

THE ROLE OF VARIATION IN DOUGLAS-FIR FOLIAGE QUALITY IN THE SILVICULTURAL MANAGEMENT OF THE WESTERN SPRUCE BUDWORM

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ABSTRACT

The objectives of this paper were to discuss 1) the consequences of phenotypic and genetic variation in known and potential host defensive chemicals (or antifeedants) in Douglas-fir to the western spruce budworm, and 2) how this variation in antifeedants, as well as primary nutrients, relates to stand composition, a major aspect in silviculture management. Significant variation in the production of host defensive chemicals and primary nutrients of the current year's foliage appears to be a widespread characteristic of Douglas-fir. Variation in these chemistries occurs among populations, within populations, within an individual tree, within a growing season, and due to aspect, thinning, and burning.

The consequence of among-population variation in Douglas-fir primary and antifeedant chemistry to the budworm was tested using reciprocal transplants of two populations of budworm among three Douglas-fir sites. Female and male budworm collected from Montana trees, when reared on Idaho and Utah trees, showed significant reduction in dry weight production as compared to their response on native Montana trees. Budworm collected from Idaho trees, when reared on Montana trees, were not significantly different in their dry weight production compared to their performance on their native Idaho trees. However, when Idaho budworm were reared on Utah trees, males and females showed significant reduction in biomass production when compared to their response on their native Idaho trees. Furthermore, it was found that tree foliage collected from all three sites differed in volatile (e.g., terpenes) and carbohydrate chemistry. Using concentrations of terpenes and acetates typically found in Douglas-fir foliage of these three populations, tricyclene, beta-pinene, camphene, limonene, bornyl acetate, geranyl acetate, and citronellyl acetate were found to increase Montana budworm mortality and decrease dry weight production when compared to the control diets. Idaho budworm mortality increased and dry weight production decreased when budworm were reared on camphene, bornyl acetate and geranyl acetate. These data suggest that the phenotypic, and likely genetic, differences among Douglas-fir populations in antifeedants may have led to genetic-based host race formation in budworm populations.

The natural variation in Douglas-fir foliage quality, if maintained, should enhance the effectiveness of the commonly recommended silvicultural practices in producing vigorous Douglas-fir stands against the budworm. In addition, abiotic and biotic stress appears to ameliorate the natural variation in Douglas-fir often resulting in increased susceptibility of a stand to the budworm. Management practices that increase tree or stand stress should be avoided.

INTRODUCTION

Silviculture, or the theory and practice of controlling the establishment, composition, constitution, and growth of forests (Society of American Foresters 1971), represents an important option toward the reduction of the adverse effects of pests and pathogens in forest ecosystems. Silvicultural treatments can result in an alteration of the forest substrate in such a manner that the population dynamics of insect pests, such as the western spruce budworm, will be adversely affected (Carlson *et al.* 1985). Furthermore, these treatments provide the significant advantage of fostering productive and vigorous forests over the long-term.

Carlson *et al.* (1985) and Wulf and Cates (1987) note that stand susceptibility to the western spruce budworm is affected by the interaction among regional climate, site climate, and tree and stand factors. Tree and stand factors include the types of tree species in the stand (i.e., shade tolerant or intolerant), species composition, degree of intraspecific genetic variation, stand vigor, stand density, height-class structure, stand maturity, and proximity to susceptible stands. Other than climatic factors, all of these factors can be changed through silviculture treatment. Stand and tree factors have been inferred to be important influences in the population dynamics of forest pests even though little experimental evidence is available to judiciously test these inferences (Carlson *et al.* 1985).

The objective of this paper is to discuss one major aspect of stand composition, that is, the magnitude of intraspecific phenotypic and genetic variation in foliage quality in Douglas-fir, to describe some of the potential consequences of this variation to the budworm, and to discuss how silviculture relates to foliage chemistry and budworm success. To accomplish this objective, first described is the variation found in volatile compounds, and to a limited extent in nitrogen, minerals, and carbohydrate content in Douglas-fir foliage. Volatiles are natural plant products produced by Douglas-fir and are typical of chemicals that are often referred to as antifeedants (Heron 1965) or host defensive chemicals. Secondly, natural patterns in the production of volatiles in Douglas-fir foliage between trees resistant and susceptible to budworm, and within the same tree but among growing seasons, will be addressed. Finally, a study will be presented showing the effect of different populations of Douglas-fir on different populations of budworm. This study shows that the dry mass production of two budworm populations responded in significantly different ways when budworm larvae were reared on three different populations of Douglas-fir. This same study also demonstrated that the Douglas-fir populations were all significantly different in their volatile (terpene, acetate, and sesquiterpene) chemistry as well as their soluble carbohydrate chemistry. Furthermore, several of the volatile compounds effectively increased budworm mortality and

reduced biomass production when budworm were exposed to these chemicals in agar diets. This paper represents a compilation of published data in combination with data published for the first time on carbohydrate chemistry variation among populations of Douglas-fir (Figure 6), the effects of terpenes on budworm mortality (Table 5), and variation in terpene chemistry among years for a single tree (Figure 5).

METHODS

Quantifying Douglas-fir Foliage Chemistry

All methods used to quantify terpenes, acetates, sesquiterpenes, unknown volatiles (hereafter referred to as terpenoids), nitrogen, and soluble carbohydrates either in foliage or synthetic diets have been published previously (Carlson and Cates, this volume). Consequently, only brief descriptions of these methods are given here for the data found in Tables 1-5 and Figures 1-6. Terpenoids and unknown volatiles were extracted from ground tissue with ether, the volume standardized, and an internal standard added. Quantification was by a capillary gas chromatograph equipped with an OV-101 or 100% methyl polysiloxane column (Cates and Zou 1990; Cates and Redak 1988, 1986). Peaks were identified by co-chromatography using authentic standards and by GCMS analysis. Percent nitrogen was determined using microkjeldahl techniques (Redak and Cates 1984) and carbohydrates by capillary gas chromatography (Carlson and Cates, this volume). Terpenoids and carbohydrate content were expressed as mg/g dry weight unless otherwise noted. Determination of terpene evenness, as defined as the degree of deviation of a tree's chemistry from the population average, was accomplished using Simpson's index calculation (Pielou 1975).

Western Spruce Budworm as a Bioassay of Douglas-fir Population Resistance or Susceptibility

Field Studies

Susceptibility of Douglas-fir trees to the budworm was determined by rearing budworm on the current year's growth as outlined in Cates and Redak (1988) and Redak and Cates (1984). Data gathered using these methods apply to Figures 2-6. Rearing budworm on trees of different populations provided some information on genetic variation in the budworm.

Reciprocal transplants of budworm from Montana and Idaho to tree populations in Montana, Idaho, and Utah involved methods described in Cates and Zou (1990). A total of 36 Douglas-fir trees of uniform age (50-70 years old), height, and crown diameter were selected at sites near Missoula, Montana, Island Park, Idaho and the Oquirrh Mountains, Utah. Budworm larvae were collected from Montana and Idaho sites, sorted to 3rd instar, and transported back to their 'natural' site and to each of the 'foreign' sites. Adults of budworm larvae 'transported' to a foreign site and then returned within two days to their native trees, were not significantly different (ANOVA, $p < 0.05$) from nontransported adults, the larvae of which were reared on their native trees. Larvae were transported in ice-cooled containers

among sites in 6-ounce cups, and were reared to pupation in nylon screen bags on the current year's growth on branch tips 45 cm long (Cates and Redak 1990). Approximately 250-500 larvae from each population were placed on trees at each site. The budworm population at the Oquirrh Mountains, Utah site was extremely sparse during this study such that insufficient numbers of larvae were available for reciprocal transplant to Montana and Idaho. Pupae were collected from trees, taken to the laboratory at the Intermountain Research Station in Missoula, or the Chemical Ecology Laboratory at Brigham Young University, and adults were allowed to emerge. Data in Tables 2 and 3 and Figures 2-5 were gathered using these methods.

In order to minimize sampling error, budworm were placed on foliage of the same developmental stage, in the midcrown of each tree, and on trees that had identical budbreak times. Larvae were placed on the trees when current year's foliage had expanded about 2.5 cm. Foliage collected for chemical analysis was collected at the same developmental stage for each population. Further details on the methods used are found in Cates and Zou (1990).

Studies Using Terpenes and Acetates in Agar Diets

In an attempt to test a cause and effect relationship between terpenoid chemistry and budworm parameters, and to lessen the concerns about foliage development differences and abiotic environmental effects, budworm were reared on agar diets containing terpenes and acetates. Methods used followed those of Robertson (1979) as modified by Cates and Zou (1990). Concentrations of nitrogen, carbohydrates, and volatiles used in the agar diets were typical of those found in current year's foliage of resistant Douglas-fir trees. Mineral concentrations were not adjusted. Larvae emerging from eggs were used as the bioassay (Cates and Zou 1990; Cates *et al.* 1987). Diets were monitored for volatiles and soluble carbohydrates by gas chromatography and for nitrogen by microkjeldahl analysis to determine the actual concentrations of chemicals in the diets during the experiments. Based on these analyses, agar diets were changed every two days to maintain constancy in nutrition and antifeedants during the experiments. Larvae were reared individually in 2.5 cm diameter petri dishes to prevent cannibalism. All experiments were carried out under controlled environmental conditions of 16-hour photoperiod, 24.6°C constant temperature, and 45% relative humidity (Cates and Zou 1990). Parameters measured for each diet containing terpenoids were average larval mortality and average adult dry weight production (Cates and Zou 1990; Cates *et al.* 1987). Data gathered using these methods are found in Tables 5 and 6.

Statistical Methods

Data in Table 1 describing the variation found in Douglas-fir were generated from several studies and involved correlation, discriminant, and ANOVA statistical analyses. Experimental designs, methods, and statistical procedures are outlined in detail in Cates and Zou (1990) and Cates and Redak (1988). To determine the effect of foliage quality from different populations of

Douglas-fir on the budworm, dry weight production was compared using a student's t-test ($p \leq 0.05$) for 1987 data and ANOVA ($p \leq 0.05$) for the 1989 study (Table 3). ANOVA was used to test whether differences in individual terpenoids existed between different Douglas-fir populations (Table 4). In an attempt to show a cause and effect relationship between budworm performance and agar diet concentrations of terpenes and acetates, larval mortality and adult dry weight production of larvae reared on diets containing terpenes and acetates were compared to mortality and dry weight production on control diets (not containing terpenes and acetates) by ANOVA ($p \leq 0.05$).

Table 1.—Types of variation in volatile terpenes, acetates, sesquiterpenes, and other volatiles, and nitrogen and soluble carbohydrate content, in current year's foliage of Douglas-fir.

Types of Variation	Chemicals		
	Terpenes	Nitrogen	Soluble Carbohydrates
Among populations throughout western U.S	X	X	X
Tissue development (or within-season) variation within a population	X	X ¹	X
Variation in same population among years	X	X	X
Among crown levels within a tree	X	--	--
Among branches within a crown level	X	--	--
Between sun and shaded branches	X	--	--
Due to site thinning or burning	X	--	X
Within a population due to aspect	X	--	--
Within a population due to water stress	X	X	--

¹Also differences between 'resistant and susceptible' trees within a population for phosphorus and potassium (after Clancy 1991).

-- = not determined

RESULTS AND DISCUSSION

Variation in Terpene and Volatile Chemistry of Douglas-fir

Table 1 summarizes several types of variation known to exist in the current year's foliage of Douglas-fir in terpenes, acetates, sesquiterpenes, and other unidentified volatile chemicals, and also in nitrogen and soluble carbohydrate content. Populations separated by only 1 km differ significantly in their quantitative production of at least 6 of 11 terpenes and acetates (Cates and Zou 1990). Populations sampled across western U. S. were shown to be significantly different, both

qualitatively and quantitatively, in individual terpene, acetate, and sesquiterpene production (Cates and Redak 1988).

As the current year's tissue develops through the growing season, some of the terpene, sesquiterpene, acetate, and tannin chemistry increases while nutrition generally decreases (Wagner *et al.* 1989; Cates *et al.* 1987; Horner *et al.* 1987). Tissue development changes in primary nutrition and secondary metabolites may be a major reason why budworm prefer young foliage as compared to mature foliage. Other types of significant variation noted were among crown levels within a tree, among branches within a crown level, and between sun and shaded branches, all of which increase the mosaic of foliage qualities that can exist within an individual tree.

We find it intriguing that trees change their terpene and volatile chemistry among years (Table 1, Figure 1). From 1981 through 1983, 75 trees in a New Mexico population were sampled and analyzed for terpene and volatile chemistry using identical methods. Stepwise discriminant analysis showed that trees in this population qualitatively and quantitatively changed their chemistry each of the three years ($p < 0.001$). Discriminant function 1, which accounted for 79% of the discriminant variation, showed that trees sampled in 1983 were higher in thujene and beta-pinene as compared to 1981 and 1982 trees (Figure 1). Trees sampled in 1982 were higher in limonene, terpinolene, linalool, sesquiterpene 4, and were all closer to the population average when compared to 1981 and 1983 trees. Trees sampled in 1981 were intermediate in these characteristics as compared to samples taken the other two years (Cates and Redak 1988). In evaluating discriminant function 2 which explained 21% of the variation, this variable also showed that trees sampled in 1982 and 1983 were closer to the population average as compared to the trees sampled in 1981.

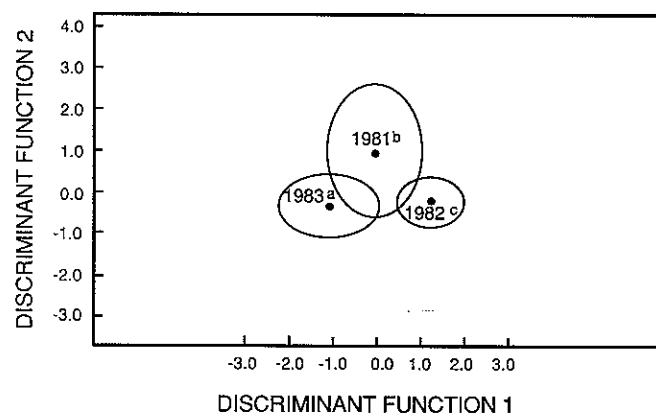


Figure 1.—Discriminant analysis showing the among-year (1981-1983) variation in terpene content of the current year's foliage of Douglas-fir at the Barley Canyon, New Mexico site. Years followed by different letters are significantly different ($p < 0.001$). Centroids are shown with a one standard deviation ellipse (after Cates and Redak 1988).

The cause of this among-year variation was not readily discernable but may have been due to 1) shifts in carbon/nutrient balances within the trees due to abiotic differences among years, 2) foliage quality changes due to an increasing budworm population, and/or 3) long-lived trees such as Douglas-fir possessing a mechanism to alter or vary qualitatively and quantitatively

defensive chemistry (Cates and Redak 1988). Sampling different sizes of young tissue was ruled out since a deliberate effort was made to obtain the same sized tissue from all trees for each of the three years. Although no abiotic environmental data were taken, a weather station within a short distance of the site revealed no recognizable changes among years in weather patterns. Field and laboratory experiments are underway to test the ability of Douglas-fir to genetically vary secondary metabolite production, and, if this occurs, to test the effect of this variation on budworm.

Thinning (Carlson and Cates, this volume) and prescribed burning (Carlson and Cates, unpublished) can increase variation in the production of secondary metabolites and are approaches that maintain a vigorous, highly productive forest. The potential of using fire and thinning as tools to create and maintain tree vigor and chemical diversity in foliage quality is discussed in the Summary section.

Table 1 also shows the interactive effect that aspect and water stress can have on Douglas-fir foliage quality. For example, control trees vigorously growing on a gentle south-facing slope did not differ in their terpenoid chemistry or nitrogen content when compared to vigorously growing trees located in the bottom of these gentle-sloping canyons. However, when a water stress was applied, trees on the south-facing slope showed significantly greater water stress compared to their controls and compared to water-stressed trees in the canyon bottoms. As noted by numerous authors (e.g., Wulf and Cates 1987; Carlson *et al.* 1985; Johnson and Denton 1975) drought or water stress often (but not always) predisposes trees (Cates *et al.* 1983) and stands to greater stand susceptibility and vulnerability. Budworm outbreaks mostly occur across warm, dry interior Douglas-fir types but also are documented in cool, moist subalpine/spruce types, albeit at varying frequencies and infestation intensities. It does appear that a common feature among these outbreaks is some type of physiological stress among trees and stands. Stresses may be due to abiotic factors such as drought, improper stocking levels on certain sites, 'mismatches' between species and site, or too high population levels of insect pests and/or pathogens (Carlson *et al.* 1985). We suggest here that its overall effect is to reduce the tremendous variation in foliage antifeedant chemistry (and tree bole quality with regard to bark beetle-pathogen complexes) that is noted in Table 1 for Douglas-fir. The outcome appears to eventually result in increased insect and pathogen problems due to enhanced nutrition that results when imbalances between tree physiological processes, within-tree carbon/nutrient allocation, and site resource availability occur (e.g., water, light, nutrient availability) (Wulf and Cates 1987; Cates *et al.* 1983; White 1974).

The variation described above is typical of Douglas-fir, as well as other gymnosperm and angiosperm woody perennials (Wagner *et al.* 1989; Denno and McClure 1983; Gambliel *et al.* 1985; Smith 1977; von Rudloff 1973). Whether this magnitude of variation is typical of other coniferous species is unknown although similar levels of population variation across the range of a species has been described for spruce, firs, and ponderosa pine (Smith 1977; Zavarin 1975; von Rudloff 1972). This variation does raise important questions: What is the significance of this variation and why has it been selected for within this species? We suggest below that this variation has arisen, at least in part, due to the interaction of trees with their

physical environment and in mediating the coevolutionary interactions between host, insect pests, and pathogens (Cates and Zou 1990; Cates and Redak 1988).

Effect of Terpenes, Acetates, and Unidentified Volatiles on Different Populations of Western Spruce Budworm

Data from field studies where different budworm populations were reared on various populations of Douglas-fir indicate that this coevolutionary scenario between budworm and Douglas-fir foliage chemistry variation appears to have occurred (Table 2). A 3-year study using budworm from Taos, New Mexico, and rearing them on a population of Douglas-fir at Barley Canyon, New Mexico, indicates that beta-pinene, limonene, bornyl acetate, and some unidentified volatiles were inversely related to female dry weight production. Alternatively, camphene, myrcene, terpinolene, and terpene evenness were all positively related to female dry weight production. However, success of budworm (as measured by larval density and defoliation level) from a Boulder, Montana site, when reared on trees at the same site, was inversely related to myrcene, bornyl acetate, the acetate fraction of the foliage, and to some unidentified volatiles (Table 2). Only beta-pinene and terpene evenness were positively related to budworm performance (as measured by larval density and defoliation level) at this site.

Table 2.—The response of western spruce budworm populations to terpenes, acetates, and unidentified volatiles in different populations of Douglas-fir. P = a positive relationship between the foliage quality variable the level of budworm success¹. I = an inverse relationship between the foliage quality variable and budworm success.

Foliage Quality Parameter	Budworm Population	
	Taos, N.M.	Boulder, MT
Tricyclene ²		
Alpha-pinene		
Beta-pinene	I	P
Camphene	P	
Myrcene	P	I
Limonene	I	
Terpinolene	P	
Bornyl acetate	I	I
Acetate fraction ³		I
Unidentified volatiles	I	I
Terpene evenness	P	P

¹For positive relationships success equates to increased dry mass production or greater budworm densities and defoliation levels (for MT); for inverse relationships success equates to reduced dry mass production or reduced budworm densities and defoliation (for MT).

²Blanks indicate that the foliage quality parameter did not significantly contribute to the correlation model.

³At least 67% of the acetate fraction is composed of bornyl acetate. (Modified from Cates and Redak 1988; Cates and Redak 1986; Cates *et al.* 1983).

These data suggest that budworm from different populations do not respond to terpenes and other volatiles in the same way; i.e., all budworm populations are not alike. Data in Table 2 show that the same chemical may adversely affect budworm from one population but be positively related to budworm

performance in another. There are, however, two general patterns that we note in these data and in other studies. Those are 1) bornyl acetate seems to be highly toxic to most budworm populations, and 2) terpene evenness, as calculated using Simpson's index, is a reasonably good predictor of budworm success. Consequently, the closer to the population average that the chemistry of a tree is, or the greater a tree's terpene evenness, the greater its susceptibility to the budworm. This appears to be accurate for about 65% of the trees within a Douglas-fir population. However, a high Simpson's index, or a high level of terpene evenness, does not always indicate a high level of susceptibility to the budworm (see discussion below concerning Figure 5).

Patterns in Chemical Production Between Resistant and Susceptible Trees

We have studied how secondary metabolites vary between resistant and susceptible Douglas-fir trees by rearing budworm on trees, analyzing the current year's foliage for secondary metabolites and relating the quantity and patterns of production of these chemicals to budworm dry weight production (e.g., Cates and Zou 1990; Cates and Redak 1988). Patterns in the production of terpenoids was quantified using Simpson's index of diversity (Pielou 1975). A high Simpson index value indicated that the trees' chemistry approached that of the population average; the lower the index the greater the trees diverged from the population's average chemistry. The former also indicates a high level of terpene evenness and the latter a low level of evenness. Consequently, two values were available to assess the level of resistance or susceptibility of a tree to the budworm. These were the actual budworm bioassay value (i.e., dry weight production per tree) and the Simpson's index or level of terpene evenness for each tree. For each of the approximately 75 trees that were studied in 1981, 1982, and 1983 from the Barley Canyon, New Mexico site, budworm dry weight production and a Simpson's index were determined. Trees were then ranked from the lowest to the highest Simpson's index. For each year the six trees with the lowest index and the six with the highest index were selected. ANOVA was used to test whether the indices were significantly different between trees judged to be resistant (small Simpson's index) or susceptible (large Simpson's index). ANOVA also was used to determine if female dry weight production within a given year was different between the presumably resistant and susceptible tree groups.

Cates and Zou (1990) showed that for 1981, trees that were resistant (produced small females) to budworm showed an average Simpson's index of 0.69 whereas trees that produced large female budworm averaged 0.81 ($p=0.001$) (Figure 2). Female dry weight production was significantly higher on trees with larger Simpson's indices as compared to dry weight production of trees with smaller indices ($p=0.001$) (Figure 2). The most significant differences in chemistry were the higher levels of camphene, linalool, and especially bornyl acetate in resistant trees as compared to susceptible trees. Furthermore, smaller differences in increased levels of alpha-pinene, beta-pinene, and limonene existed in the resistant tree terpene pattern (Figure 2).

Similar chemical patterns for six resistant and six susceptible trees emerged for trees sampled in 1982 and 1983 (Figures

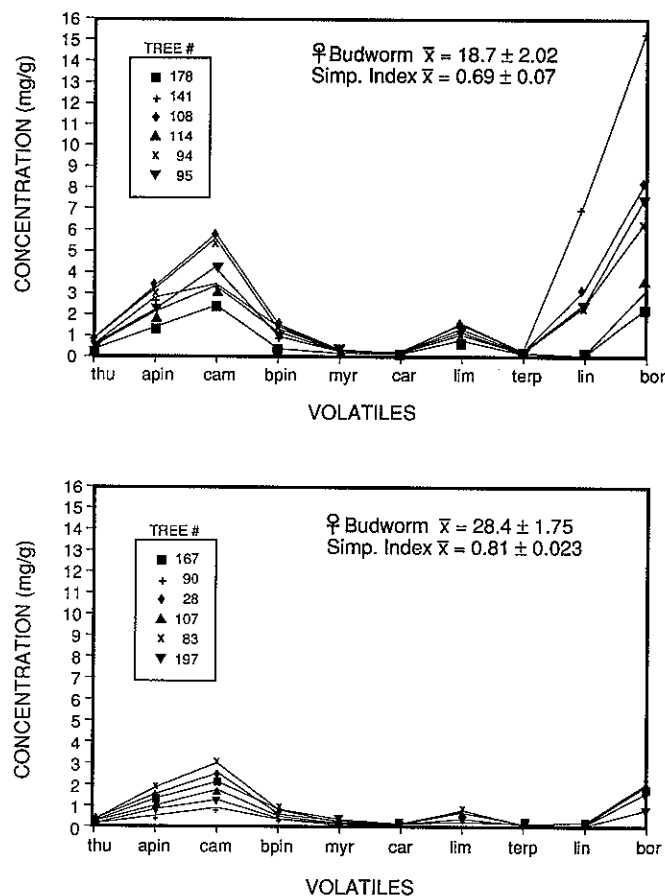


Figure 2.—Patterns in terpene production between resistant (upper panel) and susceptible (lower panel) trees for 1981. For each set of trees, female budworm dry biomass (mg) and Simpson's index values are given (\bar{x} ,sd). Legend: thu = thujene, apin = alpha-pinene, cam = camphene, bpin = beta-pinene, myr = myrcene, car = carene, lim = limonene, terp = terpinolene, lin = linalool, bor = bornyl acetate. (after Cates and Zou 1990).

3 and 4) (Cates and Zou 1990). Resistant trees were higher in alpha-pinene, camphene, and bornyl acetate content as compared to susceptible trees. As in 1981, resistant trees from 1982 and 1983 produced significantly smaller female biomass production and had smaller Simpson's indices as compared to susceptible trees. In addition, 1982 foliage of resistant and susceptible trees contained three sesquiterpenes (cadinene and sesquiterpenes 3 and 4) (Figure 3) that were not detected in the foliage collected during 1981 (Figure 2). Foliage collected in 1983 contained the sesquiterpene copanene which was not detected in either 1981 or 1982 foliage (Figure 4).

Furthermore, the chemical patterns typical of resistant and susceptible trees remained the same for each of the three years (Figures 2, 3, and 4). However, the 1981 resistant and susceptible trees depicted in Figure 2 were not the same set of trees observed for the 1982 data set (Figure 3), but several trees reappeared in the 1983 data set (Figure 4). No trees switched completely from one category to another; that is, relatively resistant or susceptible trees in 1981 remained relatively resistant or susceptible in 1982 and 1983 (Cates and Redak 1988).

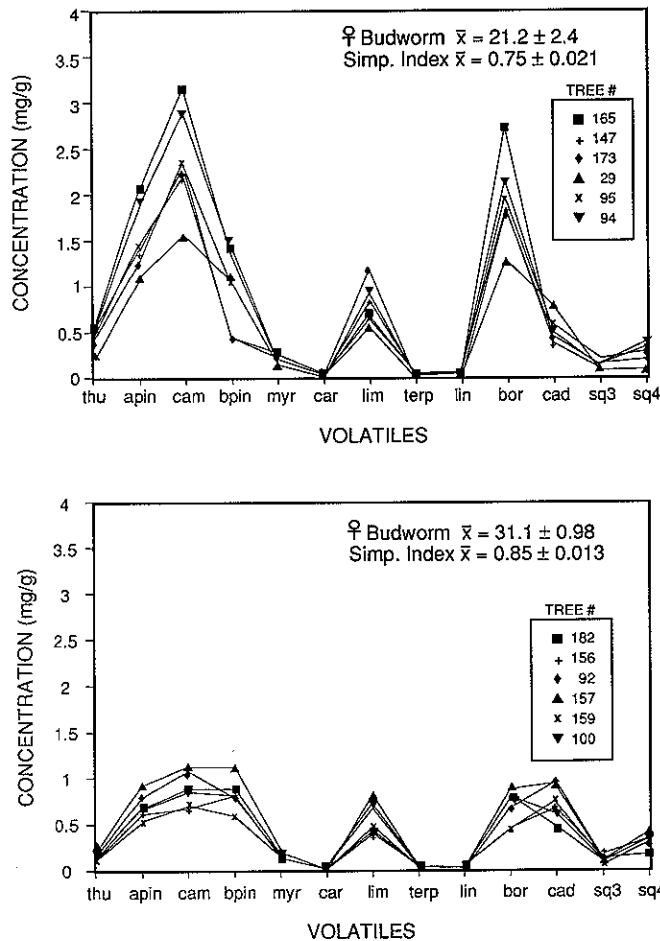


Figure 3.—Patterns in terpene production between resistant (upper panel) and susceptible (lower panel) trees for 1982. For each set of trees, female budworm dry biomass (mg) and Simpson's index values are given (\bar{x} ,sd). Legend: thu = thujene, apin = alpha-pinene, cam = camphene, bpin = beta-pinene, myr = myrcene, car = carene, lim = limonene, terp = terpinolene, lin = linalool, bor = bornyl acetate, cad = cadinene, and sq3 and sq4 = unidentified sesquiterpenes (after Cates and Zou 1990).

Shifts in Terpene, Sesquiterpene, and Volatiles Among Years but Within the Same Tree

The above patterns between resistant and susceptible trees were typical of about 60% of the trees in the population. Another pattern that characterized about 15% of the trees is shown in Figure 5. For 1981, tree 133 showed the same basic pattern noted above, that is, foliage high in alpha-pinene, camphene, beta-pinene, limonene, and bornyl acetate. However, 1982 foliage showed a significant decrease in overall terpene quantity as compared to 1981 foliage. Also noted were relatively higher concentrations of beta-pinene and cadinene in 1982 as compared to 1981 and a decrease in alpha-pinene, camphene, and bornyl acetate in 1982 as compared to 1981. Foliage from 1983 was typical of the qualitative pattern showed in 1981 but with significant decreases in quantity of the major peaks. These terpenoid patterns were associated with average female budworm dry weight productions of 16.1 mg for 1981, 20.5 mg

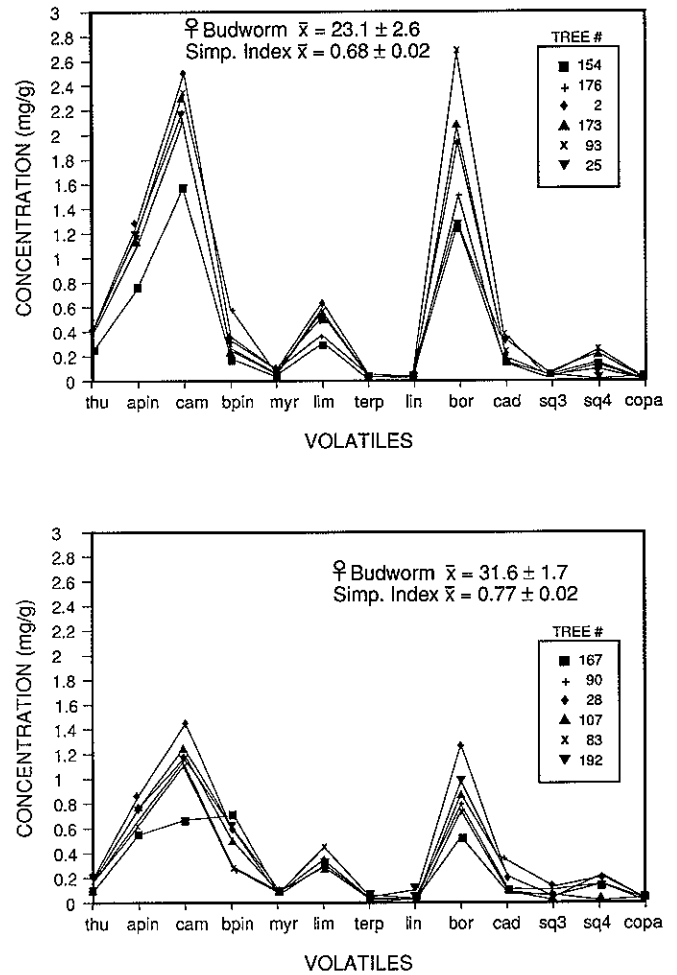


Figure 4.—Patterns in terpene production between resistant (upper panel) and susceptible (lower panel) trees for 1983. For each set of trees, female budworm dry biomass (mg) and Simpson's index values are given (\bar{x} ,sd). Legend: thu = thujene, apin = alpha-pinene, cam = camphene, bpin = beta-pinene, myr = myrcene, car = carene, lim = limonene, terp = terpinolene, lin = linalool, bor = bornyl acetate, cad = cadinene, sq3 and sq4 = unidentified sesquiterpenes, copa = copanene (after Cates and Zou 1990).

for 1982, and 19.5 mg for 1983. All of these values were typical of budworm dry weight data recorded in Figures 2, 3, and 4 for resistant trees. However, the Simpson's indices, or the level of terpene evenness, were not consistent in predicting the degree of susceptibility of this tree to the budworm. The indices were 0.81 for 1981, 0.79 for 1982, and 0.78 for 1983. All of these values were typical of susceptible trees and not resistant trees (see Figures 2-4). It appears that Simpson's index may be useful in predicting the degree of susceptibility of most of the trees in a population but not all of them. This statement is made under the assumption that the Barley Canyon Douglas-fir population structure is 'typical' of most populations. Based on the variation noted in Douglas-fir and the varied habitats in which it grows, this assumption clearly needs further testing. We are currently evaluating other indices that may be more robust in their predictive nature.

Data presented in Figures 2, 3, 4, and 5 show just two patterns among resistant and susceptible trees through time. These,

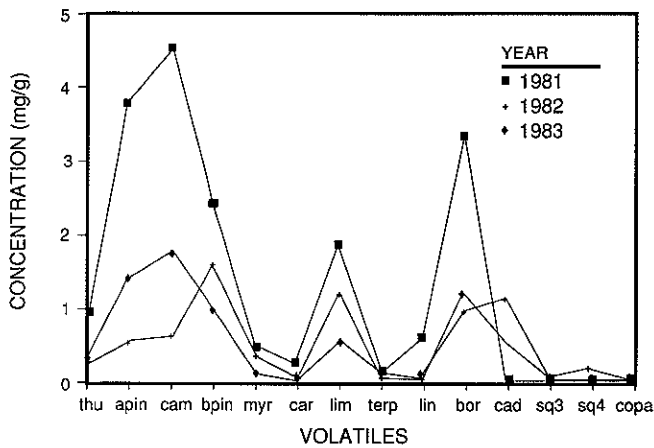


Figure 5.—One example of a variable pattern in terpene production within a single tree among years. Legend: thu = thujene, apin = alpha-pinene, cam = camphene, bpin = beta-pinene, car = carene, lim = limonene, terp = terpinolene, lin = linalool, bor = bornyl acetate, cad = cadinene, sq3 and sq4 = unidentified sesquiterpenes, and copa = copanene.

along with other individual tree patterns not shown here, increase the heterogeneity of food resources available to the budworm and increase the mosaic of foliage qualities that larval budworm face during the selection of individual host trees.

Coevolutionary Consequences of Douglas-fir/Budworm Interactions

In order to provide greater understanding about the relationship between variation in foliage quality of Douglas-fir populations discussed above, and the response of budworm populations to this variation, several field and laboratory experiments were undertaken. These experiments were designed to determine how different populations of Douglas-fir affected different populations of budworm.

Budworm Reciprocal Transplants Among Douglas-fir Populations

Male and female budworm from the Greenough, Montana site, when reared on trees at the Island Park, Idaho, and Utah sites, resulted in adults that produced significantly less biomass as compared to adult dry matter production on Montana trees (Table 3) (Cates and Zou 1990). Reduction in biomass production was greater on the Idaho and Utah trees in 1989 as compared to the 1987 experiment. A similar pattern emerged when Idaho budworm were reared on Utah trees, but Idaho budworm on Montana trees were not adversely affected by Montana tree foliage quality. It appears that budworm from Idaho would survive equally as well on Montana trees as they do on Idaho trees.

Based on these two budworm populations, and the response of those from Barley Canyon, New Mexico and Boulder, Montana, budworm populations may be as variable in response to foliage quality differences, as is the foliage of their host populations. The next step was to determine if the Douglas-fir populations were significantly different in their chemistry.

Table 3.—Dry Weight production (mg) of adult western spruce budworm reared on their native tree population and on a foreign tree population.

Reciprocal Transplant	Year	Male		P	Female		P
		\bar{x}	s d		\bar{x}	s d	
Montana Budworm							
Montana BW on							
Montana trees	1987	18.5±4.4			38.4±8.7		
(control)	1989	16.1±3.7			32.2±6.0		
Montana BW on							
Idaho trees	1987	13.8±4.8	<0.05		28.4±9.3	<0.05	
	1989	11.6±2.4	0.0001		11.6±7.9	0.0001	
Montana BW on							
Utah trees	1987	10.4±4.4	<0.05		22.3±0.6	<0.05	
	1989	3.5±0.6	0.0001		7.8±2.4	0.001	
Idaho Budworm							
Idaho BW on Idaho							
trees	1987	15.9±3.6			32.5±8.3		
	1989	12.0±3.5			26.6±8.0		
Idaho BW on							
Montana trees	1987	15.3±3.8	NS		31.8±9.2	NS	
(control)	1989	12.1±2.3	NS		27.6±4.3	NS	
Idaho BW on							
Oquirrh trees	1987	11.6±3.3	<0.05		17.3±4.2	<0.05	
	1989	5.0±0.8	0.0001		10.1±4.1	0.003	

*Within each year and sex, vertical means were compared using student's t-test for 1987 data and ANOVA for 1989 data.

Volatile and Carbohydrate Chemistry of Montana, Idaho, and Utah Douglas-fir

When the current year's foliage from each of the three Douglas-fir populations was analyzed for terpenes and other volatiles, it was found that all populations were chemically different. Concentrations of 11 of the 16 chemicals were significantly different between Montana and Idaho foliage (Table 4). Fifteen of the 16 chemicals were significantly different between Montana and Utah foliage, and 13 of the 16 chemicals differed when the chemistry of the Idaho population was compared to that of Utah trees. In addition, Idaho trees contained the greatest total concentration of the chemicals analyzed (13.3 mg/g fresh weight), followed by Utah trees (10.5 mg), and then the Montana trees (5.3 mg).

Possibly the Montana trees were susceptible to Idaho budworm simply because their total terpene production was significantly lower. In addition, individual compounds known to be toxic to the budworm (Cates and Zou 1990; Cates *et al.* 1987) were significantly higher in concentration in the Idaho foliage. For example, bornyl acetate was about twice the concentration in Idaho foliage as compared to Montana foliage (Table 4). Total production of terpenes, however, is not likely to be the only reason that the Utah population adversely affected Montana and Idaho budworm. The Utah population was significantly higher in several unidentified terpenes, as well as producing a high quantity of other terpenes toxic to the budworm such as bornyl acetate. These unidentified compounds may have contributed to the toxicity of Utah trees, and Montana and Idaho budworm may not be well adapted to these

Table 4.—Comparison of terpene chemistry* of Douglas-fir populations used in reciprocal transplant studies of budworm (modified from Cates and Zou 1990).

	Douglas-fir Population			F		
	Montana \bar{x}	Idaho \bar{x}	Utah \bar{x}	MT vs ID	MT vs UT	ID vs UT
Tricyclene	0.25	0.52	0.35	0.0001	0.0001	0.0001
Alpha-pinene	1.03	1.84	1.53	0.0001	0.0001	0.0027
Camphene	1.68	3.36	2.38	0.0001	0.0001	0.0001
Beta-pinene	0.51	0.76	0.32	0.0003	0.0017	0.0001
Myrcene	0.71	0.15	0.18	0.0001	0.0001	0.0001
Limonene	0.37	0.79	0.85	0.0001	0.0001	0.1375
Terpinolene	0.03	0.1	0.07	0.0001	0.0001	0.0014
Bornyl acetate	1.99	3.9	2.6	0.0001	0.0014	0.0001
Junipene	0.03	0.08	0.03	0.0001	0.8869	0.0002
Alpha-humulene	0.12	0.14	0.04	0.2619	0.0002	0.0001
Unknown 3	0.10	0.13	0.24	0.2984	0.0001	0.0006
Unknown 5	0.08	0.09	0.16	0.5014	0.0001	0.0092
Unknown 6	0.15	0.15	0.28	0.9014	0.0001	0.0004
Unknown 8	0.05	0.07	0.15	0.1074	0.0001	0.0001
Unknown 9	0.13	0.28	0.37	0.003	0.0001	0.1154
Unknown 10	0.12	0.87	0.98	0.0001	0.0001	0.5660
Total (mg/g)	5.3%	13.3	10.5	--	--	--

*Chemistry data were analyzed by ANOVA. Data are expressed as mg/g fresh weight.

chemicals. Current efforts in the Chemical Ecology Laboratory are attempting to isolate and identify these chemicals.

With regard to soluble carbohydrates significant variation existed among the Montana, Idaho, and Utah populations (Figure 6). Although all populations produced some level of the compounds depicted in Figure 6, the Montana population was higher in the alcohol inositol, and in the carbohydrates fructose and mannose. Alternatively, the Montana trees were lowest in sucrose, glucose, galactose, citric acid, and shikimic acid as compared to the Utah and Idaho trees. Utah trees were highest in sucrose, glucose, and galactose, and the foliage tended to have less variation in the concentrations among trees (carbohydrate evenness) as compared to the Montana population. Utah trees also were higher in citric and shikimic acids as compared to the Montana foliage. Idaho trees tended to be somewhat intermediate, but were shunted toward higher concentrations of sucrose, glucose, galactose, citric acid, and shikimic acid, and showed less variation among trees in the production of these compounds compared to Montana foliage.

We note that populations of trees from Idaho and Utah showed the greatest resistance to the budworm when compared to the Montana trees. Also, Idaho and Utah trees produced the highest concentrations of total terpenes and other volatiles (13.3 and 10.5 mg/g fresh weight, respectively) compared to Montana trees (5.3 mg/g). Taken together, these data indicate that phenotypic resistance and vigor of Idaho and Utah trees are greater than the Montana trees, and therefore, trees from these populations may be less susceptible and less vulnerable to budworm attack. Possibly genetic differences in resistance exists among these populations as well.

Budworm Population Response to Terpenes and Acetates in Agar Diets

Reciprocal transplants of budworm showed that budworm biomass production, with one exception, was adversely affected

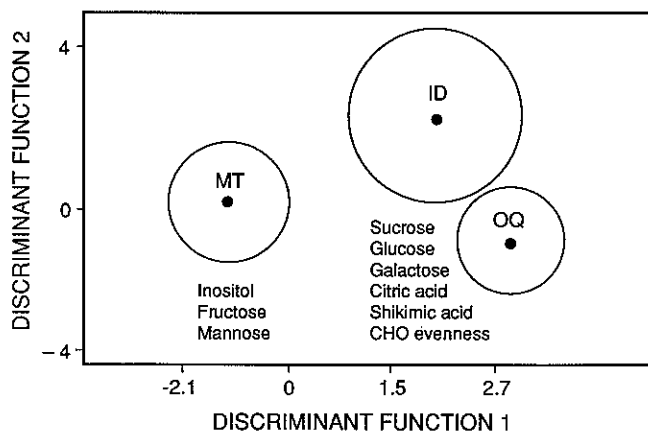


Figure 6.—Discriminant analysis showing the among-population variation in carbohydrates, an alcohol, and 2 acids among the Montana (MT), Idaho (ID), and Utah (OQ) sites. All populations are significantly different from one another at $p < 0.001$.

when budworm were reared on a 'foreign' population. In addition, the Douglas-fir populations were shown to be significantly different in several terpenes, an acetate, sesquiterpenes, and unidentified volatiles, as well as in soluble carbohydrates, an alcohol, and two acids. A logical next step was to determine if a cause and effect relationship existed between the terpenoids and budworm populations.

Budworm were reared on synthetic diets containing terpenes and acetates, nitrogen, and carbohydrates in concentrations similar to those found in the foliage of Douglas-fir (Cates and Zou 1990). Camphene, limonene, bornyl acetate, citronellyl acetate, and geranyl acetate significantly affected Montana budworm mortality when compared to the controls (Table 5). Idaho budworm mortality, however, was significantly affected by camphene and bornyl acetate, and to a limited extent by limonene and terpinolene ($p=0.08$). For the Montana and Idaho budworm

populations, bornyl acetate rendered the greatest larval mortality (88.6% and 86.7%, respectively). Camphene was significant in its effect on larval mortality as compared to the controls, but the level of mortality was 55% and 57%, respectively, for the two populations (Table 5).

Table 5.—Average percent mortality of Montana and Idaho budworm when reared on agar diets containing terpenes and acetates.

Terpenes	% Mortality			
	Montana*		Idaho*	
	%	P	%	P
Tricyclene	19.0	0.33	27.8	0.53
Alpha-pinene	11.5	0.85	30.0	0.43
Beta-pinene	20.6	0.25	19.0	0.98
Camphene	55.2	0.00	57.1	0.00
Myrcene	12.9	0.72	20.0	0.93
Limonene	35.5	0.01	38.5	0.08
Terpinolene	24.0	0.17	45.0	0.08
Bornyl Acetate	88.6	0.00	86.7	0.00
Geranyl Acetate	31.0	0.03	33.3	0.27
Citronellyl Acetate!	44.4	0.00	37.5	0.17
Control	11.1	--	18.0	--

* N = 36 larvae per treatment

Several terpenes and acetates reduced dry weight production of both females and males from the two budworm populations (Table 6) (Cates and Zou 1990). For the Montana budworm population, tricyclene, beta-pinene, and camphene significantly reduced female dry biomass production when compared to the controls. For the Idaho population, geranyl acetate significantly reduced female dry mass production. For males from the Montana population, tricyclene, alpha-pinene, camphene, myrcene, and terpinolene significantly reduced dry mass production as compared to the controls (Table 6) (Cates and Zou 1990).

Bornyl acetate caused such a high level of larval mortality (Table 5) that less than four larvae pupated. This resulted in too few male and female adults emerging from pupae to carry out a statistical analysis comparing adult dry biomass production between the control diet and that containing bornyl acetate (see Table 6). However, we can indicate the adverse impact that this compound imparts to budworm pupae by comparing Montana and Idaho pupal weights between diets. Montana female pupae from larvae reared on the control and bornyl acetate diets weighed 19 mg and 14 mg, respectively ($p < 0.0007$). For the Idaho budworm, female pupae on control diets weighed 16 mg while those on diets containing bornyl acetate weighed 13 mg ($p < 0.006$). For male budworm, Montana pupae from larvae reared on control and bornyl acetate containing diets weighed 11 mg and 9 mg, respectively ($p < 0.01$). Idaho male pupae on control vs. the bornyl acetate diet weighed 10 mg and 7.5 mg, respectively ($p < 0.026$). Consequently, the few larvae that did survive on the bornyl acetate diets produced significantly lighter pupae compared to those on the control diets.

Taken together, these data show that not only are the Douglas-fir populations different in at least secondary metabolites and carbohydrates, but, as the reciprocal transplant data suggested,

so are the two budworm populations. Furthermore, different chemicals adversely affect male and female budworm.

Table 6.—Dry weight production (mg) of Montana and Idaho budworm when reared on terpenes and acetates incorporated into an agar diet.

Sex/Compound	Population			
	Montana	P*	Idaho	P*
Female				
Tricyclene	0.024	0.0001	0.033	0.70
Alpha-pinene	0.033	0.28	0.034	0.44
Beta-pinene	0.029	0.007	0.035	0.23
Camphene	0.02	0.0001	0.028	0.36
Myrcene	0.031	0.06	0.028	0.28
Limonene	0.031	0.06	0.028	0.34
Terpinolene	0.03	0.089	0.025	--**
Bornyl acetate	--**	--**	--**	--**
Geranyl acetate	0.033	0.56	0.025	0.05
Citronellyl acetate	0.035	0.99	0.032	0.74
Control	0.035	--	0.031	--
Male				
Tricyclene	0.011	0.0001	0.013	0.63
Alpha-pinene	0.014	0.021	0.014	0.41
Beta-pinene	0.015	0.073	0.015	0.25
Camphene	0.011	0.0001	0.012	0.66
Myrcene	0.013	0.0005	0.011	0.20
Limonene	0.014	0.07	0.012	0.36
Terpinolene	0.013	0.013	0.012	0.38
Bornyl acetate	--**	--**	--**	--**
Geranyl acetate	0.015	0.10	0.013	0.94
Citronellyl acetate	0.015	0.09	0.014	0.54
Control	0.017	--	0.013	--

*Comparison of budworm dry weight of control vs. agar diet with terpene by ANOVA.

**Only 1-3 adults of the initial 35 larvae survived resulting in a sample size too small for statistical analysis for bornyl acetate. For terpinolene, only 3 females ended up in this diet. All the rest were males.

SUMMARY

Relationship Among Variation in Foliage Chemistry, Genetic Control, and Budworm Responses

Stand composition is suggested to be one major factor determining the degree of susceptibility of a stand to budworm. Factors included in stand composition are the number of different species and the proportion of each in the stand, the successional status of the stand, and the genetic variation in the host species (Carlson *et al.* 1985). We have discussed one aspect of stand composition, that being the role of phenotypic and genetic variation in the production of Douglas-fir foliage chemical characteristics, and have shown some of the consequences of this variation to the budworm.

Significant variation in the production of terpenoid secondary metabolites, or potential antifeedants, and in the primary nutrients (nitrogen, minerals, and carbohydrates) of the current year's foliage appears to be a widespread characteristic of Douglas-fir (von Rudloff and Rehfeldt 1980). Populations sampled as close as 1 km, as well as populations sampled across the western U.S., were shown to be qualitatively and quantitatively different in the production of terpenoids including the

highly toxic compound bornyl acetate (Cates and Redak 1988). Part of this variation is due to sampling Douglas-fir populations that include two varieties (coastal and inland or Rocky Mountain) both of which are known to differ in leaf oil components (i.e., terpenes, acetates, and sesquiterpenes) (von Rudloff 1973). But within each of these varieties large phenotypic variation occurs in foliage quality characteristics. Within populations, individual trees, crown levels, tissue types, and branches displayed quantitative variation in terpenes, acetates, alcohols, sesquiterpenes, and unidentified volatiles.

One source of variation that appears to be absent, or at least less common, in the current year's foliage of Douglas-fir is that of long-term induction (Haukioja *et al.* 1985, Denno and McClure 1983). Long-term induction of secondary metabolites is described by incremental yearly increases, up to a point, in potential defensive compounds in response to defoliation. None of the data accumulated by Cates and colleagues suggests induction in needle terpenes and volatiles to the same extent observed in deciduous species (Cates and Redak 1988). Possible reasons for the lack of long-term induction of secondary metabolites in Douglas-fir and most evergreen conifers and angiosperms may be related to the needles functioning as a storage organ to a greater degree than do the leaves of deciduous species (Cates and Redak 1988; Kramer and Kozlowski 1979). Well described, however, is an induction of terpenoids in the bole of Douglas-fir and other conifers (Gambliel *et al.* 1985 and references therein). The nitrogen and carbohydrate substrates needed to drive this type of induction are present in the phloem and sapwood. Consequently, long-term induction may be highly tissue dependent.

However, there are several types of induction described for secondary metabolites (Gambliel *et al.* 1985). One type includes increase in quantities of compounds that previously were not detected in plant tissues. This was described for Douglas-fir where the same trees changed their chemistry quantitatively and qualitatively each of three years. The effect of this type of variation and long-term induction are the same; that is, they provide an element of 'surprise' to the budworm in foliage quality characteristics. The among-year variation needs further investigation particularly in documenting how common it is, under what circumstances it occurs, and the genetic mechanism, if such exists, that controls this variation.

Sufficient evidence exists supporting the genetic control of the production of terpenes, acetates, and sesquiterpenes (Gambliel and Croteau 1984, and references therein; Hanover 1975). This evidence is further supported by the observation that individual Douglas-fir trees, as well as trees within other species, show strong phenotypic resistance against the budworm (Wulf and Cates 1987; McDonald 1985). The reciprocal transplant studies among 'native' and 'foreign' populations of Douglas-fir presented in this paper, and elsewhere (Cates and Zou 1990), also indicate significant phenotypic resistance in Douglas-fir against the budworm. This contention is further enhanced by the robust among-population variation in terpenoid production in Douglas-fir (Cates and Redak 1988). Finally, in progeny tests McDonald (1985) has shown a strong family heritability for defoliation, and a significant relationship between oviposition behavior and source stand. Resistance to budworm feeding had a heritability of 0.42. These data suggest that

significant genetic gains could be obtained through intensive breeding programs.

The recent attention given to the role that variation in carbohydrates, nitrogen, and other minerals play in Douglas-fir/budworm interactions has yielded interesting data. Carbohydrates are known to vary significantly among Douglas-fir populations (see above) and between resistant and susceptible trees (Clancy 1991; Clancy *et al.* 1988). With regard to individual carbohydrates Zou and Cates (submitted for publication) have shown using agar diet studies that galactose is highly toxic to the budworm as compared to other individual carbohydrates and to the control diets. Significant variation among trees within a population, among at least four Douglas-fir populations, is known to exist for nitrogen (Clancy 1991; Horner *et al.*; Cates *et al.* 1983). Furthermore, larvae from two budworm populations from New Mexico and Idaho show different growth rate responses to varying nitrogen levels (Cates *et al.* 1987). Concentrations of nitrogen and phosphorus are significantly lower whereas potassium is higher in the foliage of susceptible trees compared to resistant trees (Clancy 1991).

The variation described above is consistent with the hypothesis that primary and secondary metabolites of the current year's foliage of Douglas-fir interact to form a mosaic of variation that can influence budworm success in a negative manner (Cates and Zou 1990; Cates *et al.* 1983). This mosaic in foliage quality among- and within- Douglas-fir populations has led to genetic divergence in budworm (Whillite and Stock 1983). Essentially, budworm have become somewhat specialized and adapted to local population foliage quality characteristics, and patterns in the production of these characteristics. The result is a coevolutionary interaction with one selective force; for example, budworm response to a variable resource, 'feeding' back upon an already variable foliage (Cates and Rhoades 1977; Rhoades and Cates 1976). Budworm as a selective pressure may have favored greater diversity, variation, and divergence in Douglas-fir chemistry.

Different budworm populations do not respond to terpenes and other volatiles in the same manner. Data presented above suggest that the same chemical from one Douglas-fir population may adversely affect one budworm population, but may be positively related to the performance of another budworm population. Furthermore, the sexes are affected differently by the chemistry of Douglas-fir. Males tend to be much more susceptible to foliage quality characteristics than females.

Tree and Stand Stress in Relation to Forest Management Practices

It is important to note that biotic and abiotic stress can adversely modify the genetic control of foliage quality in Douglas-fir. When physiological stress occurs, the result is usually a change in foliage quality that favors the budworm. Male and female adult budworm from larvae reared on water stressed trees showed 20% and 30%, respectively, greater biomass production as compared to the controls (Cates *et al.* 1983). In addition, male and female larval survivorship on stressed trees was significantly greater. It appeared that not only were more budworm larvae surviving on stressed trees, but the adult dry mass production was greater. The magnitude of this dry mass change

is even more important when it is cast in the context that greater dry matter production is significantly related to greater egg mass production (Redak and Cates 1984). The observed relationship between tree physiological stress and high outbreak frequency and intensity appears to be the rule rather than the exception (but see Cates and Redak 1988, page 328; Wagner pers. communication). We suggest that generally the effect of stress is to decrease the natural variation found in Douglas-fir foliage quality, and thereby favor budworm growth, survival, and reproductive effort.

Some management practices of the 1900s have favored the development of stands and forests that appear to be moisture, nutrient, and light stressed, and hence, have become highly susceptible to the budworm (Carlson *et al.* 1983). For example, intensive fire prevention and reduced fire frequency have resulted in shade tolerant, budworm-susceptible conifer species becoming established over large areas (Arno 1980; Dickman 1978). In addition, certain selective harvesting practices remove the vigorously growing trees leaving low vigor, suppressed, and shade-tolerant trees (Schmidt *et al.* 1983; Sutherland 1983; Williams 1967). In general, it appears that these fire management and selective harvesting practices have increased forest and stand susceptibility to the budworm. Carlson *et al.* (1983) suggest that greater stand susceptibility has occurred because these past practices have increased the biomass of shade-tolerant trees, favored low-vigor-trees, created multistoried canopies, increased stand density and therefore moisture and nutrient stress, increased the proportion of hosts to nonhosts, and resulted in host types growing over large expanses (Fauss and Pierce 1969). Some of our current studies are designed to investigate the effects of stress in stand and forest susceptibility.

Phenotypic and Genetic Variation in Silvicultural Management

Although some other silvicultural treatments may be effective in certain circumstances, Table 7 shows the commonly recommended silvicultural practices that will result in vigorous forests and habitats and environments less favorable for the budworm (Carlson *et al.* 1985). Current evidence suggests that phenotypic and genetic variation is the 'name of the game' in Douglas-fir not only with regard to foliage quality parameters but also with respect to ecotypic variation in seed germination, growth rate, and other physiological adaptations (von Rudloff and Rehfeldt 1980; Rehfeldt 1979). That variation needs to be fostered with regard to insect pests and pathogens.

Each of the approaches outlined in Table 7 will maintain and enhance phenotypic and genetic variation in host as well as non-host tree species. Although not discussed in this paper, diversifying tree species composition within a stand is another source of foliage quality variation that is common to sympatric species (Wulf and Cates 1987). Where appropriate and representative of sound silvicultural practices, diversifying a stand with different host species will result in an enhancement of foliage chemical diversity (Wagner *et al.* 1989). This results in qualitatively and quantitatively different defensive mechanisms among host species that may increase energy expended by the budworm in detoxifying different compounds (Rhoades and Cates 1976).

Table 7.—Silvicultural practices suggested to reduce stand susceptibility to budworm (from Carlson *et al.* 1985).

- Strive for stand diversity in species composition by favoring seral trees and removing or otherwise discriminating against the most shade-tolerant host trees.
- Regulate stand density through appropriate release cuttings and thinnings to improve and maintain tree vigor and stand growth.
- Create and maintain even-aged stand structures by using even-aged regeneration systems, followed by periodic low and crown thinnings.
- Promptly remove all overwood trees once regeneration is established in seed-tree and shelterwood cuttings.
- Improve stand vigor by removing diseased, heavily infested, or otherwise unhealthy trees in all cuttings.
- Capitalize on phenotypic and genetic resistance to budworm by selecting the most heavily defoliated trees for removal. Retain the lightly or nondefoliated trees for seed trees; direct cone-collection programs to those phenotypes.
- Regenerate host stands at or before biological maturity as indicated by the culmination of annual growth.
- Diversify the host forest by creating seral stands in homogenous areas of late successional or climax stands.

Potentially, practices outlined in Table 7 increase vigor of individual trees, increase the proportion of non-hosts to hosts thereby reducing foliage available to the budworm, diversify the surrounding stands, and decrease the adverse effect of light, moisture, and nutrient stress. Biotic stresses from budworm defoliation also should be reduced. In addition, these practices should not only effectively manage against insect pests but should increase tree vigor against pathogens. Increased tree vigor feeds back on the original investment thereby further enhancing resistance, productivity, and vigor in the stands.

More information is needed with regard to the degree of short- and long-term effectiveness of these silvicultural approaches. Also, the benefit of these practices may vary given different sites, habitat types, and tree species conditions. We are undertaking research efforts to help answer these and other pertinent questions.

Research is needed concerning the positive effect that may be gained when certain practices are combined or sequenced. Fire and thinning represent an example of the potential that could be gained from using these practices at different sequences on different sites, on sites composed of different compositions and densities of host and nonhost species, in different habitat types, stages of stand development, or in stands presently susceptible to the budworm. For example, preliminary data suggest that fire may have an immediate effect on enhancing tree vigor and increasing variation in foliage quality (Carlson and Cates unpublished). Alternatively, the effect of thinning appears to enhance tree growth, vigor, and variation in foliage quality at a slower rate. However, thinning may provide significant benefits to the stand over a longer time period. Also, fire and thinning may change the carbon/nutrient balance in such a way that different types of variation in foliage quality parameters occurs, or that different types of antifeedants are favored.

In this paper we have mentioned only terpenes, acetates, alcohols, and sesquiterpenes in the foliage of Douglas-fir. However, numerous other genetically controlled secondary metabolites (Stafford 1990) in the monomeric phenolic and

tannin classes are present in Douglas-fir, some of which are known to be antifeedants (Hemingway and Karchesy 1989; Denno and McClure 1983; Rosenthal and Janzen 1979). Present studies in the Chemical Ecology Laboratory not only suggest that there are significant adverse effects attributable to the interaction between some soluble carbohydrates (e.g., galactose) and defensive chemical levels. The role of phenotypic and genetic variation in foliage quality parameters, budbreak (Wulf and Cates 1987; Cates *et al.* 1983), and other physical and physiological processes in the silvicultural management of the budworm, and other insect pests and pathogens, appears to be insufficiently explored.

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