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Stem galls affect oak foliage with potential consequences for herbivory

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Abstract. 1. On two dates, foliar characteristics of pin oak, *Quercus palustris*, infested with stem galls caused by the horned oak gall, *Callirhytis cornigera*, were investigated, and the consequences for subsequent herbivory assessed.

2. Second-instar caterpillars of the gypsy moth, *Lymantria dispar*, preferred foliage from ungalled trees.

3. Ungalled trees broke bud earlier than their galled counterparts.

4. Galled trees produced denser leaves with higher nitrogen and tannin concentrations, but foliar carbohydrates did not differ among galled and ungalled trees.

5. Concentrations of foliar carbohydrates in both galled and ungalled trees increased uniformly between the two assay dates. Nitrogen concentrations were greater in leaves from galled trees, and decreased uniformly in galled and ungalled trees over time. Foliar tannins were also greater in foliage from galled trees early in the season; however, foliar tannins declined seasonally in galled tissue so that by the second assay date there was no difference in tannin concentrations between galled and ungalled foliage.

6. In spite of differences in foliar characteristics, performance of older, fourth instar gypsy moth caterpillars did not differ between galled and ungalled trees.

Key words. Budburst phenology, Cynipidae, gypsy moth, horned oak gall, insect–plant interactions, phytochemistry, pin oak, *Quercus*.

Introduction

Plant galls are complex entities that develop under the influence of both the host plant and the inducing organism. In response to stimuli from the gallmaker, plant cells undergo abnormal differentiation and hypertrophy, resulting in characteristic growths that harbour the gallmaker (Mani, 1964). The complexities of gallmaker–host plant interactions are well recognised, and a variety of hypotheses have been evoked to elucidate these relationships (Abrahamson & Weis, 1987; Price *et al.*, 1987; Hartley, 1999; and others). These hypotheses vary in their focus and in their explanation of the driving mechanism(s). Some view the gallmaker–host plant relationship as non-adaptive (Bequaert, 1924) or mutualistic (Cockerell, 1890; Bronner, 1983). Some have taken a plant-centric view, perceiving gall formation as a mechanism of plant defence (Mani, 1964). A corollary to this view is that gallmakers act as *large rhizobia* (*sensu* Hartley, 1999), and may manipulate the production of plant phenolics that serve as the biochemical signals mediating interactions between the host plant and the invading gallmaker. Other hypotheses, such as the nutrition hypothesis (Price *et al.*, 1987; Weis *et al.*, 1988; Hartley & Lawton, 1992), acknowledge that galls may begin as plant defence, but contend that the inducing insects subvert gall growth to enhance their own fitness. Plant galls act as nutrient sinks (McCrea & Abrahamson, 1985; Abrahamson & Weis, 1987), and gallmakers manipulate concentrations of nutrients and other compounds to enhance the nutritional substrate (Price *et al.*, 1987), thereby creating a more hospitable environment for their developing larvae (Hartley & Lawton, 1992; Hartley, 1998; Nyman & Julkunen-Titto, 2000). Thus, gall formation is an adaptation of the insect.

The phenological synchrony hypothesis suggests that synchrony of host plant phenology with the gall inducers' life cycle is essential to the success of the gallmaker, and the insects adapt by synchronising their life cycle with host plant phenology. Temporal variation in tissue availability is extremely important for gall-formers, since they require host tissue in an undifferentiated state to initiate a gall (Weis *et al.*, 1988). Tight synchrony between gallmakers

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and their host plants has been documented in a variety of systems, including herbaceous perennials (McCrea & Abrahamson, 1985), conifers (Cumming, 1968), and deciduous trees (Moser, 1965; Schultz *et al.*, 1982 Clancy *et al.*, 1986; Rehill & Schultz, 2002). This is particularly critical for those exploiting highly ephemeral resources such as plant buds. Plant phenology also affects the distribution and abundance of free-living herbivores, specifically folivores, by producing temporal variation in host plant quality and quantity (Watt & McFarlane, 1991; Hunter, 1992; Hunter & Elkinton, 2000; Rehill & Schultz, 2002; and others). Many early season defoliators, especially those in forest systems, synchronise their egg hatch with budbreak in order to feed on higher quality foliage (Dixon, 1976; Martinat & Barbosa, 1987; Hunter, 1992; Hunter & Lechowicz, 1992; Hunter & Elkinton, 2000).

An additional facet of a gallmaker–host plant system, namely the downstream effects of stem galls on host plant foliage, and subsequent effects on foliar herbivory, are examined in this study. Plant galls may alter concentrations of nutrients and defensive compounds in leaves and other plant parts (Price *et al.*, 1987; Hartley, 1998), and so could affect subsequent herbivores utilising the same food source. Analysis of some systems shows altered nitrogen (Hartley & Lawton, 1992) and tannin (Taper & Case, 1987) concentrations in galls themselves, but examination of adjacent foliage has been relatively neglected (but see Hartley, 1998). In willow leaf galls caused by a tenthridinid sawfly, gall tissue contains elevated phenolic compounds relative to surrounding leaf tissue, and the concentration of these phenolics decline as the gallmaker develops (Hartley, 1998). Hartley (1998) also found that in an oak–cynipid leaf galling system, nitrogen concentrations change within the galls depending on gall density, position on the leaf, and age.

In this study, indirect interactions between the gall-forming and leaf-feeding herbivore guilds were assessed to determine if galling induces changes in the host plant that could influence subsequent herbivory. The model system consisted of pin oak, *Quercus palustris* Muenchhausen, infested by the horned oak gall, *Callirhytis cornigera* (Osten Sacken) (Hymenoptera: Cynipidae). The gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae), was the model herbivore. Pin oak is a favoured host of the gall wasp, which forms large (~40 mm), globular woody stem galls and small leaf galls (Taft & Bissing, 1988; Johnson & Lyon, 1989). The gamogenetic, stem-galling generation requires ~33 months to develop, and wasp emergence from stem galls coincides with budbreak in early spring. The agamic generation exploits these expanding buds, forming small leaf galls; this generation is much shorter lived (2–3 months) (Eliason & Potter, 2000a,b). The gypsy moth is an early season, polyphagous herbivore capable of widespread defoliation, and pin oak is a highly suitable host (Falco & Rieske, 2001; Foss & Rieske, 2003). Gypsy moth caterpillar development is strongly affected by phenolic concentrations (Rossiter *et al.*, 1988; Bourchier & Nealis, 1993) and host plant quality (Valentine *et al.*, 1983; Lindroth *et al.*, 1993; Rieske & Raffa, 1998; Foss & Rieske, 2003), both of which vary seasonally (Feeny & Bostock, 1968; Scriber & Slansky, 1981; Makkar *et al.*, 1991).

To characterise the interactions between stem galling, foliar characteristics, and subsequent effects on leaf herbivory, foliage from galled branches of galled trees, ungalled branches of galled trees, and ungalled trees were examined. Differences in budburst phenology, herbivore preference and performance, and foliar characteristics were assessed.

Materials and methods

A cohort of 45 pin oak street trees in Lexington, Kentucky (U.S.A.) infested with *C. cornigera* were chosen for this study. All trees were approximately 6 m tall, of the same age, and in close proximity to one another. The number of stem galls on each tree were counted, and infestation levels naturally fell into three classes: light (<10 galls per tree), moderate (20–60 galls per tree), and severe (>100 galls per tree).

Budburst phenology

Budburst phenology was monitored from 17 April to 1 May 2002. Two branches on the south side of each tree were flagged, and the terminal 20 buds were assessed for bud expansion every other day for 15 days. Each bud was rated on a scale from 0 to 5, where: 0, buds are tight, oval, and dormant; 1, buds are oval and swelling, still pointed, and light brown; 2, bud scales are expanding, leaf tissue is visible; 3, buds are expanding, scales are open, red or green tips visible; 4, leaf expansion beyond the bud scales, leaves hard and deeply grooved, still pink to red; and 5, leaves completely open, spreading, vertically drooping, and green (Adams & Rieske, 2001). The mean value was determined for each tree on each date.

Plant sampling

Ten moderately galled trees (20–60 galls per tree, hereafter referred to as *galled*) and 10 very lightly galled trees (<10 galls per tree, subsequently referred to as *ungalled*) were chosen for sampling. Moderately galled trees were used because no ungalled branches could be found on trees classified as severely galled to provide plant material for the second treatment, ‘foliage from ungalled branches of galled trees’.

The east half of each tree was divided into two quadrants (north and south), and the quadrant and canopy level (lower, mid, and upper) of each sampled branch was recorded. From each galled tree, three galled and three ungalled branches, about 75 cm long, were removed. Galled branches were cut ~10 cm behind the galls to include them in the samples. Three branches of similar lengths were cut from each ungalled tree. Thus there was foliage from galled branches of galled trees (g/g), ungalled branches of galled trees (u/g), and ungalled trees (u/u). Branches ($n = 30$ for each of the three galling categories) were carefully transported in florists' water picks in ice coolers back to the laboratory, and measured for branch diameter, length of branch from the gall or from the leaf whorl nearest the end of the branch, mean diameter of each gall, and number of leaf whorls. Diameter measurements were determined by taking the mean of two perpendicular measurements. Oak lecanium scale, *Parthendecanium quercifex* Fitch (Homoptera: Coccidae), was prevalent on most of the trees, so per cent of each branch infested by scale was determined visually. In addition, the infrequent occurrence of 10–15 mm *roly poly* galls caused by a gall wasp, *Dryocosmus* spp. (Hymenoptera: Cynipidae) was noted.

The terminal whorl or whorls of foliage were used for insect assays, and leaves from the next remaining whorls on the same branches were used for phytochemical analysis.

Caterpillar assays

Gypsy moth caterpillars (USDA-AHIS Laboratory, Otis AFB, MA, U.S.A.) were maintained on a wheat germ-based artificial diet (Southland Products Inc., Lake Village, AR), and were removed from the diet 24 h before use. All caterpillar assays were conducted in a growth chamber with a LD 15:9 h photoperiod at 23 °C.

Preference trials. On 6 May, caterpillar preference was assessed using two-choice tests with second instars, coinciding with the natural period of caterpillar dispersal and host selection in early spring. Three sets of preference tests were set up using leaves from the terminal whorl(s). For each assay, two 15-mm leaf discs from different galling categories (g/g, u/g, u/u) were randomly chosen and pinned adjacent to one another in a 50-mm wax-bottomed Petri dish lined with moistened filter paper. One newly moulted second instar caterpillar was placed in each Petri dish ($n = 30$ per paired comparison), and allowed to feed for 7 h. Leaf discs were then scanned and digitised, and the leaf area consumed was calculated by subtracting the remaining leaf area from the initial leaf area.

Performance trials. Performance trials were set up on 17 May using fourth-instar caterpillars, when caterpillars in wild populations are of the same age. Branches were collected as described above from the same 20 trees (10 *galled* and 10 *ungalled*) used in the preference trials. Whole leaves with their petioles intact were removed from the terminal whorl, surface-sterilised, weighed, and placed individually in florists' water picks in 7 × 21 cm clear plastic rearing boxes. One newly moulted, fourth-instar caterpillar was weighed and placed in each rearing box ($n = 60$ per galling category), and monitored at 4 h intervals for the duration of the trial. Leaves were replaced using foliage from the same branch, and water was replenished as needed. The assay was terminated when the insect moulted. At the completion of the assay, caterpillars were sexed by noting the presence of abdominal sex pores located ventrally on the eighth and ninth abdominal segments in females (Stehr, 1987). Caterpillars, frass, and remaining leaf material were oven-dried at 40 °C for 5 days prior to weighing. To quantify caterpillar performance, relative consumption rate (RCR = leaf area consumed (mg) × initial larval weight $(\text{mg})^{-1}$ × time $(\text{day})^{-1}$), relative growth rate (RGR = [final larval weight (mg) − initial larval weight (mg)] × initial larval weight $(\text{mg})^{-1}$ × time $(\text{day})^{-1}$), and development time (length of fourth stadium (day)) (Scriber & Slansky, 1981) were assessed.

Plant characteristics

Leaf density. On 2 May, branches containing five whorls of leaves, adjacent to those monitored for budburst, were removed from galled and ungalled trees and transported in water picks back to the laboratory. Leaves were excised, the petioles removed, and leaf area was measured with an electronic meter (LI-3100, LiCor, Lincoln, NE). Foliage was weighed before oven-drying at 40 °C for 5 days, re-weighed, and leaf density ($\text{mg} \times \text{cm}^{-2}$) calculated. Five leaf density measurements were calculated for each branch to obtain a mean leaf density measurement for each tree.

Phytochemical analysis. Concurrent with the caterpillar preference and performance trials (6 May and 17 May respectively), leaves from the sub-terminal whorls of the same branches used in the insect assays were excised, packed in wet paper towels, 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 (VirTis 1251, Gradiner, NY), and stored at −80 °C. Foliar total non-structural carbohydrate analysis was conducted with an anthrone/thiourea reagent (Quarmby & Allen, 1989). Foliar nitrogen was assessed using a Leco TN-300 nitrogen determinator (Leco, St. Joseph, MI). Tannin concentrations were analysed as foliar protein binding capacity using a radial diffusion assay (Hagerman, 1987).

Statistical analysis

Budburst data was analysed using a repeated measures mixed model analysis of variance (SAS Institute, 1997) with mean budburst rating per tree as the dependent variable and gall level (light, moderate, severe) as the independent variable. The data were further analysed using the GENMOD procedure, which treats the budburst ratings as ordered categorical variables, and assesses differences in budburst for each sample date based on gall infestation level (light, moderate, severe). The GENMOD procedure fits a generalised linear model, and then uses generalised estimating equations to generate the parameter estimates, which are appropriate estimates for repeated measurements that are correlated with one another. Caterpillar preference was assessed using a paired sign test. Caterpillar performance was assessed using a multivariate analysis of covariance (SAS Institute, 1997), with galling category and caterpillar sex as the independent variables, relative growth rate, relative consumption rate, and development time as the dependent variables, and initial caterpillar weight as a covariate. Foliar density (in the early season assay only), non-structural carbohydrates, nitrogen, and tannins were analysed using a multivariate analysis of variance, with galling category as the independent variable. Tukey's HSD was used to analyse differences among the three galling categories. A multivariate canonical correlation analysis (SAS Institute, 1997) was performed to assess the relationship between insect performance (RCR, RGR, and development time) and foliar characteristics (carbohydrate, nitrogen, and tannin concentrations).

Results

Budburst phenology

The GENMOD analysis of each sample date demonstrates that bud expansion on 17 April was significantly more advanced for lightly galled trees than for moderately and severely galled trees, which were similar (Fig. 1). There were no differences in bud expansion between gall levels on 19 April. On 21 April and for all subsequent sample dates, lightly galled trees were more phenologically advanced than their severely galled counterparts, but there was no significant difference between lightly and moderately galled trees, or between moderately and severely galled trees. Thus, heavily galled trees broke bud more slowly than lightly galled trees throughout the monitoring period. In the repeated measures analysis, budburst did not vary among trees with different gall infestation levels ($F_{2,37} = 1.1$, $P = 0.35$), nor was there a significant interaction between gall level and sample date ($F_{14,37} = 1.37$, $P < 0.22$). As expected, sample date strongly influenced budburst phenology ($F_{7,37} = 50.36$, $P < 0.001$).

Caterpillar assays

Preference trials. Second instar caterpillars preferred leaves from ungalled trees (u/u) over leaves from ungalled branches of galled trees (u/g) (Table 1), but there was no preference shown in the other pairings.

Performance trials. In the multivariate analysis, overall herbivore performance (consumption, growth, and development time) was only weakly affected by galling ($F_{6,206} = 1.76$, $P = 0.10$), but was strongly affected by initial caterpillar weight ($F_{3,103} = 6.39$, $P = 0.0005$). In the univariate analysis, individual caterpillar performance parameters did not differ among caterpillars fed foliage from each of the three galling categories (Table 2).

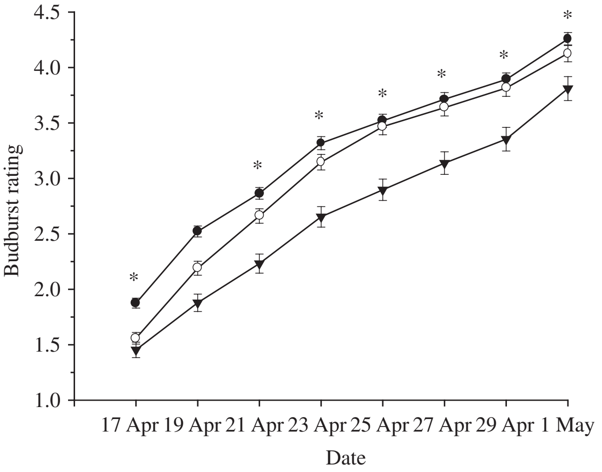

Fig. 1. Mean (± SE) budburst ratings for pin oaks lightly (●, <10 galls), moderately (○, 20–60 galls), and severely (▼, >100 galls) infested with *Callirhytis cornigera* stem galls. * indicates significant ($P < 0.05$) difference in bud expansion.

Plant characteristics

The multivariate analysis demonstrated that, early in the season, there were strongly significant differences in foliar characteristics (density, carbohydrate, nitrogen, and tannin concentrations) (MANOVA, $F_{8,140} = 3.53$, $P = 0.0009$) between the three galling categories. These differences were maintained through the second sample period (MANOVA, $F_{6,168} = 5.13$, $P < 0.0001$).

Leaf density. Leaves sampled near the time of preference tests (2 May) from galled trees were significantly ($P = 0.001$) denser than were leaves from ungalled trees [0.46 (± 0.01) mg cm^{-2} for galled trees, vs. 0.42 (± 0.01) mg cm^{-2} for ungalled foliage].

Phytochemical analysis. In leaves sampled concurrently with the caterpillar preference tests (6 May), foliar carbohydrates were equivalent for all leaf types (Table 3). Results were similar for foliage sampled on 17 May, concurrent with caterpillar performance tests. Foliar carbohydrates increased significantly and uniformly in all galling categories, increasing by approximately 65% in the 11-day period between samples (Table 3).

Table 1. Relative preference of second-instar gypsy moth caterpillars for pin oak leaves from galled branches (g/g), leaves from ungalled branches of galled trees (u/g), and leaves from ungalled trees (u/u).

Combination	u/g vs. g/g	u/u vs. g/g	u/u vs. u/g
Consumption [mean (SE)]†	53.0 (12.6) vs. 55.6 (11.3)	23.2 (7.4) vs. 26.8 (8.7)	117.0 (17.1) vs. 79.8 (12.9)
Paired sign *P*-value	0.71	0.83	0.02

†Area consumed.

Table 2. Performance [mean (SE)] of gypsy moth larvae on pin oak foliage from three galling categories.

	Caterpillar performance parameter‡		
Galling category†	RCR	RGR	Development time
g/g	1.16 (0.099) a	0.18 (0.012) a	9.52 (0.20) a
u/g	1.28 (0.092) a	0.22 (0.011) a	9.23 (0.19) a
u/u	1.13 (0.090) a	0.20 (0.011) a	9.07 (0.18) a

Means within columns followed by the same letter are not significantly different ($P < 0.05$).

†Includes foliage from galled branches of galled trees (g/g), ungalled branches of galled trees (u/g), and ungalled trees (u/u).

‡Includes caterpillar relative consumption rate [$\text{RCR} = \text{mg} \times (\text{mg})^{-1} \times (\text{day})^{-1}$], relative growth rate [$\text{RGR} = \text{mg} \times (\text{mg})^{-1} \times (\text{d})^{-1}$], and development time [length of fourth stadium (day)].

Foliar nitrogen levels in leaves sampled on 6 May were significantly different among galling categories (Table 3). Leaves from ungalled trees (u/u) had lower nitrogen levels than leaves from ungalled branches of galled trees (u/g). Differences were more prevalent in foliage sampled 17 May, when leaves from ungalled trees (u/u) were significantly lower than both galling categories from galled trees (u/g and g/g). Nitrogen concentrations declined uniformly from the first to the second sampling date for all galling categories (Table 3).

Tannin concentrations of leaves sampled on 6 May differed significantly among galling categories (Table 3), and were lower in leaves from ungalled trees (u/u) compared to leaves from galled trees (u/g and g/g). By 17 May, these differences had disappeared. From 6 to 17 May, tannin levels in galled trees (u/g and g/g) decreased, while tannins in leaves from ungalled trees remained low (Fig. 2 and Table 3).

The canonical correlation analysis demonstrated a significant relationship between plant characteristics and performance of caterpillars fed foliage from ungalled branches of galled trees (u/g) ($F_{12,82.3} = 2.51$, $P = 0.007$), which explained about 38% of the variability (squared canonical correlation = 0.376). The relationship was positively correlated with carbohydrates (0.89) and nitrogen (0.44), showed no correlation with tannins (−0.067), but demonstrated a weak negative correlation with infestation by oak lecanium scale (−0.19). The corresponding relationship with herbivore performance included a strong positive correlation with growth (0.87), and a weakly positive correlation with caterpillar consumption (0.18) and development time (0.25). This suggests that for caterpillars fed ungalled foliage from galled trees, performance was enhanced by elevated foliar carbohydrates and nitrogen, unaffected by foliar tannins, and negatively affected by the presence of the secondary scale insect. No clear patterns emerge, however, since there were no significant correlations between plant characteristics and caterpillar performance for the other two galling categories (u/u and g/g).

Discussion

Due to their endophagous habits and relative immobility, an intimate association develops between insect gall formers

Table 3. Foliar carbohydrate, nitrogen, and tannin concentrations [mean (SE)] on two dates of foliage from three galling categories of pin oak sampled concurrently with caterpillar preference and performance assays.

		Date		
Foliar component	Gall category†	6 May	17 May	Between-date differences (F, P)
Carbohydrates (%)	g/g	3.74 (0.18) a	5.04 (0.15) a	34.33, <0.0001
	u/g	3.80 (0.18) a	5.16 (0.15) a	30.72, <0.0001
	u/u	3.98 (0.18) a	5.24 (0.15) a	30.62, <0.0001
		$P = 0.61$	$P = 0.62$	
Nitrogen (%)	g/g	3.24 (0.10) ab	2.68 (0.06) b	18.77, <0.0001
	u/g	3.36 (0.10) b	2.75 (0.06) b	32.13, <0.0001
	u/u	2.99 (0.01) a	2.44 (0.06) a	26.34, <0.0001
		$P = 0.03$	$P = 0.0007$	
Tannins	g/g	0.32 (0.03) b	0.30 (0.01) a	15.30, <0.0001
	u/g	0.34 (0.02) b	0.29 (0.01) a	2.74, 0.10
	u/u	0.25 (0.02) a	0.27 (0.01) a	0.43, 0.51
		$P = 0.003$	$P = 0.083$	

For each foliar component, means within columns followed by the same letter are not different.

†Includes foliage from galled branches of galled trees (g/g), ungalled branches of galled trees (u/g), and ungalled trees (u/u).

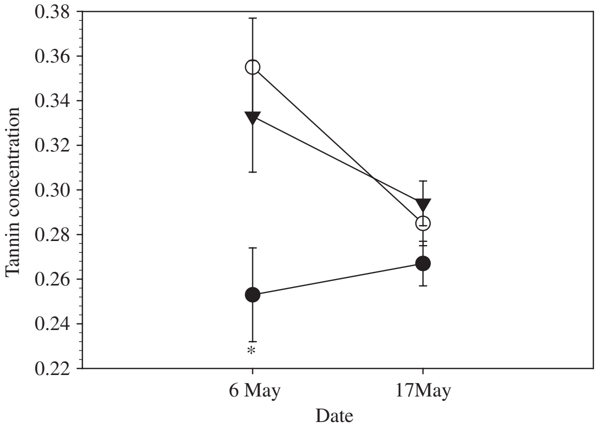

Fig. 2. Foliar tannins (mean ± SE) (6 May and 17 May) from branches of ungalled trees (●), ungalled branches of galled trees (○), and galled branches (▼). * indicates significant difference ($P < 0.05$) in tannin concentrations between galling categories.

and their host plants, and these constraints make gall formers an intriguing group in which to assess herbivore–plant relations. In this study, gall-induced changes in the characteristics of a woody plant host were assessed, and also the subsequent effects these changes may impose on a later occurring, foliage-feeding caterpillar.

Stem galls caused by *C. cornigera* cause phenological, physical, and chemical differences in pin oak foliage that may directly or indirectly affect foliage feeders. Pin oaks that were heavily infested with stem galls were slower to break bud than were their lightly galled or ungalled counterparts. Foliage from ungalled trees was also less dense, and had lower nitrogen and tannin concentrations, presumably due to resource reallocation caused by galling (McCrea & Abrahamson, 1985). The more phenologically advanced, ungalled pin oaks potentially created a more accessible food source that was preferred by gypsy moth caterpillars.

Gypsy moths consume terminal whorls before moving to adjacent branches or sub-terminal foliage, so both the caterpillar preference and performance trials utilised foliage from terminal whorls. As with many lepidopteran defoliators, there is a fair amount of host discrimination in the early instars, when caterpillar preference was assessed; however, host plant requirements relax as caterpillars' age, making preference tests with older caterpillars much less meaningful. Consequently, in this study only herbivore performance was assessed with the older caterpillars. In addition, there was a limited quantity of foliage available, so adjacent sub-terminal whorls were sampled concurrently with caterpillar feeding trials to assess foliar characteristics. Although branch position was controlled for in sampling, differences in phytochemical and physical characteristics due to whorl position cannot be fully discounted.

These results on gall-induced differences in budburst phenology differ from those of Eliason and Potter (2000b). Working with larger trees, they found that budbreak of pin oaks lightly infested with the horned oak gall (<10% of branches with stem galls) was similar to that of heavily galled (>80% of branches with galls) trees. It is possible that the trees used in their study were units too large to be affected by galling, and the buffering capacity of a mature tree exceeds one's ability to detect meaningful differences. Rehill and Schultz (2002) found, similar to the work reported here, that *Hamamelis virginiana* trees that broke bud later had greater densities of a gall-forming aphid. This apparent contradiction suggests that budbreak in deciduous trees is highly variable, and may be independent of galling pressure. Regardless, pronounced differences in tree phenology can lead to substantial differences in the structure of the herbivore community (Crawley & Akhteruzzaman, 1988). The elevated tannin concentrations induced by the gallmaker in this study are consistent with findings in similar systems (Hartley & Lawton, 1992; Hartley, 1998), and corroborate the hypothesis that gallmakers may be manipulating biochemical signals that mediate host plant–gallmaker interactions (Hartley, 1999). In spite of the elevated nitrogen and tannin levels in foliage from galled trees, budbreak phenology and foliar accessibility appear to be the driving forces behind the preference of early instar gypsy moth caterpillars (Lechowicz, 1983), as it is with many folivores (Brues, 1920; Scriber & Slansky, 1981; Du Merle, 1988; Hunter, 1992; Choong, 1996).

These results demonstrate that galling strongly impacts pin oak foliar characteristics, but these differences only very weakly effect caterpillar performance. Foliage from galled trees contained significantly greater nitrogen levels, perhaps due to physiological stress (White, 1984) caused by galling, but this did not impact herbivore performance in predictable ways. The presence of the oak lecanium scale further confounds these results. There was a weak inverse correlation between caterpillar performance, foliar carbohydrates and nitrogen, and scale infestations. Scales are immobile herbivores with sucking mouthparts that could potentially drain photosynthate and nutrients, producing the observed reduction in caterpillar performance. It would be predicted that increases in foliar nitrogen would result in decreases in herbivore consumption, since available nitrogen is frequently the limiting factor in herbivore growth (Mattson, 1980; Slansky & Scriber, 1985; Mattson & Scriber, 1987). These data do not support that view, but the results may be confounded by the overwhelming effects of initial caterpillar weight. However, these data are consistent with earlier work showing that gypsy moth preference and host utilisation are not deterred by the presence of foliar tannins (Lechowicz, 1983; Montgomery & Wallner, 1988).

Galling strongly impacted foliar characteristics, including budbreak, foliar nitrogen, and foliar tannins, but additional factors or a combination of these characteristics may be responsible for subsequent caterpillar preference and performance. An optimal combination of these foliar components may serve to maximise host suitability for generalist herbivores.

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