

Species-specific differences in oak foliage affect preference and performance of gypsy moth caterpillars

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Abstract

The gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), is an introduced defoliator that preferentially feeds on oaks, *Quercus* spp. (Fagaceae) in the north-eastern USA. As the gypsy moth expands its geographic range, the extensive oak component in forests and urban environments of the USA assure its successful establishment. Given their economic and ecological importance, and the gypsy moth's potential to cause mortality, we evaluated caterpillar preference and performance on various oaks prevalent in the central hardwoods region. Most of the physical and chemical characteristics we measured, from budbreak phenology to foliar chemistry, varied significantly among the oak species tested. Similarly, insect preference and performance varied significantly, though not always in predictable ways. Caterpillar preference was compared for black, *Q. velutina* Lamarck, burr, *Q. macrocarpa* Michaux, cherrybark, *Q. pagoda* Rafinesque, northern red, *Q. rubra* L., pin, *Q. palustris* Muenchhausen, swamp white, *Q. bicolor* Willdenow, white, *Q. alba* L., and willow, *Q. phellos* L., oaks. Gypsy moth preference was greatest for black and burr, and least for northern red, pin, and willow oaks. We assessed foliar characteristics and caterpillar performance on foliage from burr, cherrybark, northern red, pin, and willow oaks. Caterpillar preference did not always correlate with performance. Gypsy moth consumption and growth were highest, and development most rapid, on pin oak, which had high nitrogen and tannin levels, and was among the least preferred. Northern red and willow oaks were also among the least preferred and were the least suitable tested, producing caterpillars with moderate to low consumption and growth rates, as well as the longest development. Northern red oak contained the lowest foliar tannins; willow oak foliage was lowest in carbohydrates and nitrogen. Our results suggest that a combination of foliar characteristics may be responsible for gypsy moth preference and performance, and that an optimal combination of foliar components serves to maximize host suitability. These data will provide information useful for planning and managing urban forests in the presence of expanding gypsy moth populations.

Introduction

The gypsy moth, *Lymantria dispar* (L.) is an introduced, early season defoliator capable of outbreak behavior and extensive defoliation of deciduous trees. The extremely broad larval host range and the non-discriminating oviposition behavior of adult females has allowed the gypsy moth to disperse and become established through much of north-eastern USA (Doane & McManus, 1981).

Gypsy moth caterpillars feed on over 500 plant species (Liebhold et al., 1995), but they are tannin-adapted insects (Barbosa & Krischik, 1987) and preferentially feed on oaks, *Quercus* spp. The extensive oak component in forests and urban environments of the central hardwoods region of the eastern USA assures its successful establishment as the gypsy moth expands its geographic range.

Oaks suffer compromised growth and increased mortality in response to gypsy moth defoliation (Fajvan & Wood, 1996), and defoliated trees have lowered resistance to other biotic and abiotic factors (Doane & McManus, 1981). The two-lined chestnut borer, *Agrilus bilineatus* (Weber) (Coleoptera: Buprestidae), Armillaria root rot, *Armillaria mellea* (Fries) Kummer, and drought are major contributors

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to oak mortality following gypsy moth outbreaks in North America (Elkinton & Liebhold, 1990).

The ecological implications of gypsy moth defoliation include changes in forest succession patterns and watershed characteristics, stand patchiness, and sporadic masting, all of which can affect wildlife distribution patterns (Twery, 1990; Fajvan & Wood, 1996). In urban landscapes, human health concerns are associated with high populations of mobile caterpillars with urticating hairs, as well as copious frass production (Doane & McManus, 1981).

The relative preference and growth of gypsy moths on various oak species common to the central hardwoods region of the eastern USA has not been fully characterized (but see Barbosa et al., 1983; Falco & Rieske, 2001). Host plant preference is often an indicator of host suitability (Martinat & Barbosa, 1987), and is affected by phenology (Hunter, 1992) and foliar chemistry (Schultz et al., 1982). Gypsy moth development is strongly affected by the characteristics of its food plant, including plant phenology and foliar accessibility (Hunter, 1993), foliar carbohydrates (Valentine et al., 1983), nitrogen (Mattson, 1980; Lovett et al., 1998), and defensive compounds (Rossiter et al., 1988; Bouchier & Nealis, 1993), all of which vary among oak species (Feeny & Bostock, 1968; Schultz et al., 1982; Makkar et al., 1991; Hunter & Lechowicz, 1992; Hunter, 1992). Gypsy moth adult fecundity is positively correlated with larval growth rate and pupal weight (Elkinton & Liebhold, 1990; Bouchier & Nealis, 1993).

Given the economic and ecological importance of oaks in forest and urban settings, and the gypsy moth's potential to cause oak mortality, we evaluated gypsy moth larval preference and performance on various oaks prevalent in the central hardwoods region. We also compared budburst phenology and physical and chemical foliar characteristics that may be responsible for any differences in caterpillar preference or performance. This information will provide tools for urban foresters and natural resource managers with which to gauge the defoliation potential and impact of expanding gypsy moth populations.

Materials and methods

Eighteen oak species were obtained as 2-year-old whips from commercial nurseries and planted in 1997 at the University of Kentucky's (UK) Spindletop Research Farm, Lexington, KY. Species were planted in a randomized block design with six replications. In 2001, eight species were selected for experimental use, based on their prevalence in forests and urban landscapes of the central hardwoods region, including black, *Q. velutina* Lamarck, burr, *Q. macrocarpa* Michaux, cherrybark, *Q. pagoda* Rafinesque, pin, *Q. palustris* Muenchhausen, swamp

white, *Q. bicolor* Willdenow, and white, *Q. alba* L., oaks. Because of limited availability at the Spindletop site, we used the northern red oak, *Q. rubra* L., foliage from trees of a similar age, planted at UK's Horticultural South Farm, and willow oak, *Q. phellos* L., leaves from trees located on the UK campus. All trees were about the same size and 6–10 years of age. A branch at the midcanopy level on the south side of each tree was flagged ($N =$ five per species), and foliage was collected from the terminal whorls of this branch for each of the following experiments. However, only three black oak trees were available, so an additional branch on two trees served as replicates, and only four cherrybark and pin oak trees were available, so an additional branch on one tree of each respective species served as a replicate.

First instar gypsy moth larvae were obtained from the Insect Rearing Facility at Otis Air Force Base, MA (USA), and held in a growth chamber with a L15:D9 photoperiod at 23 °C. Beginning at eclosion, caterpillars were fed a wheat germ-based artificial diet (Southland Products, Lake Village, AR). They were removed from the diet and starved for 24 h before experimental use. All assays were performed in the UK Forest Entomology Gypsy Moth Quarantine Facility.

Plant characteristics

Budburst phenology and leaf expansion was monitored at the Spindletop site in early spring 2001. On 27 March and 10, 15, 21, and 27 April 2001, each tree was rated on a scale from 0 to 5, where 0 = buds dormant, dark and oval, 1 = buds light brown, oval and swollen or pointed, 2 = bud scales expanding, green tissue visible between scales, 3 = buds with red tip or with leaves visible, but not expanded, 4 = leaves clearly extend beyond bud scales, but still pink or red; leaf expansion started, but leaves remain hard and deeply grooved, 5 = leaves completely open, spread, and vertically drooping. Budbreak was monitored only on black, burr, cherrybark, and pin oaks; northern red and willow oaks were recruited later from alternate sites.

On 23 May, leaves ($N = 6$) from the predetermined branch on each tree were collected. We measured foliar toughness as the force (mg) necessary to penetrate leaf tissue using a force gauge fitted with a pointed cone attachment (Mark 10, Hicksville, NY). Leaf area was measured with an electronic meter using a photoelectric cell (LI-3100, LiCor, Lincoln, NE) before oven-drying the foliage at 60 °C for 5 days and calculating leaf density (g/cm^2).

On 31 May, additional foliage was sampled for phytochemical analysis ($N = 5$ trees per species). Leaves were excised, packed in a wet paper towel, and transported to the laboratory in an ice chest. Petioles were removed and the leaves were flash-frozen in liquid nitrogen, ground to a

fine powder, freeze-dried (125L VirTis Freezemobile, Gradiner, NY), and stored at -80°C prior to phytochemical analysis. Foliar total non-structural carbohydrate analysis was conducted with an anthrone/thiourea reagent (Quarmby & Allen, 1989) using sucrose standards. Foliar nitrogen was assessed using a Leco TN-300 nitrogen determinator (Leco, St. Joseph, MI). Tannin concentrations were analyzed as the protein binding capacity using a radial diffusion assay developed by Hagerman (1987).

Caterpillar assays

Over a 4-day period in mid-May 2001, a series of two-choice host preference tests was set up using second instar larvae, coinciding with the natural period of caterpillar dispersal and host selection in early spring. Eight oak species were used in the preference tests, including black, burr, cherrybark, northern red, pin, swamp white, white, and willow oaks, in a total of 18 paired combinations.

For each oak species, leaves were excised with petioles intact, placed between wet paper towels, and transported in an ice-filled cooler back to the laboratory. Two 15 mm leaf discs from different species were pinned adjacent to one another in a 50 mm wax-bottomed Petri dish lined with moistened filter paper. One newly molted second instar gypsy moth caterpillar was placed in each Petri dish ($N = 25$ per paired comparison) and allowed to feed.

On 11 May, black, burr, pin, and white oaks were assayed in six combinations. On 12 May, cherrybark, northern red, swamp white, and willow oak were assayed. On 14 May, five species from the previous two dates were paired against one another: black, burr, cherrybark, northern red, and swamp white oaks were assayed. Because of the limitations in available foliage, only five of the eight oak species initially used were repeated on the third day, so not all species were tested against one another.

Assays were conducted in a growth chamber at 25°C , L15:D9, and terminated after 7 h, or when there was a visual difference greater than 50% between leaf discs of the area consumed by caterpillar feeding (Rieske & Raffa, 1998). We scanned and digitized leaf disc areas, and calculated leaf area consumed by subtracting the remaining leaf area from initial leaf area (in pixels). To rank the oak species in order of preference, we devised a Preference Index by dividing the number of times a species was preferred in the pairings by the total number of pairings conducted with that species, yielding a value between 0 (least preferred) and 1 (most preferred).

We set up performance tests on 29 May using fourth instar caterpillars, when caterpillars in wild populations are of the same age. Five oak species from the preference tests were chosen, including burr, cherrybark, northern red, pin, and willow. Foliage was collected from the

predetermined branches as described above. Whole leaves with intact petioles were surface-sterilized in 0.1% sodium hypochlorite solution, weighed, and placed individually in florists' water picks in 7×21 cm clear plastic rearing boxes. One newly molted, fourth instar caterpillar was weighed and placed in each rearing box ($N = 25$ per oak species) and monitored at 6 h intervals for the duration of the assay, which was terminated when the insect molted. Leaves and water were replenished as needed. At the completion of the assay, caterpillars, frass, and remaining leaf material were oven-dried at 60°C for 5 days prior to weighing.

To quantify caterpillar performance, we calculated a relative consumption rate [$\text{RCR} = \text{leaf area consumed (mg)} \cdot (\text{initial larval weight (mg)})^{-1} \cdot (\text{time (h)})^{-1}$], relative growth rate [$\text{RGR} = \text{larval biomass gained (mg)} \cdot (\text{initial larval weight (mg)})^{-1} \cdot (\text{time (h)})^{-1}$], and development time (length of fourth stadium (h)).

Statistical analysis

Budburst phenology was analyzed using a repeated measures ANOVA. Foliar carbohydrates, nitrogen, tannins, leaf toughness, and leaf density were analyzed using a multivariate analysis of variance (MANOVA, SAS Institute, 1997), with oak species as the independent variable. Gypsy moth preference was analyzed using paired t-tests of leaf area consumed in each oak species combination. A square root ($x + 0.5$) transformation was used to normalize data prior to analysis. We assessed differences in larval performance on the five oak species using a multivariate analysis of covariance (MANOCOVA, SAS Institute 1997), with initial gypsy moth weight as a covariate, and with relative consumption rate, relative growth rate, and stadium length as the dependent variables. The Wilks lambda test statistic was used to assess the overall significance of the multivariate models, which was followed by a univariate analysis of individual response variables. We used Tukey's HSD to analyze differences among the five oak species. Lastly, we performed a multivariate canonical correlation analysis (CANCORR, SAS Institute, 1997) to link overall herbivore performance (consumption, growth, and development) with oak species' foliar characteristics (toughness, density, and carbohydrate, nitrogen, and tannin concentrations).

Results

Plant characteristics

Seasonal bud development (Figure 1) was equivalent across species through the 15 April observation date. On 21 April, black oak bud expansion lagged behind the remaining species ($F = 3.98$; d.f. = 2,15; $P = 0.041$), but by 27 April, bud development was complete for all species.

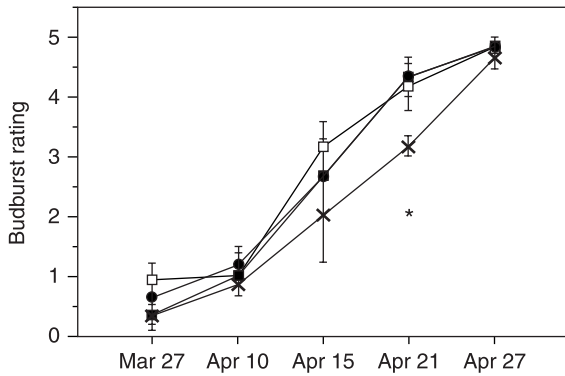


Figure 1 Seasonal bud expansion (mean ± SE) for black (x), burr (□), cherrybark (■), and pin (●) oaks used in caterpillar assays. *Indicates significant difference in bud expansion. Cherrybark oak monitored only to 15 April.

A multivariate analysis of the foliar traits we measured (leaf toughness, leaf density, foliar carbohydrates, nitrogen, and tannins) indicated strongly significant differences between oak species ($F = 9.36$; d.f. = 20,50.7; $P < 0.0001$). Foliar toughness was greatest for burr oak, and least for cherrybark and pin oaks (Table 1). Leaf density was equivalent across species. Foliar carbohydrates varied among species, and were highest in burr oak, but not significantly greater than carbohydrate concentrations in northern red oak. Pin oak foliar carbohydrates were equivalent to northern red and cherrybark oaks, and willow oak foliage had significantly lower carbohydrates than the other species. Foliar nitrogen was also significantly lower in willow oak than the other species, all of which were similar. Levels of foliar tannins varied among species, and were highest in burr, pin, and willow oak foliage. Cherrybark and northern red oak had significantly lower foliar tannins, containing approximately 50% of the concentrations found in burr, pin, or willow oak leaves.

Caterpillar assays

Black oak was preferred in more pairings than any other species assayed, and had the highest preference index (Table 2). Burr oak had the second highest preference index among the oaks tested, and was the only species that gypsy moth caterpillars marginally preferred ($P = 0.07$) over black oak. Caterpillar preference for burr oak foliage was equivalent to that of cherrybark and white oak, but was greater than caterpillar preference for northern red, pin, and swamp white oaks. Swamp white oak had a preference index equal to burr oak (Table 2). Caterpillar preference for swamp white oak was equivalent to cherrybark, but greater than caterpillar preference for northern red and willow oaks. Cherrybark oak ranked fourth in relative preference (Table 2), and was significantly preferred over northern red and willow oak. White oak ranked fifth in relative preference; caterpillar preference was greater for white than pin oak. Finally, northern red, pin, and willow oaks were not preferred in any pairings (Table 2).

The multivariate analysis with gypsy moth relative consumption rate, relative growth rate, and development time, indicated strong differences in herbivore performance based on oak species ($F = 7.37$; d.f. = 12,198.72; $P < 0.0001$). In the univariate analysis, gypsy moth relative consumption rate differed among species (Table 3), and was greater for pin oak than the remaining oak species, but was equivalent between pin and northern red oaks. Caterpillar consumption of burr, cherrybark, northern red, and willow oaks was equivalent. Gypsy moth relative growth rate was greatest for those reared on pin oak, intermediate for those fed burr, cherrybark, and willow oaks, and lowest for those fed northern red oak. Development time was most rapid for caterpillars fed foliage from burr, cherrybark, and pin oaks, which were equivalent; those fed foliage from northern red and willow oaks developed the slowest.

The multivariate canonical correlation analysis, which generates a linear combination of plant variables (toughness,

Table 1 Foliar characteristics [mean (SE)] of oak species used in gypsy moth caterpillar performance assays. Means followed by the same letter do not differ (Tukey's HSD, $P < 0.05$)

Oak species	Foliar characteristic				
	Toughness (mg)	Density (mg/cm ²)	Carbohydrates (%)	Nitrogen (%)	Tannins (diam ² /mg)
Burr	35.54(3.3)a	0.79(0.06)a	9.48(0.29)a	2.12(0.10)a	184.38(14.99)a
Cherrybark	21.80(2.98)b	0.84(0.05)a	7.27(0.26)c	2.24(0.09)a	75.01(13.41)b
Northern red	24.07(2.98)ab	0.80(0.05)a	8.65(0.26)ab	2.21(0.09)a	62.90(13.41)b
Pin	22.10(2.98)b	0.79(0.05)a	7.74(0.26)bc	2.26(0.09)a	151.87(13.41)a
Willow	23.03(2.98)ab	0.84(0.05)a	5.36(0.26)d	1.21(0.09)b	148.66(13.41)a
$F_{d.f.}$	$F_{4,23} = 3.2/$	NS	$F_{4,23} = 33.4/$	$F_{4,23} = 25.7/$	$F_{4,23} = 14.5/$
Pr > F	$P < 0.03$		$P < 0.0001$	$P < 0.0001$	$P < 0.0001$

Table 2 Rank, preference index^a, and relative preference based on two-choice tests (N = 25), of second instar gypsy moth caterpillars for selected oak species (t/P, N = 25). A positive t-value indicates that the oak species in the column heading is the preferred species in each pairing. NT, not tested

	Rank	Preference index	Black	Burr	Cherry bark	Northern red	Pin	Swamp white	White
Black	1	0.83							
Burr	2	0.60	-1.91/0.07						
Cherry bark	4	0.40	2.04/0.05	0.05/0.96					
Northern red	6	0.0	2.98/0.01	2.43/0.02	2.78/0.01				
Pin	7	0.0	2.08/0.05	8.65/< 0.01	NT	NT			
Swamp white	3	0.60	2.25/0.03	2.89/0.01	-0.19/0.85	-1.08/0.29	NT		
White	5	0.33	3.98/< 0.01	1.58/0.13	NT	NT	-2.24/0.04	NT	
Willow	8	0.0	NT	NT	4.19/< 0.01	1.48/0.15	NT	2.49/0.02	NT

^aPreference Index = number of times preferred/total number of pairings conducted.

Table 3 Performance [mean (SE)] of fourth instar gypsy moth caterpillars on selected oak species (N = 25). Means followed by the same letter do not differ (Tukey's HSD, P < 0.05)

Oak species	Caterpillar performance parameter		
	RCR ^a	RGR ^b	Development time ^c
Burr	1.19(0.17)b	0.18(0.01)ab	6.1(0.25)a
Cherrybark	1.29(0.18)b	0.19(0.01)ab	6.7(0.26)ab
Northern red	1.94(0.21)ab	0.15(0.02)b	7.7(0.31)bc
Pin	2.53(0.17)a	0.22(0.01)a	6.5(0.24)a
Willow	1.77(0.17)b	0.20(0.01)ab	7.9(0.24)c
F _{d.f.} /	F _{4,24} = 9.5/	F _{4,24} = 3.9/	F _{4,24} = 10.6/
Pr > F	P < 0.0001	P < 0.006	P < 0.0001

^aRCR = mg(mg)⁻¹(h)⁻¹.

^bRGR = mg(mg)⁻¹(h)⁻¹.

^cLength of fourth stadium (days). Analysis performed on development time measured in h.

density, carbohydrates, nitrogen, and tannins) that correlates mostly closely with a linear combination of insect performance variables (RCR, RGR, and development time), yielded a strongly significant correlation between plant characteristics and herbivore response variables (F = 3.01; d.f. = 15,254.37; P = 0.0002). The best linear combination of plant variables generated was strongly correlated with nitrogen (0.71) and carbohydrates (0.79), which were significantly and inversely correlated with caterpillar development time (0.93).

Discussion

Herbivore host acceptance and suitability is a complex process that depends on physiological aspects of the herbivore, as well as the physical and chemical characteristics of the potential host. Insect herbivores that demonstrate extreme polyphagy, such as the gypsy moth, tend to have more stringent host acceptance standards as early instars, which relax later in development (Barbosa, 1978; Elkinton & Liebhold, 1990). These relatively stringent

standards may be based on host availability or accessibility (Du Merle, 1988; Choong, 1996), on the nutritional aspects of expanding leaves (Mattson, 1980; Scriber & Slansky, 1981), or on concentrations of foliar defense compounds (Schultz, 1988). Foliar characteristics that dictate herbivore preference and performance, including phenology and chemistry, change rapidly over time (Rossiter et al., 1988; Haukioja et al., 2002), as does caterpillar development. Although neonate larvae are the primary dispersal and host selection stage in gypsy moths, second instar caterpillars readily silk and are capable of dispersal and subsequent host selection (Leonard, 1967). Budbreak in deciduous trees is highly variable, and pronounced differences in tree phenology can lead to substantial differences in the structure of the herbivore community (Crawley & Akhteruzzaman, 1988). Most of the physical and chemical characteristics we measured, from budbreak phenology to foliar chemistry, varied significantly among the oak species tested. Similarly, insect preference and performance varied significantly, though not always in predictable ways.

Black oak had the highest preference index, and also lagged behind the other species in budbreak. Enhanced preference for black oak foliage could be attributed to the phenologically younger tissue providing a more accessible food source. Food quality tends to decline with leaf age (Scriber & Slansky, 1981), and an enhanced preference for phenologically young tissue has been demonstrated with gypsy moth caterpillars on other hosts (Hunter, 1993; Rieske & Raffa, 1998). Because of the limitations of available host material, we did not assess caterpillar performance on, and foliar characteristics of, black oak.

Burr oak was among the most preferred species, and caterpillars fed burr oak consumed relatively small amounts of foliage and developed rapidly, but obtained only a moderate growth rate. Burr oak foliage contained the highest levels of carbohydrates and tannins, and only moderate levels of nitrogen, and ironically had the toughest leaves of the species we measured. However, our test of insect preference occurred 21 days prior to our tests of leaf toughness and insect performance, which occurred simultaneously. Burr oak foliar toughness may not have been elevated during the preference assay with younger caterpillars, and so was not an issue with host accessibility. The low consumption and rapid development of caterpillars fed burr oak suggests that this species is a highly suitable host. Low consumption also suggests that burr oak is less likely to suffer extensive defoliation.

Cherrybark oak was intermediate in both preference and performance. It was phenologically advanced relative to the highly preferred black oak, and although it was high in foliar nitrogen, it was among the lowest in carbohydrates and tannins. Northern red and willow oaks had a low preference index in our study, and because they were recruited from alternate sites, we have no data on bud expansion. However, both species proved marginal with respect to caterpillar consumption, growth, and development. There were no consistent trends with respect to foliar characteristics and insect performance among these less preferred species.

Young gypsy moth caterpillars demonstrated a very low preference for pin oak foliage, and the pin oak trees in our study broke bud more rapidly than the highly preferred black oak. In spite of this, older caterpillars fed pin oak had the greatest consumption and growth rates, and developed most rapidly, making pin oak the most optimal host of the species tested, and also the species most likely to suffer extensive defoliation. Foliage from pin oak contained high levels of nitrogen and tannins, and had moderate carbohydrate levels.

Our results are generally consistent with related work, and any differences in relative suitability could be attributed

to species-specific or site-specific variation in leaf chemistry, leaf phenology, or both. Barbosa et al. (1983) found that caterpillars reared on white oak foliage developed most rapidly, and produced larger pupae, than caterpillars fed willow oak. Martinat & Barbosa (1987), who tested some of the same oak species for gypsy moth acceptability, found that caterpillar preference was greatest for white oak, followed by black oak and lastly willow oak. In our experiments, gypsy moths strongly preferred black over white, followed by willow oak. However, we found that willow oak was inferior to pin oak as a host for fourth instar caterpillars with respect to caterpillar development time.

In our study, oak species that had moderate to high levels of carbohydrates, nitrogen, or tannins (i.e., burr and pin) appeared to be superior hosts, while those with low amounts of one or more of these components (i.e., northern red and willow) were poorer hosts. Our data support earlier work which stated that gypsy moth preference and host utilization are not deterred by the presence of foliar tannins (Lechowicz, 1983). In spite of the elevated nitrogen and tannin levels in pin oak foliage, which supported enhanced caterpillar performance, budbreak phenology and the availability of accessible foliage appear to be the driving forces behind the preference of early instar gypsy moth caterpillars (Lechowicz, 1983), as is the case for many folivores (Scriber & Slansky, 1981; Du Merle, 1988; Hunter, 1992; Choong, 1996). Our data suggest that a dynamic combination of foliar characteristics may be responsible for gypsy moth preference and performance, and an optimal combination of these foliar components may serve to maximize host suitability.

Our results have implications for urban foresters, arborists, and natural resource managers who want to minimize the impact of gypsy moth defoliation on the landscape. Choosing oak species which are less optimal hosts for gypsy moth development, and less susceptible to defoliation, could reduce the risk of defoliation and help to dampen expanding gypsy moth populations.

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