

THINNING, FOLIAGE CHEMISTRY, AND DEFOLIATION BY BUDWORM IN IMMATURE NORTHERN ROCKY MOUNTAIN DOUGLAS-FIR STANDS: A PRELIMINARY ASSESSMENT

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ABSTRACT

Defoliation by western spruce budworm (*Choristoneura occidentalis* Freeman) in thinned and control immature Douglas-fir stands in western Montana was assessed two years after treatment. All stands were in a dry Douglas-fir/ninebark habitat type on south-facing slopes. Defoliation declined significantly ($P \leq 0.05$) in all stands regardless of treatment. The general decline in defoliation was associated with change in foliage chemistry (nonstructural carbohydrates and terpenes) across all treatments between 1986 and 1988. Defoliation decreased from a mean of 66% in 1986 to about 28% in 1988. During the same period, sucrose increased significantly nearly four-fold from 4 mg/g dry weight to 17 mg/g, while fructose decreased from 26 to 15 mg/g, glucose decreased from 22 to 11 mg/g, and mannose decreased from 4 to 2 mg/g. Among the terpenes, tricyclene increased from 0.60 to 0.75 mg/g, limonene increased from 0.89 to 1.09 mg/g, and terpinolene decreased from 0.13 to 0.04 mg/g. All of these changes were statistically significant. Bornyl acetate did not change significantly: 3.80 mg/g in 1986 and 3.76 in 1988. Discriminant analysis on classes of defoliation change showed that change class was related to change in foliage chemistry. Nearly 68% of the cases in class 3 (where defoliation decreased more than 40%) were correctly classified with a function based on change in chemistry. Because the change in chemistry was similar among control and thinned units, the general change probably was induced by factors outside the scope of our experiment. A cause/effect relationship between foliage chemistry and budworm feeding is postulated. Results presented in this paper are considered preliminary because full exploitation of a growing site by leave trees following thinning takes longer than two years, the time interval considered here, and may take as long as five years. The study will be evaluated again in 1991, five years following thinning.

Keywords: *Choristoneura*, terpenes, carbohydrates, stand density

INTRODUCTION

Western spruce budworm (*Choristoneura occidentalis* Freeman) is a damaging pest of western Northern American forests. Budworm has a wide ecological amplitude and is noteworthy in dry Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Biessn.] Franco) habitat types to moist subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) (Carlson *et al.* 1985b).

Damage attributed to this defoliator can be significant and is especially important when stands receive multiple infestations throughout a rotation (Van Sickle *et al.* 1983; Alfaro *et al.* 1982.). Immature stands are particularly vulnerable because intense feeding causes death of tree tops, significantly reduced height growth, and serious defect.

Amelioration of potential impact of budworm is of immediate concern to land managers in the Northern Rockies. Forest Service lands of the Northern Region contain at least 430,000 acres of immature Douglas-fir stands (45-75 years old) on lands already harvested once (Chew, pers. comm.). A number of pesticides are effective in reducing current populations of the insect but apparently do not have long-term beneficial effects (Fellin 1983). Thinning has been proposed as a remedy (Carlson *et al.* 1985a), but documented evidence supporting this activity is minimal and has been contradicted by others (Wickman, pers. comm.). The study by Carlson *et al.* (1985a) was a case study, having only one replicate. Nevertheless, the difference in defoliation between the thinned and control stands was significant—only 15% in the thinned but 43% in the control—and the conclusion that thinning adversely affected the insect seems justified in that case. Reasons given for the effect observed were hypothetical. Larval mortality may have been increased in the thinned stand, increase in foliage biomass may have masked otherwise similar numbers of larvae between treatments, the foliage chemistry in the thinned stand may have changed to the detriment of western spruce budworm, or perhaps some combination of all three hypotheses may have been the cause (Carlson *et al.* 1985a).

Change in foliar chemistry was a particularly intriguing hypothesis because foliage of Douglas-fir trees under experimentally induced moisture stress in New Mexico possessed a different chemistry, quantitative and qualitative, than nonstressed trees (Cates *et al.* 1983). Competition by trees for moisture and nutrients in overstocked Douglas-fir stands is high compared to more open, thinned stands and may result in weakened defensive chemistry. The study reported here was designed to test relations among stand density, defoliation by western spruce budworm, and foliar chemistry of immature Douglas-fir in the Northern Rocky Mountains. The data represent conditions only two years after thinning and must be considered preliminary.

METHODS

Study Area

The study area is about 12 air miles east of Missoula, Montana, on the south-facing slopes of the Greenough Creek drainage. Greenough Creek is a small tributary of the Clark Fork River, flowing generally from west to east, entering the river from the southwest. The predominant habitat type is Douglas-fir/ninebark (*Physocarpus malvaceus* [Greene]

Kuntze), and the slopes are steep, consistently between 40 and 50%. Much of the dominant ponderosa pine (*Pinus ponderosa* Dougl.) and Douglas-fir were harvested from the south-facing slopes during the 1960s. More than 99% of the understory remaining is Douglas-fir, most of which originated following the intense wildfire of 1910. Fire has been absent in this area since then, and previous understory has grown substantially and now dominates the site. Most of the Douglas-fir stands are overstocked, typical of more than 400,000 acres supporting similar stands in the Northern Rockies. In 1986, when the study was installed, budworm was moderate to heavy in Greenough Creek. Visible defoliation on Douglas-fir exceeded 50% over most of the area, and some top-kill was evident, mostly on the intermediate to suppressed trees.

Experimental Design

Study Layout

The study was installed during late summer 1985. The experimental design was a randomized block ANOVA (Analysis of Variance). Three blocks were selected to be uniform in important site characteristics. Habitat type was Douglas-fir/ninebark, slopes varied from 40-50%, aspect was generally south, and Douglas-fir thickets were common. Preliminary estimates at time of study installation indicated that budworm defoliation was about equal among block and treatments. Treatment units were identified, and thinning and control treatments were assigned at random, one of each to each block. Thinning was completed in October 1986. We conducted a crop tree thinning with final spacing of about 20 feet by 20 feet. Crop trees left were free to grow, with little or no crown competition. Ten circular plots each 1/25 acre in size were installed uniformly throughout each treatment unit. Plot centers were permanently marked with steel reinforcing rod. Two dominant/codominant Douglas-fir within or adjacent to each plot were selected for repeated sampling, and an identifying metal tag was affixed to each sample tree. Four branches in upper-mid crown, on the cardinal directions, were selected and tagged on each sample tree. Selected branches were dominant at their location and were the basis for all subsequent determinations of chemistry and defoliation. In each year then, 480 branches were sampled (3 blocks \times 2 treatments \times 10 plots \times 2 trees \times 4 branches).

Variables Measured

Data were taken prior to thinning in 1986 and two years after treatment treatment, in 1988. At the plot level, basal area and number of trees by species for all trees over 1 foot high were recorded on each 1/25-acre plot. Diameter at breast height (DBH), total height, and height to sample branches were recorded for each plot tree.

Foliage samples for chemical analyses were collected during the first week of July of each year, at the time when most budworm larvae were late 4th instar and active feeders. Four to six newly explained shoots were clipped from each sample branch, placed in a labeled plastic vial, and immersed immediately in liquid nitrogen or placed on dry ice to prevent decomposition of present chemistry. In 1986, due to resource constraints, samples were composited by tree, but in 1988 we kept samples separate by branch.

Chemical analyses were done at the Chemical Ecology Laboratory at Brigham Young University. An aliquot of tissue from each sample was placed in a mortar and pestle containing liquid nitrogen. The sample was ground to a powder, extracted each of three times with ethyl ether, and the extracts were combined. This formed the extract for the analysis of terpenes and other volatiles. To the remaining ground tissue was added 10 ml of 80% methanol and 20% water. The tissue was ground again in the extraction solution, the process was repeated two more times, and all three aliquots were combined. This formed the extract for the analysis of the nonstructural carbohydrates and shikimic acid. All compounds (terpenes, nonstructural carbohydrates, and shikimic acid) were analyzed using a Hewlett Packard capillary gas chromatograph equipped with an autosampler-injector and a 100% methyl polysiloxane capillary column. For the ether and the methanol/water extracts, gamma-terpinene and erythritol were used as internal standards, respectively. Derivation of the carbohydrates and other compounds in the methanol/water extract was accomplished using hexamethyldisilazane and trimethylchlorosilane (Pierce Chemical Company, Rockford, IL).

Injector temperature was 250°C and detector temperature was 260°C. For the carbohydrate analysis initial temperature was 100°C for 1 minute. Ramp programs were 2.5°C per minute to a final temperature of 200°C for 0 minutes, and 15°C per minute to a final temperature of 245°C for 15 minutes. For the volatile analysis initial temperature was 60°C. Ramp programs were 15°C per minute to a final temperature of 220°C for 1 minute, and 5°C per minute to a final temperature of 250°C for 5 minutes. Identification of peaks was accomplished on a Hewlett Packard GCMS accompanied by a 70,000 compound library, and by co-chromatography of standards using different columns. Data are expressed as mg/g dry weight.

Defoliation was estimated following pupation of western spruce budworm, usually after mid-August of each sampling year. Each of 25 new shoots selected equally around the main terminal shoot of each permanent sample branch was inspected and rated for defoliation, using a six-class system (Carlson *et al.* 1982):

Class Code	Percentage Defoliation
0	0
1	1-25
2	26-50
3	51-75
4	76-99
5	100

Percentage defoliation for the branch was derived by multiplying the frequency of each code by the mid-point of the percentage class, summing the values for each code, and then dividing by total frequency.

Growth of the terminal leader of each branch was measured each year as an index of release of the thinned stands. Each primary leader was tagged during installation of the study so that leader growth could be indisputably followed each year.

¹The use of trade or firm names in this paper is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Data Analyses

Change between 1986 and 1988 of variables measured was estimated using t tests for paired samples. For Discriminant Analyses, magnitude of defoliation change between years was coded into three classes (increase, or 0-15% decrease = class 1; 16-40% decrease = class 2; and over 40% = class 3). Differences among classes of defoliation change were tested, using change in plot characteristics and foliage chemistry as independent variables in the discriminant functions. Nested ANOVA was used to test for treatment effect on defoliation and tree chemistry in 1986 and 1988, with Plots, Trees, and Branches as the nesting variables. Significance was assessed at $P < 0.05$.

The generalized ANOVA was:

Source of Variation	Degrees of Freedom
Blocks	2
Treatments	1
Blocks \times Treatments	2
Plots within (Blocks \times Treatments)	54
Trees within Plots	60
Branches within Trees	360
Total	479

Mean squares for Blocks, Treatments, and the interaction Blocks \times Treatments, were tested against the mean square for Plots/Blocks \times Treatments.

RESULTS AND DISCUSSION

Change Between 1986 and 1988

Significant changes occurred in the chemistry and defoliation of sampled trees, regardless of treatment, between 1986 and 1988. Defoliation decreased significantly from about 66% in 1986 to only 28% in 1988 (Table 1). Plot basal area decreased significantly due to the thinning. Shoot length did not change, but foliage chemistry shifted significantly. Of the nonstructural carbohydrates analyzed, mannose, fructose, glucose, and inositol decreased significantly, where as sucrose increased from 3.99 mg/g (dry wt) to 16.71 mg/g (Figure 1). Monoterpenes, including tricyclene, alpha-pinene, camphene, beta-pinene, myrcene, limonene, terpinolene, and an unknown terpene, increased significantly (Figure 2). Bornyl acetate did not change nor did terpene evenness as computed by Simpson's index (Pielou 1975).

The significant shift in chemistry between 1986 and 1988, associated with the three-fold decrease in defoliation, raises the question of cause and effect: did the thinning induce a change in foliage chemistry, resulting in reduced defoliation? Nested ANOVA, done separately for 1986 and 1988, offers no support for that contention. In 1986, just before thinning, plot basal area, shoot length, defoliation, and foliage chemistry were not different between treatments (Table 2). This was desirable, giving credibility to the experimental design and demonstrating similarity among the treatment units prior to treatment. In 1988, two years after thinning, no changes due to treatment were observed. Defoliation, internode growth, and foliage chemistry were not different between treatments (Table 2). This was

Table 1.—Paired t-tests of plot basal area, shoot length, defoliation, and foliage chemistry (mg/g, dry wt) between 1986 and 1988.

Variable	Means		Diff	N ¹	T	Prob
	1986	1988	88-86			
Plot basal area, sq. ft.	4.71	3.68	-1.03	60	-5.79	.0001
Shoot length, in.	1.27	1.25	-0.02	480	-0.54	.5882
Defoliation, percent	66.1	27.8	-38.33	480	-26.93	.0001
Shikimic acid	8.70	6.82	-1.88	115	-4.28	.0001
Mannose	4.03	2.20	-1.33	115	-12.81	.0001
Fructose	25.64	14.76	-10.88	115	-12.54	.0001
Glucose	22.53	10.66	-11.87	115	-16.06	.0001
Inositol	1.04	0.904	-0.134	115	-3.587	.0005
Sucrose	3.92	16.69	12.77	115	17.75	.0001
Tricyclene	0.595	0.750	0.155	115	7.51	.0001
Alpha-pinene	2.56	3.18	0.622	115	7.53	.0001
Camphene	4.00	5.01	1.011	115	7.37	.0001
Beta-pinene	1.33	1.47	0.146	115	3.47	.0007
Myrcene	0.168	0.222	0.054	115	5.79	.0001
Limonene	0.889	1.09	0.203	115	6.60	.0001
Terpinolene	0.128	0.042	-0.086	115	-6.90	.0001
Bornyl acetate	3.80	3.76	-0.04	115	-0.31	.7602
Unknown terpene #6	0.124	0.184	0.060	115	5.52	.0001
Total terpenes	14.22	16.45	2.23	115	4.64	.0001
Total sugars	57.16	45.22	11.94	115	6.84	.0001
Terpene Evenness ²	0.694	0.701	0.007	115	1.89	.060

¹Average values per tree were used for foliage chemistry; five samples were lost, leaving 115 trees for the paired t-tests.

²Computed using Simpson's diversity index (Pielou 1975).

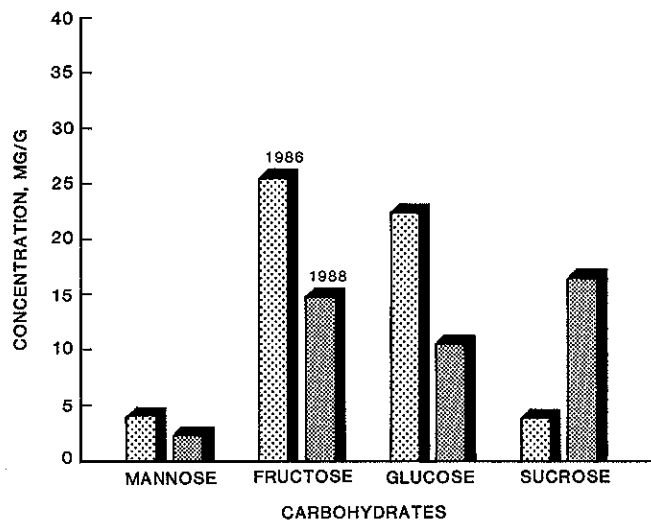


Figure 1.—Change in concentrations of four sugars (mannose, fructose, glucose, and sucrose) between 1986 and 1988 in Douglas-fir foliage at Greenough Creek.

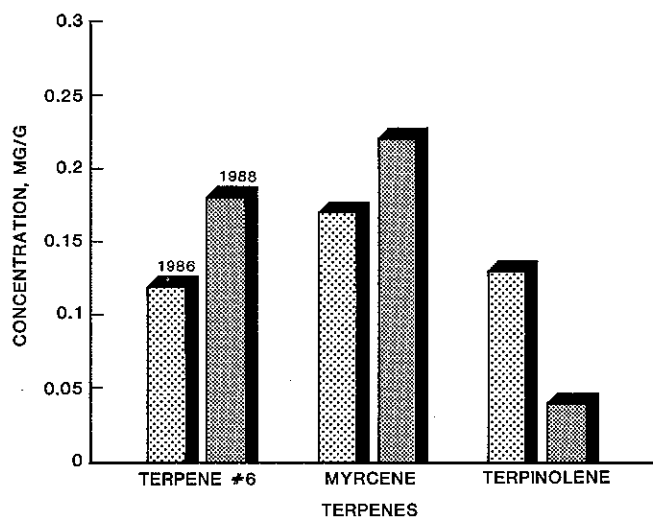


Figure 2.—Change in concentrations of three terpenes between 1986 and 1988 in Douglas-fir foliage at Greenough Creek.

desirable, giving credibility to the experimental design and demonstrating similarity among the treatment units prior to treatment. In 1988, two years after thinning, no changes due to treatment were observed. Defoliation, internode growth, and foliage chemistry were not significantly different between the thinned units and the controls (Table 3), indicating that the thinning was not responsible for the demise of budworm between 1986 and 1988 at Greenough Creek.

The lack of a treatment effect does not rule out the hypothesis that budworm feeding activity declined in response to change in foliage chemistry between 1986 and 1988. In fact, discriminant analysis suggests a strong affiliation between defoliation and foliage chemistry (Table 4). Of 21 trees that had little change in defoliation, 16 (76%) were classified correctly ($P < 0.05$) using a linear discriminant function based on change in foliage chemistry between 1986 and 1988. Of 59 trees experiencing

a large reduction in defoliation, 40 (68%) were classified correctly.

Table 2.—Analysis of variance of tree density, defoliation, and foliage chemistry (mg/g, dry wt) in 1986, prior to thinning.

Variable	Means		F Ratio	Prob
	Thinned	Control		
Plot basal area, sq. ft.	4.97	4.46	1.00	.3277
Shoot length, in.	1.18	1.31	1.43	.2349
Defoliation, percent	62.3	70.0	3.38	.0717
Shikimic acid	8.95	8.39	0.37	.5458
Mannose	4.25	3.79	2.24	.1403
Fructose	26.90	24.26	2.24	.1404
Glucose	23.61	21.28	2.32	.1335
Inositol	1.07	0.995	0.97	.3287
Sucrose	4.70	3.24	1.55	.2183
Tricyclene	0.569	0.617	1.35	.2508
Alpha-pinene	2.48	2.63	0.77	.3854
Camphene	3.81	4.18	1.62	.2083
Beta-pinene	1.27	1.36	0.61	.4386
Myrcene	0.160	0.174	0.46	.4983
Limonene	0.853	0.917	1.06	.3037
Terpinolene	0.133	0.120	0.19	.6620
Bornyl acetate	3.56	4.02	2.05	.1584
Unknown terpene #6	0.135	0.111	1.38	.2452
Terpene Evenness ¹	0.696	0.694	1.57	.2179

¹Computed using Simpson's index (Pielou 1975).

Table 3.—Analysis of variance of tree density, defoliation, and foliage chemistry (mg/g, dry wt) in 1988, two years after thinning.

Variable	Means		F Ratio	Prob
	Thinned	Control		
Plot basal area, sq. ft.	2.90	4.46	15.72	.0002
Shoot length, in.	1.34	1.16	2.97	.0904
Defoliation, percent	25.9	29.7	1.75	.1916
Shikimic acid	6.61	7.09	1.65	.2046
Mannose	2.21	2.21	0.00	.9743
Fructose	14.81	14.90	0.01	.9108
Glucose	10.75	10.61	0.04	.8382
Inositol	0.919	0.892	0.58	.4506
Sucrose	17.14	16.30	1.26	.2659
Tricyclene	0.758	0.742	0.24	.6271
Alpha-pinene	3.21	3.14	0.26	.6099
Camphene	5.05	4.96	0.20	.6564
Beta-pinene	1.47	1.49	0.08	.7784
Myrcene	0.222	0.221	0.03	.8618
Limonene	1.09	1.09	0.05	.8328
Terpinolene	0.044	0.039	0.29	.5949
Bornyl acetate	3.82	3.68	0.57	.4531
Unknown terpene #6	0.192	0.177	1.07	.3060
Terpene Evenness ¹	0.701	0.701	0.00	.9443

¹Computed using Simpson's index (Pielou 1975).

These preliminary analyses suggest a cause/effect relationship between foliage chemistry and budworm success (as measured by defoliation). The chance that changes in defoliation and chemistry were independent events seems unlikely. But the question is, what was the cause? Did budworm numbers decline due to factors other than foliage chemistry, with foliage chemistry changing perhaps because of decreased budworm pressure? Or did the chemistry change because of budworm feeding, a type of induced response by Douglas-fir? The latter

Table 4.—Classification summary for discriminant functions on defoliation at Greenough Creek.

Actual defoliation class	Predicted defoliation class ¹			Total
	1	2	3	
1	16 76.2	1 4.8	4 19.1	21 100
2	9 25.7	18 51.4	8 22.9	35 100
3	10 16.9	9 15.3	40 67.8	59 100

¹Class 1 = defoliation reduced less than or equal to 15%;

Class 2 = defoliation reduced from 15 to 40%;

Class 3 = reduction greater than 40%.

hypothesis is supported somewhat by data from this study. The increase in the disaccharide sucrose likely is linked to the decrease in the monosaccharides fructose and glucose (Devlin 1975). Heavy defoliation, as we measured in 1986, may interrupt sucrose production as the monosaccharides are mobilized extensively for growth and synthesis of defensive compounds. Terpenoid synthesis follows more complicated secondary metabolic pathways but ultimately is dependent on primary accumulation of sugars, or conversion of stored carbohydrates (Geissman and Crout 1969). Nonstructural carbohydrates were significantly lower in 1988 than in 1986, while total terpenes increased significantly during the same period (Table 1). This suggests that Douglas-fir at Greenough Creek may have responded to budworm defoliation by synthesizing increased quantities of terpenoids as a defensive mechanism, perhaps at the expense of other physiologic functions.

Other work supports our hypothesis of mobilized defenses. In New Mexico, terpenes changed significantly among five sampling dates between bud break in early June until July 8 (Cates and Redak 1988). Trees sampled at the same Julian date but in different years also varied significantly in qualitative and quantitative terpene chemistry. Also, different populations of Douglas-fir were significantly different in the types and quantities of terpenes present (Cates and Redak 1988). Budworm success, as indexed by female dry weight production, was both inversely and positively associated with terpene chemistry, depending on the specific terpenes (Cates and Redak 1986). Furthermore, sampling of the same trees at the New Mexico site in 1981 and 1982 revealed that different factors were affecting the budworm, suggesting that defensive chemistry of the trees changed through time. In 1981, female budworm dry weight production was inversely related to beta-pinene concentration and internode length. In 1982, however, high concentrations of bornyl acetate, camphene, and carene, along with d.b.h. and sapwood basal area ratio were inversely related to female dry weight production. Infestation intensity, another index of budworm success, decreased as the acetate fraction, myrcene, and an unidentified terpene increased (Cates *et al.* 1983). This highly variable nature of terpenoids in Douglas-fir, along with accumulating evidence that terpenoids are at least one defense against budworm (Cates *et al.* 1987), suggest a triggering mechanism by the host Douglas-fir in response to certain stimuli to manufacture these defensive compounds.

Douglas-fir and budworm, both native to western North America, have evolved together. Thus, the host should have evolved some means to defend against budworm. Results from several major field studies involving more than 660 trees testify to a significant level of within-and among-population variation in Douglas-fir terpene, nitrogen, and carbohydrate chemistry (Cates and Redak 1988, and this report). Furthermore, it appears that the budworm is highly variable and that a population of budworm adapted to Douglas-fir in Montana or Idaho, when moved to a 'foreign' population of Douglas-fir, is ill-adapted to the foliage chemistry (Cates *et al.* this symposium). Many of these interactions appear to be mediated by natural product chemistry of the foliage, including primary nutrients (carbohydrates, nitrogen) as well as secondary metabolites (terpenes and other volatiles) (Cates and Redak 1988), the mechanisms of which need more exploration.

Data reported here raise more questions than they answer and perhaps open several areas of interest about the interrelationships between the ecology of budworm and Douglas-fir and how this system can be more appropriately managed. It is much too early in the study to dismiss the hypothesis that thinning may have an effect on foliage chemistry and budworm. Normally, trees respond to thinning about 3 years after treatment. This period until release likely would be longer for trees under stress from budworm such as our sample trees at Greenough Creek. Therefore, we do not believe enough time has yet elapsed since treatment for an effect to be observed. We will sample the Greenough Creek study again in 1991, which will give us a five-year response period since treatment. This should put us in a better position to judge the experiment.

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