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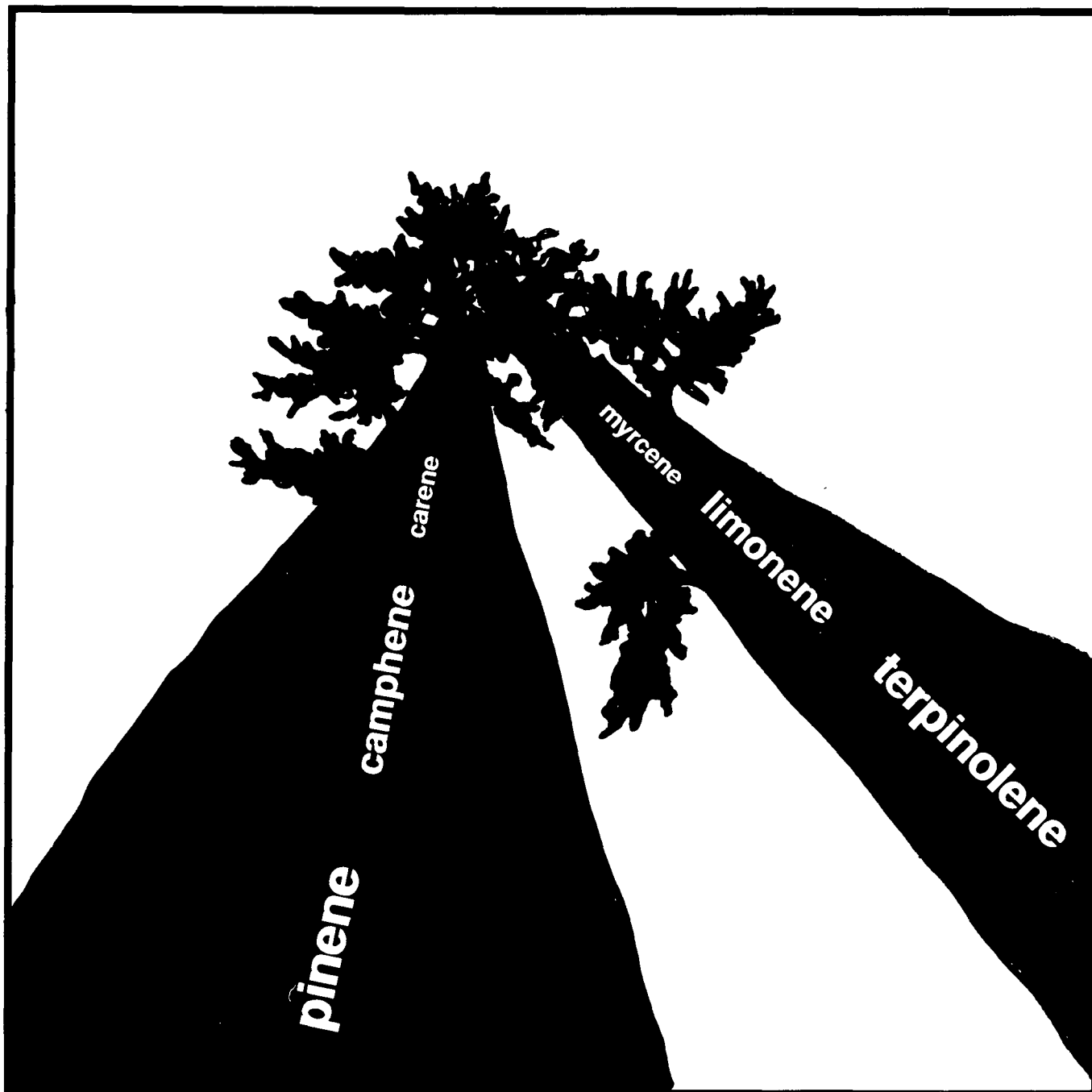
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Variation in Phenology and Monoterpene Patterns of Defoliated and Nondefoliated Douglas-Fir (*Pseudotsuga menziesii* var. *glauca*)

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Abstract

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Foliage was collected from paired Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) trees characterized as either "resistant" or "susceptible" western spruce budworm (*Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae) attack. Resistant trees produced more foliage monoterpenes and broke bud 7 to 10 days earlier than susceptible trees.

Keywords: Spruce budworm (*Choristoneura occidentalis*), Douglas-fir, phenology, monoterpenes.

Contents

1	Summary
1	Introduction
2	Methods
4	Results and Discussion
7	Acknowledgments
7	Literature Cited

Summary

The monoterpene composition of new foliage taken from phenotypically varied Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) growing in northeast Oregon was investigated. Foliage was collected from 10 pairs of trees characterized as apparently resistant or susceptible to western spruce budworm (*Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae)) based on previous year's defoliation. Seven major monoterpenes were identified from *P. menziesii* foliage, and relative amounts present were determined. Although there were no compositional differences in terpenes, foliage from nondefoliated trees produced a greater amount of monoterpenes than foliage from susceptible trees.

Phenology patterns between these two groups of trees differed greatly; severely defoliated trees broke bud 7 to 10 days earlier than nondefoliated trees. Results may have application in breeding Douglas-fir less susceptible to western spruce budworm.

Introduction

Plant-herbivore interactions involve several factors. Resistance-susceptibility polymorphology has been demonstrated for many host-pest systems (Feeny 1976, Futuyma 1983, Jermy 1984) and often is exhibited as variation in the host, including intraspecific host genetic variation (Simms and Fritz 1990). Variability in plant quality could be developmental (for example, Kearsley and Whitham 1989), genetic (for example, Berenbaum and others 1986, McCrea and Abrahamson 1987), or environmental (for example, Mattson and Haack 1987, Mihaliak and others 1987).

Host secondary chemistry composition also is believed to be a strong indicator of host resistance or susceptibility. Given two hosts, an herbivore will generally attack those plants or tissues containing low levels of secondary metabolites (Rhoades 1985). Host-insect phenologic asynchrony has also been implicated as affecting defoliation levels (for example, Perry and Pitman 1983, Redak and Cates 1984).

Variation within and between host trees seems to affect attack behavior by western spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae), a major defoliator of coniferous forests in Western North America (Clancy and others 1988; McDonald 1979, 1981; Perry and Pitman 1983). There are recorded observations of individual Douglas-fir *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco that have remained relatively nondefoliated during severe budworm outbreaks, which occur periodically in the Rocky Mountain and Intermountain regions (Johnson and Denton 1975). Adjacent defoliated and resistant trees have been noted in several Western National Forests (McDonald 1981), including the Wallowa-Whitman National Forest in northeast Oregon, which has experienced a severe outbreak of western spruce budworm for the past 10 years.

Previously tested hypotheses to determine overriding influences of differential levels of defoliation involve larval feeding preference, including such aspects as foliage nutrient and water content (Bryant and others 1987, Clancy and others 1988) and defensive chemistry (secondary compounds) (Feeny 1976, Cates and others 1983, Mattson and others 1983, Rhoades and Cates 1976).

Lack of synchronization between larval emergence and bud swelling may be why some trees are less susceptible to defoliation; such between-tree variation diminishes the predictability of the resource (Feeny 1976). Furthermore, asynchrony has been shown to adversely affect insect performance (Blake and Wagner 1986, Eidt and Little 1970, Krischik and Denno 1983), and also may contribute to insect densities failing to reach outbreak levels (Embree 1985).

Such asynchrony has been associated with host resistance (Redak and Cates 1984, Witter and Waisanen 1978). Eidt and Little (1970) have considered using delayed budburst for controlling of the spruce budworm (*Choristoneura fumiferana*) (Clemens) on balsam fir (*Abies balsamea* (L.) Mill. Western spruce budworm-host asynchrony has been associated with the collapse of two outbreaks in British Columbia (Thomson and others 1984). Many studies have demonstrated the predictability of insect development by temperature (Dennis and others 1986, Kemp and others 1986, Wickman 1976), but controlling factors inherent in plant development are not fully understood.

Although resistance traits are controlled genetically, their phenotypic expression can be modified substantially by environmental factors (Hanover 1975, Mattson and Haack 1987). Although environmentally induced phenotypic variation would be minimal for individuals of the same species occupying a relatively comparable microsite, they exhibit differential levels of defoliation (McDonald 1979, 1981; Perry and Pitman 1983). Because foliage quality, particularly secondary chemicals, seem to play a significant role in plant-host susceptibility and resistance, the heritability of chemicals such as monoterpenes (Squillace 1976) may be beneficial for tree breeding. An important question is whether observed differences in defoliation by Douglas-fir provide a potential management opportunity, that is, whether they would be useful in tree improvement. One of our objectives was to determine if differences in the monoterpene composition of new foliage contribute to differences observed between severely and slightly defoliated Douglas-fir trees. We tested this by examining pairs consisting of each type of tree in an area that is currently undergoing a severe budworm outbreak.

A second objective was to determine differences in foliage phenology between trees resistant and those susceptible to budworm to assess if this attribute makes some trees resistant to spruce budworm.

Methods

The study area was about 8 kilometers east of Cove, Oregon, in the Wallowa-Whitman National Forest at 1640 meters elevation. Ten pairs of Douglas-fir trees were selected in a mixed-conifer stand experiencing heavy defoliation by *C. occidentalis*. Estimates of insect densities for 6 years before the study indicated outbreak populations of 91 to 417 instar IV larvae per square meter of branch area.¹ We chose pairs of trees that had similar diameters and microsites and showed large differences in levels of *C. occidentalis* defoliation (table 1). Each tree was within 3 meters of its counterpart. Slopes at the site ranged from 15 to 40 percent and were the same for each tree pair. One tree of each pair exhibited minimal previous-year defoliation, and the other tree exhibited medium to heavy defoliation. The extent of defoliation from previous years was estimated visually.

Percentage of budburst was monitored every few days from the onset of bud swelling until 100 percent of the buds on sampled branches had flushed. The percentage of buds flushed on two midcrown branches on each tree was estimated. Buds were considered flushed if they were at the "split stage" (Shepherd 1983), where the bud cap splits to reveal green needles, still held tightly together.

¹ Torgersen, T., unpublished data. On file with: Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850.

Table 1—Characteristics of paired trees

Diameter at Breast Height		Age		Defoliation	
D ^a	R ^b	D	R	D	R
--- Centimeters ---		-----Years-----		----- Percent -----	
26.9	53.3	46	94	85	15
34.0	46.0	74	73	90	10
62.5	53.8	69	80	100	5
31.0	57.4	81	67	100	10
44.4	32.3	48	51	100	5
43.4	32.3	48	51	100	5
19.8	19.1	28	25	50	5
17.8	30.0	17	34	95	15
59.7	37.1	93	59	75	25
14.2	8.4	20	16	95	0

^a D = Defoliated.

^b R = Resistant trees.

Data on degree-day accumulation were collected during the same period. Air temperature was recorded with an Omnidata TA51² biophenometer in a weather station. The biophenometer measured the temperature every 10 minutes and calculated degree-days; a threshold temperature of 5.5 °C was used to calculate degree-days.

Foliage samples were collected at random from the midcrown area during the heaviest period of budworm feeding; that is, when the larvae were fourth and fifth instars, and when there was adequate foliage to sample. About 5.0 grams of new foliage was removed from each tree, immediately placed in precooled glass test tubes, and then sealed with gas-impermeable serum caps. The samples were kept frozen (−2 °C) until analyzed.

For chemical analysis, 2.5 grams of frozen needles was chopped into about 1-millimeter lengths, placed into 5 milliliter glass vials, covered with chromatographic-grade pentane, sealed with Teflon-lined caps, and refrigerated at 4 °C until analyzed. Monoterpenes were analyzed by using a Varian gas chromatograph equipped with a thermal conductivity detector and linked to a Hewlett Packard 3390A Integrator. The column was 0.3 millimeters by 2.4 meters stainless steel packed with B B' oxydipropionitrile liquid support 5 percent chromosorb with AW solid support. The column temperature was maintained at 65 °C with 155 °C injector and detector temperatures. All samples were treated identically, and injection volume was the same for all.

² The use of trade, firm, or corporation names is for the information and convenience of the reader. Such use does not constitute an official endorsement by the U.S. Department of Agriculture of any product or service to the exclusion of others that may be suitable.

All results of the analyses were reported by percentage of monoterpene, the content of each monoterpene being relative to total monoterpenes present in the sample. The area under the peak of the graph for each monoterpene was determined and divided by the total area under all monoterpene peaks in the sample, that is, normalized area. This is a simple, rapid, and accurate measure (Squillace 1976) and is most often used in genetic studies. Relative composition on a total monoterpene basis is strongly inherited and is not strongly associated with variation in total monoterpene content (von Rudloff 1975a, Zavarin and others 1971).

Data were analyzed by using paired t-tests to compare terpene differences between resistant and defoliated trees and repeated measures analysis of variance by using a general linear regression model to examine phenological variation (SAS 1987).

Results and Discussion

Budburst began in the heavily defoliated trees at about 133 degree-days accumulation (June 3). The rate at which these trees flushed was significantly greater than the "resistant" trees (fig. 1). One-hundred-percent budburst occurred 7 to 9 days earlier in the heavily defoliated trees ($P < 0.0001$, repeated measures analysis of variance).

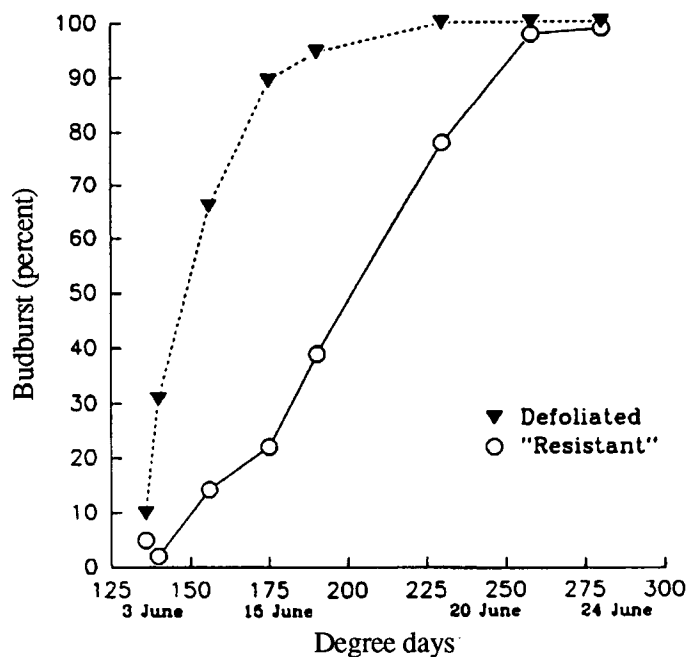


Figure 1—Contrasting phenology patterns of defoliated and undefoliated (resistant) Douglas-fir. The earlier flushing of the defoliated trees was significantly different ($P < 0.0001$).

Previous defoliation in these conifers may have resulted in earlier budburst, whereas in deciduous trees previous defoliation (particularly early season) causes delayed budbreak (Tuomi and others 1989). Delayed budburst seems to be a valuable defense for birch (Haukioja and others 1985). Early flushing seems to be a defense mechanism in *Acer rubrum* L. resistance (Townsend 1989).

In a previous study, Cates and others (1983) showed that trees that burst bud later in the growing season suffer less damage from *C. occidentalis* attack. Eidt and Little (1970) determined that spruce budworm (*C. fumiferana* (Clemens)) survival is reduced on late-flushing foliage. By using gypsy moth, *Lymantria dispar* L., Sheppard and Friedman (1990)

found that foliar phenology has a significant impact on larval performance, particularly nutritional indices. Early flushing may be advantageous for *C. occidentalis*, in that these trees offer a refugium for dispersing second instar larvae. Conversely, delayed budburst can adversely affect the immobile, early feeding larvae. A similar phenomenon has been noted with *P. menziesii* infected by dwarf mistletoe (*Arceuthobium douglasii* Engelman) (Briede and others 1991), possibly because of an altered source-sink relation. The phenological pattern could have to do with only resource availability and have no correspondence with plant strategy, and would not represent a defensive response.

Plant-herbivore interaction theory suggests that unpredictability in space or time may be an effective mechanism for reducing the adverse effects of monophagous herbivores on young ephemeral tissues. The current data suggest that escape in time may be more beneficial for Douglas-fir resistance.

Young foliage is the preferred food for the spruce budworms, and many other insects, probably owing to the high nitrogen and water content. When *C. occidentalis* fed on mid-season to late-season foliage, they often did not survive to pupation (Blake and Wagner 1986). Because selection strongly favors rapid development and growth to a level contributing to the net primary productivity of the plant, selection is postulated to favor a defensive system that takes the least amount of energy to produce; that is, secondary chemical production is likely minimized. Alternately, selection also could also favor defense of nutrient-rich bud tissues via secondary chemicals, particularly in plants adapted to growth under resource-poor environments.

Seven major monoterpenes were separated, but many other components were present in small or trace amounts. The compositional patterns were the same for both types of tree; that is, α -pinene, β -pinene, and camphene were the dominant compounds. There were no differences in the relative proportions of the principle monoterpenes between the defoliated and nondefoliated trees (fig. 2). When all terpenes (major and minor) are

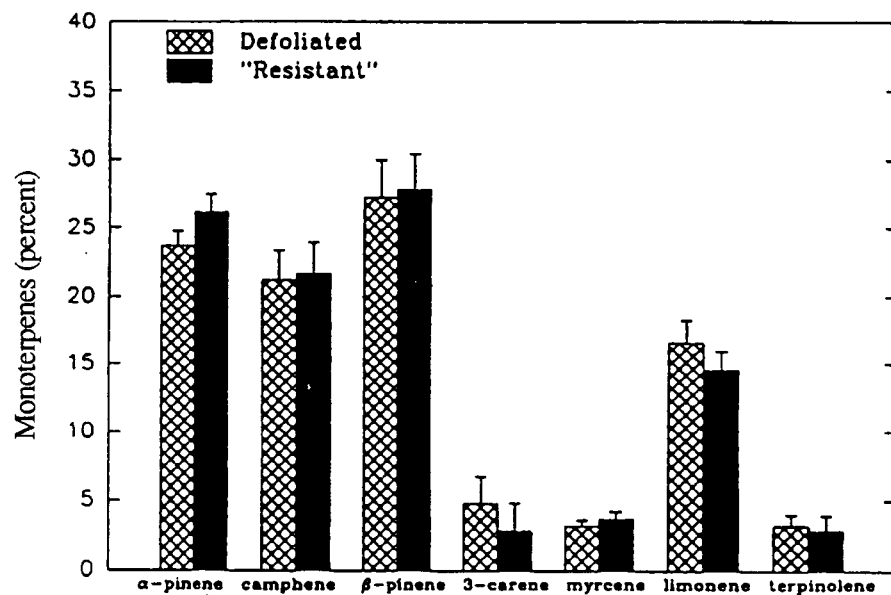


Figure 2—Average concentrations (%) $\pm$ SE of seven terpenes identified from *Pseudotsuga menziesii*. There were no significant differences in concentrations of individual terpenes between defoliated and undefoliated (resistant) trees.

summed, however, foliage from nondefoliated trees produced a significantly ($P = 0.02$) greater volume of total monoterpenes than foliage from defoliated trees. These results support findings by Radwan and Ellis (1975), who found that Douglas-fir resistant to browsing by deer produced more terpenes than trees susceptible to browsing. That terpenes are more abundant in the resistant trees may be a function of the greater leaf area of these nondefoliated trees. Wright and others (1979) found that defoliation decreases monoterpene production in stems of grand fir (*Abies grandis* (Dougl.) Lindl.).

Certain studies suggest no relation between *C. occidentalis* feeding preference and terpenes. Perry and Pitman (1983), for example, have found no convincing relation between terpenes and resistance to larval feeding. Similarly, putatively resistant and susceptible Douglas-fir produced similar amounts of terpenes in a study by Clancy (1991). Terpenes have been identified as factors possibly influencing weight gain and adult weight in budworm in other studies, however. Several investigators (Cates and others 1983, Mattson and others 1983, Redak and Cates 1984) found negative correlations between concentrations of terpenes and adult budworm dry weights.

Notable changes in terpenes occur from budburst to total needle elongation and throughout the growing season (Wagner and others 1989). Studies of seasonal variation of monoterpenes from blue spruce (*Picea pungens* Engelm.) (von Rudloff 1975b), coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) (Maarse and Kepner 1970), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) (Zavarin and others 1971) confirm the observation that large quantitative changes occur in monoterpene composition of new leaves from budburst to the end of leaf elongation, that is, at the time of maximum insect activity. Qualitative changes in individual terpenes also have been recorded (von Rudloff 1975b), and these factors, separately or together, may affect larval feeding.

Although inducible defenses may be manifest where there has been previous defoliation, there is no evidence of an induced response of the hosts. Such theory maintains that a plant may induce resistance in response to defoliation or stress (Karban and Myers 1989, Tuomi and others 1990). Defoliation of the susceptible trees here did not seem to affect foliage quality in terms of the secondary chemicals we identified.

This study may indicate that several mechanisms are contributing to defoliation resistance. It still is unclear whether terpenes, acting as toxins, are responsible for reduced budworm success. Other compounds may be influencing the patterns observed. Other experimental work with natural populations of *P. menziesii* and *C. occidentalis* are needed to determine cause and effect, but these data seem to corroborate findings that the terpene chemistry aspect of plant-herbivore interactions may be a main factor toward understanding tree resistance and susceptibility to western spruce budworm attack and lead to development of novel approaches to the control of herbivores.

Perhaps both terpene content and phenologic asynchrony affect foliage resistance to budworm attack, but it remains difficult to assess the relative contributions of each. Because there were no differences among terpenes, the individual variation may not be as meaningful as total terpene concentrations. Our data suggest that phenology may represent a critical factor responsible for differential feeding by the insect.

Acknowledgments

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