DOUGLAS-FIR NUTRIENTS AND TERPENES AS POTENTIAL FACTORS INFLUENCING WESTERN SPRUCE BUDWORM DEFOLIATION

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INTRODUCTION

Variation in levels of herbivory within and among plants can be attributed to many mechanisms, such as differences in a) host nutritional quality, b) suitability of the physical environment, and c) abundance of competitor consumers or natural enemies (Mattson et al. 1982, Denno and McClure 1983, Mattson and Scriber 1987, Clancy et al. 1988a, 1988b, Mattson et al. 1988). To test the hypothesis that variation in host plant nutritional quality is a significant mechanism in plant resistance against herbivores, I have selected western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), and Douglas-fir, *Pseudotsuga menziesii*, for use as a model system.

C. occidentalis is one of the most abundant defoliators of true fir and Douglas-fir coniferous forests in western North America (Brookes et al. 1987). The larvae preferentially feed on the opening buds and the newly developing needles of their host trees. Several lines of evidence suggest that both foliar concentrations of nutrients, such as nitrogen, sugars, and minerals, and allelochemicals, terpenes in particular, could have important effects on budworm survival and reproduction (Harvey 1974, Kemp and Moody 1984, Redak and Cates 1984, Cates 1985, Wagner and Tinus 1985, Cates and Redak 1988, Clancy et al. 1988a, 1988b, Wagner et al. 1989, 1990).

This study was designed, therefore, to compare levels of foliar nutrients (N, sugars, and several mineral elements) and allelochemicals (terpenes) between phenotypically "resistant" and "susceptible" Douglas-fir trees. Differences in biochemical characteristics between trees that have experienced light versus heavy defoliation may provide clues to which nutrients or terpenes are connected with resistance to budworm attack. In addition, I compared the results with those from artificial diet experiments that were designed to ascertain the budworm's response curves to important host plant nutrients.

EXPERIMENTAL METHODS

Field Study

The study site was a high-elevation, mixed-conifer forest with a history of western spruce budworm infestation in the Pike National Forest near Deckers, Colorado. At the time of the study, in 1988, most of the trees at the site had sustained moderate to severe budworm defoliation for at least several years, as determined from their growth form and general condition.

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

I selected 12 resistant trees by identifying mature (at least 20 years old, or well beyond juvenile stage) individual Douglas-fir trees with a full crown and good form, as distinct from most of the nearby trees that had clearly been defoliated for several successive years. The resistant trees were obviously healthy and vigorous and appeared to have sustained little or no defoliation. To pair with each resistant tree, I selected a nearby tree (within 30 m) of similar size (height and diameter) and microsite (slope and aspect) that was manifestly susceptible to budworm defoliation.

In late June of the 1988 growing season, corresponding to the late instar feeding period of the western spruce budworm, I collected current-year foliage from the 24 study trees for chemical analyses. One branch was clipped at random from the mid-crown area of the north, south, east, and west quadrants of each tree. All the current-year shoots were immediately removed, bagged, and stored on dry ice. The foliage was later transferred to an ultralow freezer and stored at -90°C until analyzed. The needles were pulled off the stems in preparation for the chemical analyses, and a composite subsample of all the current-year needles collected from each tree was analyzed.

Foliage samples were analyzed by the Analytical Services Laboratory of the Ralph M. Bilby Research Center, Northern Arizona University, for the following: total Kjeldahl nitrogen and phosphorus (colorimetrically); potassium, calcium, magnesium, and zinc (by flame atomic absorption spectroscopy); sugars--including xylose, fructose, glucose, galactose, mannose, sucrose, maltose, lactose, and erythrose (by high-performance liquid chromatograph); and terpenes--28 individual monoterpenes, sesquiterpenes, and oxygenated monoterpenes (by capillary column gas chromatograph) (Wagner et al. 1989). The same procedures were used to analyze nutrient concentrations in artificial diets.

Data were analyzed using paired *t*-tests ($P \leq 0.05$) to determine whether resistant and susceptible trees contained different concentrations of the several nutrients and of terpenes.

Artificial Diet Experiments

I evaluated the budworm's response curves to sugars, P, K, Ca, Mg, and Zn using a multiple generation bioassay and various artificial diets containing defined levels of the nutrients. My experimental base diet had concentrations of N, water, sugars, and most minerals similar to those provided by Douglas-fir foliage (Clancy in press).

I formulated other diets that encompassed the range of mineral (K, Mg, and Ca) and sugar concentrations typical for host foliage. However, the P and Zn experiments did not include responses at the lower limit because the concentrations of these minerals in the base diet were near the middle of the usual range for foliage.

My insect bioassay procedure measured survival and reproduction for three consecutive generations (Clancy in press). The P_1 generation of the experiments started with egg masses from my laboratory colony of nondiapausing western spruce budworm. Survival rates were determined for three periods: early to late larval instars, late instars to pupal stage, and pupal to adult stage. These rates were multiplied together to estimate cohort survival to the adult stage. I also incubated egg masses produced by the adult moths to determine the proportion that was viable. The bioassay for each treatment and generation started with 10 egg masses, which usually produced 200 to 300 first instar larvae. At the late instar stage, up to 150 live larvae were transferred to fresh diets to complete larval development. From 50 to 120 larvae typically pupated and produced about 40 to 100 moths, which laid a total of 25 to 75 egg masses on average. Pupae were weighed and the average female pupal mass for each treatment and generation was used to predict fecundity, e.g. the number of oocytes in the adult moth (Wagner et al. 1987). Experiments were replicated twice to evaluate repeatability.

Data obtained from these experiments were used in the following population growth model to get a composite measure of the effects on budworm performance of different nutrient levels:

$$\text{no. } F_1 \text{ larvae} = (\text{no. } P_1 \text{ larvae}) \cdot (P_1 \text{ \% cohort survival to adult stage}) \cdot (P_1 \bar{x} \text{ female fecundity}) \cdot (F_1 \text{ \% viable egg masses})$$

The number of F_2 and F_3 larvae was calculated using data for the appropriate generation. The model estimates the number of first instar larvae alive at the beginning of the F_1, F_2, and F_3 generations, assuming that all the treatments in an experiment have equal populations at the beginning of the P_1 generation, i.e. the number of P_1 larvae was 1 for all treatments. I plotted the number of F_1 to F_3 larvae against the nutrient concentrations for the different treatments in an experiment and determined the optimal concentration of each nutrient tested based on the level that produced the most F_3 larvae.

RESULTS

The foliage of trees susceptible to western spruce budworm defoliation contained lower levels of N ($P < 0.001$), sugars ($P = 0.004$), and P ($P = 0.009$), but higher levels of K ($P = 0.018$) than that of resistant trees (Table 1). Foliar concentrations of Ca, Mg, and Zn were not different between resistant and susceptible trees ($P \geq 0.265$) (Table 1).

I also examined ratios of sugars and minerals to N because experimental results had indicated that N may determine the amount of food a budworm larva ingests, which in turn affects the amount of other nutrients or allelochemicals consumed (unpubl. data). Susceptible trees had higher ratios of P, K, Mg, and Zn to N than resistant trees ($P < 0.001$) (Table 1) and a tendency toward higher Ca/N ratios ($P = 0.069$). The two types of trees did not differ in sugars/N ratios ($P = 0.487$) (Table 1).

The foliage of susceptible trees had concentrations of sugars and K, plus ratios of P, K, Ca, and Zn to N, which were closer to the optimal levels determined by artificial diet experiments than those of foliage from resistant trees (Table 1). The optimal Mg/N ratio estimated from diet studies was between the mean values for resistant and susceptible trees. Levels of P in resistant trees were nearer the diet experiment optimum. It should be noted, however, that for sugars, P, P/N, K, and Zn/N the optimal diet values either were barely contained in the ranges observed for trees or were outside the ranges. Furthermore, none of the optimal diet values would be included in 95 percent confidence intervals for average tree values.

Resistant trees had higher levels of foliar N than susceptible trees, contrary to findings by Cook et al. (1978) for *Picea glauca* and by Piene (1980) for *Abies balsamea*. I was not surprised at this result, however, because experiments conducted with varying levels of N in artificial diets had demonstrated that N alone is not a limiting nutrient for *C. occidentalis* (unpubl. data).

There were no detectable differences in foliar terpene concentrations between resistant and susceptible Douglas-firs ($P \geq 0.334$) (Table 2). Likewise there was no distinction in total terpene/N ratios ($P = 0.992$) (Table 2). The terpene concentrations were calculated on a fresh mass basis because the foliage from all the trees was collected at the same phenological stage and moisture contents were thus similar.

Table 1. Comparison of foliar nutritional chemistry for 12 pairs of Douglas-fir trees that appeared to be resistant versus susceptible to western spruce budworm defoliation and the optimal concentrations of sugars and minerals determined by artificial diet experiments

Response variable[a] (units)	Douglas-fir foliar chemistry[b]			Artificial diet experiment optimum[c]
	P^d	Resistant	Susceptible	
N (%)				
$\bar{x}$	<0.001	1.14	0.93	--[e]
SE		0.031	0.021	
Range		1.02-1.39	0.80-1.07	
Sugars (%)				
$\bar{x}$	0.004	11.2	8.9	6.4
SE		0.43	0.49	
Range		9.5-14.0	5.7-11.9	
Sugars/N ratio				
$\bar{x}$	0.487	9.9	9.5	5.2
SE		0.39	0.39	
Range		7.6-12.4	7.1-11.8	
P (mg/g)				
$\bar{x}$	0.009	2.03	1.93	3.36
SE		0.042	0.044	
Range		1.84-2.32	1.71-2.23	
P/N ratio (x 10)				
$\bar{x}$	< 0.001	1.78	2.08	2.73
SE		0.024	0.056	
Range		1.67-1.97	1.71-2.40	
K (mg/g)				
$\bar{x}$	0.018	8.89	9.94	12.73
SE		0.180	0.369	
Range		7.80-9.65	8.16-12.2	
K/N ratio (x 10)				
$\bar{x}$	< 0.001	7.85	10.76	10.35
SE		0.232	0.521	
Range		6.54-9.23	8.08-14.13	
Ca (mg/g)				
$\bar{x}$	0.695	2.78	2.71	3.95
SE		0.191	0.154	
Range		1.80-4.01	1.91-3.82	

Table 1. Continued

Response variable[a] (units)	Douglas-fir foliar chemistry[b] P[d]	Resistant	Susceptible	Artificial diet experiment optimum[c]
Ca/N ratio (x 10)				
$\bar{x}$	0.069	2.49	2.93	3.21
SE		0.212	0.188	
Range		1.59-3.71	2.15-4.29	
Mg (mg/g)				
$\bar{x}$	0.265	0.90	0.92	1.04
SE		0.030	0.022	
Range		0.73-1.07	0.80-1.02	
Mg/N ratio (x 10)				
$\bar{x}$	< 0.001	0.79	1.00	0.85
SE		0.026	0.039	
Range		0.68-0.98	0.79-1.17	
Zn (μ/g)				
$\bar{x}$	0.631	27.8	27.3	85.6
SE		0.90	0.53	
Range		24-36	24-30	
Zn/N ratio (x 1,000)				
$\bar{x}$	< 0.001	2.44	2.95	6.96
SE		0.052	0.084	
Range		2.24-2.75	2.43-3.30	

[a]All concentrations are based on the dry mass of the foliage or diet.

[b]Current-year needles collected in late June 1988, when western spruce budworms were in the late-instar feeding period.

[c]The concentration that produced the best budworm survival and reproduction when larvae were reared on the diet for three consecutive generations.

[d]Probability level for a paired t-test comparing foliar chemistry for resistant and susceptible Douglas-fir trees, df = 11.

[e]Experiments conducted with different levels of N in artificial diets demonstrated that responses to N were dependent on levels of minerals in the diet. Thus I predict the optimal N concentration will vary according to levels of minerals (and other nutrients and allelochemicals) present in the food.

Table 2. Comparison of foliar terpene chemistry for 12 pairs of Douglas-fir trees that appeared to be resistant versus susceptible to western spruce budworm defoliation[a]

Response variable		Douglas-fir foliage[b]	
	P^c	Resistant	Susceptible
		(μg/g fresh mass)	
Tricyclene			
$\bar{x}$	0.670	84.8	77.8
SE		14.54	11.24
Range		24-165	22-171
α-pinene			
$\bar{x}$	0.495	367.2	321.0
SE		66.05	42.01
Range		131-795	96-643
Camphene			
$\bar{x}$	0.495	544.0	471.0
SE		96.74	74.12
Range		190-1110	114-1097
β-pinene			
$\bar{x}$	0.351	275.3	207.5
SE		66.70	36.40
Range		82-813	0-359
Myrcene			
$\bar{x}$	0.920	56.9	55.7
SE		8.10	9.71
Range		22-98	25-142
Menthene-1			
$\bar{x}$	0.788	246.1	231.1
SE		32.06	44.67
Range		121-411	82-626
Bornyl acetate			
$\bar{x}$	0.922	471.2	461.5
SE		81.75	85.50
Range		105-924	99-1194
Total monoterpenes			
$\bar{x}$	0.334	1742.2	1411.9
SE		279.52	199.56
Range		590-3347	404-3100

Table 2. Continued

Response variable	P^c	Douglas-fir foliage[b] Resistant	Susceptible
		(μg/g fresh mass)	
Total oxygenated monoterpenes			
$\bar{x}$	0.981	477.4	475.1
SE		84.93	89.67
Range		105-978	99-1248
Total terpenes			
$\bar{x}$	0.437	2219.6	1887.0
SE		357.62	285.63
Range		775-4325	503-4348
Total terpenes/N ratio		ratio x 1,000	
$\bar{x}$	0.992	202.1	201.7
SE		35.26	28.66
Range		68.6-408.0	55.9-430.5

[a]Concentrations of six monoterpenes (tricyclene, α-pinene, camphene, β-pinene, myrcene, menthene-1) and one oxygenated monoterpene (bornyl acetate), the principal components of the oleoresin of these trees, are presented. Additional monoterpenes (α-phellandrene, Δ-3-carene, ℓ-limonene, terpinolene) and oxygenated monoterpenes (cis-β-terpineol, ℓ-borneol) that were minor components of the oleoresin were included when calculating terpene totals.

[b]Current-year needles collected in late June 1988, when western spruce budworms were in the late-instar feeding period.

[c]Probability level for a paired t-test comparing foliar chemistry for resistant and susceptible Douglas-fir trees, df = 11.

CONCLUSIONS

Foliar analyses of 1988 new growth revealed that defoliation susceptible Douglas-fir had lower levels of N and sugars in their foliage than nearby defoliation resistant trees. Susceptible trees, moreover, had higher mineral/N ratios for P, K, Ca, Mg, and Zn. These field data are consistent with predictions made from laboratory diet experiments that high mineral/N ratios favor spruce budworm population growth. In other words, the susceptible trees had sugar concentrations and mineral/N ratios closer to the optimal levels for the spruce budworm than did the resistant trees. The results, therefore, support the hypothesis that variations in levels of foliar nutrients among individual trees may be an important mechanism in Douglas-fir resistance to *C. occidentalis* damage. Resistant trees may suffer low defoliation because they provide a food source that is poorly matched to the budworm's nutritional requirements with respect to concentrations of sugars and balances of key minerals to N.

A potential caveat must be attached to these results, however. Although there were detectable differences in sugar concentrations and mineral/N ratios between apparently resistant and susceptible trees, neither group was close to the optimal levels estimated from diet experiments. This implies that host plants rarely provide a food resource which closely matches the budworm's most favorable conditions for growth and reproduction.

Terpenoid compounds did not appear to be related to resistance to budworm attack because there were no detectable differences between monoterpene concentrations in putatively resistant and susceptible trees. This result was somewhat surprising because terpene compounds have frequently been implicated as important determinants of western spruce budworm performance (Redak 1982, Cates et al. 1983a, 1983b, 1987, Perry and Pitman 1983, Redak and Cates 1984, Cates 1985, Shepherd 1985, Wagner and Tinus 1985, Cates and Redak 1986, 1988, Campbell 1987, Hermann 1987, Wulf and Cates 1987, Wagner et al. 1989, 1990). However, the sample size was small (12 pairs of trees) and observations were highly variable, so the significance of the failure to detect differences may be open to question. Moreover, I only measured monoterpenes and sesquiterpenes, not larger terpenoids such as resin acids.

Several possible alternatives may explain why foliar nutrients were different between susceptible and resistant Douglas-fir trees. First, the susceptible trees may truly have inherently different nutrient levels owing to their genetic make-up. Second, the foliar chemistry of resistant versus susceptible trees may have been induced by the dissimilar defoliation histories, which are a consequence of some unmeasured tree properties (Piene 1980). If this is the case, it implies that budworm defoliation has a positive feedback for subsequent generations, as in the "resource regulation hypothesis" proposed by Craig et al. (1986). Third, it is possible that resistant trees support budworm populations equal to those supported by susceptible trees, but the larvae consume less of the annual foliage increment because a) the food contains more N and b) the trees produce more foliage. In other words, resistant trees suffer substantially less defoliation. A fourth plausible explanation involves phenology of budbreak. Resistant trees may break bud later than susceptible trees and consequently be consistently asynchronous with budworm emergence. I am investigating these alternative explanations in greenhouse bioassay experiments with replicated isogenic lines of resistant and susceptible trees.

SUMMARY

The western spruce budworm (*Choristoneura occidentalis*) and Douglas-fir (*Pseudotsuga menziesii*) provide a good model system by which to test the hypothesis that variation in host plant nutritional quality is a mechanism for plant resistance to herbivore attack. In this study I compared levels of several nutrients (nitrogen, sugars, phosphorus, potassium, calcium, magnesium, and zinc) and terpenes in foliage of Douglas-fir trees that were phenotypically resistant and susceptible to western spruce budworm defoliation. The field results were compared with the results of artificial diet experiments designed to determine the budworm's response curves to individual nutrients.

This first year's (1988) field data revealed that susceptible Douglas-fir trees had lower levels of foliar N and sugars than resistant trees, agreeing with predictions made from laboratory diet studies. Moreover, the susceptible trees had mineral/N ratios (for P, K, Ca, and Zn) which were closer to the optimal levels established in artificial diet studies. There were no detectable differences in monoterpenes between susceptible and resistant Douglas-fir trees.

ACKNOWLEDGMENTS

I would like to thank R.M. King, R.W. Tinus, and M.R. Wagner for their comments on the manuscript. I am grateful to J.K. Itami for assistance with the field work and to R. Foust and T. Huntsberger for conducting the chemical analyses. My western spruce budworm colony was started with egg masses obtained from the Insect Production Unit of the Forest Pest Management Institute, Forestry Canada, in Sault Ste. Marie, Ontario.

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