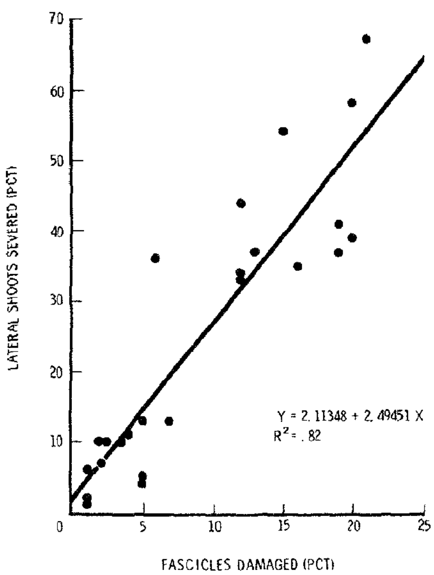

Figure 5. Relationship of the percent of fascicles fed on and the percent of lateral shoots severed by western spruce budworm larvae.

Conclusions

Fertilization is still in its infancy in forests of the Northern Rockies, but as management intensifies, it may become a practical forest management tool. Like many management practices, the introduction of fertilizers into a natural ecosystem can be expected to affect elements of the system other than that to which the practice is directed. In this study, the objective of the fertilization treatment was to accelerate tree growth, but we discovered that the fertilizers also influenced the feeding behavior of western spruce budworm larvae. Our evaluation for the first 6 years after fertilization showed that:

1. Fertilization increased all types of budworm feeding on young western larch, including fascicle feeding, needle feeding on the lateral shoots, lateral shoot mining, and severances of lateral and terminal shoots.

2. All fertilizer combinations tested resulted in increases in budworm feeding.

3. Those combinations of fertilizers that included nitrogen increased the incidence of budworm feeding the most with an intermediate effect shown by the fertilizer that had no nitrogen (PK).

4. Fertilizers that included nitrogen increased the incidence of budworm feeding in the general range of one and a half to twice that found on the control plots.

5. Fertilizer effects on budworm-feeding appeared relatively short-lived, with the effects most pronounced the second year after treatment and declining rapidly after that.

6. Practically none of the trees, even on the control plots, escaped some type of budworm feeding the second year after fertilization, a year that coincided with a generally heavy budworm infestation.

7. Budworm feeding was most pronounced in the upper crowns of both fertilized and nonfertilized trees with no apparent changes in this feeding pattern due to fertilization.

8. The effects of fertilization on budworm feeding, in relation to the controls, were relatively consistent from area to area, in spite of differences in budworm populations on the different areas.

9. The most severe forms of budworm feeding--shoot severances--were increased the most by fertilization.

10. Damage to the terminal shoots was the most pronounced of any of the damage categories, and from determinations we made from earlier studies, can be expected to have the most pronounced effect on tree development.

Why these fertilizer treatments affected the feeding behavior of western spruce budworm larvae is not explained by this study. Our study areas were relatively small and our sampling indicated that larvae were evenly distributed. Therefore, the condition of the tree--the feeding substrate for the budworm--must be the major factor affecting the budworm larvae response to the fertilizers. We postulate that at least two factors may help explain this feeding response: (1) The nutritional status of needle and shoot components of fertilized larch trees are improved by fertilization. This more favorable diet may result in more vigorous and active budworm larvae capable of increased feeding activity. (2) Budworm larvae find the fertilized trees a more favorable substrate and fewer of them disperse from the tree to the forest floor where they succumb to unfavorable physical and biological conditions.

Nutritional studies may help explain why some of these interactions between budworm larvae and fertilized trees occur. In the meantime, it appears that fertilization of larch stands within areas of heavy budworm infestation should be delayed until budworm populations decline. During a heavy infestation, the positive effects of fertilization on larch tree growth and vigor can be largely negated by increased budworm feeding.

Literature Cited

Behan, M. J. Fertilization in western larch forests. Note 6. Missoula, MT: Montana Forest and Conservation Station, School of Forestry, University of Montana; 1968. 28 p.

Carrow, J. R. Chemical fertilizers to combat the balsam woolly aphid. In: Procedures 18th Annual Western Forest Insect Work Conference; 1967 February 28-March 3; Las Vegas, NV. 1967: 71.

Carrow, J. R.; Graham, K. Nitrogen fertilization of the host tree and population growth of the balsam woolly aphid, *Adelges piceae* (Homoptera: Adelgidae). Can. Entomol. 100(5): 478-485; 1968.

Eidmann, H. H.; Ingestad, T. Nutritive condition, growth and insect attack in a pine plantation. Rev. Appl. Entomol. 53(8): 369-424; 1963. Abstract. In German.

Fellin, David G.; Schmidt, Wyman C. Spruce budworm larvae sever stems of western larch shoots in Montana. J. For. 65(4): 258-260; 1967.

Fellin, David G.; Schmidt, Wyman C. How does western spruce budworm feeding affect western larch? Gen. Tech. Rep. INT-7. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1973a. 25 p.

Fellin, David G.; Schmidt, Wyman C. Frost reduces western spruce budworm populations and damage in Montana. Agric. Meteorol. 11: 277-283; 1973b.

Hughes, R. H.; Jackson, J. E. Fertilization of young slash pine in a cultivated plantation. Stn. Pap. 148. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station; 1962. 14 p.

Merker, E. Insect control in the forest by fertilizing stands. For. Abstr. 19: 4578; 1958. Abstract. In German.

Merker, E. What causes the injurious effect of forest fertilizing on insects? For. Abstr. 22: 4774; 1961. Abstract. In German.

Merker, E. The direct and indirect effects of fertilizers upon forest pests. For. Abstr. 24(2): 2366; 1962. Abstract. In German.

Merker, E. Control of *Pristiphora abietina* through fertilizing. For. Abstr. 24(4): 5329; 1963. Abstract. In German.

Mustanoja, K. J.; Leaf, A. L. Forest fertilization research, 1957-1964. Bot. Rev. 31(2): 151-246; 1965.

Oldiges, H. The effect of fertilizing in the forest on injurious insects. For. Abstr. 21: 3133; 1959. Abstract. In German.

Schmidt, Wyman C.; Fellin, David C. Western spruce budworm damage affects form and height growth of western larch. Can. J. For. Res. 3: 17-26; 1973.

Schmidt, Wyman C.; Lotan, James E. Phenology of common forest flora of the Northern Rockies--1928 to 1937. Res. Pap. INT-259. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1980. 20 p.

Shaw, G. G.; Little, C. H. A.; Durzan, D. J. Effect of fertilization of balsam fir trees on spruce budworm nutrition and development. Can. J. For. Res. 8(4): 364-374; 1978.

Stark, R. W. Recent trends in forest entomology. Annu. Rev. Entomol. 10:303-324; 1965.

Thalenhorst, W. The effect of density-dependent factors on infestation in fertilizer trials. For. Abstr. 26(3): 3947; 1964. Abstract. In German.

Xydias, G. K.; Leaf, A. L. Weevil infestation in relation to fertilization of white pine. For. Sci. 10(4): 428-431; 1964.

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