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SEASONAL CHANGES IN FOLIAR TERPENES INDICATE SUITABILITY OF DOUGLAS-FIR BUDS FOR WESTERN SPRUCE BUDWORM

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Abstract—The terpene composition of current-year buds of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, was analyzed from before budburst to after buds were fully flushed. Terpene composition was measured at weekly intervals for several seasons at eight different locations in the southern interior of British Columbia, Canada. Discriminant functions relating terpene composition to suitability of buds for newly emerged western spruce budworm, *Choristoneura occidentalis* Freeman, were developed based on terpene profiles of the buds and bioassays measuring the suitability to budworms of a sister group of buds. Changes in percent composition of bud terpenes before and during budburst were closely associated with changes in the suitability of the buds to utilization by budworms at both the tree and site by date levels. Use of a degree-day scale for bud suitability removed much of the year-to-year variation, but remaining differences among sites suggest additional sources of variation influencing the insect–host plant relationship. The success of correctly classifying bud suitability using terpene profiles demonstrates the value of foliar terpenes as indicators of seasonal changes in suitability of Douglas-fir foliage during the critical spring emergence period of western spruce budworm. This indicator could be used to screen individual trees susceptible to budworm damage and identify sites at high risk of damaging defoliation.

Key Words—Douglas-fir, *Pseudotsuga menziesii*, western spruce budworm, *Choristoneura occidentalis*, foliar terpenes, host suitability, phenology, seasonal development, chemical indicators.

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INTRODUCTION

The western spruce budworm, *Choristoneura occidentalis* Freeman, is an important native defoliator of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, in western North America. This insect–host plant association extends over highly varied climatic zones. Analysis of historical defoliation and impact records suggest that regional-scale outbreaks are associated with areas of optimal synchrony between bud development of the host tree and budworm-feeding activity (Thomson et al., 1984). Synchrony between budworm activity and foliage development also influences local patterns of defoliation. Differences in relative severity of defoliation of putatively "resistant" vs. "susceptible" Douglas-fir during outbreaks are the result of intertree differences in foliage phenology and relative synchrony with local, developing budworms (Chen et al., 2003). Thus, the relationship between phenology of budburst of Douglas-fir and of western spruce budworm development may provide insight into the host–plant relationship at several ecological scales.

Thomson and Moncrieff (1982) produced a robust, empirical method of predicting budburst in Douglas-fir, but their model was not referenced directly to insect performance. Shepherd (1983) used a system of photographs to classify seasonal development of Douglas-fir buds into nine stages ranging from fully closed winter buds to expanded summer shoots. He then identified the critical stages of bud development in terms of survival of western spruce budworm as: (1) the overwintering bud stage when budworms could not penetrate the hard bud; (2) the swollen, soft bud stage that could be penetrated by budworms; and (3) the stages following bud flush when budworms became exposed feeders (Shepherd, 1992). His analysis of budworm survival focused on stages following bud penetration by the budworm and during the period of exposed feeding. Similarly, investigations of the role of associated changes in foliage nutrients and terpene composition in budworm fitness have been restricted to the period of development following budworm penetration of the current-year buds (Wagner et al., 1989; Cates and Zou, 1990; Chen et al., 2002). Little information has been available on foliar chemistry or budworm survival early in the season as buds are just becoming available as a resource to foraging budworms (Clancy et al., 1993). Host–plant relationships at this early seasonal stage play an important role in the population ecology of conifer-feeding budworms (Campbell, 1993; Nealis, 2003).

Nault (2003) examined seasonal changes in terpene composition of Douglas-fir foliage over a 3-year period at several sites in British Columbia (BC), Canada. Measurements began in early spring before budburst and included the earliest phases of bud development identified by Shepherd (1983). The results revealed highly dynamic shifts in relative concentrations of different terpenes during the early spring period in contrast to their relative stability over the remainder of the growing season (Nault, 2003). Seasonal changes in several terpenes characteristic of Douglas-fir buds resembled seasonal changes in the suitability of vegetative buds to spring-emerging larvae in other budworm systems (Nealis and Lomic, 1994). It seemed likely that these changes in terpenes could serve as indicators of bud suitability for western spruce budworm. Such an indicator would be less subjective than methods that rely on photographic interpretation (Shepherd, 1983) and would extend our understanding of the relationship between budworms and foliage chemistry to the critical period when budworms are foraging for feeding sites immediately following spring emergence.

This paper describes a set of discriminant functions based on terpene composition of current-year buds of Douglas-fir that accurately classify the suitability of those buds to exploitation by newly emerged western spruce budworm in early spring. The accuracy of predictions using terpenes as indicators of bud suitability is compared to predictions based on a degree-day model. Use of foliage chemistry results in models that are robust over a wide range of environmental conditions and allow rapid assessment of foliage suitability. This indicator can be used to quantify synchrony between local trees and budworms to interpret risk rating at the stand level as well as to identify relative susceptibility to defoliation of individual trees within a site.

METHODS AND MATERIALS

General. We used plant material collected directly from field sites. Eight sites were selected over a range of elevations where Douglas-fir dominates the forest community (Table 1). Sites 1 to 5 were in the Nicola Valley near Merritt, BC, and sites 6 to 8 were in the Okanagan Valley near Peachland, BC. All sites were in the Interior Douglas-fir (IDF) zone except site 5 which is an enclave of Douglas-fir within the Ponderosa Pine (PP) zone (Meidinger and Pojar, 1991). Temperature profiles for these sites for 1998 to 2003 were constructed from records obtained from the Meteorological Service of Canada for the two weather stations closest to the study sites: (1) Merritt STP (station #1125079, 50°7′N, −120°48′, 588 m); and (2) Peachland (station #1126070, 49°47′N, −119°43′, 345 m). Temperature regimes for each site were calculated using the program BioSIM (Régnière, 1996), which uses these nearest weather stations and adjusts for differences in location and elevation at the target sites based on estimated thermal gradients (Régnière and Logan, 2003). Daily degree-day accumulations above a temperature threshold of 4°C were calculated using daily maximum and minimum temperatures.

In seven sites, 10 codominant Douglas-fir trees were chosen at ∼10- to 20-m intervals along a 200-m transect. Only five trees were similarly selected at

TABLE 1. LATITUDE, LONGITUDE, AND ELEVATION OF SAMPLE SITES AND FREQUENCY OF SAMPLING FOR BIOASSAYS AND FOLIAR CHEMICAL ANALYSIS IN TWO REGIONS OF THE SOUTHERN INTERIOR OF BRITISH COLUMBIA, CANADA

Region and site	Latitude (N), Longitude (W)	Elevation (m)	Sampling frequency (April to July)			
			1998	1999	2000	2003
Nicola valley						
1	50°08′, 120°45′	1100	3	–	–	3
2	50°14′, 120°49′	950	4	–	–	4
3	50°11′, 120°40′	1050	4	8	5	4
4	50°14′, 120°39′	1350	4	12	7	5
5	50°11′, 120°40′	750	4	10	6	3
Okanagan valley						
6	49°45′, 119°48′	600	5	10	4	–
7	49°47′, 119°46′	850	5	10	3	–
8	49°47′, 119°46′	1050	4	10	4	–

site 5 in 1998 and 1999, but this was increased to 10 trees after 1999. Samples were taken approximately weekly and consisted of a single 45-cm branch tip removed without regard to directional quadrant from the midcrown of each tree at each sample date using pole pruners equipped with a cutting head. Branches were bagged, labeled, and returned to the laboratory where they were stored at 2°C in the dark until buds could be excised, usually within 3 days. Defoliation estimates were made by applying the method of Fettes (1950) to branches sampled in August after feeding was complete. Defoliation estimates were expressed as percentage defoliation of current-year foliage for each tree in all years (V.G. Nealis, unpublished data).

Western spruce budworm used in bioassays were derived from wild populations collected as late-instar larvae or pupae in the previous season. These insects were reared to adult and allowed to mate in the laboratory. Female moths were provided cut host foliage on which to lay egg masses. Egg masses were placed into a Petri dish covered with parafilm to which a triple-layer patch of cheesecloth had been attached to the inside surface, facing the egg masses. The dish was placed into a paper envelope with a window cut to expose the cheesecloth patch and incubated at 20°C L:D 16:8 hr. As budworms hatched, they moved toward the light, became embedded in the cheesecloth, and spun hibernacula. After 2 wks at 20°C, hibernating larvae were stored at 2°C to satisfy their diapause requirements until needed the following spring. To activate the budworms, the cheesecloth patch with the budworms was saturated with water, placed into a dry glass tube, and incubated at 20°C.

Bioassays to Determine Bud Suitability. Current-year buds and 2-years' previous shoot growth were excised from each branch on each sample date to determine their current suitability for western spruce budworm. The cut end of the shoot was inserted into a hole in a cork (3-cm diam). The cork served as a stand for the shoot. Freshly emerged western spruce budworms that were not fed yet were introduced to the base of the shoot at a ratio of one budworm per bud. Five buds per tree and five insects were used on samples from the earliest dates in the season. This was increased to 10 buds and 10 insects during the period of budburst and expansion. Thus, there were five or 10 buds tested for each of 10 trees on each sampling data at the site level.

A glass tube (3.5 cm in diam 15 cm long) was placed over the set-up to cage the budworms and the buds. These units were placed at 20°C, L:D 16:8 hr for 2 days to allow budworms to forage. After that time, the number of budworms that had successfully penetrated a bud was scored. This number was converted into a proportion of the cohort, ρ, that successfully established in buds and used as a measure of bud suitability for each tree on each sample date. An analogous measure for the site, P, was obtained by pooling across all trees within a site on each sample date.

Foliage Chemistry Assays. Detailed methods used to extract and analyze foliar terpenes are described by Nault (2003). Briefly, current-year vegetative buds were cut from the same branches as bioassay material and stored at −5°C until terpenes could be extracted (less than 1 mo). Sufficient buds from each branch sample were selected randomly to ensure a minimum total mass of ~0.3 g. To extract terpenes, tissues were homogenized in a solution of cold water, methanol, hexane, and an internal standard (methyl palmitate in iso-octane). The homogenized samples were centrifuged and the terpenes recovered in the hexane layer. Extracted terpenes in solution were analyzed on a gas chromatograph. Individual terpenes were identified by peak retention times. Identifications were confirmed by gas chromatography—mass spectrometry and gas chromatography—Fourier transform infrared spectroscopy. In all cases, blank samples without tissues were used to verify solvent purity. Individual terpenes were calculated as percent contribution to the total peak area recorded on the chromatogram and as milligrams per gram of green sample.

Analysis. Discriminant function analysis (STATISTICA, version 6.0; StatSoft Inc., Tulsa, OK) was used to develop classification algorithms distinguishing samples in which buds from individual trees were either unsuitable ($\rho < 0.5$) or suitable ($\rho \geq 0.5$) for budworms. The frequency of sampling and often rapid transition of buds from unsuitable to suitable (Figure 1A) precluded using more than two categories.

We explored several possible discriminant functions relating bud suitability to its terpene profile by dividing the available data into various, mutually exclusive training and test sets. To form a training set, the sample set was first divided into six, ordinal categories based on ρ values between 0 and 1. In order to avoid overrepresentation of extreme values ($\rho = 0.0$ or 1.0) and to ensure adequate

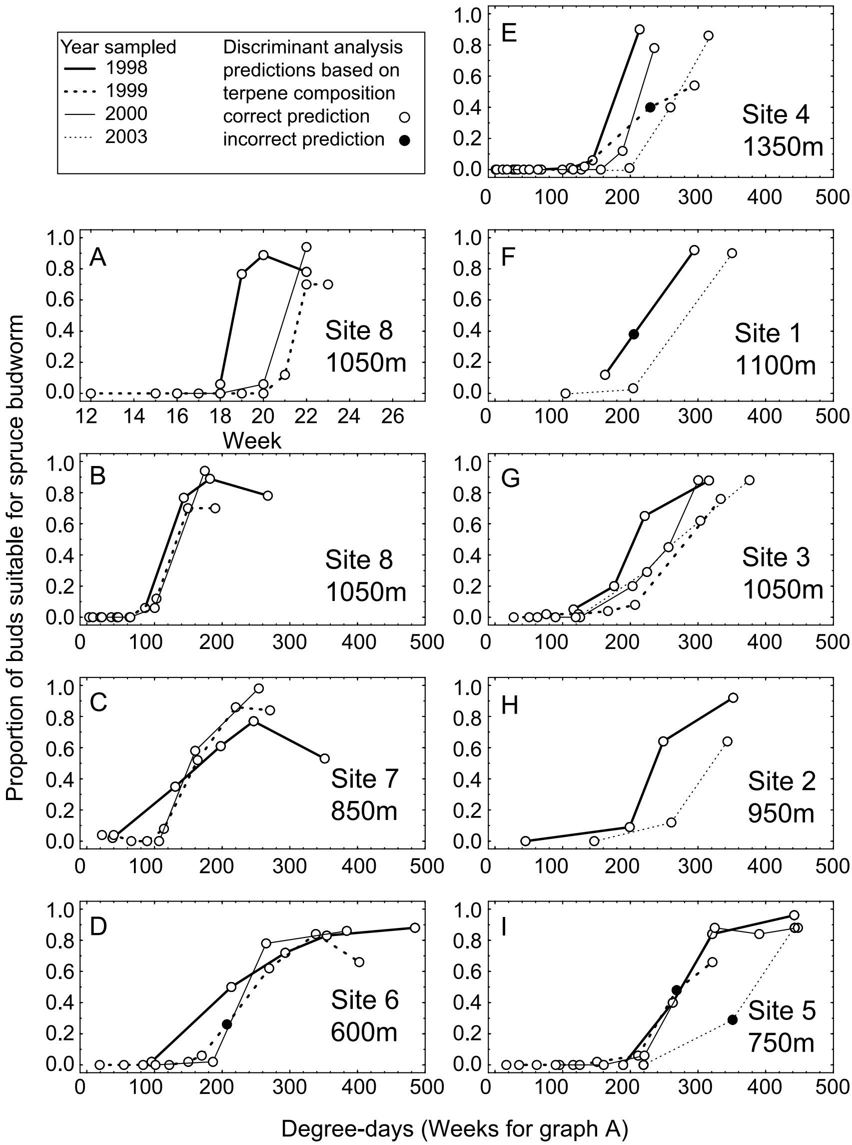

FIG. 1. Seasonal changes in bud suitability, *P*, for western spruce budworm **A** by week at site 8 and **B**–**I** by accumulated degree days above 4°C at all sites between 1998 and 2003. Open symbols indicate correct classifications and closed symbols indicate incorrect classifications using discriminant function B (Tables 2 and 3).

representation of observations throughout the range of ρ values, an equal number of samples was then randomly chosen from each of these six categories. Several discriminant functions were developed and tested as follows:

(1) Function A. Data were stratified by year(s) (1998–2000 vs. 2003) pooled over all sites (Table 2). The training set consisted of an equal number of samples from all sites from the 1998 to 2000 group selected as described above. The test set used all samples from all sites in 2003. The procedure was repeated using 2003 data to compile the training set and all 1998 to 2000 data as the test set. The discriminant functions distinguished suitable and unsuitable buds based upon percent composition of terpenes. Results are presented for each procedure as well as the sum of the two test sets combined. The identical procedures using actual terpene concentrations instead of percent composition of terpenes as the measure returned similar, but slightly less accurate, predictions and are not reported further.
(2) Function B. Data were stratified by sites pooled over all years (Table 2). The training set consisted of samples randomly chosen from four sites (two from each valley) in all years, and the test set was comprised of samples from the remaining four sites in all years. As in (1), the procedure

TABLE 2. CLASSIFICATION FUNCTIONS STRATIFIED BY YEAR OR SITE USING EITHER PERCENT COMPOSITION OF TERPENES OR DEGREE DAYS ABOVE 4°C AS VARIABLES

Classification				Percent correct predictions for test sets[a]	
Function	Stratum	Training set	Test set	Tree	Site by date
Variables are percent composition of terpenes					
A	Year	1998, 1999, 2000	2003	92.7 (179)	100 (18)
A	Year	2003	1998, 1999, 2000	88.7 (1010)	94.2 (120)
A	Year		**Combined**	**89.3 (1189)**[b]	**94.9 (138)**
B	Site	2, 5, 6, 7	1, 3, 4, 8	91.6 (669)	97.3 (73)
B	Site	1, 3, 4, 8	2, 5, 6, 7	82.5 (520)	95.4 (65)
B	Site		**Combined**	**87.6 (1189)**	**96.4 (138)**
Variable is degree days					
C	Year	1998, 1999, 2000	2003	73.7 (179)	72.0 (18)
C	Year	2003	1998, 1999, 2000	79.5 (1010)	81.7 (120)
C	Year		**Combined**	**78.6 (1189)**	**80.4 (138)**
D	Site	2, 5, 6, 7	1, 3, 4, 8	84.6 (669)	89.0 (73)
D	Site	1, 3, 4, 8	2, 5, 6, 7	82.9 (520)	86.2 (65)
D	Site		**Combined**	**83.9 (1189)**	**87.7 (138)**

[a] Percent correct predictions given for indicated test sets by sample tree and by averages per site by date
[b] Sample sizes given in parentheses. Bold figures represent mean for combined sets.

distinguished suitable and unsuitable buds based on percent composition of terpenes. Also, as in (1), the training and test sets were reversed and the procedure was repeated. Results are presented for each procedure as well as the sum of the two test sets combined.

(3) Function C. The same stratification and procedure were used as in Function A except degree-day data rather than terpene composition was used to develop the discriminant function.

(4) Function D. The same stratification and procedure were used as in Function B except degree-day data rather than terpene composition was used to develop the discriminant function.

To evaluate the performance of these discriminant functions at the site by date, rather than the tree level, an average bud suitability, P, and an average classification [unsuitable ($P < 0.5$) or suitable ($P \geq 0.5$)] for each site on each date was calculated from the test sets. These were compared to classifications at the site by date level just as was done for classifying suitability of trees (ρ).

To examine the possibility that fewer terpenes may provide equally good predictive value, training and test sets were developed using Function B, but selecting only the two best terpenes as determined by the stepwise procedure in STATISTICA for prediction.

RESULTS

Foliar Terpenes and Bud Suitability. Classifications using percent terpene composition predicted bud suitability for western spruce budworm correctly more than 80% of the time at the tree level and more than 90% of the time at the site by date level irrespective of whether data were stratified by year (Function A) or by site (Function B) (Table 2). Thus, terpene composition of buds provided highly accurate indicators of bud suitability for western spruce budworms over a wide range of site conditions with all of their attendant seasonal and annual variations in weather.

Analysis of misclassifications of individual samples ($N = 147$) revealed that misclassified samples were not necessarily statistical outliers (i.e., two or more standard deviations from the mean for a given site and date). Of more ecological interest, there was no difference in previous defoliation levels of misclassified and correctly classified samples [mean (SD) percent defoliation 30% (29%) vs. 31% (32%), respectively]. Thus, defoliation by the western spruce budworm does not seem to influence the reliability of terpenes as indicators of bud suitability. This confirms similar results of Chen et al. (2002) and further generalizes the utility of the indicator.

Each of the training sets in Table 2 provides a distinct set of coefficients to discriminate between unsuitable and suitable buds. The most accurate discrimination of bud suitability that we found was Function B using site = 2, 5, 6, 7 as the training set (Table 2). The coefficients for Function B using that training set along with the corresponding mean percent composition of the various terpenes are given in Table 3. To use for predictions, observed percent composition of each terpene is multiplied by its corresponding coefficients in Table 3, one for an unsuitable score and one for a suitable score. These products are summed to provide separate scores for unsuitable and suitable categories. The greater of the two scores is accepted as the prediction (suitable vs. unsuitable). Table 2 indicates the expected accuracy of such a prediction.

Comparison of percent terpene composition between suitable and unsuitable buds (Table 3) provides additional insight into the patterns of particular terpenes as buds change from unsuitable to suitable for western spruce budworm. The two dominant terpenes, α-pinene and β-pinene, reverse their relative positions with α-pinene more abundant in unsuitable buds and β-pinene more abundant in suitable buds. Some of the largest relative differences, however, are in the less dominant terpenes. For example, the percent composition of Δ-3-carene is, on average, almost twice as high in unsuitable than in suitable buds, while percent composition of camphene is almost twice as high in suitable than in unsuitable buds (Table 3).

TABLE 3. COEFFICIENTS FOR DISCRIMINANT FUNCTION B (TABLE 2, TRAINING SET IS SITE = 2, 5, 6, 7) AND MEAN (SD) PERCENT COMPOSITION OF TERPENES IN BUDS THAT WERE UNSUITABLE OR SUITABLE FOR WESTERN SPRUCE BUDWORM[a]

	Coefficients		Mean percent composition (SD)	
Terpene	Unsuitable	Suitable	Unsuitable	Suitable
Tricyclene	–	–	1.4 (0.8)	1.9 (0.9)
α-Pinene	0.902	0.755	35.3 (12.4)	24.3 (4.7)
Camphene	–	–	7.6 (5.5)	11.9 (5.9)
Sabinene	–	–	4.7 (4.2)	4.5 (5.3)
β-pinene	0.704	0.734	25.8 (10.9)	35.6 (9.5)
Myrcene	1.055	0.951	5.0 (3.0)	3.8 (1.8)
Δ-3-Carene	1.309	1.123	2.8 (3.5)	1.4 (1.6)
Limonene	1.123	0.985	10.9 (5.1)	9.7 (4.2)
β-Phellandrene	5.323	4.102	1.2 (0.6)	1.0 (0.2)
Terpinolene	–	–	2.7 (2.2)	1.8 (1.8)
Bornyl acetate	–	–	2.7 (1.9)	4.2 (2.7)
Constant	−39.425	−32.342		

[a] Blanks indicate cases where discriminant function did not utilize that particular terpene.

We found that good predictions could be obtained by using fewer terpenes. The best single terpene to use was α-pinene, a relatively dominant terpene that decreases rapidly in its contribution to total terpenes early in the season as budburst proceeds (Nault, 2003) and buds become suitable to budworms (Table 3, Figure 1). Using training and test sets described under Function B, predictions using α-pinene alone were 78.5% accurate at the tree level and 89.9% accurate at the site by year level compared to 87.6% accurate and 96.4% accurate, respectively, using as many as six terpenes (Tables 2, 3). Further increasing the accuracy of prediction using the single terpene by adding a second or third terpene was not straightforward because the second-best terpene added in stepwise development of the discriminant function varied with the selection of the training set. In other words, one would need to measure α-pinene plus several other candidate terpenes to obtain accuracies approaching those provided by all terpenes. More practically, there is no gain in either efficiency or cost by selecting a subset of terpenes to measure because the collecting, processing, and analytical procedures described above must be followed whether one is measuring one or many terpenes. Therefore, we consider the larger set of terpenes to be the preferred basis for prediction using the coefficients in Table 3.

Influence of Temperature. Classifications based upon accumulated degree days were not as accurate as classifications based on percent terpene composition whether stratified by year or site (Table 2: compare corresponding predictions from Functions A vs. C and B vs. D, respectively). Nonetheless, predictions based on degree days were also acceptably accurate as might be expected by the strong correlation between cumulative degree days and percent composition of individual terpenes (Nault, 2003). Analysis of cases of misclassification at the site by date level revealed that errors using terpenes tended to occur within a narrow range of bud suitability ($0.26 < P < 0.48$) whereas misclassifications using degree days covered almost the entire range ($0.0 < P < 0.94$).

The relative success of using terpene composition over degree days for classification suggests that terpenes are a more sensitive indicator of bud condition, probably because terpene levels are the result of biological integration of many more factors than air temperature alone. Degree days are useful, however, for scaling both changes in terpene composition (Nault, 2003) and bud suitability to budworms under different temperature regimes. For example, expressing changes in bud suitability on a degree-day scale removes much of the year-to-year variation at the site level (Figure 1A vs. B). Similarly, the degree-day scale reduces variation associated with elevation in any single year. However, interesting differences, remain at the site level. Note that within each region (Figure 1B–D and E–I, Okanagan and Nicola Valleys, respectively), there appears to be a negative correlation between degree days required for buds to become suitable and site elevation. In the Okanagan Valley, buds are mostly unsuitable for budworms until accumulated degree days ≥ 200 in the low elevation site (Figure 1D), whereas almost all buds are suitable at the corresponding number of degree days at the higher elevation (Figure 1B). Similarly, in the Nicola Valley, buds do not become suitable for budworms until degree days ≥ 220 at 750 m (Figure 1I), but are ~50% suitable by that same thermal point at 1350 m (Figure 1E). There are other apparent site-related interactions that reduce the accuracy of using degree days to discriminate groups. Compare, for example, Figure 1B and G, both at 1050 m, but in different regions. Whereas expressing suitability in terms of degree days removes much of the year-to-year variation in site 8 (Figure 1B), there remains considerable year-to-year variation in site 3 (Figure 1G). Despite these complex site-related differences in the relationship between temperature and bud phenology, terpene composition predicted bud suitability to western spruce budworm very well in all sites (compare open vs. closed symbols in Figure 1). The fact that terpene composition tracks these site-to-site differences illustrates the value of this tool in detecting patterns that may be relevant in explaining spatial variation in defoliation caused by the western spruce budworm.

DISCUSSION

The suitability of current-year Douglas-fir buds to western spruce budworm following spring emergence depends upon the state of development of the buds (Shepherd, 1992). The phenology of this suitability varies by site and by date largely as a function of individual tree responses to ambient temperature. Discriminant functions based on percent terpene composition of buds can be used to indicate their biological suitability to budworm both at the tree and site levels. Using foliar chemistry as an indicator of bud suitability is an objective and repeatable method of describing plant phenology. We found that terpene profile was a consistent means of distinguishing buds that were suitable or unsuitable for penetration by the western spruce budworm in spite of considerable variation in site-specific and annual variation in ambient temperature and levels of previous defoliation. Thus, persistent differences in the response of particular trees or in specific site conditions and the effect of these differences on suitability to western spruce budworm can be investigated. Results can be used to provide real-time information to augment hazard-rating systems that are typically based on historical patterns as well as to identify individual trees with desirable phenological characteristics associated with reduced susceptibility to defoliation by the western spruce budworm.

Experimental studies exploring the possible role of terpenes as constitutive or induced plant defenses in the Douglas-fir/western spruce budworm system have focused on the midseason phenological stages when shoots were elongating and budworms were feeding actively (e.g., Cates and Zou, 1990; Clancy et al., 1993). The results provided equivocal or little evidence of a role for terpenes as plant defenses (Clancy, 2002). The terpene profiles of Douglas-fir shoots during the later feeding stages of the western spruce budworm, however, are relatively stable compared to the dynamic shifts occurring in those profiles earlier in the season when buds are swelling and budworms are just attempting to establish feeding sites (Nault, 2003). Thus, although our results stress the use of terpenes as the indicators, not the causes, of foliage suitability, they may provide insight in the search for trees with lower susceptibility to western spruce budworm by revealing how variation in early-season rates of change in terpene chemistry are associated with host suitability.

Chen et al. (2003) showed the relative susceptibility of Douglas-fir to defoliation by the western spruce budworm was related to differences in the relative phenology of the tree's foliage and the budworm's development. Further, their experimental results indicate that relative susceptibility is determined by early-season phenology; once buds were penetrated by the insects, differences between susceptible and resistant trees was reduced or reversed. Our results show that these phenological differences among trees that determine host suitability for the western spruce budworm can be related directly to the terpene profile of individual trees early in the growing season. The relative phenology of bud development, and, therefore, susceptibility to western spruce budworm can be ascertained easily for individual trees, irrespective of their defoliation history—indeed, even in the absence of defoliation. This could provide an objective basis upon which to select desirable developmental characteristics of trees because both terpene characteristics and phenological development have a strong heritable component (von Rudloff and Rehfeldt, 1980; Chen et al., 2003).

The use of terpenes as indicators also has an application in population studies. Surveys of terpene profiles of trees within sites could identify the degree of homogeneity of particular phenological patterns in the host population. The degree of homogeneity in budburst phenology in combination with measures of population rates of change in budworms or severity of defoliation provides a direct link between weather, host–plant relationships, and outbreak dynamics. Similarly, known geographic differences in terpene profiles (von Rudloff and Rehfeldt, 1980) could help interpret large-scale patterns of outbreak behavior. We found systematic differences in the thermal requirements for buds to become suitable to budworm on trees at different elevations. If these differences reflect local adaptations by trees to ambient climate, then the relationship between insect outbreak behavior and weather may be mediated by the response of the host tree. The indicator provided by changes in the profile of terpenes makes this pathway tractable.

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