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EFFECTS OF NITROGEN FERTILIZATION ON MONOTERPENES OF JACK
PINE SEEDLINGS AND WEIGHT GAIN OF JACK PINE BUDWORM
(LEPIDOPTERA: TORTRICIDAE)

Deborah G. McCullough^{1,2} Paul D. Swedenborg¹, and Herbert M. Kulman¹

ABSTRACT

Nine-month old jack pine (*Pinus banksiana*) seedlings were grown in a greenhouse under four nitrogen fertilization regimes. Levels of total nitrogen and five monoterpenes in new foliage were measured. Fertilization resulted in four significantly different levels of foliar nitrogen; means ranged from 1.8–4.5 percent dry weight. Contrary to predictions of resource availability theory, seedlings grown under the highest fertilization regime had higher foliar monoterpene levels than seedlings in the other treatments.

Newly molted, sixth-instar female jack pine budworm (*Choristoneura pinus pinus* [Lepidoptera: Tortricidae]) larvae were allowed to feed for four days on new foliage of the seedlings. Larvae that fed on low-nitrogen seedlings gained less weight and processed more vegetation than did larvae on high-nitrogen seedlings. Larval weight gain was positively related to foliar nitrogen.

Quality of host plant tissue for herbivorous insects is a function of many factors, including levels of nutrients and allelochemicals. Nitrogen (N) is particularly important, and survival, development and fecundity of defoliating insects are often closely tied to foliar N levels (White 1974, 1984, McNeil and Southwood 1978, Mattson 1980, Mattson and Scriber 1987). However, insect performance may be reduced by plant secondary compounds even under optimal N conditions (Scriber and Slansky 1981). Recent theories have suggested that availability of growth-limiting nutrients such as N may determine the extent of plant investment in allelochemicals (McKey et al. 1978, Bryant et al. 1983, 1987; Coley et al. 1985, Larsson et al. 1986, Hermes and Mattson 1992). Nitrogen-limited plants should theoretically allocate high amounts of carbohydrate reserves to carbon-based defenses, since foliage lost to herbivory would be costly to replace.

We tested this hypothesis by manipulating N availability and observing effects on monoterpene production in jack pine (*Pinus banksiana*) foliage. We examined effects of four levels of N fertilization on production of monoterpenes in jack pine seedlings and subsequent feeding activity of jack pine budworm larvae (*Choristoneura pinus pinus* Freeman) [Lepidoptera: Tortricidae]. Jack pine is a disturbance-adapted species, typically found on sandy, nutrient-poor sites in the Lake States and Canada (Rudolf 1958, Wilde et al.

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1964, Rudolph and Laidly 1990). Jack pine stands are often N-limited, as evidenced by significant increases in growth following N fertilization (Morrison et al. 1981, Morrow and Timmer 1981, Weetman and Fournier 1984). Jack pine budworm is the primary defoliator of jack pine, with extensive outbreaks occurring at 6-10 year intervals (Howse 1984, Volney 1988). Outbreaks can severely reduce growth and may result in top-kill and mortality (Kulman et al. 1963, Kulman 1971).

Several monoterpene compounds, which are carbon-based allelochemicals, are present in conifer foliage, including jack pine. Synthesis and accumulation of monoterpenes may be an important mediator of interactions between plants and herbivorous insects, affecting feeding, development, host location and pheromone synthesis (Borden 1982, Redak and Cates 1984, Cates et al. 1987, Cates and Redak 1988, Wilkinson 1985, Leather et al. 1985, Brooks et al. 1987a, Mihaliak et al. 1987). Monoterpene production is under genetic control (Smith 1964, Thorin and Nommik 1974), but in some plant species, amounts of compounds or total monoterpene levels may vary seasonally (von Rudloff 1975, von Rudloff and Granat 1982, Brooks et al. 1987b, Bernard-Dagen 1988) or in response to availability of light, water and nutrients (Burbot and Loomis 1967, Fretz 1976, Clark and Menary 1980).

MATERIALS AND METHODS

Jack pine seed from McKinnon Lake, Quebec was germinated in March 1988 and grown in a greenhouse at 18:6 light/day, 24-32°C and 65-85% RH. Potting medium consisted of a 4:1.5:2 ratio of peat, perlite and vermiculite. Osmocote, a slow release (NPK) fertilizer (19-7-10), was incorporated into the potting medium. After four months of growth, 136 seedlings were transplanted into pots, 15 cm in diameter, containing the same potting medium plus Osmocote. Seedlings were supplied with moisture through automatic drip irrigation. Seedlings were grown under 250 watt sodium lamps (18:6 light/day, illumination: 310-800 $\mu\text{E}(\text{m}^{-2})(\text{sec}^{-1})$) for six months. Seedlings were then exposed only to natural light (illumination: 210-230 $\mu\text{E}(\text{m}^{-2})(\text{sec}^{-1})$) for 5 months during winter. Seedlings were returned to sodium lamp radiation in early May, which stimulated expansion of new foliage.

Fertilization treatments

Fertilization treatments were initiated in January 1989 and 34 seedlings were randomly assigned to each of four N regimes. Seedlings assigned to the very high (VH) treatment received 170 ml of a balanced nutrient solution weekly (Peters' solution, 20-19-18, 4 ml solution per liter of water). This was supplemented with bi-monthly additions of NH_4NO_3 at a rate equal to either 88 kg/ha or 44 kg/ha N, on an alternating basis. Fertilizer was distributed in a granular form on the surface of the potting medium. Seedlings assigned to the medium (MED) treatment similarly received weekly applications of Peters' solution. They also received a single monthly application of NH_4NO_3 equivalent to a rate of 44 kg/ha N. This N regime was roughly equivalent to that used in cultivation of jack pine seedlings in Minnesota state nurseries (MN Dept. Nat. Resources, pers. comm.). Seedlings assigned to the control (CONT) treatment received only 170 ml of Peters' solution weekly. Seedlings in the low (LOW) treatment received Peters' solution weekly for two months, then received only 170 ml of water and no nutrient solution. In addition, 2.6 g (ca 110 kg/ha) of sawdust were distributed over and lightly incorporated into the top few centimeters of the potting medium of each LOW treatment seedling.

This was designed to increase the C:N ratio and reduce availability of N to the seedlings.

Growth and biomass measurements

Height and root collar diameter (RCD) of seedlings were measured when seedlings were transplanted and at 10–14 week intervals thereafter, until seedlings were harvested. Relative growth rates (RGR) per month (28 days) were calculated for height and RCD growth where $RGR = (\ln L_2 - \ln L_1) / (t_2 - t_1)$, and L_1 and L_2 are tree height or RCD at times t_1 and t_2 (van den Driessche 1988). Measurement period 1 corresponded to growth occurring between times t_1 (transplanting) and t_2 , about 2.3 months. Measurement periods 2, 3 and 4 corresponded to the subsequent 3.4, 3.3 and 3.7 months, respectively.

Biomass of above-ground components was determined after six months of fertilization, following the larval bioassay described below. All currently expanding (new) foliage was removed from each seedling and immediately frozen on dry ice for subsequent analysis. Frozen samples were weighed and one-third of each sample was returned to the freezer for monoterpene analysis. Remaining foliage was dried at 70°C for 8 days, weighed and ground in a Wiley mill to pass through a 20-mesh screen. Moisture content was determined for each dried sample and used to calculate total dry weight of new foliage for each seedling. Stems of seedlings were clipped off level with the top of each pot. Remaining old foliage was separated from woody material. Wood and foliage were dried and weighed. Total weight of foliage (new + old foliage) and total above-ground biomass (total foliage + wood) were determined.

Foliar analysis

Dried and ground current-year foliage from each seedling was analyzed for total N using microKjeldahl techniques. Nitrogen analyses were performed by the University of Minnesota Soils Laboratory, St. Paul, MN. Foliar levels of alpha-pinene, camphene, beta-pinene, myrcene and bornyl acetate were analyzed with a Hewlett-Packard (HP) 5890 gas chromatograph equipped with FID coupled to an HP 3396A integrator and an HP automatic injector (Hewlett-Packard Co., Avondale, PA). Preliminary experiments and results of related studies indicated that these were the most abundant monoterpene compounds in jack pine foliage. Frozen foliage was analyzed using p-Cymene as an internal standard (Aldrich Chemical Co., Milwaukee, WI), due to its absence in jack pine foliage within detection limits (Raffa and Steffek 1988). Detailed methods of monoterpene extraction and quantification were described in detail in McCullough and Kulman (1991a, 1991b). Simpsons' index of diversity was calculated to examine differences in monoterpene profiles in each seedling (Magurran 1988). Relatively high values are indicative of equitable within-plant distribution of the compounds sampled.

Jack pine budworm feeding trial

Second-instar jack pine budworm larvae were collected from an outbreak population near L'Anse, MI, and reared on jack pine foliage in the laboratory. Newly-molted female-sixth instars were removed from rearing boxes, weighed, and individually placed into small cages on one lateral shoot of randomly selected seedlings in each treatment. Seedlings that lacked new foliage or seedlings that appeared to be near death were excluded from the study. Twelve to 20 seedlings per treatment were infested with budworm larvae. Late instar larvae were used for feeding trials since most consumption and growth occurs then (Miller 1977, Retnakaran 1983), and to avoid injuring

young larvae through handling. Cages were 100 ml, 7 cm long, transparent plastic cups, which enclosed two to three shoots of foliage, each about 3 to 6 cm long. The open end of cups was covered with white nylon netting material. Modelling clay was used to secure cages to seedlings. At least 4 to 5 cm of new foliage was available in each cage. Larvae were allowed to feed for four days, then were removed from cages and immediately re-weighed. Feeding trials were limited to four days to ensure that new foliage would be available for the duration of the trial in all treatments. Larval survival and weight gain during the four day feeding trial was determined. Frass was collected from the bottom of cups, dried and weighed. In a few cases, fungus grew on the frass and dry weight could not be accurately measured. The ratio of (frass dry weight: weight gain of larvae) was calculated for each surviving larva.

Statistical analysis

The experiment was designed and analyzed as a completely randomized one-way analysis of variance. Effects of the four levels of N fertilization on tree and budworm variables were analyzed using BMDP Statistical Software (Dixon et al. 1990). The Levene test was used to test for homogeneity of variance (Brown and Forsythe 1974). Diagnostic plots were used to select appropriate transformations where homogenous variances did not occur. Quantities of monoterpene compounds, ratio of frass weight: budworm weight gain, and dry weight of woody material were log-transformed; dry weight of new foliage was square-root transformed. Differences among treatments were determined with Fishers LSD procedure (Milliken and Johnson 1984). Foliar N concentration was analyzed with the nonparametric Kruskal-Wallis test, since variance could not be normalized. Nonparametric Spearman correlation coefficients were calculated to examine relations between foliar N and other variables. All analyses were conducted at the 0.05 level of significance.

RESULTS

Nitrogen fertilization treatments resulted in four significantly different levels of foliar N concentration (Table 1) (Kruskal-Wallis test statistic = 93.7, $P < 0.001$). Mean concentrations ranged from 1.8 % (LOW), and 2.6% (CONT), up to 3.5% (MED) and 4.5% (VH). Moisture content of new foliage did not vary among treatments ($F = 1.40$, $P < 0.25$), with means ranging from 72 to 76% dry weight.

Seedling growth

Seedling growth and survival were significantly affected by fertilization regime. Survival of seedlings ranged from 91 to 97% except in the VH treatment, where only 60% survived. Drooping shoots, an atypical abundance of foliage, and discolored foliage were first noted on four-month-old VH seedlings, with several dying over the next six weeks. Only two seedlings in the MED treatment died, but several others also showed symptoms of N toxicity after six months. Seedlings in the MED and VH treatments were significantly shorter ($P < 0.001$) and had smaller diameters ($P < 0.001$) than LOW and CONT seedlings (Table 1).

Significant differences in relative growth rates were observed 3-6 months after fertilization treatments began (Table 1). Seedlings in the MED and VH treatments had significantly lower rates of height ($P < 0.001$) and diameter growth ($P < 0.001$) than seedlings in the LOW and CONT treatments.

Although total above-ground biomass of seedlings did not differ among

Table 1. Mean foliar nitrogen concentration, biomass and growth rate of one-year old jack pine seedlings after six months of nitrogen fertilization treatments. Letters following values indicate significant differences among treatments. RGR refers to relative growth rate during the final 3 months of fertilization. LOW, CONT, MED, and VH refer to low, control, medium and very high nitrogen fertilization regimes.

	LOW	CONT	MED	VH
Foliar nitrogen (% dry wt)	1.83 ^a	2.61 ^b	3.54 ^c	4.50 ^d
SE	0.06	0.11	0.08	0.16
New foliage (g)	4.5 ^a	10.6 ^b	4.8 ^a	2.6 ^c
SE	0.35	0.76	0.58	0.58
Total foliage (g)	30.6 ^a	39.7 ^b	36.1 ^b	35.9 ^b
SE	1.35	1.57	1.57	2.57
Woody biomass (g)	16.1 ^a	13.5 ^b	11.6 ^c	9.9 ^c
SE	1.06	0.96	0.60	0.63
Aboveground biomass (g)	46.6 ^a	53.3 ^a	47.6 ^a	45.8 ^a
SE	2.25	2.37	2.11	3.15
RGR—height (cm/month)	0.039 ^a	0.045 ^a	0.009 ^b	0.008 ^b
SE	0.007	0.007	0.002	0.002
RGR—diameter (cm/month)	0.040 ^a	0.040 ^a	0.008 ^b	0.011 ^b
SE	0.005	0.006	0.004	0.006

treatments (Table 1) ($P < 0.116$), distribution of biomass among components varied significantly. Seedlings in the CONT treatment produced more new foliage than seedlings in other treatments ($P < 0.001$). Seedlings in the LOW treatment had less total foliage ($P < 0.001$) and allocated more resources to wood production than seedlings of other treatments (Table 1). Heavily fertilized seedlings in the MED and VH treatments produced less woody material than CONT or LOW seedlings ($P < 0.005$) and were characterized by thin, drooping shoots.

Monoterpenes

Foliar monoterpene levels differed significantly among the four treatments (Table 2) ($P < 0.045$). Seedlings in the VH treatment had the highest concentration of all compounds, but differences among other treatments were small. Beta-pinene, alpha-pinene and myrcene were the most abundant foliar monoterpenes. Simpson's index of diversity differed little among the four treatments, indicating that equitability of monoterpene distribution was not affected by fertilization treatment.

Spearman correlation coefficients were used to examine linear relations among the five individual monoterpenes and foliar N concentration. Bornyl acetate, which accounted for only 2 to 3% of the total monoterpene content, was inversely related to foliar N concentration ($r = -0.33$). No other monoterpene compound was significantly related to foliar N.

Jack pine budworm feeding trial

Larval survival during the 4-day feeding trial was 79% for larvae on LOW and MED seedlings and 82% for larvae on VH seedlings. Survival was highest for larvae caged on CONT seedlings, where 94% survived.

Weight gained after four days of feeding by sixth instars was used as a simple index of host plant suitability. Weight gained during the feeding trial differed significantly among treatments (Fig. 1) ($P < 0.001$). Budworm larvae that fed on MED and VH seedlings gained about 50% more weight than larvae caged on LOW and CONT seedlings.

Table 2. Mean concentration (ng/g dry needle weight) of five monoterpene compounds from current-year foliage of jack pine seedlings. Diversity refers to Simpsons' index of diversity. Letters after values indicate significant differences ($P < 0.05$) among treatments. LOW, CONT, MED and VH refer to low, control, medium and very high nitrogen fertilization regimes.

		LOW	CONT	MED	VH
Alpha-pinene	mean	34.9 ^a	33.6 ^a	47.1 ^a	57.7 ^a
	SE	(3.7)	(3.7)	(7.8)	(10.4)
Beta-pinene	mean	45.1 ^a	28.4 ^a	36.7 ^a	60.3 ^b
	SE	(8.4)	(3.5)	(5.5)	(9.3)
Myrcene	mean	44.5 ^a	38.2 ^a	34.1 ^a	74.7 ^a
	SE	(8.0)	(6.7)	(8.5)	(20.2)
Bornyl acetate	mean	3.8 ^a	3.7 ^a	2.1 ^a	6.6 ^b
	SE	(0.4)	(0.8)	(0.6)	(2.9)
Camphene	mean	1.6 ^a	1.7 ^a	1.4 ^a	2.8 ^a
	SE	(0.1)	(0.3)	(0.2)	(0.9)
Total	mean	129.9 ^a	105.6 ^a	121.3 ^a	202.2 ^b
	SE	(15.6)	(10.5)	(16.2)	(34.2)
Diversity	mean	2.53 ^a	2.70 ^a	2.50 ^a	2.72 ^a
	SE	(0.08)	(0.10)	(0.08)	(0.13)

The ratio of frass production to larval weight gain also differed significantly among treatments (Fig. 1) ($P < 0.002$). Larvae feeding on LOW and CONT seedlings processed 4 to 9 times as much foliage for each unit increase in weight as larvae feeding on MED and VH treatment seedlings. Spearman rank correlation coefficients indicated that there was a significant positive relationship between foliar N concentration and budworm weight gain ($r = 0.39$, 39 d.f.) and an inverse association between foliar N and ratio of frass production to weight gain ($r = -0.42$). Correlation coefficients were not significant between monoterpene abundance (individual compounds and total) and budworm weight gain, and the budworm frass to weight gain ratio were not significant.

DISCUSSION

Growth and foliage production were greatest for CONT seedlings. Mean foliar N concentration of CONT seedlings (2.6%) was very similar to the 2.58% N concentration recorded by Swan (1970) when jack pine seedlings were fertilized with an optimal nutrient solution. These N values are relatively high compared to concentrations previously reported for mature jack pine in the field (Morrison 1972, 1973, Green and Grigal 1980, Morrow and Timmer 1981, Weetman and Fournier 1984, Stergas and Adams 1989). However, seedlings and young trees often have higher foliar N levels than mature trees (Miller et al. 1981, Gordon and van Cleve 1987), especially when seedlings are grown in pots (Munson and Timmer 1989). In addition, we measured foliar N during a period of active growth and needle expansion, when new foliage acts as a strong sink for N. The studies cited above measured foliar N in late summer or fall, when N concentration of current-year foliage is lower and more stable as trees enter dormancy (Binkley 1986). Quantification of N status during periods of growth may be more indicative of growth-limiting N deficiencies than measurements during dormancy (Waring and Youngberg 1972, van den Driessche 1974).

We originally hypothesized that monoterpenes would be inversely related to foliar N levels (Bryant 1983, 1987, Coley et al. 1985). Jack pine typically

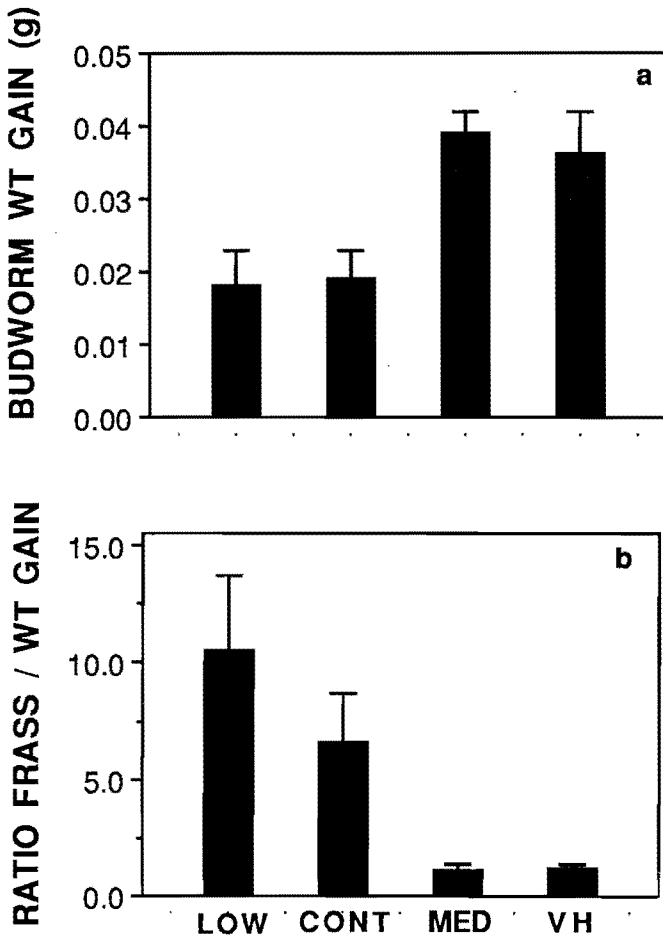


Figure 1. Mean values for jack pine budworm larval weight gain (a) and the ratio of dry weight of frass produced: weight gain (b) during a four day feeding trial. Error bars represent one se. LOW, CONT, MED, and VH refer to low, control, medium and very high nitrogen fertilization regimes.

grows on nutrient-poor sites where C:N ratios are high. Monoterpenes are produced from nonstructural carbohydrates (Croteau 1984) and should theoretically be abundant when nutrients limit growth (Bryant et al. 1983). Nitrogen fertilization decreased the C:N ratio of tissue and resulted in decreased nonstructural carbohydrates in Douglas-fir seedlings (Margolis and Waring 1986), reduced phenolics in aspen (Bryant et al. 1987), and reduced terpene levels in *Heterotheca subaxillaris* (Lam.) Britton and Rushy (Mihaliak and Lincoln 1985, 1989).

Contrary to our expectations, however, increased levels of available N did not result in decreased production of monoterpenes, and the highest monoterpene levels were found in seedlings in the VH treatment. Similarly, Muzika et al. (1989) did not demonstrate an overall negative relationship between monoterpenes and N when *Abies grandis* seedlings were fertilized. They observed that while four monoterpenes decreased at the highest level of fertilization, six other monoterpenes were unaffected and no compounds were affected by an intermediate level of N fertilization. Other studies with conifers have failed to show a consistent relation between foliar N and monoterpene levels in foliage (Fretz 1976) or oleoresin (Thorin and Nommik 1974). Relations between monoterpene production and foliar N may be nonlinear in jack pine. Stress due to either extremely high or low N availability may limit growth and result in increased allocation of carbon to secondary compounds such as monoterpenes.

Obtaining adequate amounts of N is crucial for defoliating insects (e.g. White 1974, 1984, Mattson 1980, Strong et al. 1984) and may regulate the amount of foliage consumed (Clancy 1992). In our study, late-instar jack pine budworm larvae responded positively to high N levels in MED and VH seedlings. Weight gained by these larvae during the four-day feeding trial was double that gained by larvae on LOW and CONT seedlings. Large amounts of frass produced by larvae on LOW and CONT seedlings indicated larvae compensated for low N levels by increasing feeding rates, a pattern frequently noted in studies of other herbivores (Slansky and Feeny 1977, Mattson 1980, Scriber and Slansky 1981). Implications of compensatory feeding may include prolonged larval development and exposure to natural enemies or poor weather, and increased impact of budworm defoliation on low-nitrogen trees.

Fertilization can increase levels of free amino acids in jack pine seedlings (Kim et al. 1987, Durzan and Stewart 1967), which may be nutritionally superior to proteins or more available to herbivores (Cockfield 1988). Nitrogen fertilization increased feeding rates, survival and fecundity of other *Choristoneura* species (Shaw et al. 1978, Schmidt and Fellin 1983, Schmitt et al. 1983). Mattson and Koller (1983) found adult female weight was consistently related to N levels and proposed a minimal foliar N concentration of 2.1 percent for optimal performance of *Choristoneura fumiferana* (Clemens). Brewer et al. (1985) found *Choristoneura occidentalis* Freeman benefitted from increased N until foliar N concentrations reached 3.9–4.4%, where larval mortality rose significantly. Clancy (1992) found survival of *C. occidentalis* was good at very high (3.9% and 7.6%) and very low (1.2–3.0%) levels of N, but was not convex or linear. Addition of minerals at high N levels affected the response to N. She concluded that compensatory feeding to acquire adequate N in low N diets ensured that larvae obtained a proper balance of many different nutrients. Nutritional ecology of jack pine budworm may be similar, but long-term multiple generation studies are needed to more fully investigate this.

Amount, composition and diversity of terpenes have been previously found to affect growth and survival of other budworm species (Cates et al. 1983a, 1983b, 1987; Mattson et al. 1983, Redak and Cates 1984, Cates and Redak 1988). Mattson et al. (1991) observed variable effects of monoterpenes on *C. fumiferana* when terpene compounds were incorporated into artificial diet at rates much higher than what occurred in host foliage. They concluded that *C. fumiferana* could readily cope with normal loads of monoterpenes in its host plants. Similarly, we detected no effect of monoterpenes on jack pine budworm larvae. Larvae feeding on seedlings in the VH treatment, which had the greatest amount of monoterpenes, showed no signs of toxic effects. Monoterpene diversity varied little among treatments and was not related to weight gain or frass production. Longer exposure may be needed before effects of terpenes can be observed. If terpenes act in a quantitative manner and induce metabolically expensive detoxification enzymes (Brattsen et al.

1977), their importance may relate to adult fecundity or multigenerational influences not observable here. Work with *Spodoptera eridania* (Cramer) similarly failed to demonstrate a relation between leaf monoterpenes and insect success (Lincoln and Couvet 1989). Morrow and Fox (1980) found leaf N in *Eucalyptus* spp. to be much more important than terpenes in explaining herbivore success.

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