

WHITE ALDER AND DOUGLAS-FIR FOLIAGE
QUALITY AND INTEREGG-MASS INFLUENCES ON
LARVAL DEVELOPMENT OF GYPSY MOTH,
Lymantria dispar

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Abstract—Individual families of gypsy moth collected from a single population exhibited different degrees of fitness when fed diets of white alder, a suitable broadleaf host, and Douglas-fir, an unsuitable conifer host. Members of families on diets of Douglas-fir had significantly lower survival, longer larval periods, lower pupal weights, and shorter pupal periods than members of the same families fed alder. Foliar nutritional quality, including nitrogen level and allelochemical composition (terpenes and phenols), was considered the key factor responsible for these differences. Growth parameters differed significantly for families within diet treatments, indicating that the genetic resources of a family did affect performance somewhat. The influence of a family's genetic resources on larval survival was most notable when larvae were under the greatest nutritional stress.

Key Words—Douglas-fir, *Pseudotsuga menziesii*, gypsy moth, *Lymantria dispar*, Lepidoptera, Lymantriidae, insect-host plant relations, phenolics, terpenes, white alder, *Alnus rhombifolia*.

INTRODUCTION

Developmental rate and survival of the gypsy moth are influenced by many factors, including host species (Hough and Pimentel, 1978; Barbosa et al.,

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1986); constitutive and induced chemical variation within the host species (Rhoades, 1983; Rossiter et al., 1988); genetic variation among and within insect populations (Leonard, 1966); and environmental variables, such as temperature and humidity (Elkinton and Liebhold, 1990). Previous studies relating the suitability of hosts to gypsy moth fitness have suggested that certain allelochemicals, such as alkaloids, influence fitness parameters, such as larval development (Doskotch et al., 1981; Barbosa et al., 1983, 1990a,b; Barbosa and Krischik, 1987; Miller and Hanson, 1989a). Plants containing iridoids and alkaloids appear to be poor hosts (Barbosa and Krischik, 1987; Miller and Hanson, 1989a, 1990a), but many other plants containing a wide array of allelochemicals permit successful development (Miller and Hanson, 1989a). Lechowicz (1983) suggested that suitable plants are characterized by precipitable (hydrolyzable) tannins and sclerophylly (a combined measure of leaf toughness and water content).

Goldschmidt (1934) and Leonard (1966, 1969) noted significant intra- and interpopulation variance in larval development that was related to the parental source (egg mass) of the larvae. Variation in growth among individuals in a population may be influenced by genetic differences between families that also may influence suitability of hosts, particularly those newly encountered.

The gypsy moth is not an established pest in the forests of the Pacific Northwest of North America. Isolated infestations were detected in Pacific Coast states in the early 1980s, when egg masses were accidentally transported from sites with major infestations in the northeastern United States. Oregon had a serious problem in 1984 (Daterman et al., 1986). Spraying with *Bacillus thuringiensis* in 1985 and 1986 successfully controlled the outbreak. As long as large infestations exist in the United States, new introductions of gypsy moth into western forests remains a possibility.

The objective of this research was to determine the range of certain developmental parameters relative to the parental source of larvae and the allelochemical content of the diet. Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], a conifer, was selected for study because of its prominent status in forests of the Pacific Northwest, and its limited suitability as a host (Miller and Hanson, 1989b; Miller et al., 1991). White alder (*Alnus rhombifolia* Nutt.) was chosen to represent the highly suitable woody angiosperm hosts that commonly grow intermixed or adjacent to Douglas-fir forests. The differences in host suitability of these two species was believed to be due to significant differences in the allelochemical contents of their foliage.

METHODS AND MATERIALS

Insects. Egg masses were obtained at the end of January from an oak woodland in Seneca Creek State Park, Montgomery County, Maryland, and stored at 4°C until May. Eight large egg masses (each containing ca. 700–1000

eggs) were selected for evaluation of larval performance on Douglas-fir; eggs from four of these masses also were evaluated on alder. Large egg masses were chosen to ensure against selecting two egg masses from the same parents (Doane and McManus, 1981), thus assuring that each egg mass was of a separate family line.

Foliage Collection. Foliage was collected from three alder trees initially selected for their differences in nitrogen content after a preliminary analysis; two trees had higher nitrogen levels (tree-type A) than the third (tree-type B). These differences in nitrogen did not persist, however, resulting in nearly identical nitrogen contents for the two alder types when foliage collection began. Douglas-fir foliage was collected from five trees. Two were 10 years old and had high levels of foliar nitrogen resulting from fertilization (tree-type A); the other three, ranging in age from 10 to 15 years old, were unfertilized and had low foliar nitrogen (tree-type B).

Collections for laboratory feeding trials began in May and were completed by the end of June, coincident with the natural life cycle of gypsy moth larvae in Oregon. Only one tree of each type was harvested on collection days, with the same tree harvested on subsequent days until the foliage became limited; then a new tree of the same type was selected. The freshly gathered foliage was immediately transported to the laboratory, where it was subsampled for chemical analysis and then prepared for feeding by surface sterilizing in 0.25% sodium hypochlorite, rinsing in distilled water, and briefly air-drying.

Larval Feeding Experiment. Upon eclosion, 80 larvae from each of eight families were randomly selected for rearing on Douglas-fir foliage; an additional 42 larvae were selected from each of four of these families and reared on alder foliage. Larvae on Douglas-fir diets were reared in 145-ml cups, 10 per cup until the third instar and three per cup for the remaining instars. Larvae on alder diets were reared in groups of three per cup throughout.

Larvae were reared at 24°C, 45–50% relative humidity, and 16:8 (light-dark) hr photoperiod. Foliage was replaced every two days for early instars and daily for later instars. Larvae were observed every three days to determine percent survival. Pupae were weighed 48 hr after pupation. Days to pupation and pupal period also were determined by daily observations.

Nitrogen Analysis. Subsamples of foliage for nitrogen analysis were washed in dilute soap solution, rinsed three times with distilled H₂O, oven-dried at 60°C for 48 hr, and ground in a Wiley mill to pass a 20-mesh screen. Nitrogen content was determined by a micro-Kjeldahl technique with an automated Technicon Autoanalyzer II (Anonymous, 1975).

Terpene Analysis. Five to twelve branch tips of Douglas-fir, similar to those used to feed larvae, were selected. One-year-old needles were detached, combined into a composite sample, sealed in double air-tight plastic bags, and stored frozen until processed for analysis.

Before analysis, samples were warmed to room temperature inside the bags.

A subsample was withdrawn, frozen with liquid N₂, and ground with a mortar and pestle. Ground tissue was transferred to a capped scintillation vial. Water content was determined on triplicate samples dried at 105°C overnight.

Terpenes were extracted from 0.5 g of the freshly ground subsamples in 1 ml MeOH-H₂O (2:1) and 2 ml of pentane containing fenchone (0.1 mg/ml) as an internal standard (Brooks et al., 1987). Samples were shaken mechanically for 60 min and then centrifuged at room temperature in a IEC HN-SII centrifuge at approximately 1000 rpm for 3–4 min. The pentane, containing the terpenes, was removed and stored at –16°C.

Terpenes were analyzed on a Hewlett-Packard 5890 gas chromatograph equipped with a flame ionization detector and a Supelcowax 10 fused silica capillary column (30 m × 0.32 mm ID, 0.25-μm film thickness, 1:50 split). Injector and detector were at 250°C. Oven temperature was programmed from 60 to 220°C at 5°/min with a 15-min pause at 220°C. Peak areas were obtained with a Hewlett-Packard 3390A integrator. Compounds were identified by a combination of gas chromatography-mass spectrometry and peak enrichment with standards. Separate response factors for hydrocarbons and monooxygenated and dioxygenated compounds were determined with standards relative to fenchone.

Total Phenol Analysis. A subsample of alder leaves was air-dried after collection and stored in plastic bags at room temperature. A portion of the fresh-frozen Douglas-fir needles analyzed for terpenes was subsampled for phenolic analysis. Before analysis, alder and Douglas-fir foliage were oven-dried for 24 hr at 60°C, ground to pass a 40-mesh screen, and redried overnight. Phenols were extracted from a 100-mg subsample in 8 ml (Douglas-fir) or 10 ml (alder) MeOH-H₂O (7:3) on a shaker for 1 hr. The mixture was centrifuged at 1000 rpm in an IEC HN-SII centrifuge at room temperature for 5 min and analyzed with Folin-Ciocalteu phenol reagent as described by Julkunen-Tiitto (1985). Percent transmittance was measured at 700 nm with a Bausch and Lomb Spectronic 21 set to zero with distilled H₂O. A standard curve was prepared with catechin containing a MeOH concentration equivalent to the samples.

Water Content. Water content of foliage samples was measured gravimetrically from freshly cut alder leaves and from frozen Douglas-fir needles stored for terpene analysis.

Statistical Analyses. One-way analysis of variance (ANOVA) was used to determine if the foliage diets contained different concentrations of nitrogen during the feeding experiment. Fisher's least significant difference (LSD) was used to compare the means. Concentrations of total phenols and terpenes were compared only for diets within species by the Student's *t* test. In order to test the effect of diet on the performance of families, each growth parameter was analyzed separately for males and females with a nested ANOVA; family within treatment was the error term for treatment, and individual larvae within families

was the error term for families. Both the family and larvae were considered random effects. Treatment means were compared by Fisher's LSD. The effect of diet on percent family survival had to be analyzed with a one-way ANOVA because there was a single value for each family; data transformation was not necessary. Significantly different means were identified by Fisher's LSD.

RESULTS

Foliar Quality. The chemical composition of alder foliage differed substantially from that of Douglas-fir throughout the feeding experiment, as illustrated by the seasonal trends (Figure 1) and averages (Table 1). The alder foliage contained higher quantities of both nitrogen and total phenols, but contained no volatile terpenes. The nitrogen contents were within expected ranges for angiosperms and conifers (Mattson, 1980); the two alder types each averaged more than 2% through the sampling period and the two Douglas-fir types averaged 1–2% (Figure 1).

Steam distillation confirmed the absence of terpenes in alder. A bulk fresh leaf sample failed to produce an oil layer above a column water trap; the water was not cloudy, and no characteristic terpene odor was detectable (Farnsworth, 1966). A fresh leaf sample extracted and analyzed like the Douglas-fir needles also exhibited no appreciable quantities of any volatile compounds. Total terpenes in Douglas-fir foliage made up about 1.75% of the dry weight (Table 1), with monoterpenes representing more than 90% of this quantity. α -Pinene, β -pinene, and sabinene were the most abundant monoterpenes.

In addition to the differences in foliar quality between species, foliar quality differed between tree types within a species. When the alder trees were selected for study, they differed substantially in their nitrogen content (3.7% tree-type A, and 2.8% tree-type B), but, as the growing season progressed, their nitrogen contents rapidly converged. By the time the feeding experiment began, their nitrogen contents were the same (Figure 1), and they did not differ when averaged over the season (Table 1). Total phenol concentrations were consistently lower in alder tree-type A (LP), than in tree-type B (HP) throughout the collection period (Figure 1), resulting in a significant difference when averaged for the season (Table 1).

In Douglas-fir, the nitrogen level was consistently higher for tree-type A (Figure 1), and the average content over the collection period differed significantly from that of tree-type B. Total phenols were most similar between the two fir types early in the collection period, May 17–25, (Figure 1); during the rest of May and nearly all of June, they generally were much higher for tree-type B, which had a significantly higher seasonal average (Table 1). Concentrations of total terpenes in the fir varied considerably (Figure 1), and there

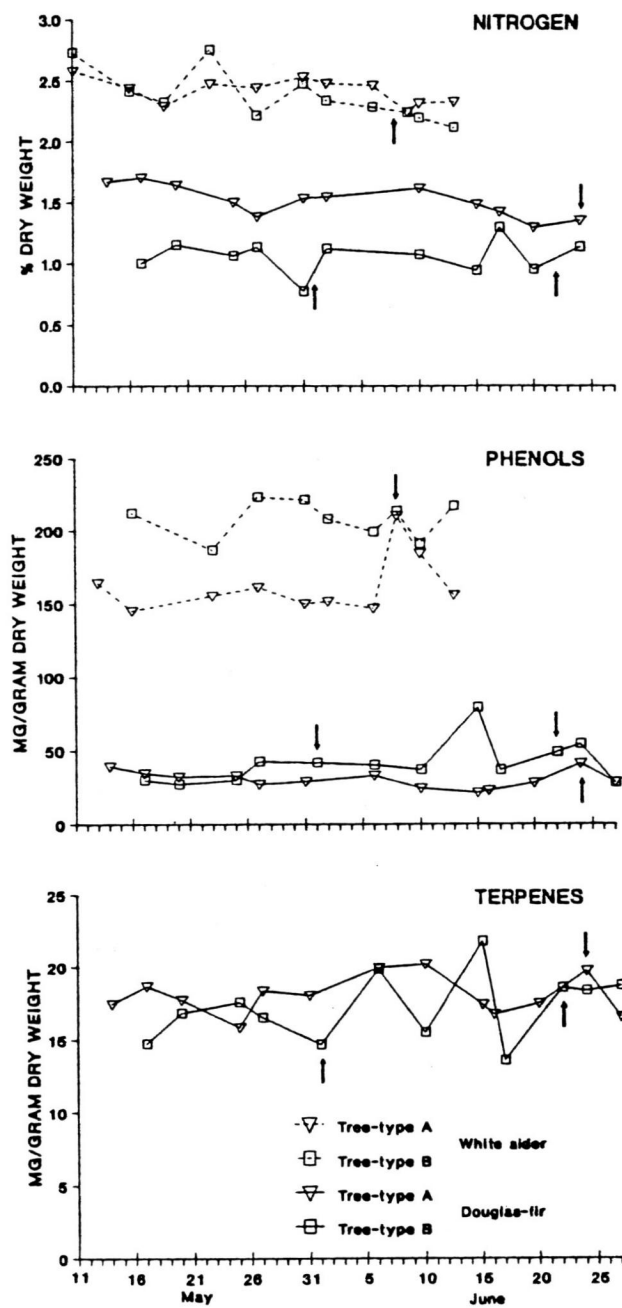


FIG. 1. Seasonal levels (1988) of foliar nitrogen and allelochemicals in white alder and Douglas-fir diets fed to gypsy moth larvae. Vertical arrows indicate when a new tree was selected for harvest within a type.

TABLE 1. SEASONAL MEAN CONCENTRATIONS (\pm SE) OF NITROGEN AND ALLELOCHEMICALS IN WHITE ALDER AND DOUGLAS-FIR FOLIAGE AND DEVELOPMENTAL PARAMETERS OF GYPSY MOTH FAMILIES FED THESE TISSUES^a

	Sex	White alder ^b		Douglas-fir ^c	
		Type A LP	Type B HP	Type A HNLP	Type B LNHP
Foliar quality					
Nitrogen (%)		2.41a (±0.03)	2.36a (±0.06)	1.51b (±0.03)	1.05c (±0.04)
Total phenols (mg catechin equiv/g) ^d		162.38 (±6.37)	207.78 (±4.35)	30.40 (±1.63)	36.94 (±2.45)
Terpenes (mg/g) ^e		0.0	0.0	17.21 (±0.69)	18.01 (±0.37)
Developmental parameters					
Survival (%)		88.3a (±6.0)	84.5a (±3.9)	16.8b (±2.7)	7.5c (±2.3)
Larval period (days)	F	38.5a (±0.7)	36.9a (±0.7)	49.7b (±1.6)	51.1b (±1.3)
	M	33.5a (±0.6)	32.3a (±0.6)	46.4b (±1.0)	47.8b (±0.2)
Pupal weight (mg)	F	1295a (±73)	1447b (±27)	846c (±27)	708c (±87)
	M	459a (±7)	510b (±16)	344c (±7)	317c (±1)
Pupal period (days)	F	11.0a (±0.1)	11.1a (±0.1)	10.4b (±0.1)	10.3b (±0.0)
	M	13.5a (±0.2)	13.7a (±0.3)	12.1b (±0.1)	12.2b (±0.1)

^a Nitrogen and survival analyzed with a one-way ANOVA; all other larval parameters were analyzed with a nested ANOVA. Multiple comparisons between means were computed with a standard LSD. Means followed by the same letters are not significantly different at $P \leq 0.05$.

^b LP = low phenols; HP = high phenols.

^c HNLP = high nitrogen, low phenols; LNHP = low nitrogen, high phenols.

^d Only intraspecific concentrations were compared statistically by the Student *t* test; alder significantly different at $P \leq 0.001$, Douglas-fir significantly different at $P \leq 0.05$.

^e Douglas-fir was compared by the Student *t* test, not significant at $P \leq 0.05$.

were no significant differences between the two tree types over the course of the experiment (Table 1). Chemically, Douglas-fir tree-type A contained higher nitrogen and lower phenolic concentrations (HNLP) than tree-type B (LNHP).

Water content of the LNHP fir diet was lower than that of the HNLP diet most of the season, averaging 55.3% and 57.1%, respectively (Joseph, 1989). There were no differences in the water content of the alder diets. In May, Doug-

las-fir diets had a lower average water content (56.2%) than alder (63.6%), whereas in June, Douglas-fir contained more water (56.2%) than alder (41.3%).

The morphology and texture of alder leaves differed substantially from that of Douglas-fir needles. Simple puncture tests in our laboratory indicated that 1-year-old needles of Douglas-fir were tougher than white alder leaves.

Larval Survival and Development. Growth and development of families fed alder foliage was much better than that of families fed Douglas-fir foliage (Table 1). Survival was significantly lower on Douglas-fir foliage than on alder; mortality in the first instar accounted for over 90% of the losses. Those families with larvae surviving through pupation on Douglas-fir had significantly longer larval periods, significantly lower pupal weights, and significantly shorter pupal periods than did families reared on alder (Table 1). Longer larval periods and lower pupal weights decrease the fitness of insect herbivores (Rhoades, 1983).

Intraspecific differences in tree nutritional quality affected family performance to some extent. The only difference between families reared on HP and LP alder foliage was the lower pupal weights of families fed the latter (Table 1). Survival, larval periods, and pupal periods did not differ. Survival of families reared on HNLP Douglas-fir was more than twice as high as survival for families reared on LNHP fir. Pupal weights and larval and pupal periods did not differ for larvae in families fed the two types of fir foliage. *F* ratios and *P* values from the nested ANOVA (Table 2) indicated significant differences between families for all parameters, except for female pupal period and male pupal weight. Nevertheless, there were even greater differences caused by the treatment, demonstrating that variation in all growth parameters was most

TABLE 2. *F* RATIOS AND *P* VALUES FOR NESTED ANOVA FOR GYPSY MOTH DEVELOPMENTAL PARAMETERS

Sex	Source of variation	Developmental parameters					
		Larval period		Pupal weight		Pupal period	
		<i>F</i> ^a	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Female	Host species and quality	31.8	0.0001	29.2	0.0001	10.9	0.0010
	Family (within treatment)	9.2	0.0001	2.1	0.0208	1.4	0.1730
Male	Host species and quality	75.5	0.0001	163.3	0.0001	11.5	0.0008
	Family (within treatment)	4.2	0.0001	0.8	0.6317	3.4	0.0002

^a *F* = *F* ratio, *P* = level of significance.

strongly influenced by the species of host tree fed to the larvae. Survival, with an F ratio of 151.4, also was greatly influenced by the host species and quality (Table 1).

Although host species strongly influenced development, differences in larval performance were associated with interegg-mass differences (Table 2), especially on diets of Douglas-fir foliage (Table 3). For the four families (I, V, VI, VII) subjected to all diets, survival and growth of each was superior on alder foliage. Only two families (I, V) had sufficient genetic resources to survive and complete development (Tables 3) on the foliage of HNLP Douglas-fir, nutritionally the more suitable of the two Douglas-fir types tested. None of the four families completed their life cycles on the most unsuitable diet, LNHP fir. Six of eight families reared on Douglas-fir survived and completed development on the HNLP foliage, but only two of the eight families were successful on the LNHP foliage, the least nutritious of the two types. Coefficients of variation for family survival on each of the four diets confirmed that survival varied least for families fed the two alder diets (CV 13.6% and 9.4% for LP and HP alder, respectively), and increased inversely as the nutritional quality of the diet declined (CV 54.0% and 168.3% for HNLP and LNHP fir, respectively). Therefore, genetic differences among families are probably most critical to survival when the nutritional quality of the diet is least satisfactory.

The performance of some families relative to the other families varied substantially with the diet (Table 3). For example, survival in family I was the lowest of all four families on both diets of alder; its survival on LNHP fir was low. On fir HNLP diets, however, family I survival was intermediate to high (Table 3) compared to the three other families in this group. Female pupal weights in family I showed similar responses. On LP alder diets, family I females had significantly greater pupal weights than females from the other three families, and family I had one of the two highest pupal weights on HP alder diets (Table 3). Only two of the four families had sufficient larval survival when fed HNLP Douglas-fir to permit measurement of pupal weights, but there were pupae from four additional families reared only on Douglas-fir. Females of family I had the lowest pupal weights of all six families measured. Not enough females survived on LNHP Douglas-fir diet for measurements. Performance of a family on a suitable host diet probably has limited utility for predicting its success and potential adaptability to a new, less suitable host.

DISCUSSION

Both genetic background and host species clearly were critical in determining survival, development, and overall fitness of gypsy moth larvae in this study. Chemical analysis confirmed the nutritional and allelochemical differ-

TABLE 3. DEVELOPMENTAL PARAMETERS (MEAN \pm SE)^a OF GYPSY MOTH LARVAE FROM EGG MASSES REARED IN LABORATORY ON FIELD-COLLECTED FOLIAGE OF WHITE ALDER AND DOUGLAS-FIR

Egg mass	Larval survival (%)	Larval period (days)		Pupal weight (mg) ^b		Pupal period (days)	
		Female	Male	Female	Male	Female	Male
Alder type A (LP)							
I	71	39.1 (±0.6)	34.3 (±0.8)	1493 (±64)	480 (±14)	11.2 (±0.2)	14.1 (±0.2)
V	99	38.5 (±0.5)	33.5 (±0.6)	1299 (±57)	454 (±11)	10.8 (±0.1)	13.3 (±0.2)
VI	91	38.8 (±0.6)	34.3 (±0.6)	1245 (±62)	456 (±11)	11.3 (±0.2)	13.7 (±0.2)
VII	92	35.8 (±0.7)	31.9 (±0.6)	1142 (±66)	446 (±10)	10.8 (±0.2)	13.0 (±0.2)
Alder type B (HP)							
I	76	36.0 (±0.7)	31.6 (±0.7)	1485 (±64)	512 (±12)	11.1 (±0.2)	13.8 (±0.2)
V	90	38.7 (±0.6)	32.5 (±0.6)	1497 (±62)	513 (±11)	11.3 (±0.2)	13.8 (±0.2)
VI	80	37.3 (±0.7)	33.8 (±0.7)	1432 (±71)	515 (±13)	11.3 (±0.2)	14.2 (±0.2)
VII	92	35.5 (±0.5)	31.3 (±0.7)	1375 (±51)	500 (±19)	10.8 (±0.1)	12.8 (±0.2)
Douglas-fir type A (HNLP)							
I	14	43.0 (±1.0)	41.0 (±1.2)	750 (±104)	313 (±21)	10.5 (±0.3)	12.0 (±0.4)
II	26	50.1 (±0.8)	47.5 (±0.8)	757 (±77)	350 (±13)	10.4 (±0.2)	12.3 (±0.2)
III	21	50.3 (±1.0)	45.6 (±0.8)	828 (±104)	343 (±15)	10.5 (±0.3)	12.2 (±0.3)
IV	15	53.3 (±1.3)	47.7 (±1.1)	940 (±127)	370 (±19)	10.3 (±0.3)	12.0 (±0.3)
V	19	48.4 (±0.9)	49.2 (±1.1)	835 (±85)	346 (±19)	10.3 (±0.2)	12.0 (±0.3)
VI	4						
VII	10						
VIII	25	53.2 (±0.7)	47.5 (±1.1)	954 (±68)	347 (±19)	10.3 (±0.2)	12.0 (±0.3)
Douglas-fir type B (LNHP)							
I	1						
II	11						
III	15	49.8 (±1.3)	48.0 (±1.5)	631 (±127)	323 (±23)	10.3 (±0.3)	12.3 (±0.5)
IV	16	52.3 (±1.3)	47.6 (±1.0)	784 (±127)	311 (±19)	10.3 (±0.3)	12.1 (±0.3)
V	0						
VI	0						
VII	7						
VIII	10						

^aBecause family was used as a random effect in the nested ANOVA, no mean separation was performed.

^bFresh weight two days after pupal formation.

ences between alder and Douglas-fir and the poor nutritional quality and limited suitability of Douglas-fir for gypsy moth development (Miller and Hanson, 1989b; Miller et al., 1991).

To what extent did each of the chemical components in the diets contribute to the differences in family performance? Comparing foliar chemistry of alder and Douglas-fir is difficult, because three principal groups of compounds that differ both quantitatively and qualitatively are involved. Relatively modest differences in nitrogen and phenols in the two Douglas-fir diets had significant effects on survival. The alder diets contained much more nitrogen and total phenols than the Douglas-fir diets. The greater nitrogen content of alder undoubtedly made it a better diet nutritionally (Mattson, 1980; Scriber and Slansky, 1981; Mattson and Scriber, 1987) and contributed to the higher survival and better larval growth.

The differences in total phenol concentrations between Douglas-fir and alder must be interpreted with caution, because the types of tannins and phenols may be quite different in the two species. Conifers, including Douglas-fir, produce condensed tannins (Swain, 1979; Stafford and Lester, 1981). Angiosperms can synthesize hydrolyzable as well as condensed tannins (Swain, 1979), and the proportion of each can differ substantially between species (Bate-Smith, 1977). Tannin and phenol composition of white alder apparently has not been reported.

In the Folin-Denis assay for total phenols, a procedure similar to that used in our study, the absorbance of tannic acid (a standard for hydrolyzable tannins) was 2.2 times greater than that of catechin (the same standard for condensed tannins that we used) when normalized (Mole and Waterman, 1987). Consequently, if two plant tissues contained equal quantities of tannins and phenols, one having predominantly hydrolyzable tannins and the other predominantly condensed tannins, the one with hydrolyzable tannins would appear to have twice the total phenol concentration, as calculated from a catechin standard curve. If alder tissues contain a significant proportion of hydrolyzable tannins, a 2.2-fold difference in concentration relative to Douglas-fir could represent no difference at all in total phenols. Total phenol concentrations in alder, however, were 4.4–6.8 times greater than in Douglas-fir. Thus, concentrations of total phenols in the alder diets probably were greater than in Douglas-fir diets, even though the precise structure and composition of the alder tannins are unknown.

The species effect of the greater phenolic concentration in alder and the interactions of phenolics with nitrogen are difficult to evaluate, because the actual tannin structures and toxicities and how toxicities may interact with nitrogen level are unknown. The two alder diets we tested differed only in their concentration of total phenols; this comparison is not complicated by interspecific differences in tannin structures or nitrogen concentrations. The greater pupal weights produced by feeding on HP alder may have resulted from increases in

the relative consumption rate, the efficiencies of conversion of ingested or digested food, or some combination of these (Waldbauer, 1968), since the larval period was unchanged. Plants containing tannins are more acceptable hosts for gypsy moth than are plants containing other allelochemicals—iridoids, sesquiterpenes, and particularly alkaloids (Barbosa and Krischik, 1987; Miller and Hanson 1989a; Barbosa et al., 1990a), and host acceptance in the field is more closely correlated with tannin content than with total phenol content of the leaves (Lechowicz, 1983). Hydrolyzable tannins may act as phagostimulants for adapted species, such as gypsy moth (Bernays, 1981; Lechowicz, 1983; Kleiner et al., 1989). The alder phenolics appear to have acted as phagostimulants in this study.

The combined effect of low nitrogen and high phenol concentrations in Douglas-fir had a greater adverse impact on survival than did either high quantities of phenols alone in alder or the HNLP diet in Douglas-fir. Part of the difference between Douglas-fir and alder, or between the two Douglas-fir diets, may be attributable to the relative amounts of condensed tannins, which are detrimental to several species of herbivorous insects (Bernays, 1981; Klocke and Chan, 1982; Reese et al., 1982; Berenbaum, 1983; Manuwoto et al., 1985; Manuwoto and Scriber, 1986). This detrimental effect has often been ascribed to formation of insoluble complexes between tannins and proteins that diminish metabolizable nitrogen (Feeny, 1976; Rhoades and Cates, 1976). This mechanism, however, does not appear to function in insect herbivores (Bernays, 1981; Manuwoto et al., 1985; J.S. Martin et al., 1985; Manuwoto and Scriber, 1986; M.M. Martin et al. 1987), including gypsy moth (Schultz and Lechowicz, 1986). Survival of gypsy moth larvae was 77% of controls, and larval weights were 40% of controls after 20 days of exposure to tannin- and phenol-rich extract of Douglas-fir (with the terpenes removed) incorporated into artificial diet (Joseph, 1989). When the nitrogen contents of the treatment and control diets were lowered, survival did not change, but weights of larvae fed low-nitrogen, phenol-rich diets were approximately 20% of the controls.

The presence of terpenes in Douglas-fir and their absence in alder is probably the greatest difference in the allelochemistry of the two host species. Two of the three major terpenes in Douglas-fir foliage, α -pinene and β -pinene, were strong phagodeterrents when applied in pure form to food of the gypsy moth (Meisner and Skatulla, 1975). Other monoterpenes, sesquiterpenes, sesquiterpene lactones, and diterpenes also have feeding deterrent activity (Doskotch et al., 1980a,b; El-Naggar et al., 1980).

The impact of terpenes alone on gypsy moth growth and development cannot be evaluated from our data, because their effects are inseparable from the influences of nitrogen and phenols. However, induction of detoxification enzymes in insects ingesting monoterpenes in their diet indicates that these compounds are nutritionally undesirable (Brattsten, 1986; Yu, 1986, 1987; Har-

wood et al., 1990). Douglas-fir terpenes isolated by steam distillation and incorporated into artificial diet at natural concentrations did not affect survival or weights of gypsy moth larvae reared on these diets for 20 days (Joseph, 1989). When the terpenes were combined in artificial diet with an extract containing Douglas-fir phenols, survival and pupal weights were greatly reduced below those on diet containing only the phenol extract, suggesting an interaction or possible synergism between these two groups of compounds.

Most larval mortality occurred during the first instar, when the small larvae were more likely to be repelled by physical barriers such as leaf toughness (Hough and Pimentel, 1978; Ohmart et al., 1985). Barbosa et al. (1986) reported mechanical barriers to biting, and consequent starvation, as a probable cause of mortality for first instars fed conifer foliage. In our experiments leaf toughness probably did affect mortality of first-instar larvae on fir, but not alder. However, the magnitude of the effect relative to foliar chemistry is not determinable from these data. We can conclude that toughness did not contribute to the differences in family performance observed between tree types within a species. Furthermore, incorporation of Douglas-fir foliage extracts into artificial diets, where needle toughness was not a factor, resulted in low survival and decreased larval weight (Joseph, 1989), as observed with our fresh foliage.

Water content is closely associated with leaf toughness; together they provide a measure of sclerophylly (Lechowicz, 1983). Foliar water content in Douglas-fir differed little from that of alder and probably did not contribute much to the differences in family performances between the two host species.

Host adaptability has important implications for potential establishment of gypsy moth in the forests of the Pacific Northwest, where preferred hosts such as Oregon white oak and alder species often are situated in or adjacent to Douglas-fir stands (Daterman et al., 1986). The genetic constitution of some families of gypsy moth clearly permits survival and successful development on an unsuitable host, such as Douglas-fir, even when this host is of low nutritional value. Furthermore, the likelihood of survival increases as the nutritional value of the Douglas-fir increases, as would be the case in fertilized plantations.

In the northeastern United States, gypsy moths effectively utilize conifers such as white pine (*Pinus strobus* L.), pitch pine (*P. rigida* Mill.), and Norway spruce [*Picea abies* (L.) Karst] as secondary hosts during low-density population phases (Rossiter, 1987), and performance and fitness improve on a two-species diet of black oak (*Quercus velutina* Lam.) and either Virginia pine (*Pinus virginiana* Mill.) or loblolly pine (*P. taeda* L.), relative to black oak alone (Barbosa et al., 1986). Utilization of secondary hosts may help to release populations from a low-density stable phase into a higher-density building phase (Campbell, 1981). Therefore, establishment of gypsy moth on Douglas-fir even at low levels might pose a serious threat, especially from larvae in later instars, which survive switching from alder to Douglas-fir (Joseph, 1989). In addition,

establishment on Douglas-fir might give rise to populations with enhanced behavioral or metabolic resistance to pathogens (Rossiter, 1987) or pesticides (Moldenke et al., unpublished data).

In summary, although nutritional quality is a primary determinant of host suitability, the genetic makeup of each family influences the degree of suitability to family members. Genetic differences between families are particularly important when the nutritional quality of the host is limited. If gypsy moth becomes established at low population densities in mixed conifer-broadleaf stands in the Pacific Northwest, some utilization of Douglas-fir can be anticipated.

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