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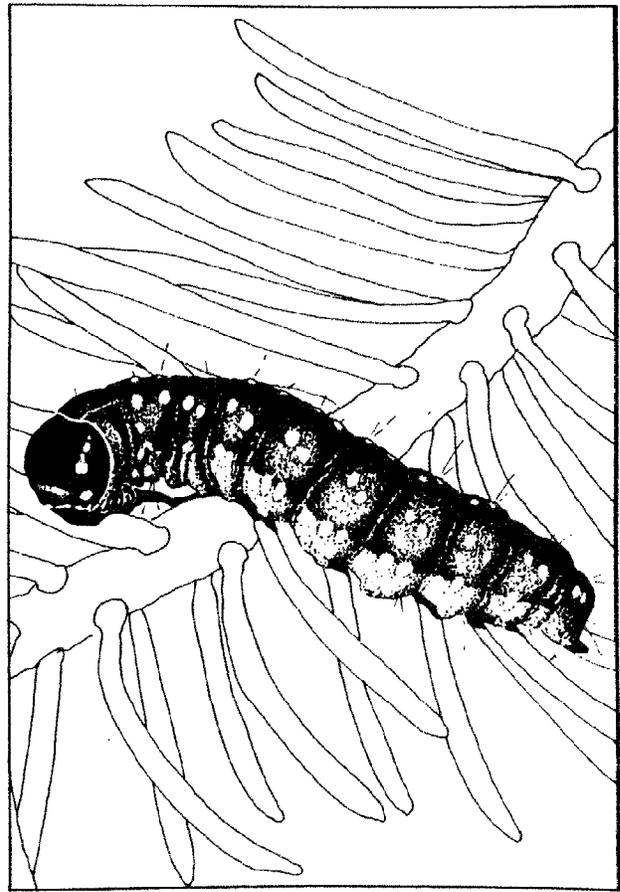
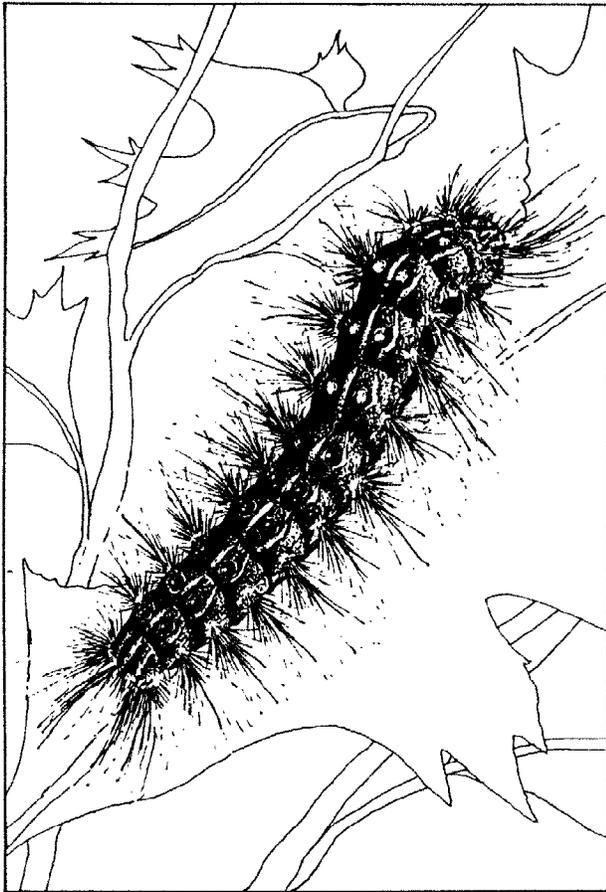
General
Technical
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Proceedings

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.

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PROCEEDINGS,

forest defoliator--host interactions:

A comparison between gypsy moth and spruce budworms

New Haven, Connecticut, April 5-7, 1983

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SPRUCE BUDWORM (CHORISTONEURA FUMIFERANA)

PERFORMANCE IN RELATION TO FOLIAR CHEMISTRY

OF ITS HOST PLANTS

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Spruce budworm growth was best on balsam fir, poorest on lowland black spruce, and intermediate on upland white and black spruce. Growth was consistently, positively linked to foliar N and negatively linked to Fe, K, and select terpenes. Survival rates were not strongly, nor consistently linked to any of the measured foliar chemical traits.

The population dynamics of the spruce budworm, Choristoneura fumiferana, is clearly an ecosystem/biome level process. The process has many parts, all of which interact to some degree, and none of which is really well understood individually, not to mention how they operate together. The process starts, as we see it, by a budworm larva taking a bite out of a plant. The plant has a complex array of nutritive and nonnutritive chemicals that together affect budworm behavior, metabolism and ultimately growth, reproduction and/or death. Our primary objective has been to examine variations in budworm performance among different host tree species in relation to the foliar chemistry of these trees. The ultimate goal is to identify the major host factors regulating budworm performance.

This paper reports on our preliminary analyses of the growth and survival of budworms in relation to total nitrogen, mineral elements, mono-terpenes, and phenolics in its diet on three tree species: balsam fir, Abies balsamea; white spruce, Picea glauca; and black spruce, Picea mariana.

This study was conducted in two locations, the main plot being about 20 miles south of International Falls, Minnesota, in Koochiching County, and the secondary plot about 15 miles west of Cloquet, Minnesota, in St. Louis County.

Methods

In 1981, we selected 122 trees for the purpose of monitoring the performance of larval budworms in relation to foliar chemistry of these trees. Among

this set were 20 white spruce, 25 black spruce, and 58 balsam fir which were divided into four classes: 24 small (1-5 m), 16 medium (5-10 m), 8 large (10-15 m), and 10 stress. Nineteen of the medium/large category were selected at random for the purpose of studying both early and late season (i.e., late summer) budworm performance.

On each tree we selected five branches at midcrown level, approximately 70° apart so as to encircle the tree. Each branch was then enclosed with a 36" long fine-mesh cloth sleeve cage which served as an enclosure for 15 second-stage larvae placed therein. Larvae were obtained from the laboratory colony of the Insect Rearing Service of the Forest Pest Management Institute, Environment Canada, Canadian Forestry Service in Sault Ste. Marie, Ontario. Each branch contained at least 30 new shoots. Budworms were removed at the pupal stage and subsequent moths were collected in the laboratory and frozen within 24 hours after emergence in preparation for freeze-drying to constant weight.

We started the experiment in all cases after shoot elongation had begun (approximately 300 degree days, using 2.8°C as the threshold and March 1 as the beginning date). Budworms normally emerge from hibernacula at about 200 degree days in northern Minnesota (Bean and Wilson 1964) whereas in New Brunswick it may be closer to 100 (Cameron et al., 1968). Our records indicate that balsam "bud break" occurred at about 238 DD in our main plot. In 1981, we placed larvae on black spruce about 1 month later (6/22/81) than on balsam and white spruce so as to avoid any possible adverse effects of the late phenology of black spruce. In 1982 all tree species received larvae at 300 DD. Furthermore, in 1981, we also placed second stage larvae on 19 medium/large balsam on July 24. This is about the time that budworm first stage larvae are normally preparing for overwintering.

Foliage chemistry was measured only once during the larval period, at approximately the commencement of the fifth larval stage. This was done because the fifth and sixth stages consume 90-95 percent of the total diet (Miller 1977, Retnakaran 1983). Foliage was gathered from all sides of the tree at midcrown, immediately stored in coolers on dry ice and then frozen at the laboratory until used for analysis. Except for terpene analyses, the foliage was separated from stems, then lyophilized and ground to pass through a 40-mesh screen on a Wiley mill. It was then stored dry in a glass container in the dark until analysis. Details of the various analyses can be obtained from the authors on request.

Because the field studies did not permit control of temperatures during larval development, temperature effects may be confounded with tree effects when comparing budworm performance on different plots and at different times. In all cases we know the daily maximum, minima, and mean temperatures for our experiments as well as the precipitation values. Once we understand the budworm's temperature-growth responses we will be able to remove possible temperature effects from host effects.

Table 1.--Mean adult female and male weights (mg dwt) reared on different hosts in 1981 and 1982

Host plant	1981		1982		1981		1982		n ^{a/}
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
	Females		Females		Males		Males		
BFir stress	21.44	5.64	22.13	5.11	10.24	1.92	12.91	2.95	10
BFir lge	19.28	4.91	22.42	4.32	9.66	2.02	12.40	2.71	8
BFir med	20.42	3.90	20.65	5.74	9.76	1.76	11.99	3.44	16
BFir sml	17.83	3.99	18.78	4.43	9.33	1.69	10.87	2.38	24
WSpr lge	16.81	5.50	18.49	6.33	7.31	1.93	12.43	3.02	10
WSpr sml	15.00	6.05	16.17	6.21	8.20	2.81	9.26	2.93	10
BSpr upld	15.06	10.37	19.04	6.01	8.12	1.89	10.67	2.78	10/20 ^{c/}
BSpr lowld	8.32	3.38	11.10 ^{b/}	3.56	4.92	1.42	6.73	1.79	15
BFir late	13.56	3.09	na ^{b/}	na	7.41	1.78	na	na	18

^{a/} Number of trees in each species class.

^{b/} No data available.

^{c/} Ten trees in 1981, twenty in 1982.

Results

Differences Among Species

Budworms clearly attained the highest adult weights on balsam fir (18-22 mg dwt), followed by white spruce (15-18.5 mg) or upland black spruce (15-19 mg) and then lowland black spruce (8-11 mg) (Table 1). The pattern was consistent between years for both sexes. The fact that white spruce-reared budworms were smaller than those from fir is contrary to results from eastern North America where such spruce-reared budworms are usually about equal to (Blais 1957, Greenbank 1963) or significantly larger (Koller and Leonard 1982, and see T. Thomas in this proceedings) than those from balsam fir. The upland black spruce data agree with previous research which suggests that it produces slightly smaller insects than does balsam fir but not necessarily less than does white spruce (Blais 1957, Greenbank 1963).

Variability in female weights was about 50 percent greater on the spruces than on balsam fir as estimated by the coefficients of variation (SD/ \bar{x}) (Table 1). This was the result of the fact that some spruce trees consistently produced very small insects (< 11 mg) while others consistently produced large insects (> 20 mg) similar to those on large balsam fir.

Generation survival rates (from second instars to the adult stage) in 1981 revealed that balsam fir was a superior host followed by white spruce and then black spruce (Table 2). The pattern changed in 1982, however, showing that white spruce and lowland black spruce were not different from balsam. Upland black spruce, however, again showed the lowest survival rates. We cannot explain differences in the survival patterns between years except to hypothesize that weather conditions may have been responsible. Mean daily temperatures were about 2.4°C higher during the larval period in 1981 than in 1982 (16.7° vs. 14.3°). Mean daily maxima averaged nearly the same (23.8° vs. 22.9°) in both years but daily minima were about 4°C higher in 1981 (9.5° vs. 5.7°).

Table 2.--Survival rates and proportion of females from different hosts in 1981 and 1982

Host plant	Survival rate		Proportion females	
	1981	1982	1981	1982
BFir stress	.290	.282	.48	.51
BFir md/lge	.305	.276	.55	.48
BFir sml	.330	.327	.54	.51
WSpr all	.232	.351	.53	.51
BSpr upld	.130	.179	.71* ^{a/}	.45
BSpr lowld	.120	.275	.60*	.51
BFir late	.157	na	.53	na

^{a/} Significantly ($p < .05$) different from .50 ratio.

Differences Among Age Classes

We studied budworm performance on three age/size classes of trees (3-5 m, 5-10 m, 10-15 m) known as small(s), medium(m), and large(l), respectively. All trees were nearly open grown so most had full tree crowns. Large trees were bearing male flowers in the upper half crown level, whereas only few of the medium and none of the small trees were flowering.

In both balsam and white spruce, there was a consistent trend for small trees to produce the smallest insects. This pattern held between years and for both sexes. For example, the female mean dry weights (mg) for each size class shown in the following tabulation are significantly different ($p < .05$) from one another:

1981	BFir:	20.35(m)	19.26(l)	17.83(s)
1982	BFir:	22.42(l)	20.65(m)	18.78(s)
1981	WSpruce:	16.81(l)	15.09(s)	
1982	WSpruce:	18.49(l)	16.17(s)	

The smallest difference between mean female weights on small and the large-medium classes ranged from 1.4 to 1.9 mg on balsam and 1.7 to 2.3 mg on white spruce. The differences imply that insects growing on large-medium trees averaged at least 10 percent larger than those from small trees and in some cases as much as 20 percent. Survival rates, however, did not vary significantly among age classes (Table 2). Therefore, although small balsam and white spruce produced smaller insects, they did not produce lower survival rates than larger trees. In general, for both balsam and white spruce, mean insect weight gains and survival rates per tree had no correlation with one another.

Differences Owing to Phenology

On July 24, 1981, we "planted" second stage budworm larvae on 19 medium-large balsams. This date is nearly 2.5 months later than budworm second stage larvae normally emerge for feeding in northern Minnesota. The larvae on these trees attained only about two-thirds the size (13.56 mg) of normal early-season larvae (Table 1). Furthermore, survival was only about half (16%) of that experienced by the similar early-season cohort (Table 2). This was not unexpected because late summer foliage conditions are drastically different from those of early season. The fact that budworms performed as well as they did, however, was surprising. Mean daily temperatures during this late season experiment were about 2°C higher (18.9° vs. 16.7°) than during the early season experiments.

Differences Owing to Stress Treatments

Ten trees (7 medium and 3 large) were trenched at a radius of 10 feet from the trunk in the spring of 1980 down to depth of about 30 inches. This depth reached well into the mineral soil layer or hit bedrock since the study plot was on top of a rock outcrop covered with shallow soils. The ground area under each tree canopy was then covered with black polyethylene plastic. Trees were monitored for moisture stress by pressure bombing twigs that were collected near the bottom of the crown. Pressure bomb readings were taken once per week and two times per day (before 8:00 a.m. and after 2:00 p.m.), during the 6-week larval growth period. The following tabulation shows the mean seasonal pressure bomb differences (stress-control) at both a.m. and p.m. samples:

	<u>a.m. difference</u>	<u>p.m. difference</u>
1981	0.50 bars	0.89
1982	0.45 bars	0.78

Mean differences in water potential between stress and control trees were usually less than one bar--suggesting that the stress treatment was relatively weak. The differences were nevertheless statistically significant on half of the sample periods each summer.

Stress trees produced significantly larger female and male insects than the control trees (all medium and large firs combined) (Table 1). However, in 1982 only males were significantly larger than

those from the control trees. The mean weight differences (stress-control) for each sex are shown in the following tabulation:

	<u>Females</u>	<u>Males</u>
1981 (Stress-Control):	1.31 mg	0.53
1982 (Stress-Control):	0.79 mg	0.80

Thus, so far, the induced stress treatment has had only a minor enhancing effect on budworm growth. However, it has not had any effect on survival rates (Table 2).

Budworm Performance in Relation to Foliar Nutrients

Theoretically an insect's performance should vary in relation to its dietary needs and a diet's deviations from these needs. In the case of the spruce budworm, no one really yet knows what the particular details of its needs are. Mattson and Koller (1981) proposed that the minimally optimal foliar N value for female performance is about 2.1 percent dwt. Harvey (1974) proposed that the minimally optimal levels of soluble sugars in the female's diet is about 4 percent fwt or 20 percent dwt. Albert et al. (1982) found that peak behavioral (i.e., feeding) response to soluble sugars (sucrose) in the diet occurs at about .03M or less than 1 percent fwt. Thus diets deviating negatively from these values probably will produce smaller insects and/or longer growth and feeding periods. Requirements for other important dietary components are really unknown.

To obtain a perspective on the budworm's needs for the mineral elements, we analyzed the nutrient levels in the bodies of adult males and females collected from the trees in our study and then compared their body levels to their food levels (Table 3). The data reveal that the elemental concentrations showing highest deviations from foliar levels are as follows for males and females:

Females: Na>N>P>Cu>Zn>Fe>Mg>K>Ca>Mn
 Males: Na>N>Cu>P>Zn>Fe>Mg>K>Ca>Mn

Sodium clearly had the highest magnification factor (MF) (60.9 and 13.4), but owing to possible errors in its measurement on our emission spectrometer we consider the results very tentative. Nitrogen, P, and Cu were clearly the next highest, with all elements down to Fe showing MF's greater than two. All the rest were smaller than one. MF is concentration in insect body divided by concentration in foliage. Studying the budworm's utilization efficiencies of mineral elements in a low-salt McMorran (1965) meridic diet gave nearly the same results as the above magnification factor array:

Cu>N>Zn>P>K>Mg>Fe>Ca>Mn

The utilization efficiencies array is somewhat different from MF array because the artificial diet does not exactly match the levels of elements contained in the foliage. The point is, though, that any variations in budworm performance on different hosts will most likely be due to variations in the limiting nutrients--those having highest magnification factors or utilization ratios.

Table 3.--Concentrations (ppm dwt) of mineral elements in the bodies of male and female spruce budworm adults, and balsam fir foliage (6/22/82), and the ratios of insect/foliage elemental concentrations

Item	Zn	P	K	Mg	Ca	Zn	Fe	Na	Cu	Mn
SNW Female										
Mean	7.97	7,539	9,932	861	290	113	73	56	12	4
SD	.44	308	800	101	97	22	43	21	4	3
SNW Male										
Mean	9.51	9,569	10,855	987	340	117	87	128	19	6
SD	.40	642	892	83	73	23	51	38	8	4
Fir foliage										
Mean	1.26	1,872	12,738	927	3,671	34	31	9	4	303
SD	.10	108	1,704	109	646	4	4	2	1	103
♀SNW/foliage	6.1	4.0	.78	.92	.08	3.3	2.4	6.1	3.3	.01
♂SNW/foliage	7.5	5.1	.85	1.06	.09	3.4	2.8	13.9	5.4	.02

Growth in Relation to N and Mineral Elements

Balsam fir. Regressing male and female dry weights against the foliar elemental concentrations they experienced as fifth and sixth stage larvae revealed that nitrogen was the only variable consistently and positively related to growth (Table 4). Calcium had a significant positive effect on female weights in 1981 but this is probably spurious owing to the fact that the larvae used only about 300 ppm calcium or less in their diets and foliage has about 15-fold this level. Calcium, of course, could be related to some other important foliar variable which in turn affects larval growth. For example, it was negatively correlated ($p < .05$) with both tannins and phenolics. Calcium may form chelates with many kinds of phenolics, perhaps rendering them less deleterious to a leaf consumer. The effects of the other elements (K, Fe, Cu) were, to our surprise, all negative. For example, based on the body/foliage magnification factors, we expected that Fe and Cu were in relative short supply, but their negative correlation with weight gain implies otherwise. However, as in the case of calcium, their correlation need not imply direct cause and effect but some indirect effect. K, for example, was significantly positively correlated with 10 monoterpenes and sesqui-terpene species in balsam fir and with the terpene grand nima. Fe, on the other hand, was negatively correlated with four terpenes and Cu positively with three. In general, all foliar elements tended to show a negative correlation with total phenols and condensed tannins.

Late season results were unlike the early season results in that K and Cu were now positively correlated with weight gain (Table 4). For both elements, however, late season levels were less on the average than they were in early season (e.g., K: 8090 vs. 10,482). Not only were they less, they were much more variable (e.g., CV-K = .22 vs. CV-K = .08). Late season Cu levels were probably below optimal, for more than half of the late

season trees had less than 0.5 ppm in their foliage. Early season trees, on the other hand, averaged about 4 ppm--none going below 2.6 ppm. When Cu occurred at similar levels (4 ppm) in the meridic diet, budworms more completely (ca. 60-75 percent) extracted it than other elements that occurred at levels comparable to early season foliage. N was not a significant late season nutrient variable for both sexes but only for males, probably owing to its relatively uniform concentration among late season trees (CV-N = .08 vs. CV-N = .14).

Table 4.--Significant variables in the regression of mean male and female adult dry weights per tree on foliar mineral element concentrations in different host trees and years

Host species	Significant Variables	R ²	a/ n
Females			
BFir-79	+N -Fe	.69	12
BFir-81	+N -Fe -K +Ca	.44	50
BFir-late	+K	.17	18
Males			
BFir-79	+N -Cu	.47	12
BFir-81	+N -Fe -K	.18	50
BFir-late	+N -Fe +Cu	.33	18
Females			
WSpr-81	+N -K -Zn	.61	18
BSpr-81	+N -K	.66	17
Males			
WSpr-81		.00	18
BSpr-81	+N -Mn -Cu	.76	17

a/
-- Number of trees in the regression.

Spruces. As with the firs, N was the only element showing a consistent, positive relation to weight gain for both sexes (Table 4). All other elements were negative; thereby corroborating the pattern seen for early season balsam fir. The consistently negative contribution of K stands out because K levels in black spruce were even lower in most cases than they were for late season balsam (6000 ppm vs. 8000 ppm). Thus one is obliged to conclude that K itself is not directly affecting weight gains but indirectly through its effect on some other plant traits. For example, plant K was positively associated with every terpene species but one in both black and white spruce. We hasten to add that none of the associations was statistically significant though. This is probably at least partially due to a small data set which will be enlarged in the next few months. As before, the negative contribution of Cu is difficult to explain because copper was close to its minimally optimal level in the foliage diet. On the other hand, manganese may be approaching deleterious levels in the foliage because it's about one-hundred fold more abundant there than in the insect's body. Moreover, excessively high levels of one mineral element can interfere with the absorption and utilization of other elements and nutrients (Maynard et al. 1979). No explanation is readily available for zinc's negative contribution because its level in the foliage (46 ppm) is hardly excessive. In fact, at this level in the artificial diet it is highly utilized and supports good growth.

Survival in Relation to N and Mineral Elements

Regressing generation survival (the arcsin transformation of the survival rate) against foliar elements revealed that none accounted for more than 50 percent of the observed variation and in most cases, they accounted for only about one-third of the variation (Table 5). Moreover, there was no consistency between years or between species. Therefore, we feel that the observed results may be entirely an artifact.

We were also surprised to learn that insect weight gains (FWT, MWT) and survival rates per tree were not significantly correlated with one another except on black spruce (*) where the relationship was negative ($p < .05$) contrary to expectation:

	<u>BFir</u>	<u>WSpr</u>	<u>BSpr</u>	<u>Late BFir</u>
FWT	.11	.13	-.51*	.23
MWT	-.03	-.28	-.56*	.16

The latter result may suggest that foliage was in short supply and hence higher survival meant less food per insect and thus lower growth. On the other hand, it also could suggest that the tree traits governing survival and growth of budworm are linked in opposing directions, or perhaps not at all in the case of fir and white spruce.

Table 5.--Significant variables in the regression of generation survival rates per tree (2d→adult) on foliar mineral elements and phenolics (PH) in different host trees and years

Host species	Significant variables	R ²	a/ n
BFir-79	+Fe -PH	.32	39
BFir-81	+Mn +Cu	.31	50
BFir-late	+N	.18	18
WSpr-81	+Cu -K -Fe +PH	.52	18
BSpr-81	+Mg	.33	18

a/ Number of trees in regression

Budworm Performance in Relation to Allelochemicals

Terpenes

Preliminary analyses reveal that several terpenes are significantly negatively correlated with weight gain for both sexes in both balsam fir and white spruce. In the case of balsam fir, the following six species of monoterpenes were negatively correlated ($p < .05$) with growth except where noted (ns):

	<u>alpha-pinene</u>	<u>beta-pinene</u>	<u>camphene</u>	<u>beta-phellandrene</u>
MWT	-.36	-.37	-.43	-.38
FWT	-.32	-.32	-.40	-.25

	<u>bornyl acetate</u>	<u>terpinolene</u>	<u>terpene grd sum</u>
MWT	-.24	-.30	-.62
FWT	-.16 ns	-.24	-.45

None of the terpenes in balsam fir, in fact, were significantly positively correlated with growth.

In the case of the white spruce, five different compounds were significantly negatively correlated ($p < .05$) with growth except where noted (ns) as shown in the following tabulation:

	<u>camphor</u>	<u>Sesquiterpenes & monoterpene</u>			<u>alcohol</u>
		<u>#1</u>	<u>#2</u>	<u>#14</u>	<u>#35</u>
MWT	-.33 ns	-.69	-.19 ns	-.32 ns	-.57 ns
FWT	-.71	-.64	-.66	-.68	-.65

Only one terpene showed a positive relation to growth. The fact that white spruce and balsam may have different terpenes regulating budworm performance is not extraordinary because the two trees have different kinds as well as amounts of the individual terpenes. For example, balsam at mid-June had a terpene grand sum of about 6,700 ppm fwt vs. 836 ppm for white spruce. In other words, balsam has roughly 8-fold more terpenes. Black spruce was similarly terpene-rich having about 6,200 ppm fwt in mid-June. This suggests that if it's the total amount of terpenes that are

deterrent, then budworm performance should be better on white spruce than on either balsam fir or black spruce, all other things being equal. The data, however, show the contrary. What is the explanation? Particular species-unique terpene compounds may be especially deterrent at low levels in white spruce (e.g., camphor). On the other hand, all other things are not equal. For example, lower plant nitrogen levels may make white spruce significantly less suitable than fir in spite of its lower terpene levels. White spruce, for example, had 20 percent less N in mid-June than did balsam fir (e.g., 1981: 1.24 percent vs. 1.52 percent). We know that this is due to the fact that white spruce grows faster than balsam fir and thereby dilutes its foliar nutrient levels similarly faster (Fig. 1).

Going back to the hypothesis of the effects of terpene grand sums on budworm growth leads us to differences between small and medium/large balsams. As we said earlier, small trees produced 10 to 20 percent smaller insects than did medium/large trees. This may have been due to the fact that small trees had 42 percent more terpenes than did medium/large trees at mid-June when larvae were in the 5th/6th instars (9,547 ppm fwt vs. 6,700 ppm). The N levels in these two age classes were nearly identical (e.g., 1981: 1.50 vs. 1.55), so this is not a large potential source of variation. We also know that mineral element differences are not a likely explanation of the difference because they appeared to be available in sufficient amounts in both age classes, barring any negative interactions with tannins and phenolics. Similarly, there were

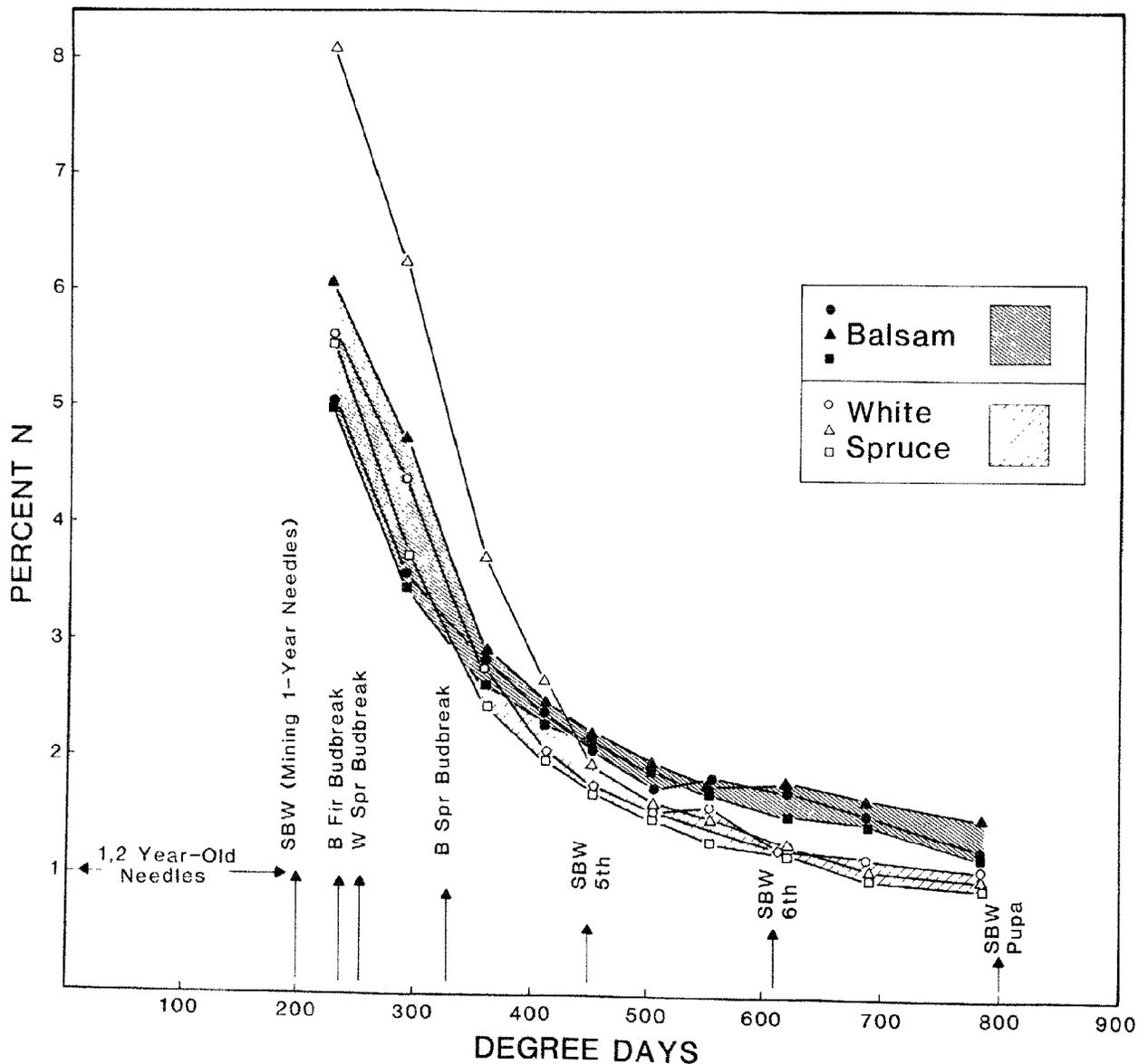


Figure 1.--Seasonal change in foliar nitrogen content (percent dwt) of three balsam and three white spruce with respect to degree day accumulations (2.8°C as base), and the phenology of the spruce budworm

no significant differences between the two groups for total phenols (2.64 percent vs. 2.59) or tannins (3.8 vs. 4.5 percent). Therefore, until the final analyses are complete, we suggest that the budworm growth difference between balsam age classes is due in large part to their terpene differences.

Small white spruce also had smaller insects and more total terpenes than did large white spruce (994 ppm fwt vs. 667 ppm). But, in this case, male and female weights were not correlated with terpene grand sums. The most likely explanation for differences in insect weight gain between white spruce age classes is the difference in levels of the one or more of individual terpene compounds listed above. There were no significant differences in tannins, total phenolics, and N levels between the two age classes just as was the case for balsam.

Phenolics-tannins

Incorporating phenolic and tannin estimates along with the mineral element data in the multiple regressions did not change any earlier conclusions for balsam fir but did in the case of male weight gain on white spruce. In this case, tannin was the only variable significantly correlated with male weight ($r = -.46$). This reflects the fact that no other variables were previously related to male weight gains.

The simple correlation coefficients between phenolics, tannins and weight gains on fir and spruce were not significant in all but two cases (*) as shown below:

	Balsam		White Spruce	
	FWT	MWT	FWT	MWT
Phenolics	-.29*	.00	.19	.02
Tannins	-.06	.13	-.20	-.46*

In general, levels of tannins and phenolics were negatively correlated with nearly all mineral elements in fir and white spruce. In the case of spruce, however, only one of the correlations was significant. This is in striking contrast to balsam where only five out of eighteen negative correlations were not significant in both 1979 and 1981, 2 years for which we have substantial data sets. The following tabulation shows the significant ($p < .05$) tannin and phenolic correlations with N in balsam fir foliage:

	N-79	N-81
	Phenolics	-.62
Tannins	na	-.42

Palmer (1982) found the same negative relationship between phenolics and N in Populus tremuloides foliage.

Previous studies on the effects of phenolics and tannins on the growth performance (via lowered protein utilization) of folivorous insects have almost unanimously come to the same general conclusion: there seems to be little or no measurable deleterious effect, except perhaps at extraordinarily high tannin concentrations (Lawson et al. 1982, Bernays 1981, Fox and McCauley 1977).

While our analyses are too preliminary to come to any firm conclusions, we believe that there may also be long-term, subtle effects that have been overlooked in the typical growth bioassays which usually measure insect performance (nutritionally and behaviorally) for only one or two instars, or at most for the whole feeding period of one generation. Tannins and/or phenols could have some chronic, subtle effects, such as through the chelation of micro-nutrients like Cu, Zn, and Fe--which then renders them less available to the insects. Such effects would have to be monitored over two or more successive generations to see the impacts of chronic micronutrient deficiencies. The chelation of such micronutrients may also be an important plant defense against microorganisms and could also thereby affect essential gut microbes or pathogens in those consumers having such microsymbionts (Swinburne 1981, Radhakrishnan and Sivaprasad 1980, Roy and Mukherjee 1979, Shieh et al. 1968, Emery 1982).

Budworm Growth Response to N Levels

The analyses have indicated that budworm weight gains are consistently but not exclusively linked to variations in plant foliar N levels. In those cases where N was not implicated, there was usually only very little variation in N levels among plants. Therefore, to add strength to the N hypothesis, we planned two experiments to raise the level of nitrogen offered to larvae, thereby hoping to elicit increased growth. The first experiment was designed to raise dietary N for just the first three instars (2, 3, and 4), whereas the second was designed to raise N for the whole larval life span, but particularly for late stage (5, 6) larvae.

Diet/Foliage Transfer Experiment

In the early spring before budbreak occurs, second stage budworm larvae mine 1-year-old or sometimes 2-year-old needles for 1 to 2 weeks (Blais 1979, McGugan 1954). After molting to the third instar, larvae then move to the newly opening buds or male flowers for feeding. During the needle mining period budworms subsist on very little N, such needles, usually having between 0.95 and 1.1 percent N. The newly flushed foliage, on the other hand, is very N rich (as high as 8 percent) but very ephemeral because shoots and needles are rapidly expanding thereby causing a precipitous decline in most foliar elements (Fig. 1), probably owing to a dilution effect. The decline takes the form of a negative exponential ($\%N = aX^{-b}$) as has also been reported by Shaw and Little (1977). By the fifth larval stage N levels are < 1.5 percent in balsam, and somewhat less in white spruce owing to its faster development and nutrient dilution (Fig. 1). Since the fifth and sixth larval stages eat about 95 percent of the whole food budget for the larval period, (Retnakaran 1983, Miller 1977) we asked whether a consistently high N diet for the first three feeding stages (2, 3, 4) would have any enhancing effect on ultimate weight gain if these larvae were then transferred at the 5th instar to a low N foliage diet. To test this hypothesis we simultaneously grew insects on meridic diet (McMorran 1965) having about 4.4 percent N and also on the natural hosts, balsam and white spruce. At the fifth larval stage, ten females were

transferred from the diet to each of 48 balsam fir and 20 white spruce trees for completion of feeding. At pupation all insects were removed and later weighed for adult body size. The results on balsam showed that diet/foliage reared larvae were significantly larger (9 percent) than foliage/foliage reared insects (20.51 vs. 18.87 mg). Furthermore, plotting mean female weights of each group from a tree against the foliar N values they experienced as fifth and sixth stage larvae gave nearly identical regressions except for the intercepts which reflect their mean differences in body size:

$$\begin{array}{l} \text{diet/foliage} \quad \text{FWT} = 12.06 + 5.42\%N \quad r^2 = .19 \\ \text{foliage/foliage} \quad \text{FWT} = 10.37 + 5.46\%N \quad r^2 = .22 \end{array}$$

Thus the early diet ration seems to have "bumped up" final adult weights.

On the other hand, the same experiment on white spruce gave opposite results; diet/foliage insects were about 9 percent smaller (14.18 vs. 15.50 mg where $.1 < p < .05$). There was no significant regression of either group on foliar N values but the two groups nevertheless performed similarly on the set of 20 spruce as evidenced by the significant regression between their respective mean adult weights:

$$\text{FWT (d/f)} = 6.72 + .481 \text{ FWT (f/f)} \quad r^2 = .30$$

These results are in direct contrast with those reported by Thomas (this proceedings) who found that diet to current white spruce foliage transfers (at the 6th larval stage) produced larger insects (ca. 21 mg) than similar transfers to balsam fir (ca. 15 mg). The explanation for this divergence from our results could be due to several factors: different populations of insects, different physical environments, and different host materials. The latter one entails at least two variables. Thomas used excised branches of both fir and spruce whereas we used intact branches. Perhaps even more important is the fact that the eastern populations of white spruce and fir are known to differ (phytochemically) from the more western populations such as the one we studied in northern Minnesota (Wilkinson et al. 1971, von Rudloff 1974, Zavarin and Snajbeck 1972, and Lester 1974). For example, von Rudloff (1975) reported that camphor levels are nearly twice as high in some western populations of white spruce than in eastern ones. However, until more is known about the nutrient levels of the eastern host materials, it's impossible to explain the causes of the apparent differences in budworm performance.

To recapitulate, the balsam fir transfer experiment suggested that giving young larvae a high protein diet enhanced their performance by an amount that was constant, when the N effect on late larvae was accounted for. On the other hand, the spruce transfer experiment suggested that the early high protein diet was not enhancing, for these larvae attained smaller size than those having spent their early instars on spruce. Nevertheless both diet and tree insect groups performed similarly with respect to the trees they were on. The following tabulation summarizes the transfer effects on adult female dry weights relative to the

meridic diet control:

	<u>diet/wsp</u>	<u>wsp/wsp</u>	<u>bfir/bfir</u>
Mean female weight (mg)	14.18	15.50	18.87
	<u>diet/bfir</u>	<u>diet/diet</u>	
Mean female weight (mg)	20.51	26-31	

Obviously, feeding for the fifth and sixth larval stage on a tree was not as good as feeding on the diet. White spruce insects achieved about half, and balsam insects about two-thirds of their potential size. Why the meridic diet experience enhanced growth on fir but disenanced it on spruce is an enigma. Perhaps early season spruce foliage is superior to the artificial diet. On the other hand, later in the season, it is plainly inferior. One can speculate that there must have been significant transfer shock going from diet to trees, especially in the case of white spruce. Perhaps the shock was due to higher metabolic costs to operate the budworm's mixed-function oxidase system on spruce than on fir (Brattsdén 1983). This assumes, of course, that there were allelochemicals that elicited higher MFO activity on spruce than on fir or that there were present significant MFO inhibitors in the spruce foliage which may have rendered spruce allelochemicals more deleterious. On the other hand, the effect may have occurred at the behavioral level, for spruce foliage seems to harden off faster than balsam, and it might also possess important feeding deterrents (e.g., pungenin) (Heron 1965).

Fertilization Study

To elucidate the budworm growth response (Δ WT) to changes in foliar N (Δ N), we first regressed budworm weight gains in 1981 on foliar N levels. Secondly, we fertilized our most N-impooverished trees, the lowland black spruce (3-5 m tall and 30-45 years old) and half of the small balsam which are comparable to trees used in two earlier fertilization studies (Shaw et al. 1978, Shaw and Little 1972). In each case we had 15 treated and 15 control trees. We applied 600 lbs. N/acre (urea) around the root zone of each tree during the first week of May 1982.

Male and female weight gains (MWT, FWT) in 1981 were clearly linear functions of foliar N (using all tree species and age classes):

$$\begin{array}{l} \text{FWT} = 3.45 + 9.844 (\%N) \quad r^2 = .54 \quad n = 114 \\ \text{MWT} = 3.13 + 3.959 (\%N) \quad r^2 = .44 \quad n = 113. \end{array}$$

Scatter plots of the data revealed that female weight gains showed a clear positive trend over the full range of N values (0.47-2.05%). Furthermore, female weights increased with even higher N levels (2-4%) administered in the form of casein and wheatgerm in artificial diets. Male weights, on the other hand, showed little tendency to increase with foliar N levels above 1.5%. Moreover, administering even higher levels of N (2-4%) in the artificial diet brought about a weak response, 1-2 mg, suggesting that above 1.5% N males have a shallow response potential if any.

The linear regressions imply that the weight gain response of budworms to an increment of N is constant, e.g., $\Delta FWT/\Delta N = 9.84$, the slope of the regression line. In other words, for each unit increase in foliar N there is a concomitant 9.8 mg increase in female weight. In the case of the fertilization study, our treatment of 600 lbs. N/acre elevated foliar N levels by 0.40 and 0.45% for the black spruce and balsam fir trees, respectively. These N changes both elicited 1.38 mg changes in female mean weights as shown in the in the following tabulation:

	FWT	ΔFWT	MWT	ΔMWT	%N	$\Delta \%N$
BfirCk	18.78	} 1.38	10.87	} 0.37	1.31	} 0.45
BfirF	20.16		11.24		1.76	
BSprCk	11.10	} 1.38	6.73	} 0.96	0.85	} 0.40
BSprF	12.48		7.69		1.25	

The urea treatment caused significant ($p < .05$) increases in female weights on both tree species but significant increases in male weights only on black spruce. The fact that the males did not respond to urea fertilization on balsam lends support to our suspicion that males have a low optimal dietary N requirement (perhaps about 1.5%) and that near this level their response is nearly flat.

Using the fertilization data for females only, we calculate that $\Delta FWT/\Delta N$ for balsam and black spruce are 3.07 and 3.45, respectively. These values are not much different from those derived from the fertilization experiments of Shaw *et al.* (1978). They reported that high and low urea treatments raised foliar N values (on June 23) by 0.8 and 0.4%, respectively. These increments in turn elicited female adult dry weight gains (using formula of Mattson *et al.* 1982) of 3.33 and 1.13 mg. Thus $\Delta FWT/\Delta N$ was 4.16 and 2.83 for the high and low urea treatments, respectively. Shaw *et al.*'s high calcium nitrate treatment gave a $\Delta FWT/\Delta N$ value of 2.86. Therefore, pooling Shaw *et al.*'s and our values suggests that $\Delta FWT/\Delta N$ averages about 3.27 and ranges from 2.83-4.16. In other words, $FWT = a + 3.27 (\%N)$. This implies that for every 1% increment in foliar N, there will be a corresponding 3.27 mg dwt increment in adult female weights.

On the other hand, our earlier regression analysis suggested that $\Delta FWT/\Delta N$ should be about 9 instead of 3. What's the explanation for this discrepancy? The explanation might lie in the fact that changing foliar N through fertilization results in many other changes in foliar chemistry that are not all enhancing. For example, fertilization is also known to raise the levels of mono- and sesqui-terpenes. Moreover, the fertilization studies reported herein (Shaw *et al.* and ours) were done on young balsam fir which we have already shown to have significantly higher terpene levels than older trees. Thus the budworm responses (ΔFWT) on small trees might be significantly less than on older trees which have lower levels of terpenes. Similarly, the lowland black spruce which we fertilized probably has

levels of terpenes at least as high and total phenolics levels that are higher than the small fir. Thus the overall 1981 regression may have a higher slope or predicted weight increment per unit of N because the pooled data consists of such species as white spruce and medium/large balsam which may have higher levels of N relative to terpenes, thereby giving higher weight gains per unit N increment than would small balsams and lowland black spruce.

Changes in Fecundity

In order to obtain some idea of the potential impact of different dietary regimes on budworm population dynamics, we used the fecundity/pupal size equation of Miller (1963) and the adult dry weight/pupal size equation of Mattson *et al.* (1982) to project changes in female dry weight into changes in egg output. The resulting formula for fecundity in relation to body size is as follows:

$$F = -442.1 + 216.7 (FWT)^{.37}$$

$$\Delta F = 81.04 (FWT)^{-.63} \Delta FWT$$

The second equation says that changes in egg output (ΔF) increase directly with changes in body size (ΔFWT). In other words, a 2 mg change in body size elicits exactly twice the output of a 1 mg change and so on, holding initial body size (FWT) constant.

The question yet to be answered is how large are the differences in fecundity between insects having different sizes. For example, female budworms from small balsam averaged 32 less eggs than similar females on medium balsam (187 vs. 219) (Table 6). Similarly insects from small white spruce averaged 26 less eggs than females from large white spruce (148 vs. 174). In the case of black spruce, females from the lowland trees averaged 17 fewer eggs than those from upland trees (32 vs. 149).

In the case of the fertilization experiments, we estimated that increasing foliar nitrogen levels by 1.0% would result in roughly a 3 mg increment in female weight. This translates into 41 more eggs for females that weighed 17 mg before fertilization. If foliar N increased only 0.5%, the result would be about half as many eggs, i.e., 20 more per female.

The significance such differences in egg output have on the insect's population dynamics cannot, of course, be answered. These are questions that must be addressed through an ecosystem level model which incorporates all of the major factors regulating budworm natality and mortality.

CONCLUSIONS

Although the study is not yet completed, there are some consistencies that seem substantial enough to warrant recapitulation.

There are clear differences in budworm growth between small and large tree classes, larger trees producing larger and hence more fecund insects. Furthermore, there are differences between species--balsam giving rise to larger insects than white spruce. This pattern seems not to hold in eastern North America where the reverse is true. The explanation for this inconsistency may reside in the fact that the phytochemistry of the eastern and western tree populations are different owing to limited gene exchange, different geological histories, and different environments. There is also, of course, the possibility that the insect populations are substantially different as well.

Budworm survival rates did not vary among tree size/age classes and appeared to be highest on balsam and lowest on black spruce. Survival rates and budworm weight gain per tree were not correlated except in the case of black spruce where the association was negative. This implies that the plant traits which affect weight gain are independent of those that affect survival except perhaps in black spruce where they could be negatively linked. Budworm survival rates were not consistently linked to any variables that were measured.

Insect weight gains per tree were consistently, positively linked to foliar N and negatively to Fe and/or K. The negative associations with Fe and K are surprising because neither element occurs at levels high enough to be minimally optimal much less toxic or noxious. Nevertheless, iron levels in the insect body show a tendency to decrease with increasing levels in the diet. Iron, in fact, is the only element showing this inverse behavior. Moreover, iron concentrations in the insect are also negatively correlated with insect size. What this implies is not clear. It may mean that insects sequester less Fe per unit body weight when diets are better for growth. Fe concentration is also positively correlated with (1/N) of the diet. Since total consumption is usually positively linked to (1/N), Fe uptake by the insect may be related to the total amount of Fe passing through the digestive system.

Potassium levels by themselves may not be inhibitory to budworm growth but K is linked positively to foliar terpene levels which apparently are inhibitory.

Terpene levels were negatively linked to budworm weight gains both on balsam and on white spruce. In the case of balsam, terpene grand sums (all molecular species pooled) showed the strongest correlations whereas in white spruce individual compounds not the grand sums had the highest linkage to weight gain. Difference in budworm performance between tree age classes may be largely due to higher levels of terpenes in the younger trees. Because plant terpene profiles are known to exhibit significant east-west variation across North America, it is likely that budworm performance on these trees will similarly vary.

The significance of phenolics and tannins in the performance of spruce budworm is still uncertain. The early data suggest little effect on either survival or weight gain. However, the

spectrum of phenolic compounds in balsam and the two spruces has not yet been examined so it is entirely possible that one or more of them could have significant behavioral or physiological effects. Pungenin, for example, in white spruce could be an important feeding deterrent.

Finally, it is clear that changing insect N intake through artificial diet to foliage transfers and fertilization results in enhanced insect growth, at least on balsam fir. The data suggest that growth increment per unit nitrogen increment ($\Delta\text{FWT}/\Delta\text{N}$) is about 3, as long as the minimally optimal level of N in the diet has not yet been reached. We suspect that the growth increment per unit nitrogen increment ($\Delta\text{FWT}/\Delta\text{N}$) will vary with different host species and age classes owing to different background levels of nutrients and allelochemicals.

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