SPRUCE BUDWORM FECUNDITY AND FOLIAR CHEMISTRY: INFLUENCE OF SITE

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ABSTRACT

Two Maine spruce-fir stands having different soils were sampled to determine the relationship between spruce budworm weight (fecundity) and foliage quality. Although much of the variation in budworm weight was attributable to other factors, significant correlations between budworm weight and multiple foliar nutrient concentration variables suggest that foliage quality altering silvicultural practices such as fertilization may stimulate populations of the spruce budworm.

Introduction

One of the many questions that needs to be answered concerning the relationship between the spruce budworm (Choristoneura fumiferana Clem.) and the spruce-fir forest concerns the hypothesis that site productivity influences the susceptibility of these valuable forests to spruce budworm outbreaks. Quantification of this theoretical relationship is a highly desirable goal because the information could be used to develop a hazard rating scheme based on differential site productivity. This would facilitate decision making by forest managers or pest management specialists who must determine how and where to allocate limited time and financial resources.

In addition to the obvious variation in productivity associated with sites that have vastly different gross characteristics, it is also important to consider the more subtle variation in site productivity that may be expressed in differential foliar nutrient concentrations (Czapowskyj, 1979; Tilton, 1978). The latter is intuitively appealing because evidence suggests that nutritional, structural, and allelochemical quality of foliage consumed by budworm (Mattson and Koller, in press) may significantly alter important behavioral and population characteristics such as propensity to feed (Albert et al., 1982), survival of larvae, fecundity (Shaw et al., 1978), and oviposition (Stadler, 1974).

Forest fertilization is a means by which wood and fiber production can be increased in the spruce-fir forest. Fertilization, however, significantly alters foliar nutrient concentrations (Czapowskyj et al., 1980; Briggs et al., 1981). Inclusion of foliar nutrient information in an equation that defines the relationship between site productivity and the intensity and duration of budworm infestation would allow researchers to evaluate forest fertilization not only in the context of its primary goal of increased production, but also its impact on the spruce budworm. For example, Xydias and Leaf (1964) indicated that fertilization increased damage to white pine (Pinus strobus L.) by the white pine weevil (Pissodes strobi Peck), negating beneficial effect of this management option on tree growth and bole quality. A number of other studies have demonstrated the impact of forest fertilization and tree nutrition on insect and disease organisms (e.g., Baule, 1973; Campbell, 1976; Carrow and Graham, 1968; Cooke et al., 1978; Mitchell and Paul, 1974; Moore and Layman, 1978; Mustanoja and Leaf, 1965; Roberts and Chow, 1977; Smirnoff and Bernier, 1973; Weiner and Mirkes, 1972; White and Leaf, 1957).

The objective of our study in Maine was to quantify the relationship between selected physical characteristics of the spruce budworm and site productivity in mixed stands of red and white spruce (Picea rubens Sars.; Picea glauca (Moench) Voss.) and balsam fir (Abies balsamea (L.) Mill.) growing on two sites that differed in soil type and drainage. It is anticipated that the results of this and similar studies will contribute toward (1) the development of diagnostic criteria to evaluate the susceptibility of forest stands to budworm outbreaks based on analyses of host or site conditions and (2) elucidation of the consequences of inadvertently stimulating an increase in spruce budworm populations when spruce-fir stands are commercially fertilized.

Methods

Site Descriptions

Two study areas were selected during the 1980 field season as suitable for this investigation. The first, designated as the dry site, is located in Little Squaw Township, Piscataquis County, Maine, and is occupied by a 50-70 year-old stand consisting primarily of balsam fir and red spruce with lesser quantities of American beech (Fagus grandifolia Ehrh.) and yellow birch (Betula

alleghaniensis Britton). Stand basal area is approximately 230 square feet/acre at a density of about 470 trees/acre, with an associated site index of 53 for red spruce and 58 for balsam fir. Understory vegetation is limited to seedlings of the overstory species in addition to a number of herbaceous species. The soils belong to the Chesuncook catena and consist of a complex of the Telos and Chesuncook series. These soils were developed in glacial till derived from slates, phyllites, and a mixture of other dark and low grade metamorphic rocks. The Telos soil is a deep, somewhat poorly drained soil with a seasonal high water table depth of about eight inches. Internal drainage is moderate through the solum of this soil, with much of the water moving laterally across the surface of very compact glacial basal till that occurs at a depth of about 16 inches, which marks the depth of maximum root penetration. The deeper Chesuncook soil has a seasonal high water table depth of about 16 inches and exhibits tree root penetration to a depth of 18 inches. A compact layer of basal glacial till occurs at a 20 inch depth. Both the Telos and Chesuncook soils are classified as coarse-loamy, mixed, frigid, Aquic Dystrochrepts.

The second area, designated as the wet site, is located in Thorndike Township, Somerset County, Maine, and is occupied by a stand of similar age and composition to that on the dry site except for the presence of sugar maple (Acer saccharum Marsh.) and northern white cedar (Thuja occidentalis L.). Stand basal area is approximately 205 square feet/acre at a density of 55 trees/acre, with an associated site index of 48 for red spruce and 49 for balsam fir. The soils also belong to the Chesuncook catena but are members of the Monarda series of coarse-loamy, mixed, frigid, Aeric Haplaquepts. On this soil, root growth is restricted to an organic mat and an underlying cobble and gravel zone 2-6 inches thick. Although the seasonal water table depth varies with local precipitation, the root zone in this soil may not drain until several days after precipitation events (Schiltz and Grisi, 1980).

Budworm/Foliage Sampling and Analysis

A total of 38 randomly selected dominant and codominant balsam fir and red spruce trees with relatively full crowns and no evidence of excessive budworm feedings or other damage were chosen for analysis. Late stage larvae (sixth instar) and pupae were collected during the period of June 30-July 15, 1980, from 45 cm long midcrown branch tips taken from the midcrown of each of the sample trees using a pole pruner with basket attachment. When the population density permitted, enough healthy insects were collected to insure that 20 female moths would be obtained from each sample tree. The pupae were weighed the day of collection or within 24 hours of formation and placed in separate cups until moth emergence, at which time moths were weighed within eight hours of ecolsion, frozen, oven-dried at 60°C to constant weight, and reweighed.

Current (1980), one year (1979), and two year-old (1978) foliage for element analysis was collected in late August and early September from the upper third of the crown, Foliage analyzed for organic materials was obtained in early July from the same midcrown branches used for samples of late stage larvae. All foliage was put on ice in the field, and transferred to freezers the day of collection. Foliage for element analyses was oven-dried at 60°C to constant weight and ground in a Wiley Mill equipped with stainless steel fittings to a size that permitted passage through a 1 mm sieve. Subsample foliar N concentration were determined using the macro-Kjeldahl method (Wilde et al., 1972). Additional foliar subsamples were dry-ashed (Parrow, 1976) and analyzed for P using the amonium-molybdate-vanadate method (Jackson, 1958) and K, Ca, and Mg using atomic absorption spectrophotometry.

For organic analyses, freeze-dried foliage was ground to pass through a 100 micron sieve. A 70 mg subsample was mixed with 3 ml of methanol:chloroform:water (12:5:3), placed in an ultrasonic bath for ten minutes, centrifuged, and the supernatant decanted. This extraction process was repeated twice. To the combined supernatant, 2 ml chloroform and 4 ml water were added followed by mixing and centrifugation. Top layer volume was recorded and aliquots taken for phenolic and sugar analyses.

Total phenols were determined with Folin-Denis reagent using procedures recommended by Rosenblatt and Peluso (1944) on a semi-micro scale. Specifically, a 25 to 100 microliter extract was diluted with water to 7 ml followed by the addition of 0.3 ml of Folin-Denis reagent and 0.6 ml of a saturated solution of sodium carbonate. The solution was read at 730 nm after 30 minutes against a reagent blank. Gallotannin was used as a reference standard.

Flavanol content, including dihydrochalcones and proanthocyanidin oligimers, was determined with freshly prepared 1% vanillin in 70% sulfuric acid reagent (Swain and Hillis, 1959). A 25 microliter extract was added to each of two test tubes containing 1 ml water in an ice bath. One tube received 2 ml of reagent and the other 2 ml 70% sulfuric acid followed by mixing. The tubes were removed and read after 15 minutes against a blank of 25 microliters methanol, 2 ml reagent, and 1 ml water. Catechin served as a reference standard.

Condensed tannin content was estimated by forming anthocyanidins. This was accomplished by heating a 50 to 200 ml sample of extract in 5 ml of 5% concentrated hydrochloric acid in 1-butanol for 1.5 hrs at 95°C. The sample was read at 548 nm against a reagent blank. Correction for interfering pigments prevalent in early season samples was made by placing the sample in acetic acid, ethanol, 1-butanol, (1:3:16). A purified condensed tannin from July red oak leaves served as a reference standard.

Sugars were analyzed by gas chromatography. A 4 ml aliquot of extract was dried under nitrogen and silylated sugar oximes formed using hydroxylamine hydrochloride and hexamethyldisilazane in pyridine (Pierce Handbook and General Catalog, 1979-80). Phenyl-Beta-glucopyranoside was added as an internal standard and commercially available

reagent grade sugars serves as references. Chromatography was on a 2 m x 2 mm column of 3% OV-17 using a temperature program of 170 to 275°C at 10 C/min with detection by FID. Peak areas were integrated to mg/sample by the internal standard method.

Statistical Analyses

Using foliar nutrient concentration as measures of site productivity, Pearson correlations (Snedecor and Cochran, 1967) were generated to relate average pupal wet weight, moth wet weight, and moth dry weight to the N, P, K, Ca, Mg, fructose, glucose, sucrose, total free sugar, total phenol, flavanoid, and condensed tannin concentrations in the foliage from the different age classes on an individual tree basis aross both sites and species. Additionally, general linear models were constructed to determine which factors accounted for a significant amount of the variation in the budworm variables. In addition to the foliar nutrient concentration values, dummy variables that defined the different study sites and species examined were tested for inclusion in these models (Freund and Littell, 1981).

Results and Discussion

The correlation coefficients between the budworm and foliar nutrient concentration variables are provided in Table 1. Both budworm variables were highly significantly correlated with foliar N concentrations in all foliage age classes. The strongest correlations occurred in current year foliage. Both budworm variables were also highly significantly correlated with glucose, fructose, and total free sugar concentrations in current year foliage. These findings are consistent with the results of Harvey (1974, 1975), Shaw and Little (1977), and others, who demonstrated that the spruce budworm develops better on foliage that contain sugars and nitrogenous compounds at higher levels. Both budworm variables were also significantly correlated with Mg, total phenol, and flavanoid concentrations in current year foliage, while pupal weight was significantly correlated with P, Ca, and condensed tannin levels in current year foliage and with K concentrations in two year-old foliage. In all cases the significant correlation coefficients were positive. While it was not surprising to find pupal weights positively correlated with nutrients and carbohydrates since these are required for growth, the positive correlation with phenolic and tannin levels was unexpected. These compounds supposedly function as digestion inhibitors by binding with protein (Feeney, 1969); hence, would be expected to be negatively correlated with weight gain.

The data indicate that foliage with higher nutrient concentrations is likely to foster development of spruce budworm pupae and moths with greater individual mass and, presumably, fecundity. This suggests that high foliar nutrient concentrations caused by inherent differences in site quality or the result of silvicultural practices such as fertilization may increase the fecundity of the spruce budworm to such an extent that the net effect of such practices may actually be a reduction in wood and fiber production.

The linear models containing the factors that account for a significant amount of the variation in the budworm variables are provided in Table 2. The model with pupal weight as the dependent variable produced an r-square value of 0.29, while the model with moth dry weight as dependent variables yielded a r-square of 0.69. In both models, the dummy variables specifying site and specific differences were statistically significant. The only

Table 1. Pearson correlation coefficients between pupal weight or adult dry weight and foliar chemistry.

	Pupal wet weight Foliage age			Pupal dry weight Foliage age		
	Two-year	One-year	Current	Two-year	One-year	Current
N	0.471***	0.520***	0.634***	0.460***	0.849***	0.583***
P	-0.094	-0.025	0.415	-0.248	-0.205	0.197
K	0.355**	0.191	-0.365	0.254	0.176	-0.144
Ca	-0.063	0.046	0.466***	-0.163	-0.050	0.308
Mg	-0.036	0.217	0.567***	-0.029	0.201	0.493***
Fructose	0.487	-----	0.688***	0.422	-----	0.621**
Glucose	-0.109	-----	0.750***	0.649**		
Sucrose	0.139	-----	0.347	0.124	-----	0.263
Total free sugars	0.319	-----	0.731***	0.272	-----	0.706***
Total phenols	0.105	-----	0.634**	0.207	-----	0.483*
Flavanoids	-0.281	-----	0.614**	-0.183	-----	0.501*
Condensed tannins	0.438	-----	0.502*	0.551	-----	0.440

*, **, and *** indicate significance at the alpha = .10, .05, and .01 levels, respectively.

foliar nutrient concentration value that contributed a significant amount of information about the budworm variables after differences due to site and species were accounted for was the K level in current year foliage, which was included in the model where moth dry weight was the dependent variable. The significant relationship between budworm variables and concentrations of foliar chemicals (Table 1) are totally masked by the inclusion of dummy variables specifying site and species differences. However, these variables have likely achieved significance due to the significant differences in nutrient concentrations that exist between sites (Table 3) and species (Table 4).

Table 2. Significant sources of variation in pupal weight and moth dry weight including estimates of regression coefficients and means.

Dependent Variable: Pupal Weight (g) r^2=0.29

Parameter	Estimate	Std. Error	T value	P > T
Intercept	0.0499	0.0035	14.39	0.0001
Site	0.0105*	0.0041	2.56	0.0159
Species	0.0101#	0.0040	2.53	0.0172

Table 2. continued

Dependent Variable: Moth Dry Weight (g) r^2=0.69

Parameter	Estimate	Std. Error	T value	P > T
Intercept	0.0018	0.0039	0.45	0.6556
Site	0.0040*	0.0014	2.89	0.0106
Species	0.0084#	0.0018	4.71	0.0002
K levels in current year foliage	0.0111	0.0043	2.61	0.0190

	Pupal Weight		Adult Dry Weight	
Site	Mean	Std. Error	Mean	Std. Error
Dry	0.066	0.003	0.018	0.001
Wet	0.056	0.003	0.013	0.001
Species				
Balsam Fir	0.064	0.003	0.020	0.001
Red Spruce	0.054	0.003	0.013	0.001

*Multiply by 1 if site = dry, 0 if site = wet.
#Multiply by 1 if species = balsam fir, 0 if species = red spruce.

Table 3. Mean concentrations (%) of foliar chemicals in current, one and two year-old foliage by site.

	Two year		One year		Current	
	Dry	Wet	Dry	Wet	Dry	Wet
N	1.133	1.022*	1.221	1.110*	1.260	1.156
P	0.082	0.105*	0.092	0.111*	0.120	0.139
K	0.486	0.504	0.556	0.597	0.737	0.910
Ca	0.612	1.280*	0.760	1.405*	0.572	0.605*
Mg	0.103	0.142*	0.149	0.188*	0.175	0.155
Fructose	1.704	1.349	1.383	1.928	1.866	1.256
Glucose	3.016	3.270	2.450	1.652	3.591	0.999*
Sucrose	0.627	0.674	0.058	0.118	0.401	0.056
Total free sugars	5.345	5.171	4.890	3.700	6.005	2.311*
Total phenols	8.050	8.375	6.290	4.300	4.228	3.068*
Flavanoids	6.950	8.668	5.550	3.050	3.905	2.263*
Condensed tannins	5.800	5.148	3.540	3.100	2.902	2.282

*Indicates statistical significance between site at the alpha = 0.05 level.

Table 4. Mean concentrations (%) of foliar chemicals in current, one and two year-old foliage by species.

	Two year		One year		Current	
	Fir	Spruce	Fir	Spruce	Fir	Spruce
N	1.261	0.870*	1.304	0.990*	1.420	1.119*
P	0.097	0.098	0.101	0.108	0.136	0.129
K	0.533	0.463	0.578	0.589	0.637	0.906*
Ca	1.467	0.611	1.775	0.605*	1.032	0.418*
Mg	0.147	0.111	0.226	0.125*	0.245	0.132*
Fructose	1.420	-----	1.383	1.928	2.030	1.479*
Glucose	3.219	-----	2.450	1.652	5.555	1.313*
Sucrose	0.665	-----	0.058	0.118	0.720	0.069*
Total free sugars	5.206	-----	4.890	3.700	8.307	3.001*
Total phenols	8.310	-----	6.290	4.300	6.014*	2.755*
Flavanoids	8.324	-----	5.550	3.050	5.320*	2.377*
Condensed tannins	5.278	-----	3.540	3.100	3.646*	2.219*

*Indicates statistical significance between species at the alpha = 0.05 level.

Examination of respective site and species means indicated that pupae and moths from the dry site were significantly heavier than those from the wet site, and pupae and moths from balsam fir trees were significantly heavier than those that fed on red spruce. Although both site and species factors are significant, the differences attributable to species are greater than those due to site.

Conclusions

The results of this study support the hypothesis that size (fecundity) of the spruce budworm adults is, in part, related to site productivity as measured by obvious physical differenes in sites and/or foliar nutrient concentrations. The budworm variables examined in this study were significantly correlated with a number of foliar nutrient concentration values. Dummy variables that specified differences in sites and species sampled were statistically significant for all budworm variables examined in general linear models designed to identify sources of variation in budworm characteristics.

However, r-square values for the linear models are not satisfying, in that a large proportion of the variation in the budworm variables could not be accounted for by differences in site productivity as expressed by the variables selected. This, however, is not unexpected in view of the diverse extrinsic and intrinsic factors that may influence budworm fecundity (Miller, 1963). Furthermore, similar relationships must be determined for a range of site conditions and budworm population histories to assure that the results obtained are representative of and applicable to a broader range of field conditions. This is especially important in view of interstand differences that may exist in regression models that describe fecundity as a function of budworm size (Miller, 1957). Numerous studies have demonstrated a relationship between insect fecundity and food quality. The question that must be addressed now concerns the biological significance of statistically significant results. For example, how many eggs are represented by a difference of 0.010 g in mean pupal weight? Is this difference enough to significantly alter the population dynamics of the budworm?

Although experimental results are not conclusive and are based on a limited number of samples, evidence suggests that those interested in improving spruce-fir forest productivity through fertilization will need to balance the opportunity to generate additional revenue from increased outputs of wood and fiber against the possibility that elevated foliar nutrient concentrations will stimulate destructive populations of the spruce budworm.

Acknowledgements

The authors gratefully acknowledge the CANUSA project for supporting this research effort and for the contributions of Ann Kenney and Sharon Nygaard.

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