USDA United States Department of Agriculture

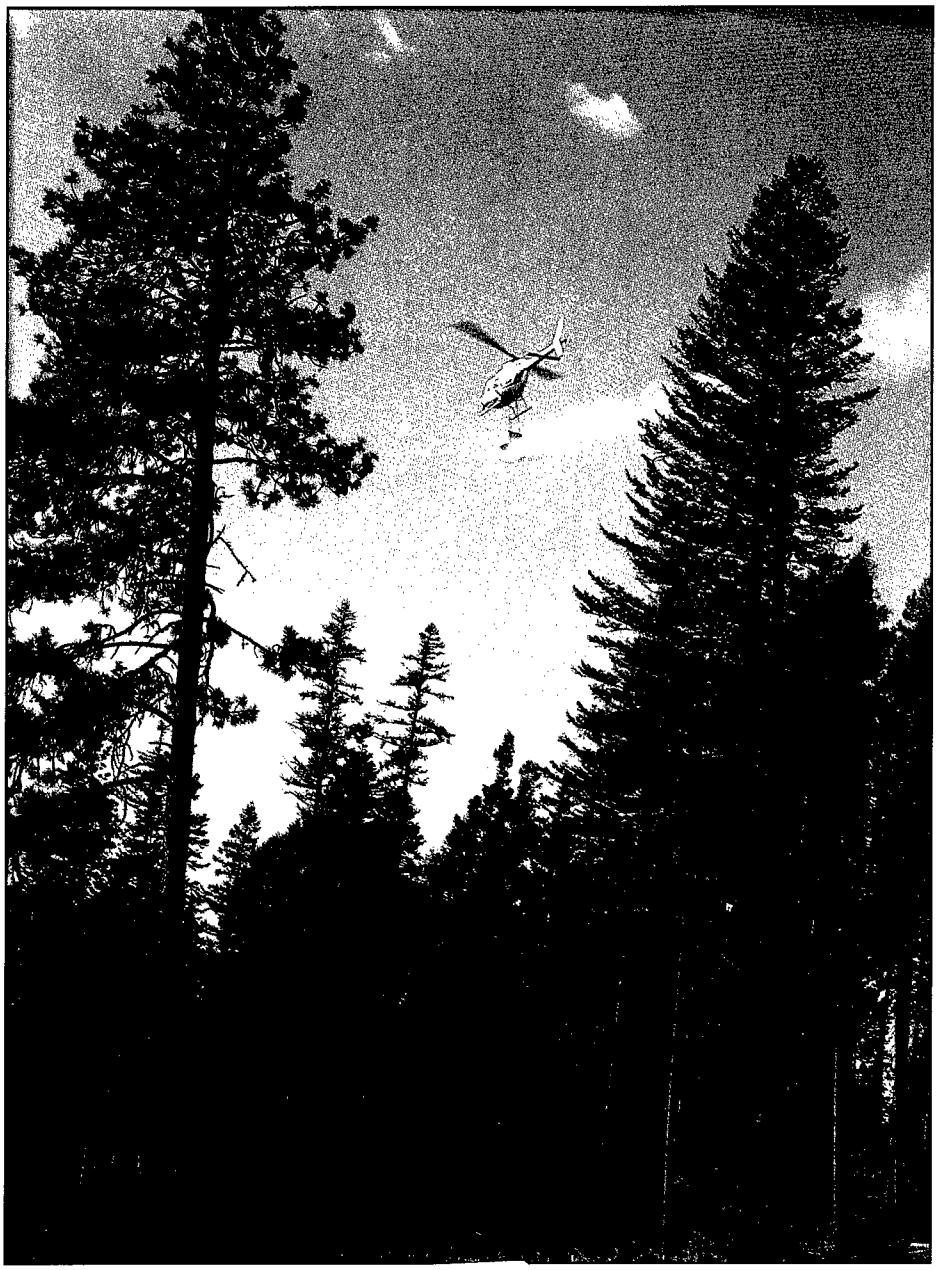
Forest Service

Pacific Northwest Research Station

Research Paper
PNW-RP-506
May 1998

A Pilot Experiment of Forest Fertilization During an Outbreak of the Western Spruce Budworm in Northeastern Oregon

R.R. Mason, B.E. Wickman, H.G. Paul, and T.R. Torgersen



Authors

R.R. MASON was principal insect ecologist (now retired), T.R. TORGERSEN is principal research entomologist, and H.G. PAUL is a forestry technician, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850-3399. B.E. WICKMAN is emeritus scientist, Pacific Northwest Research Station, Deschutes National Forest, 1645 East Highway 20, Bend, OR 97702.

REPORT DOCUMENTATION PAGE

Form Approved
OMB No. 0704-0188

PB98-152952

k)

2. REPORT DATE	3. REPORT TYPE AND DATES COVERED
May 1998	Research Paper

4. TITLE AND SUBTITLE

A Pilot Experiment of Forest Fertilization During an Outbreak of the Western Spruce Budworm in Northeastern Oregon

5. FUNDING NUMBERS

6. AUTHOR(S)

R.R. Mason, B.E. Wickman, H.G. Paul, and T.R. Torgerson

7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)

Pacific Northwest Research Station
Communications Group
P. O. Box 3890
Portland, OR 97208-3890

8. PERFORMING ORGANIZATION REPORT NUMBER

FSRP-PNW-506

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)

Same as number 7

10. SPONSORING/MONITORING AGENCY REPORT NUMBER

11. SUPPLEMENTARY NOTES

12a. DISTRIBUTION/AVAILABILITY STATEMENT

Release unlimited

12b. DISTRIBUTION CODE

13. ABSTRACT *(Maximum 200 words)*

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14. SUBJECT TERMS

Insect defoliators, defoliation, tree growth, silvicultural control, western spruce budworm, Choristoneura occidentalis.

15. NUMBER OF PAGES

25

16. PRICE CODE

17. SECURITY CLASSIFICATION OF REPORT	18. SECURITY CLASSIFICATION OF THIS PAGE	19. SECURITY CLASSIFICATION OF ABSTRACT	20. LIMITATION OF ABSTRACT
Unclassified	Unclassified	Unclassified	

Abstract

Mason, R.R.; Wickman, B.E.; Paul, H.G.; Torgersen, T.R. 1998. A pilot experiment of forest fertilization during an outbreak of the western spruce budworm in northeastern Oregon. Res. Pap. PNW-RP-506. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 25 p.

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Keywords: Insect defoliators, defoliation, tree growth, silvicultural control, western spruce budworm, *Choristoneura occidentalis*.

Summary

Three fertilizer treatments—nitrogen and two application rates of a combination of nitrogen, phosphorus, potassium, and sulfur—were tested for their effects on trees and insects in mixed-conifer stands infested with outbreak populations of the western spruce budworm (*Choristoneura occidentalis* Freeman). The fertilizers were applied by helicopter in fall 1988 to 4-hectare plots in a randomized block design. Treatment results then were evaluated for 3 to 5 years afterward by responses of the budworm and other arthropod populations, and the growth of primary tree hosts, grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco).

A total of 25 response variables, 15 insect related and 10 tree related, were analyzed. The most significant effects of fertilization on budworm were an improvement in the survival of larvae and an increase in the weight of pupae the first year after treatment. Neither response translated, however, into a detectable effect on change in budworm numbers. Treatments had no measurable effect on the abundance of other insect defoliators or on arboreal spiders. Fertilization also did not significantly affect the impact of defoliation on shoot and foliage weight, radial increment, budworm-caused tree mortality, or tree recovery for the first 2 years after the outbreak. Although fertilizing had little influence on insects and trees, highly significant differences in measured variables commonly were associated with years and host-tree species. Tree mortality and topkill also were strongly affected by crowding and overtopping in the stands. Radial increment in dominant grand fir and Douglas-fir on study plots ultimately was reduced 80 percent by budworm defoliation. The absence of statistically significant responses of trees to fertilizing was attributed to variable soil and site conditions, which made detection of growth differences difficult, and to the extaordinarily high densities of budworm that severely impacted all phases of tree growth during the study.

Contents

Introduction

Fertilization is receiving increased emphasis as a way to enhance the health and vigor of western forests (Chappell and others 1992). Much information already is available on the response of trees and stands to fertilization and on the importance of forest nutrition in maintaining long-term productivity (Miller and others 1992). Less is known, however, about the response of important insects and diseases to increased nutrient levels or the practicality of using fertilizers to alleviate some pest problems (Mika and others 1992). What is known on the subject often is hypothetical and, when put into practice, has produced inconsistent or contradictory results (Lesniak 1986, Muzika 1993, Stark 1965, Waring and Schlesinger 1985, White 1993). The influence of fertilization on forest insects or diseases is a complex process strongly dependent on behavior of the pest species, as well as on tree and stand conditions and the balance of key nutrients (Mika and others 1992). When measured against this array of variables, it is not surprising that fertilization in pest management is fraught with uncertainties.

Recent results of a controlled study at King Mountain in the Malheur National Forest (Oregon) indicate that fertilization may have practical use in the management of some outbreaks of western spruce budworm (*Choristoneura occidentalis* Freeman) (Mason and others 1992, Waring and others 1992, Wickman and others 1992). In this replicated experiment, grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) stands infested with western spruce budworm were fertilized with urea at 350 kilograms of nitrogen (N) per hectare. Although budworm densities and population trends were unaffected by the treatment, overall vigor and tolerance of the stands to defoliation were improved. The findings suggested that fertilization might have a future in budworm management by delaying adverse impact on trees until outbreaks collapse naturally. At the same time, fertilization might have other beneficial side effects, such as improving site productivity and increasing forage production for large game and domestic livestock.

The results from King Mountain were encouraging, but they had limited generality by being from relatively small plots in a single area. Questions still remained about possible effects on other insect herbivores and the general response of trees and stands if fertilizer were applied operationally on a broader scale. Foremost was the concern that additional nutrients in the environment might improve overall budworm vigor and possibly intensify or prolong outbreaks. The pilot experiment described here was the next logical step needed to test the procedure and address some of these concerns. Its primary objectives were to determine how large-scale fertilization might affect the course of an ongoing outbreak and the overall tolerance of host trees to defoliation.

Methods

Description of Study Area

The experiment, henceforth identified as the "Mount Emily" study, was conducted in the Blue Mountains of northeastern Oregon. Specific plot sites were in the Mount Emily area of the Umatilla and Wallowa-Whitman National Forests (fig. 1). Forests were a mixed-conifer type of grand fir, Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), and western larch (*Larix occidentalis* Nutt.) (see color plate A in center of this paper). The primary hosts of western budworm, grand fir and Douglas-fir, were dominant in all areas selected for intensive study. Elevation of the study area ranged from 1280 to 1425 meters, and annual precipitation was 640 to 760 millimeters, mostly in the form of snow during winter.

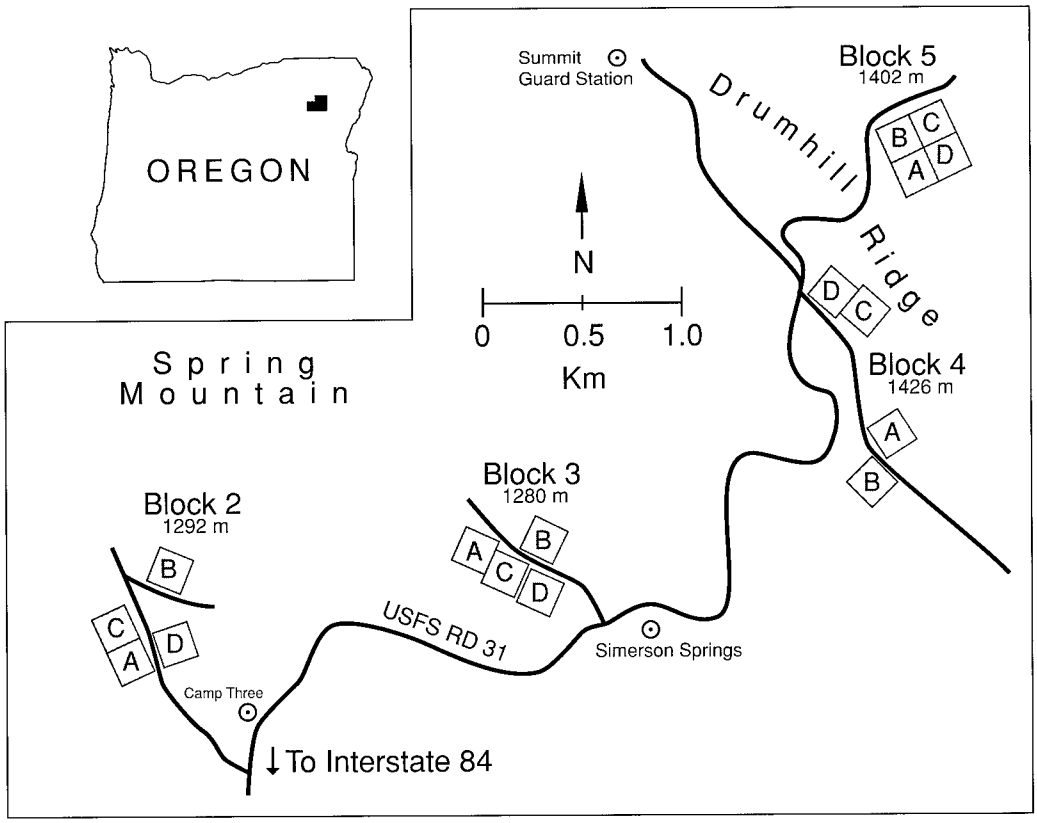


Figure 1—Geographic location of blocks and included plots in fertilization experiment. Plot treatments were A—N-fertilization, B—low NPKS-fertilization, C—high NPKS-fertilization, and D—control. Block 1 (not shown) was excluded from final analysis.

At the time of fertilization (1988) and the subsequent period of intensive measurements (1989-91), outbreak populations of western spruce budworm were present in all the study areas as well as in much of the northern Blue Mountains (fig. 2, color plates B and C). Forest conditions in which the study was conducted reflected the same diversity of sites and stands that are typical of budworm infestations. In 1992, the entire study area was included in a suppression project in which about 36 000 contiguous hectares in the Umatilla and Wallowa-Whitman National Forests were treated with the microbial insecticide *Bacillus thuringiensis* Berliner (*Bt*), which caused a sharp decline in budworm numbers (Hadfield 1992, Sheehan 1996). Ironically, most of the outbreak populations of budworm elsewhere in the Northwest also collapsed at the same time from natural causes (USDA 1995).

Experimental Design and Treatments

The study was planned and conducted originally as a randomized block experiment with five replicated 16-hectare blocks and four treatments. Treatments were randomly assigned to four 4-hectare plots in each block. Because of unexpected difficulties encountered in sampling trees in the first block (block 1), the experiment was adjusted and ultimately completed with data collected from only four replications, blocks 2, 3, 4, and 5 (fig. 1).

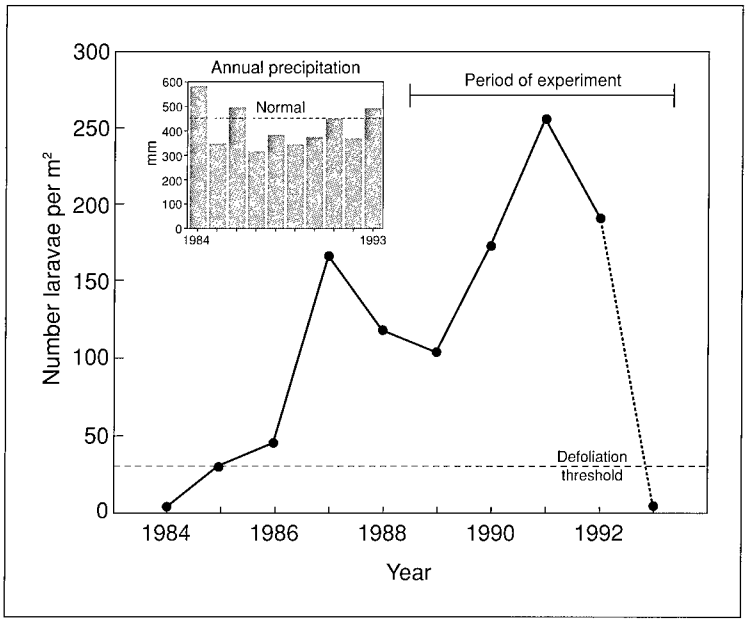


Figure 2—Overall trend of outbreak population of western spruce budworm in general area of fertilization experiment (from Mason and Paul 1996) with annual precipitation (inset) at La Grande, Oregon.

The treatments replicated in each block were:

A. N—nitrogen applied at a rate of 350 kilograms per hectare of elemental N as urea.

B. Low NPKS—nitrogen, phosphorus, potassium, and sulfur applied at rates of 100, 25, 25, and 25 kilograms per hectare, respectively.

C. High NPKS—nitrogen, phosphorus, potassium, and sulfur applied at rates of 300, 75, 75, and 75 kilograms per hectare, respectively.

D. Control—no fertilizer applied.

Treatment A (N-fertilizer) was the same application rate and formulation used previously in the 1984 King Mountain experiment in the Malheur National Forest (Mason and others 1992). The combination NPKS-fertilizers in treatments B and C were included to test the possibility that large amounts of N added alone might create a deficiency in one of the other nutrients. Perceived extant low levels of available soil sulfur, especially, were expected to be depressed even further by the addition of nitrogen.[1] The two combinations were identical except that treatment C was applied at three times the rate of treatment B. Fertilizer treatments were applied to the respective plots by helicopter on October 12 and 13, 1988 (color plates D, E, and F). The period of application was followed by cool and damp weather that minimized losses by volatilization.

[1] Tiedemann, A.R.; Mason, R.R.; Wickman, B.E. Forest floor and soil nutrients 5 years after urea fertilization in a grand fir forest. Manuscript in review.

Collection of Data

Sample trees—Effects of treatments on the density of selected arthropods and the condition of foliage were determined from a permanent sample of host trees (primary sample unit) in the interior of each 4-hectare plot. Where possible, a maximum of 10 trees each of grand fir and Douglas-fir was sampled. Most plots were dominated by grand fir, however, and 10 Douglas-firs suitable for sampling were not always available. As a result, more grand fir frequently were sampled than Douglas-fir. Sample trees ranged from 6 to 20 meters tall.

Foliage samples and arthropod densities—The secondary sample unit was two 45-centimeter branch tips clipped from the midcrown of each sample tree by using a pole pruner with attached basket (color plate G). Two samplings of tree foliage were made each year in 1989, 1990, and 1991: (1) an early sample in late June to early July for estimating arthropod density and biomass, and (2) a late sample in mid-August to estimate the density of new budworm pupal cases and evaluate shoot growth and new buds.

In the early sample, budworm larvae and other arthropods were collected in the field by beating the clipped branch tips inside a plastic drum from which all individuals were collected and preserved in alchohol vials (color plate H). In the laboratory, the preserved specimens were sorted by taxa and counted, and budworm larvae were oven-dried to a constant weight. Densities of selected arthropods and dry weights of budworm were summarized by tree species for each plot in terms of the square meters of branch area sampled by using standard procedures (Torgersen and others 1993). Developmental rate of budworm larvae was estimated for each plot by the instar composition of 100 randomly selected larvae from the preserved specimens for each tree species.

In the late sample, the number of pupal cases of emerged moths and newly formed buds on each clipped branch tip were counted and densities estimated by tree species for each plot. The 10 outermost shoots of current growth on each branch tip also were removed, oven-dried, and weighed; the results were summarized as mean dry-weight per shoot by tree species per plot. Late samples for new buds and shoot growth also were taken in 1992 and 1993 to estimate foliage recovery after collapse of the budworm population.

Pupal samples and larval subsamples—Other effects of treatments on budworm population dynamics were determined by additional collections of larvae and pupae each year. During the early sampling, 5 budworm larvae were collected from the midcrown of each of 10 randomly selected host trees in each plot and placed in rearing chambers in the laboratory. After pupation in mid-July, 100 pupae also were collected in each plot by randomly beating foliage in the lower crown. Sex of each pupa was determined, and they were weighed and reared individually. Emerging parasitoids from each budworm life stage were then recorded and identified to determine degree of parasitization in each plot.

Radial growth, tree mortality, and topkill—Radial growth of grand fir, Douglas-fir, and ponderosa pine was determined from increment cores before and after treatment. Two cores were taken at breast height from each of 15 to 20 dominant or codominant trees of each species in a plot. Cores were prepared and measured for actual increment and then rescaled to tree-ring indices by using recommended dendrochronological techniques (Swetnam and others 1985). Overall effect of defoliaton on radial growth was determined by growth series of tree-ring indices for grand fir and Douglas-fir, and corrected for weather by subtracting growth series of dominant or codominant nonhost ponderosa pine (Swetnam and others 1985). Because ponderosa pine also was expected to respond to fertilizing, "corrected" tree-ring indices cancelled the possible effects of fertilization in

growth rings of host species and could not be used for detecting treatment differences. Treatment effects on radial growth, therefore, were analyzed by using actual mean increment summarized each year by tree species and plot.

In fall 1993, two years after the last budworm defoliation, budworm-caused mortality and topkill of grand fir and Douglas-fir were estimated by an inventory of each plot. Condition of all trees >15 centimeters in diameter at breast height (dbh) was recorded by crown class (i.e., dominant, codominant, intermediate, and suppressed) in sixteen 0.016-hectare subplots in each 4-hectare plot (6.4 percent cruise). Topkill was designated when a portion of the upper live crown was dead, and mortality was tallied when the entire crown was dead.

Analysis of Data

Respective treatments were evaluated by their effect on 25 variables in each plot:

Variable	Unit of measurement
1 — Density of nominal 4th instars of western spruce budworm	Number per square meter of branch area
2 — Density of 1st and 2d instars of Douglas-fir tussock moth (*Orgyia pseudotsugata* (McD.))	Number per square meter of branch area
3 — Density of larvae of other Lepidoptera	Number per square meter of branch area
4 — Density of sawfly (Hymenoptera) larvae	Number per square meter of branch area
5 — Density of aphids (Aphididae)	Number per square meter of branch area
6 — Density of arboreal spiders (Araneae)	Number per square meter of branch area
7 — Density of budworm pupal cases	Number per square meter of branch area
8 — Developmental rate of budworm larvae	Instar number
9 — Survival of budworm larvae from 4th instar to adult	Ratio of pupal case density to 4th instar density
10 — Rate of change of budworm population	Ratio of larval densities between consecutive years
11 — Weight of individual budworm larvae	Dry weight (milligrams)
12 — Weight of budworm larvae per unit of branch area	Dry weight (milligrams)
13 — Weight of individual budworm pupae	Wet weight (milligrams)
14 — Parasitization of budworm larvae	Percentage of larvae
15 — Parasitization of budworm pupae	Percentage of pupae
16 — Density of buds on host trees	Number per square meter of branch area
17 — Weight of new shoots and foliage on host trees	Dry weight per shoot (milligrams)
18 — Topkill of host trees	Percentage of trees
19 — Mortality of host trees	Percentage of trees
20 — Radial growth of grand fir	Annual increment (millimeters)
21 — Radial growth of Douglas-fir	Annual increment (millimeters)
22 — Radial growth of ponderosa pine	Annual increment (millimeters)
23 — Rate of change in radial growth of grand fir	Ratio of annual increment between consecutive years
24 — Rate of change in radial growth of Douglas-fir	Ratio of annual increment between consecutive years
25 — Rate of change in radial growth of ponderosa pine	Ratio of annual increment between consecutive years

Treatment effects on each variable were evaluated by split plot or split-split plot analyses of variance (ANOVA)(Snedecor and Cochran 1967). In the case of variables not sorted by tree species, the ANOVA was split once by years. For variables estimated by tree species (or by sex of pupae), ANOVA was split by both tree species and years. In the case of tree mortality that was estimated just once, ANOVA was split by tree classes only. Design of a split-split plot ANOVA is illustrated below:

Source of variation	df[2]
Blocks	3
Treatments	3
Error (a)	9
Tree species	1
Treatments × tree species	3
Error (b)	12
Year	2
Treatments × years	6
Tree species × years	2
Treatments × tree species × years	6
Error (c)	48
Total	95

All data in which the unit of measurement was a percentage were transformed before analysis by using the standard arcsin transformation for proportions (Snedecor and Cochran 1967).

Results

Density and Dynamics of Budworm Population

Densities of budworm larvae remained very high over the 3 years when they were estimated (fig. 3). Sampling was well timed for larval development (nominal 4th instars) in 1989 and 1991 (mean instars 4.09 and 4.46, respectively) but was slightly late in 1990 (mean instar 5.48). Development was significantly different among years but not among fertilizer treatments or on either grand fir or Douglas-fir. There was a significant interaction, however, between years and tree species (table 1). Treatments had no significant effect on larval density on either tree species; however, densities were strongly affected by years and a tree species-year interaction ($P < 0.01$ and $P < 0.01$, table 1). The differences were due mostly to sharp increases in the number of budworm larvae on Douglas-fir in 1991. Density of pupal cases and survival of 4th instars to adults also were higher on Douglas-fir than on grand fir ($P < 0.01$ and $P < 0.01$, table 1; fig. 3). Even though fertilization did not affect overall density, it was significantly related to an improvement in budworm survival for the first 2 years after treatment ($P = 0.05$, table 1; fig. 4). In 1989, especially, average survival to adults was lowest in the control plots and highest in the low NPKS treatment for both grand fir and Douglas-fir (fig. 4).

[2] Degrees of freedom.

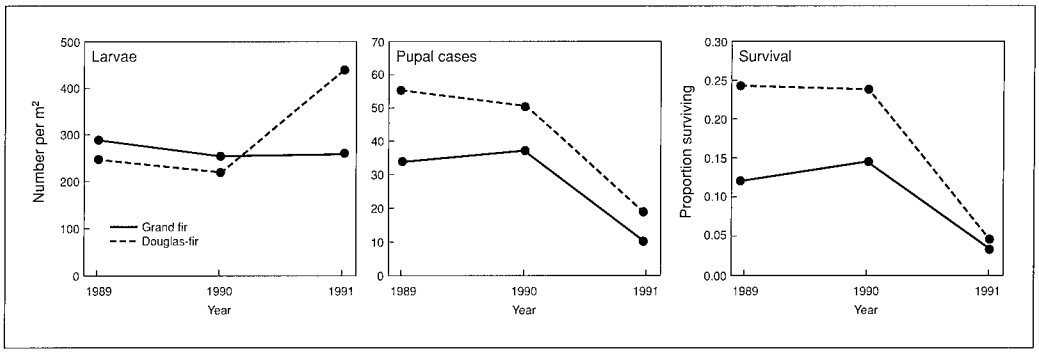


Figure 3—Mean densities of western spruce budworm larvae, pupal cases, and survival of 4th instars to pupae, by host-tree species and combined for all experimental plots, 1989-91.

Table 1—Probabilities from ANOVA tests for effects on dynamics of western spruce budworm population[a]

Sources of variation	Density of larvae	Instar development	Density of pupae	Survival to adult	Rate of change
Treatments	0.59	0.69	0.61	**0.05**	0.74
Tree species	0.25	0.29	**<0.01**	**<0.01**	**<0.01**
Treatments × tree species	0.60	0.81	0.25	0.41	0.62
Years	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**0.02**
Treatments × years	0.50	0.82	0.49	**0.05**	0.25
Tree species × years	**<0.01**	**0.03**	0.32	**<0.01**	**0.03**

[a] Probabilities ≤0.05 are in **boldface** type.

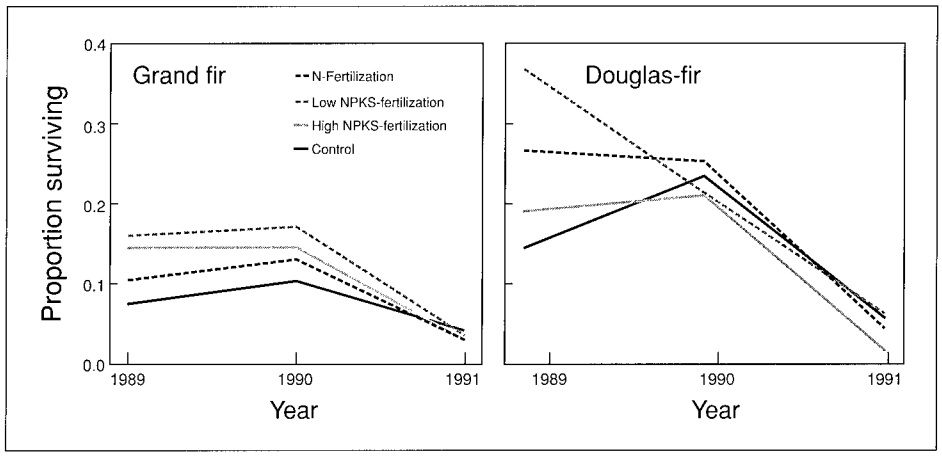


Figure 4—Survival of 4th instar budworm to pupae on grand fir and Douglas-fir, by fertilizer treatment, 1989-91.

Although rates of change in density of budworm larvae were unaffected by treatment, they were different among years ($P = 0.02$, table 1) and consistently higher for populations on Douglas-fir than on grand fir ($P < 0.01$, table 1). Calculations of survival and rate of population change in the same year were not independent, so it was not surprising that they produced similar outcomes in the ANOVA. There also are, however, valid biological reasons for survival rates to be related to intergeneration change, because egg density is determined directly by the number of surviving adults of the previous generation.

Density of Other Insect Herbivores and Spiders

Compared to budworm numbers (fig.3), densities of other insect herbivores on the foliage were relatively low (fig. 5). Fertilizer treatments had no significant effect on any other arthropod. Except for the aphids, the other herbivores were probably too few in number to detect a subtle response to the treatments. Density of each of the taxa was significantly affected, however, by the year of estimate. The number of sawflies, aphids, and spiders also was significantly influenced by the species of host tree (table 2). Sawflies were more common on grand fir and aphids were particularly abundant on Douglas-fir the first year after treatment. Arboreal spiders, which are important predators of budworm larvae, were consistently more abundant on Douglas-fir than grand fir, but differences between the species lessened over the 3 years (fig. 5) (Mason and others 1997a).

Table 2—Probabilities from ANOVA tests for effects on density of miscellaneous foliage arthropods[a]

Sources of variation	Douglas-fir tussock moth	Other lepidoptera	Sawflies	Aphids	Spiders
Treatments	0.44	0.77	0.69	0.96	0.56
Tree species	0.71	0.47	**<0.01**	**<0.01**	**<0.01**
Treatments × tree species	0.65	0.35	0.36	0.91	**0.02**
Years	**0.01**	**0.05**	**<0.01**	**<0.01**	**<0.01**
Treatments × years	0.24	0.20	0.52	0.97	0.68
Tree species × years	**0.03**	0.15	**<0.01**	**<0.01**	**0.01**

[a] Probabilities ≤0.05 are in **boldface** type.

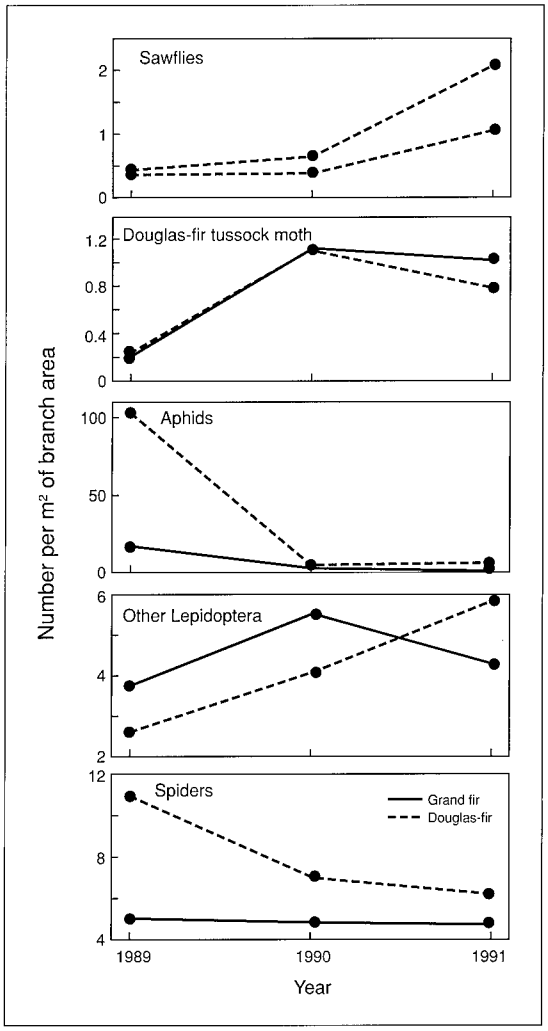


Figure 5—Mean densities of other insect herbivores and spiders, by host-tree species and combined for all experimental plots, 1989-91.

Biomass of Budworm Larvae and Pupae

Fertilization had no detectable effect on the dry weight of individual budworm larvae or on the total dry weight of larvae per unit of branch area (table 3). Individual larval weight was significantly affected, however, by tree species and years ($P = 0.01$ and <0.01, respectively; table 3). Weights would be expected to be higher in 1990 because the average age of sampled larvae was at least one instar older than in other years. In 1989, budworm larvae sampled on grand fir were heavier than larvae on Douglas-fir (fig. 6). Total larval weight also was significantly affected by years and the interactions of years with treatments and tree species (table 3). Total weight, however, was a product of both individual weight and larval number, so that these results must be interpreted only after considering larval density in combination with individual weight.

Table 3—Probabilities from ANOVA tests for effects on biomass of western spruce budworm larvae and pupae[a]

Sources of variation	Dry weight of single larvae	Dry weight of total larvae/m2	Wet weight of pupae
Treatments	0.65	0.33	**0.03**
Tree species	**0.01**	0.08	—
Treatments × tree species	0.23	0.56	—
Years	**<0.01**	**<0.01**	**<0.01**
Treatments × years	0.28	**0.03**	**0.02**
Tree species × years	0.11	**0.01**	—
Sex of pupae	—	—	**<0.01**
Treatment × sex of pupae	—	—	**0.01**
Sex of pupae × years	—	—	**<0.01**

[a] Probabilities ≤0.05 are in **boldface** type.

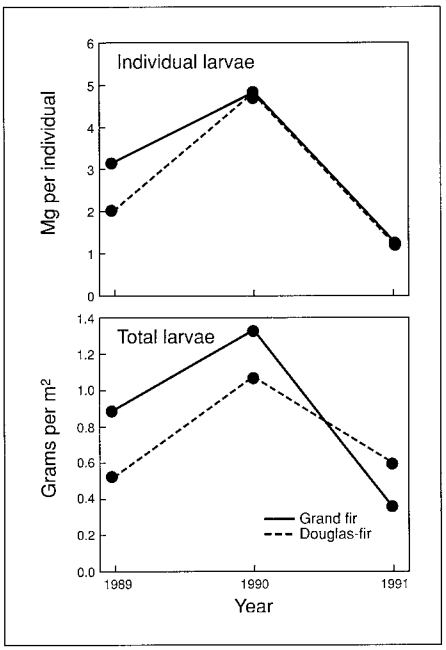


Figure 6—Mean dry weight of individual and total budworm larvae combined for all experimental plots, by host-tree species, 1989-91.

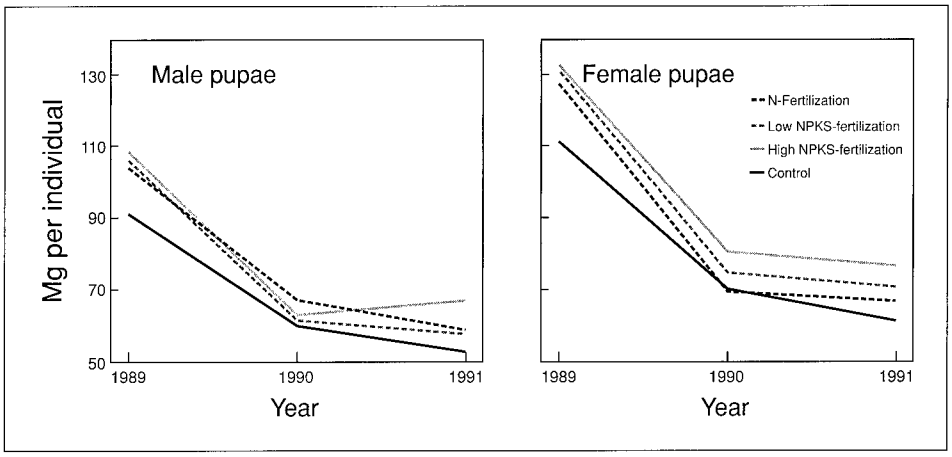
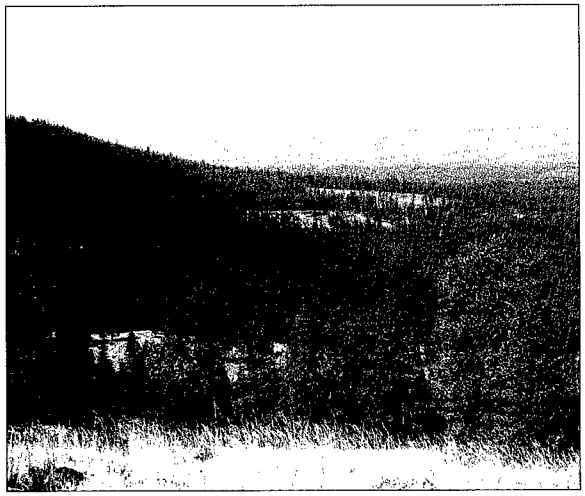


Figure 7—Fresh weight of male and female budworm pupae by fertilizer treatment, 1989-91.

Pupal weights may be the best measure of treatment effects on budworm, because they represent the same stage of development and are less variable than samples of other life stages. Fecundity also is directly related to the weight of female pupae, such that any weight increase due to fertilizer treatment implies a similar increase in egg production. Weight of pupae was significantly affected by all measured variables: treatments, years and sex ($P = 0.03$, $P < 0.01$, and $P < 0.01$, respectively; table 3). Interactions among all these variables also were significant (table 3). Trends of male and female pupal weights were almost identical over the 3 years, but the average weight of females was 19.9 percent heavier than males (fig. 7). Mean pupal weights of both sexes were 17.1, 11.4, and 16.9 percent heavier in fertilized plots than in untreated control plots in 1989, 1990, and 1991, respectively. Pupae on average also were 8.5 percent heavier in the high NPKS-fertilized plots than in other fertilizer treatments (fig. 7).

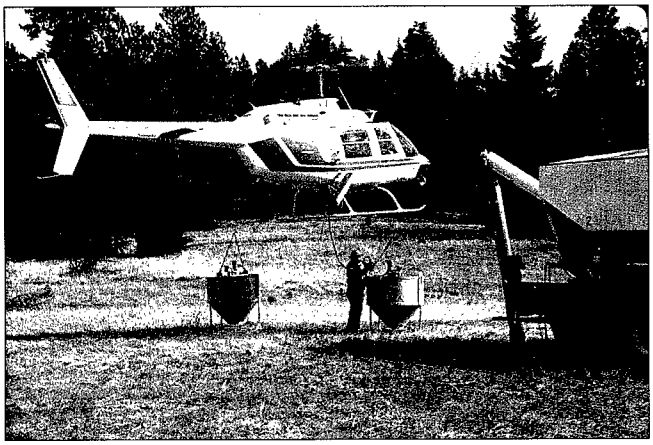
Parasitization of Larvae and Pupae

Mean larval parasitization increased from 6.1 percent in 1989 to 25.1 percent in 1990, and then declined to 13.7 percent in 1991; differences were highly significant among years ($P < 0.01$, table 4). The general trend of larval parasitization was similar in all fertilizer treatments (fig. 8). Compared to year-to-year variation, the differences among treatments were small but, nonetheless, were significant for no readily apparent reason ($P = 0.03$, table 4). The trend of parasitoids emerging from pupae was the reverse of that observed for larvae. Mean parasitization by this group fell from 11.6 percent in 1989 to only 2.1 percent in 1990, then increased again to 12.8 percent in 1991 (fig. 9). Pupal parasitization was not significantly different among fertilizer treatments but was significantly influenced by years and a treatment-year interaction ($P < 0.01$ and $P = 0.01$, respectively; table 4). For all three years, significantly more female pupae produced parasitoids than male pupae ($P = 0.01$, table 4; fig. 8). Overall, female pupae were parasitized nearly twice as often as male hosts (11.0 vs. 6.7 percent). Among all pupae reared, the ratio of females to males for the three years was 47:53. The ratio favored females in 1989 but was not significantly different in 1990 and 1991.

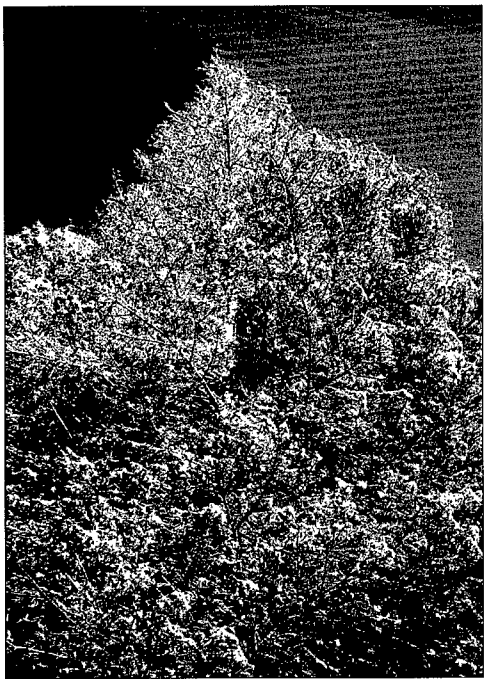


Color plate A—Overview of forests in experimental area near block 3.

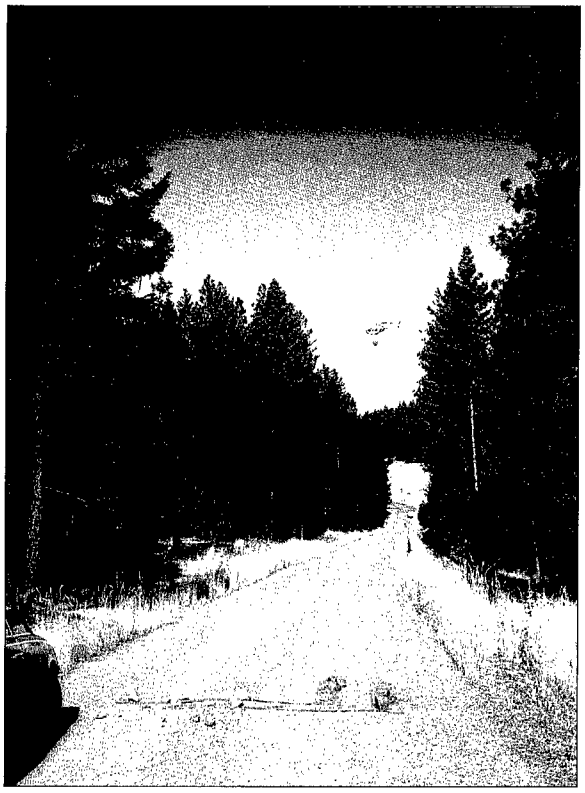
Color plate B—Larva of western spruce budworm feeding on new foliage of grand fir.



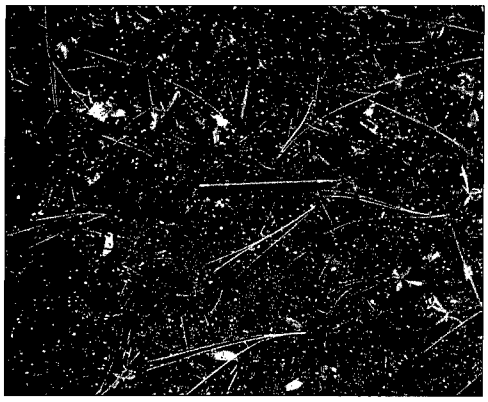
Color plate D—Helicopter preparing to lift loaded bucket used for applying fertilizer to experimental plots.



Color plate C—Tips of branches damaged by budworm feeding in crown of Douglas-fir.

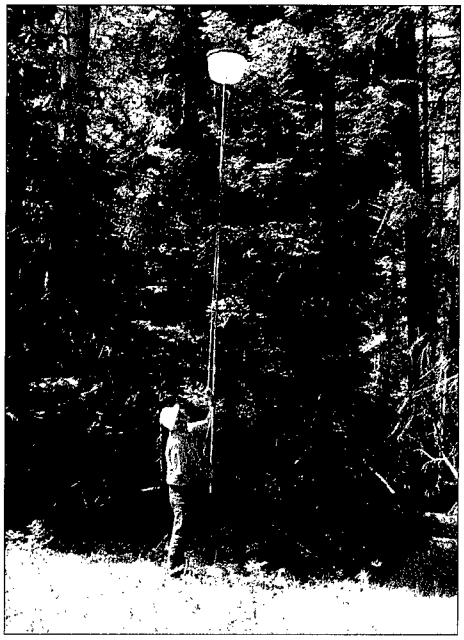


Color plate E—Helicopter applying fertilizer to plot in block 2.



Color plate F—Distribution of fertilizer on forest floor after application.

Color plate H—Processing foliage samples in the plot by beating clipped brances inside drum to remove arthropods from clipped branches.



Color plate G—Clipping a foliage sample from the crown of a sample tree by using a pole pruner with collection basket.

Table 4—Probabilities from ANOVA test for effects on parasitization of larvae and pupae[a]

Sources of variation	Parasitization	
	Larvae	Pupae
Treatments	**0.03**	0.27
Sex of pupae	--	**0.01**
Treatments × sex of pupae	--	0.86
Years	**<0.01**	**<0.01**
Treatments × years	0.64	**0.01**

[a] Probabilities ≤0.05 are in **boldface** type.

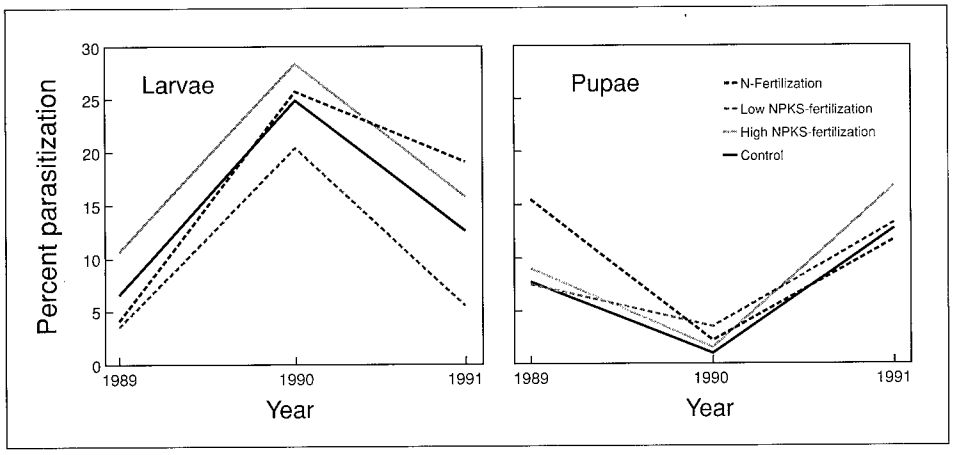


Figure 8—Parasitization rate of budworm larvae and pupae by fertilizer treatment, 1989-91.

Two species accounted for 90 percent of the larval parasitoids reared from hosts collected as nominal 4th instars: the braconid, *Apanteles fumiferanae* Vier. (47 percent), and the ichneumonid, *Glypta fumiferanae* (Vier.) (43 percent). Hosts producing these species would have been attacked as 1st instars in late summer of the preceding year. Among remaining species, the late-larval parasitic tachinid, *Winthemia fumiferanae* (T11.), and the ichneumonid, *Mesochorus tachypus* Vier., accounted for about 5 percent, and another 10 miscellaneous species represented the balance of larval parasitoids.

Pupae were affected by a guild of dipteran and ichneumonid parasitoids ovipositing in or on late-instar larvae and emerging from the pupal stage. The guild was dominated by the tachinid, *W. fumiferanae* (83 percent), and the ichneumonid, *Phaeogenes maculicornis hariolus* (Cress.) (10 percent).

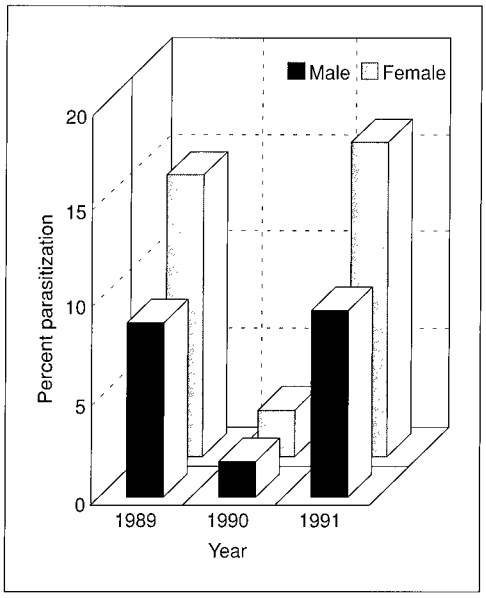


Figure 9—Mean parasitization rate of male and female budworm pupae combined for all experimental plots, 1989-91.

Shoot and Foliage Biomass and Number of Buds

From 1989 to 1991, current impact of budworm defoliation was measured at the end of the growing season by the dry weight of new shoots and the remaining foliage. Physiological response of trees was evaluated further by the density of newly set buds. Current as well as cumulative effects of defoliation were reflected by these indicators. After suppression of the budworm population in 1992, the same indicators also were estimated for 2 additional years to monitor recovery.

During the prespray period when budworm feeding was intense, both shoot and foliage weight and bud density declined significantly on grand fir and Douglas-fir ($P < 0.01$, table 5). After collapse of the budworm population in 1991, however, both indicators responded with a sharp turnaround over the next 2 years (fig. 10). Fertilization had no measurable effect on the weight of new shoots and foliage or on the number of buds in either the prespray or postspray periods (table 5). Shoots and foliage, however, were significantly heavier on grand fir than on Douglas-fir, during both defoliaton and recovery periods ($P < 0.01$, table 5; fig. 10). Density of buds was higher on Douglas-fir during the years of defoliation ($P < 0.01$, table 5), but bud production appeared to accelerate on grand fir in the second year of recovery (fig. 10).

Table 5—Probabilities from ANOVA tests for effects on weight of new shoots and foliage, and density of new buds before and after suppression of budworm population[a]

Sources of variation	Weight of new shoots and foliage		Density of new buds	
	Prespray	Postspray	Prespray	Postspray
Treatments	0.29	0.49	0.72	0.50
Tree species	**<0.01**	**<0.01**	**<0.01**	**0.01**
Treatments × tree species	0.67	0.37	0.33	0.09
Years	**<0.01**	**<0.01**	**<0.01**	**<0.01**
Treatments × years	**0.01**	0.26	0.90	0.80
Tree species × years	**0.04**	**0.02**	**<0.01**	**<0.01**

[a] Probabilities ≤0.05 are in **boldface** type.

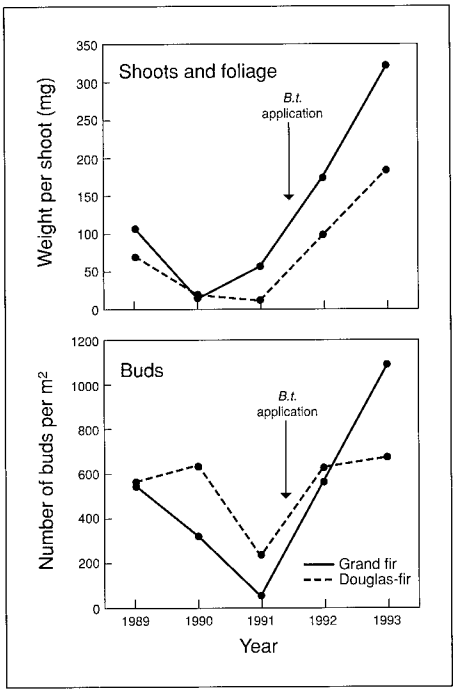


Figure 10—Mean dry weight of shoots and foliage, and number of buds by tree species combined for all experimental plots, 1989-93.

Radial Increment of Trees

Actual increment was not significantly affected by fertilization for any of the tree species in the first 4 years after treatment (table 6). Year-to-year rate of change in increment, which may be a more sensitive measure than actual growth, was significantly affected, however, in Douglas-fir (P = 0.03, table 6). These differences seemed to be due to small but consistently higher rates of change in the growth of Douglas-fir in the low NPKS-fertilized plots during the last 3 years (fig. 11).

Increment and its rate of change was highly significant among years for all species (P <0.01, table 6). In general, 1990 was a favorable growth year for all trees, but it was followed by two below-normal years for grand fir and Douglas-fir (fig. 11). Decreased growth in grand fir and Douglas-fir in 1991 and 1992 most likely reflected a delayed response at the tree base to defoliation of 2 years earlier (fig. 11).

Effects of budworm defoliation on radial increment are best measured by corrected tree-ring indices that portray growth after weather effects have been removed. In any year, a corrected index of 1.0 represents the expected increment, while larger or smaller indices imply radial growth that is better or poorer than expected. Although general trend was down, indices from 1984 to 1988 were all greater than 1.0, thereby indicating normal increment at breast height for both grand fir and Douglas-fir over that period (fig. 12). After 1989, average growth was less than expected and steadily decreased over the next 4 years. Grand fir indices were at first larger than those of Douglas-fir but then became significantly smaller during the period of rapid decline in growth (P = 0.05 and 0.02, respectively; table 7). These differences presumably were in response to higher budworm densities and greater defoliation of grand fir in 1989 and 1990 (figs. 3 and 10). The last year of significant defoliation was in 1991, but increment continued to decline through 1993. Defoliation ultimately depressed annual growth of both tree species by 80 percent (fig. 12).

Table 6—Probabilities from ANOVA tests for effects on radial increment and rate of change of increment for grand fir, Douglas-fir, and ponderosa pine[a]

Source of variation	Actual increment			Rate of increment change		
	Grand fir	Douglas-fir	Ponderosa pine	Grand fir	Douglas-fir	Ponderosa pine
Treatments	0.63	0.74	0.56	0.46	**0.03**	0.46
Years	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
Treatments × years	0.13	0.25	0.96	0.11	0.68	0.10

[a] Probabilities ≤0.05 are in **boldface** type.

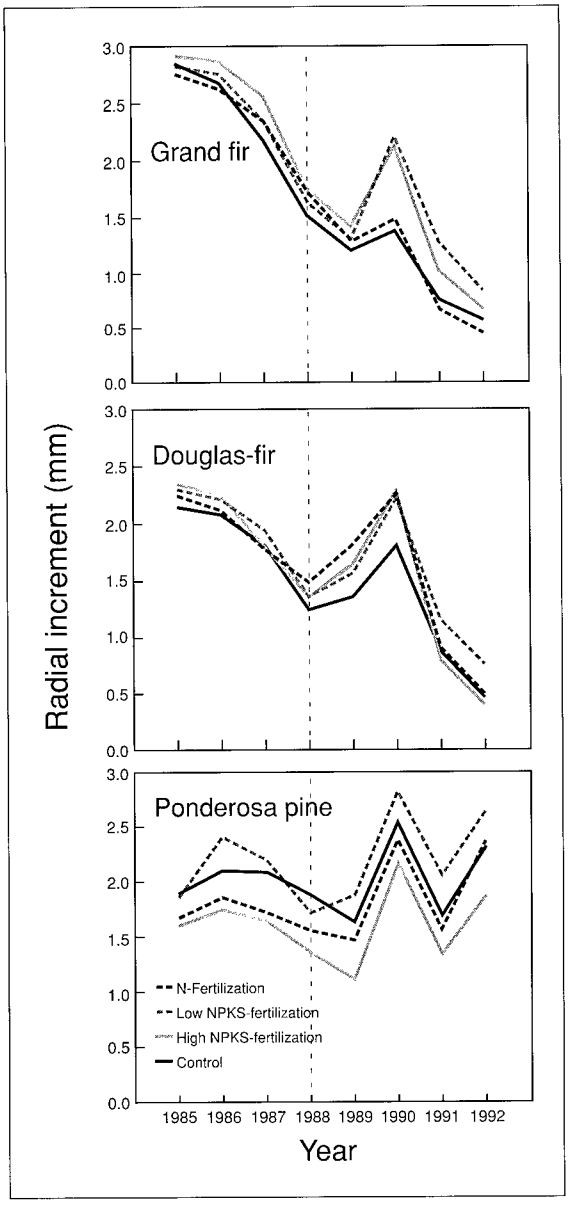


Figure 11—Radial growth of grand fir, Douglas-fir, and ponderosa pine, by fertilizer treatment, 1985-92. Vertical dashed lines mark the year of fertilization.

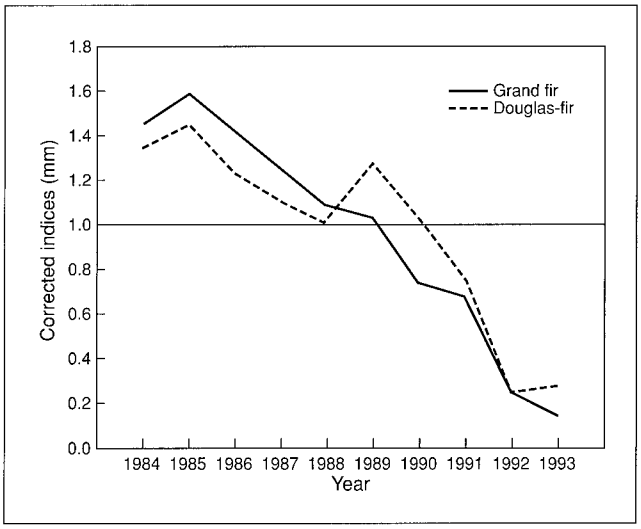


Figure 12—Mean corrected tree-ring indices combined for all experimental plots, by tree species, 1984-93. A corrected index of 1.0 is the expected index after rescaling radial growth of sample trees (Swetnam and others 1985).

Table 7—Probabilities from ANOVA tests for effects on corrected tree-ring indices, tree mortality, and topkill[a]

Sources of variation	Corrected tree-ring indices 1984-88	Corrected tree-ring indices 1989-93	Tree mortality	Tree topkill
Treatments	—	—	0.30	0.19
Tree species	**0.05**	**0.02**	**<0.01**	**0.03**
Years	**<0.01**	**<0.01**	—	—
Tree species × years	**0.01**	**0.03**	—	—
Treatments × tree species	—	—	0.51	0.22
Crown classes	—	—	**<0.01**	**<0.01**
Treatments × crown classes	—	—	0.53	—
Tree species × crown classes	—	—	0.58	0.06

[a] Probabilities ≤0.05 are in **boldface** type.

Tree Mortality and Topkill

By fall 1993, study plots had not been defoliated for two growing seasons and dead trees and tops were easily recognized. In the inventory of budworm-caused mortality and topkill, 791 host trees (568 grand fir and 223 Douglas-fir) were evaluated on subplots for effects of defoliation. Of the total, 170 trees (129 grand fir and 41 Douglas-fir), or 21.5 percent, were killed by defoliation. Another 377 trees (229 grand fir and 148 Douglas-fir), or 47.7 percent, suffered some degree of topkill. Overall, rate of tree mortality was highest in the smallest diameter trees (15-20 centimeters dbh) and declined in the larger diameter classes (fig. 13). Relatively few trees over 50 centimeters dbh were sampled, and none of these was killed.

Treatments had no significant effect on either mortality or topkill of trees sampled ($P = 0.30$ and 0.19, respectively; table 7), thereby indicating that prior fertilization did not influence tree recovery in the first 2 years after defoliation ceased. A significantly larger proportion of grand fir than Douglas-fir, however, was killed or had part of the tops killed ($P < 0.01$ and $P = 0.03$, respectively; table 7). Both mortality and topkill were strongly influenced by a tree's position in the canopy, making the effects of crown class highly significant ($P < 0.01$, table 7). In general, the percentage of trees killed or topkilled in a crown class increased with degree of competition and overtopping represented by the class. Suppressed trees were killed at three to five times the rate of dominants (fig. 14). As would be expected under these conditions, rate of mortality also was directly related to the combined basal area of grand fir and Douglas-fir in the stand (fig. 15).

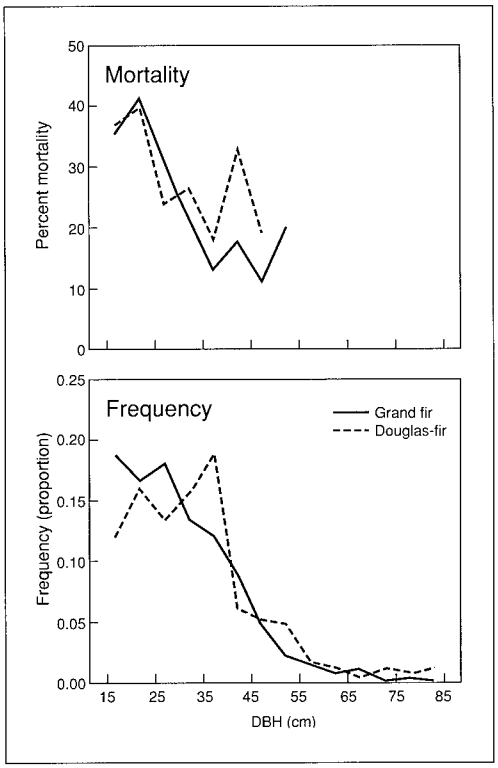


Figure 13—Frequency and mortality of trees encountered in sample cruise by diameter and species, fall 1993.

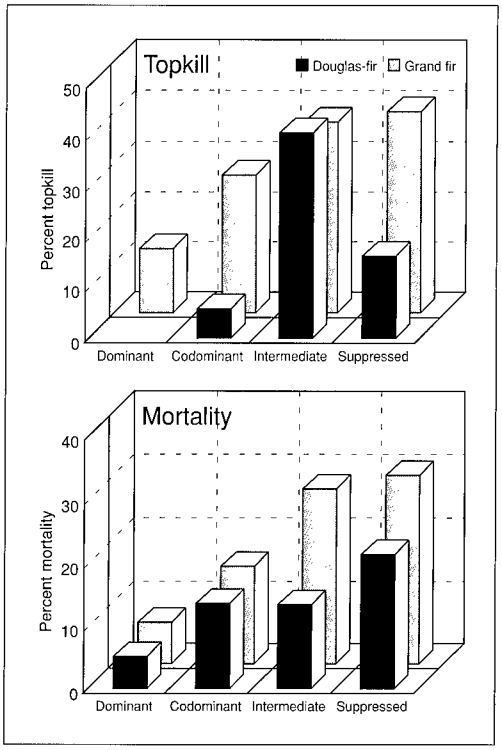


Figure 14—Mean topkill and mortality of grand fir and Douglas-fir by crown class combined for all experimental plots, fall 1993.

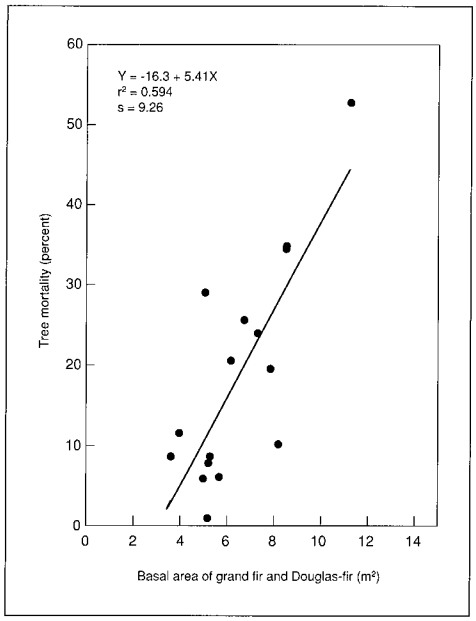


Figure 15—Relation of combined mortality in grand fir and Douglas-fir to basal area of the same species on combined experimental plots, 1993.

Discussion and Conclusions

Many of the promising results of the earlier experiment at King Mountain were not validated in this larger pilot study. At King Mountain, fertilization of stands caused significant weight gains in larvae and pupae and increased total budworm biomass; however, radial growth and the foliage of host trees also increased, thereby offsetting the impact of defoliation. In the Mount Emily study, only larval survival and pupal weight responded significantly to fertilization, while none of the tree variables apparently were affected. These generally negative findings were due in part to high variability of site and stand conditions and to budworm densities three to four times greater at Mount Emily than at King Mountain (Mason and others 1992). Both conditions undoubtedly made detection of treatment differences difficult. Dispersal of larvae and gravid moths among plots also tended to mix populations and obscure treatment effects in both studies. Despite these problems and differences in study conditions, the general lack of effect on most measured variables, particularly tree growth, still was surprising. Because of the significant positive response of pupae to fertilizing at both locations, pupal weight may prove to be the best bioassay of all for detecting nutrient changes in foliage.

Although treatment results were disappointing, other valuable findings emerged from the pilot study that should not be overlooked. Most important were the significantly different effects of grand fir and Douglas-fir on the behavior of budworm populations and the diverse responses of those species to defoliation. Year of measurement also had a significant effect on virtually all variables estimated (tables 1-7). After disregarding treatments and combining plot results by tree species and year, a large database on tree and budworm dynamics in the study area still was available for analysis. Several relations among insect-tree variables emerged from these analyses that might not be obvious from a smaller database. Budworm survival, for example, was significantly higher in 1989 and 1990 than in 1991, which likely led to the higher densities recorded in 1991, particularly on Douglas-fir. High survival in 1989 was partly linked to 1988 fertilization in the only significant treatment effect on budworm dynamics that is recorded (table 1, fig. 4). It might be hypothesized that larvae benefitted from an increased quantity and improved quality of foliage the first year after fertilization. Similarly, relatively low survival in 1991 probably caused the sharp drop in larval density observed in 1992 (figs. 2 and 3). Prior analyses of population time series in the same general area (fig. 2) have suggested that budworm populations at high densities fluctuate in response to fast-acting feedbacks, such as overcrowding and competition for foliage (Mason and Paul 1996). Significantly higher densities of larvae on Douglas-fir in 1991 (fig. 3) probably were responsible for the extremely low shoot and foliage weights and sharp reduction of new buds recorded for that species later the same year (fig. 10). Heavy feeding by budworm increases latent bud formation more on Douglas-fir than on *Abies* species (Carolin 1987), which probably explains the higher bud density on Douglas-fir during the years of severe defoliation.

Larval and pupal parasitoids likewise were affected most by differences among years. As parasitization is strongly density dependent, some of the differences undoubtedly can be explained by a changing number of budworm hosts. Unfortunately, the study was of too short a duration to clearly observe delayed responses of parasitoids to host density. Larval parasitization increased between 1989 and 1990 when budworm densities were very high (figs. 3 and 8); however, the same parasitoid species did not respond numerically in 1991 when budworm density was highest. Conversely, pupal parasitism was low in 1990 but rebounded to a relatively high rate in 1991. A most interesting result of pupal rearings was the significantly higher rate of parasitization of females than of males (fig. 9). A likely explanation is that female budworm larvae, which may have an extra instar (Carolin 1987, Schmidt and Lauer 1977), are vulnerable for a longer time to late-instar parasitization than are males.

The lack of a significant response in radial increment by any of the tree species is difficult to explain without more detailed information on soils in the area, available nutrients, soil moisture conditions, etc. Tree response to fertilization is based on complex interactions among site factors that are highly variable and difficult to predict (Brockley and others 1992). Obviously, because of the significant weight increase observed in budworm pupae on treated plots (table 3, fig. 7), some of the applied fertilizer must have been taken up by trees and become present in leaf tissue where it was ingested by feeding larvae. Forest fertilization studies are notoriously difficult to analyze, and standard experimental methods frequently are inadequate to deal with the

high variation encountered (Woollons and Whyte 1988). Because the primary objective of the experiment was to observe fertilizing effects on defoliation and possible impacts on other arthropods, it is likely that the design was insufficient to detect subtle differences in radial growth.

Overall response of radial increment to defoliation was striking on all plots (fig. 12). Maximum effects also appeared to be delayed at least 2 years because growth continued to decline after defoliation ended in 1992. Such a time lag between defoliation and growth reduction in the lower bole agreed with other recent findings in which the strongest response in grand fir and Douglas-fir to outbreak densities of larvae was delayed 3 years (Mason and others 1997b). The intense defoliation of all host trees on both treated and control plots undoubtedly had a severe impact on physiological processes, which easily could have obscured differences among treatments.

The higher rate of budworm-caused mortality in suppressed trees and smaller diameter classes in the Mount Emily study agreed with findings on tree impact reported from similar budworm outbreaks in the Malheur National Forest (Powell 1994). Overall mortality rates in our study were higher, however, than those determined in the Malheur, possibly because defoliation at Mount Emily was more intense and occurred for a longer time. Grand fir also was killed at a significantly higher rate than Douglas-fir in our study, whereas Douglas-fir was killed at twice the rate of "white fir" (i.e., *A. grandis/A. concolor)*, in the Malheur study (Powell 1994). Unfortunately, comparisons of topkill between the studies were not possible because of different procedures used for estimating dead tops.

In conclusion, our results must not be viewed as completely negative. Although fertilization failed to influence tree growth or the mortality and recovery of trees after defoliation, it also had no significant effect on budworm dynamics or on the other insects sampled. This can be viewed only as positive. Under conditions of lower budworm densities and lighter defoliation, a beneficial response of trees to fertilizing might have been more evident. Based on final results of the experiment, however, it would be difficult to recommend any of the treatments on an operational scale as a prescription for moderating the effects of insect defoliation.

Acknowledgments

The field and laboratory phases of this study were conducted over 5 years and required a large commitment of time and resources by many individuals. In particular, Katie Bobowski, Bobby Fuller, Michelle Hutton, Beth Kempton, Ellen Stennard, Wendy Sutton, and Tina Tibbs, Pacific Northwest Research Station, La Grande, OR, provided invaluable assistance during this time. Arthur R. Tiedemann (emeritus scientist), Pacific Northwest Research Station, Wenatchee, WA, recommended the fertilizer treatments, arranged for their application, and reviewed early and final drafts. David Marx, University of Nebraska, Lincoln, consulted on the original statistical design. Tim A. Max, Pacific Northwest Research Station, Portland, OR, provided statistical help during the summarization phase and did the ANOVA analyses and final statistical review. Additional technical reviews of a final draft were made by Patrick H. Cochran (retired), Pacific Northwest Research Station, Bend, OR, and David C. Powell, Umatilla National Forest, Pendleton, OR. We thank all the above for their many contributions.

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