John T. Lill · Robert J. Marquis

The effects of leaf quality on herbivore performance and attack from natural enemies

Abstract A diverse array of sublethal plant secondary compounds are commonly found in the foliage of temperate deciduous trees. These traits are thought to defend a plant in two principal ways, either directly by reducing insect oviposition, feeding, or biomass gain, or indirectly, through digestive inhibition. Such inhibition is hypothesized to slow the rate of herbivore development, thereby increasing their susceptibility to natural enemies (the slow-growth-high-mortality hypothesis). To clarify the defensive role of these compounds, field experiments were conducted to examine the relationships among oak leaf quality, herbivore family, and three herbivore performance measures: survivorship, development time, and pupal mass, for a bivoltine leaf-tying caterpillar, *Psilocorsis quercicella* (Lepidoptera: Oecophoridae). Two experiments, one for each generation of the insect, were conducted to examine the effects of intraspecific variation in leaf chemistry of its host, white oak trees (*Quercus alba*). In each experiment, full-sib neonate larvae were placed in experimental leaf ties on high- versus low-quality trees and allowed to feed for 2 weeks under field conditions. To determine the effect of the third trophic level, a portion of each family in each leaf-quality treatment was bagged to prevent attack from natural enemies. This treatment also allowed us to test a prediction of the slow-growth-high-mortality hypothesis, i.e., that development time, as measured for full sibs in the bagged treatment, should be positively correlated with mortality of their full sibs exposed to natural enemies. Low leaf quality significantly reduced survivorship of the caterpillars in the first generation but not the second. The third trophic level decreased survivorship in both generations. Larval development time was not affected by leaf quality in either generation, but varied significantly among insect families in both generations. In turn, larvae from slower-developing families did not suffer increased predation and parasitism, as predicted by the slow-growth-high mortality hypothesis. In contrast to development time, pupal mass showed a greater response to intraspecific variation in leaf quality, although the effect was only significant in generation 1. Concentrations of both total phenolics and hydrolyzable tannins in *Q. alba* foliage appear to be important negative predictors of pupal mass in *P. quercicella*. In marked contrast to development time, no main family effect was found for pupal mass in either experiment; however, significant family×environment interactions were found for the effects of the bagging treatment (generation 1) and the leaf-quality treatment (generation 2). Overall, the first trophic level had a greater influence on pupal mass (a fecundity correlate), while larval development time was determined more by the insect's family (genotype+ maternal environment). The third trophic level was a consistently strong source of mortality in both experiments, but as a whole did not respond to familial differences in development time. Thus, from the perspective of *P. quercicella*, plant quality appears to serve as a defense more through its direct effect on herbivore survivorship and fecundity than through an indirect effect on predation via changes in development time.

Keywords Parasitoids · *Psilocorsis quercicella* · *Quercus alba* · Slow-growth-high-mortality hypothesis · Tritrophic interactions

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Introduction

Our understanding of the defensive role of polyphenolics in plants remains elusive. Typically found at sublethal levels, polyphenolics in combination with low nutrients may defend a plant by decreasing oviposition, reducing feeding, or causing herbivores to move off the plant (reviewed in Ayres et al. 1997). Such effects, however, have rarely been demonstrated in the field (but see Bryant et al. 1991; Wold and Marquis 1997). For herbivores that

are not deterred from feeding on a plant, low leaf quality can also decrease the biomass attained by individual herbivores (Slansky 1993), which is typically measured as pupal mass for holometabolous insects. To the degree that herbivore biomass is related to herbivore fecundity, low leaf quality could serve as a direct defense for long-lived plants by reducing subsequent herbivore loads via a numerical response, particularly for herbivore species with limited dispersal capabilities (e.g., scale insects and microlepidopterans; Hanks and Denno 1994; Mopper and Simberloff 1995).

In addition to these direct effects, sublethal plant defenses are also postulated to act indirectly, by increasing exposure of juvenile herbivores to attack from the third trophic level. Known as the slow-growth-high-mortality hypothesis (hereafter SG-HM hypothesis; Clancy and Price 1987), this hypothesis generates two predictions: (1) low-quality tissues lengthen herbivore development time (Lindroth and Hemming 1990; Lindroth and Bloomer 1991) and/or increase the proportion of time spent feeding (Loader and Damman 1991; Benrey and Denno 1997), and (2) lengthened development time/ increased feeding results in increased mortality due to natural enemies (Rhoades 1983; Schultz 1983; Grossmueller and Lederhouse 1985; Leather 1985; Häggström and Larsson 1995; Benrey and Denno 1997; Bernays 1997; Parry et al. 1998). Results of experiments testing the predictions of the SG-HM hypothesis have been mixed, in part due to the different experimental approaches employed. One approach has been to manipulate leaf quality by rearing polyphagous herbivores on different host plant species. However, using multiple hosts introduces several possible confounding effects. For example, interspecific differences in plant architecture (Lawton 1983; Geitzenauer and Bernays 1996; see review by Marquis and Whelan 1996) and semiochemistry (McCall et al. 1993; Turlings et al. 1993, 1995; Horikoshi et al. 1997) can affect enemies directly. These direct effects may obfuscate the detection of indirect effects or actually reverse the direction of the effects predicted by the SG-HM hypothesis (e.g., Benrey and Denno 1997).

To avoid these potential complications, we designed a set of field experiments in which we simultaneously manipulated both host plant quality and exposure to the third trophic level for a single host plant species, taking advantage of naturally occurring intraspecific variation in plant quality. This approach allowed us to examine possible mechanisms (both direct and indirect) by which sublethal plant traits may defend a plant against herbivory. Moreover, because herbivore genotypes may respond differentially to host plant traits [that is, herbivore genotype×environment (G×E) interactions may exist], we included herbivore family as a factor in our experiment. The degree to which G×E interactions exist will reveal whether sublethal plant traits are effective against all or just some herbivore genotypes.

In this study, we examined experimentally the influence of oak leaf quality and herbivore family on three measures of herbivore fitness: survivorship, development time, and pupal mass. We did so for each of two generations of a leaf-tying herbivore, *Psilocorsis quercicella* Clemens (Lepidoptera: Oecophoridae), feeding on white oak (*Quercus alba* L.) trees varying in leaf quality. As an obligate leaf-tier, *P. quercicella* is easily manipulated and individuals can be followed in the field, allowing us to examine herbivore responses to plant quality within a genetic framework. These experiments were replicated in both the presence and absence of natural enemies to compare the effects of the first trophic level alone with the effects of the first plus the third trophic levels. We first predicted that natural enemy exclosures would increase survivorship in both leaf-quality treatments. Second, we predicted that larvae exposed to natural enemies and feeding on low-quality leaves would (1) develop more slowly and experience increased mortality from natural enemies, and (2) pupate at a smaller size and/or have a lower probability of completing development, compared with exposed larvae feeding on high-quality leaves.

Materials and methods

Study system

P. quercicella is a moth common throughout eastern North America (Covell 1984). Larvae feed exclusively within leaf ties that they construct by binding overlapping leaves of their host plant (primarily oaks) together with silk. *P. quercicella* is bivoltine, with a summer and a fall generation. Adults begin to emerge from overwintering pupae in late May in Missouri. After mating, summer generation eggs are laid on overlapping, mature leaves and hatch within a few days (Carroll and Kearby 1978). Larvae feed by skeletonizing the leaf surfaces inside the leaf ties, passing through five instars before pupating. Larvae rarely move from their leaf ties and typically complete development within a single tie, occasionally adding adjacent leaves if food becomes limiting. Larval development times are highly variable, both within and between generations, but average about 28 days from egg hatch to pupation (J. Lill, personal observation). Fall generation larvae can be found from mid-August to leaf drop at the end of October, and fall generation pupae overwinter in the soil. Pupal mass of *P. quercicella* varies considerably (range 5.0–19.5 mg) and is a significant positive predictor of realized fecundity in females (r^2=0.31, P=0.0012, n=31; Lill 1999b). The parasitoid community attacking *P. quercicella*, described by Pasek and Kearby (1984) and Lill (1999a) in Missouri, consists of endoparasitic wasps from the families Ichneumonidae, Braconidae, Trigonalyidae, and Eulophidae. In addition, it includes two parasitic flies: a newly described species of Cecidomyiidae (Gagné and Lill 1999) and an unidentified species of Tachinidae. Data derived from 3 years of rearing field-collected *P. quercicella* larvae (Lill 1999a) indicate that early instar *P. quercicella* larvae (1–3) are most susceptible to attack by the dominant parasitoid species [*Diadegma psilocorsis* Walley (Ichneumonidae), *Bassus calcarata* Cresson (Braconidae), and an unidentified species of Eulophidae]. A variety of predaceous arthropods, including beetle larvae, lacewing larvae, ants, stink bugs, assassin bugs, centipedes and spiders, have also been observed feeding within the leaf ties on *P. quercicella* caterpillars (J. Lill, personal observation). Since the integrity of their leaf ties increases substantially as larvae reach the later instars (larvae seal off a feeding chamber using silk and frass), the risk of attack by these generalist predators is likely to be much higher during the early instars. Predation by birds is unlikely to have a significant impact on *P. quercicella* larvae,

since caging experiments designed to exclude birds on white oak in Missouri have demonstrated that leaf-tying caterpillars are largely immune to birds (R. Marquis and C. Whelan, unpublished work).

Study site

The field portion of all experiments was conducted at Cuivre River State Park, located near Troy, Missouri. The park is a northern extension of the Ozark plateau and is a second-growth, mixed oakhickory forest. The experiments were conducted on the south-southwest facing slopes of a single 10-ha ridge containing numerous oak saplings with crowns accessible from the ground.

Experimental rationale

Each of the two experiments (E1 and E2) examined the effects of variation in white oak (*Q. alba*) leaf quality and attack from natural enemies on the performance of nine full-sib families of *P. quercicella* larvae. The two experiments coincided with the two generations of *P. quercicella* naturally occurring in Missouri (E1=summer generation, E2=fall generation). Experiments were conducted during both generations since summer-generation and fall-generation larvae are likely to experience different environmental conditions (e.g., leaf quality, natural enemy abundance, temperatures) and also differ in whether or not they will diapause as pupae for the winter (fall generation only).

Leaf quality

The leaf-quality treatments in each of the two experiments were established by screening 15–18 white oak trees for leaf nitrogen (percent dry mass) and protein-binding capacity, one measure of the combined effects of leaf tannins and other leaf phenolics on the ability of insect herbivores to utilize leaf material (Hagerman 1987). A tree's leaf quality was estimated as mean percent nitrogen/ mean protein-binding capacity in milligrams of tannic acid equivalents (N/PBC; see also McKey and Gartlan 1981). From the 15–18 trees sampled per experiment, the two trees with the highest and lowest mean leaf quality were selected for use in a given experiment (*n*=4 trees per experiment). Screening took place 2 weeks prior to the start of each experiment. By this time in the season, all leaves on a tree were mature and hardened.

Three undamaged leaves were collected haphazardly from each tree crown, sealed in plastic bags and stored in a cooler on ice. In the laboratory, the leaves were weighed before and after freeze-drying to determine water content. The petiole and midvein of each dried leaf were removed and the remaining tissue was ground in a cyclone sample mill and stored in 20-ml scintillation vials. Nitrogen content was determined by microcombustion (Perkin Elmer Series II CHNS/O Analyzer 2400, Norwalk, Conn., USA). The protein-binding capacity of each leaf was measured using the Hagerman radial diffusion assay (Hagerman 1987; Wold and Marquis 1997), with each leaf extract run on three different plates (55-µl aliquots/well). The average of the three plates was used to determine the equivalent tannic acid concentration for each leaf. The standard for this assay was tannic acid (T-8406, Sigma Chemical Co., St. Louis, Mo., USA). Means for leaf quality were then compared using ANOVA (followed by Duncan's a posteriori mean comparison test) to determine if the selected trees differed significantly for each leaf quality parameter.

Bulked leaf material from each of the trees used in E1 and E2 was also examined ex post facto for total phenolics and condensed and hydrolyzable tannins using the Folin-Denis (Swain and Hillis 1959), butanol-HCl (Bate-Smith 1977), and a modification of the potassium iodate assay (Schultz and Baldwin 1982), respectively, by J. Schultz and H. Appel, Pennsylvania State University. Tannic acid was used as a standard for the total phenolics and hydrolyzable tannin assays whereas purified quebracho tannin was the standard for the hydrolyzable tannin assay.

Herbivore source population

In the summer of 1997, full-sib families of *P. quercicella* larvae were generated through controlled laboratory matings of moths collected from the field site as larvae during fall generation of 1996. Virgin male and female moths were continuously paired by emergence time in mating/oviposition chambers containing branchlets of two or three white oak leaves clipped together with a lightweight hair curler clip. The leaves were inspected after approximately 7 days for the presence of *P. quercicella* eggs, which were then placed in 500-ml clear plastic deli containers containing moist filter paper and additional fresh white oak leaves. These containers were then monitored for eclosion of the neonate larvae. Two sets of nine full-sib families were used to conduct E1 and E2, respectively. Mating male moths with more than one female to produce half-sib families was not feasible due to the short-lifespan of adult moths and difficulties in sexing live adult moths. The nine families used in each experiment were selected based on the number of offspring produced (at least 20 viable larvae/ family) and the timing of eclosion (across families, eclosion had to occur simultaneously in order to control for the age of larvae).

Experimental design and analysis

The four experimental trees selected for use in each experiment were paired according to spatial proximity (<10 m apart), with each block (=pair) containing one high- and one low-quality tree. The limited number of simultaneously eclosing larvae per family prohibited a completely factorial experiment. Thus, the nine full-sib families were randomly assigned to one of the two blocks, with four or five families nested within each block. Half of the larvae from each family were placed in artificially constructed leaf ties (one larva/tie) on each of the two trees (one high-quality, one low-quality) comprising a block. Artificial leaf ties were made by clipping undamaged (<5% leaf area missing) adjacent leaves together with a curler clip. A no. 2 insect pin was used to transfer the neonate larvae from their container to the ties. The family identity of each larva was marked on the clip and families were distributed haphazardly throughout the crown of each tree. Once ten exposed leaf ties of a given genotype had been created on both trees within a block, the remaining larvae were evenly distributed on the high- and low-quality trees and each individual tie was enclosed within a sheer organza bag, the end of which was closed with a twist tie to protect the larva from being attacked by natural enemies. All larvae within a block were transferred on the same day. In transfer experiments conducted in the laboratory with *P. quercicella* larvae, we have found that 97% of larvae establish in the leaf tie in which they are placed (J. Lill and R. Marquis, unpublished data).

After 14 days (the minimum recorded development time for *P. quercicella* in the laboratory; Lill 1999), leaf ties were individually harvested and returned to the laboratory. The content of each tie was recorded, noting the status (present/missing) and condition (alive/dead) of each *P. quercicella* larva. Within 24 h of collection, the head capsule width of all living larvae was measured to the nearest 0.01 mm using a stereomicroscope fitted with a video camera allowing measurements of images using digital image analysis system (DIAS) software (C-Squared Corporation 1987). These measurements were used to assign instars (1–5) to each larva at the time of collection based on published data (Carroll 1977). Larvae were then individually reared in covered 500-ml deli containers and their fate, total development time, sex (of the pupae), and pupal mass were recorded (48–72 h after pupating, once pupal mass had equilibrated). Leaves were replaced as needed with fresh leaves collected from the tree on which the larva was placed in the field. All containers contained moist filter paper, and larvae were reared at 23°C under a 14 h:10 h light:dark cycle.

In using total development time (from egg-hatch to pupation), we assumed that the growth rate of a larva in the field during the 14-day exposure period was negatively correlated with its total development time (laboratory+field) [i.e., larvae that develop rapidly in the field (and are thus collected in later instars) have

shorter total development times compared with larvae that develop slowly in the field]. To test this assumption, we examined the relationship between instar at the time of collection and total development time; the two variables were negatively correlated in both experiments (E1: $r=-0.57$, $n=323$, $P<0.0001$; E2: $r=-0.56$, $n=207$, $P<0.0001$).

Logistic analysis using the LOGISTIC procedure of SAS (Stokes et al. 1995) was performed to assess the effects of block, leaf quality, bagging, and all two-way interactions on larval mortality. For this analysis, larvae were placed into two categories, those that survived to pupation and those that died. The latter category included caterpillars that were parasitized and preyed upon, as well as caterpillars that were missing from the harvested ties, since these were presumed to have died (once established, larvae rarely move from their ties). Larvae that died during rearing but were not parasitized were excluded from analysis, since the cause of death could not be determined. Because these models contained both dichotomous response variables (survived to pupation or died) and dichotomous predictor variables (treatment high vs. low, bagged vs. non-bagged, block 1 vs. block 2), we analyzed results using conditional odds ratios. A conditional odds ratio compares how one level (e.g., feeding in a protected tie) affects the risk of mortality relative to the other level (e.g., feeding in an unprotected tie), independent of other factors in the model (Stokes et al. 1995).

For larvae that survived to pupation, mixed-model ANOVA (GLM procedure, SAS Institute 1989) was used to test for the main effects of leaf quality, sex, block, bagging, and family (nested within block) on larval development time and pupal mass. Type III sums of squares were used in all analyses because of the unbalanced nature of the data. The full model with all possible interactions was computed initially and then used to guide the construction of reduced models that included only significant and/or biologically meaningful interactions. Family (nested within block) and its interactions were considered random effects, while all other factors were considered fixed. Block was considered a fixed effect since it was not a random sample of all possible blocks but was chosen based on spatial proximity of the high- and low-quality trees, with only two possible combinations of high and low trees (Newman et al. 1997). The TEST option of SAS was used to compute F statistics with the appropriate MS error denominators (SAS Institute 1989). The methods employed and analyses conducted were identical for E1 and E2, except that in E2 the bagging treatment was only possible for six of the nine families because of restricted family sizes.

The relationships between each of the three additional leaf-quality measures (total phenolics, condensed tannins, and hydrolyzable tannins) and mean herbivore performance (development time and pupal mass) in E1 and E2 were examined using linear regression. These analyses should be viewed as exploratory, since the experiment was designed to be analyzed with leaf quality as a discrete class variable (in ANOVA) rather than as a continuous predictor variable. Because sample sizes were small ($n=4$ per regression), statistical power was limited in these analyses. The interrelationships among these three leaf chemistry parameters and the N/PBC ratio were also examined using non-parametric correlation analysis.

Slow-growth-high-mortality hypothesis

To test the SG-HM hypothesis, the relationship between mean family mortality of exposed larvae (i.e., the larvae in non-bagged ties) and the mean family development time of protected (i.e., bagged) larvae was examined with regression for each experiment; a significant positive relationship is predicted by the SG-HM hypothesis. Both total mortality and mortality due only to parasitoids was examined. To improve normality, values for percentage mortality were transformed prior to analysis with Johnson and Kotz's improved angular transformation (Sokal and Rohlf 1981).

We also examined the relationship between mean family development time and mean family fitness in the presence and absence of the third trophic level by comparing the slopes of this relationship

in the protected vs. exposed treatments. If the regression coefficients differ in the two environments, it indicates that the third trophic level is selecting on development time. This analysis was conducted for each leaf-quality treatment separately in both experiments. Our measure of mean family fitness incorporated individual survival and fecundity by using individual pupal mass as our measure of fitness, with individuals killed by the third trophic level assigned a fitness of zero. The regression coefficients calculated for the protected and exposed treatments were compared using an F-test for equality of slopes of two regression lines (Sokal and Rohlf 1981). Since the probability of committing a type I error is high in an analysis involving eight regressions, we used an alpha-level of $0.05/8=0.006$ for significance testing.

It is important to note that by fixing the amount of time each larva was exposed to natural enemies to 14 days, these experiments did not allow us to examine the response of natural enemies to the total duration of larval development (Häggström and Larrson 1995), but rather examined their response to larvae with narrower or wider "windows of vulnerability" (i.e., slower developing larvae spend proportionately more time in early, more vulnerable instars than faster developing larvae; Craig et al. 1990). This window is concentrated in the early instars in *P. quercicella*. In this study, we took this approach for three reasons: (1) the early instars (1–3) of *P. quercicella* are the most susceptible to attack by parasitoids and predators and thus, variation in the rate of development during this stage is likely to have the greatest effect on the risk of attack; (2) several other studies (Craig et al. 1990; Loader and Damman 1991; Leather and Walsh 1993; Benrey and Denno 1997) have demonstrated that plant quality affects an herbivore's window of vulnerability, which is positively correlated with its risk of attack; (3) the alternative, continuous monitoring of the status of *P. quercicella*, would involve regularly opening the leaf ties, a disturbance likely to influence larval performance and attack rate by natural enemies, confounding interpretation of the results.

Results

Leaf chemistry

Significant intraspecific variation in leaf-quality measures was found for both E1 and E2 (Table 1). As a result, average N/PBC ratios of high-quality trees were 89–145% (E1) and 63–88% (E2) greater than the low-quality trees used in the experiments. There was also evidence for a seasonal decline in leaf quality: both leaf nitrogen and leaf water content were significantly lower in the E2 trees compared to the E1 trees (nitrogen: two-tailed $t_s=3.23$, $df=6$, $P=0.018$; water: two-tailed $t_s=4.64$, $df=6$, $P=0.004$). Additionally, the high-quality trees used in E2 had lower ratios of leaf nitrogen to protein-binding capacity (PBC) than the high-quality trees used in E1. Combining the leaf chemistry data from E1 and E2 ($n=8$ trees), the measure of leaf quality (N/PBC) used to establish experimental treatments was not significantly correlated with any of the three leaf phenolic measures obtained ex post facto ($P>0.05$ for all rank correlations). Among the three leaf phenolic measures, total phenolics and hydrolyzable tannins were significantly positively correlated (Kendall's rank correlation, $\tau=0.65$, $n=8$, $P=0.047$, Sokal and Rohlf 1981), whereas condensed tannin concentration was not significantly correlated with either total phenolics ($\tau=-0.36$, $n=8$, $P=0.25$) or hydrolyzable tannins ($\tau=-0.29$, $n=8$, $P=0.30$).

Table 1 Leaf-quality measures of trees used in the summer (E1) and fall (E2) generation experiments. *Values* presented are means of 3–5 leaves per tree and *values in parentheses* are 1 SD. Within an experimental run, means with the same *letter* are not significantly different using Duncan's post hoc test following one-way ANOVA. All ANOVA models were significant ($P<0.05$), except percentage nitrogen in E2. Data from three phenolic assays (the lower three rows) are reported without variance estimates, since the assays were run on bulked samples. The results of all three phenolic assays are presented in units of mg standard equivalents per mg dry leaf material (*TAE* tannic acid equivalents)

	Summer generation experiment				Fall generation experiment			
	Block 1		Block 2		Block 1		Block 2	
	Low[a]	High[a]	Low[a]	High[a]	Low[a]	High[a]	Low[a]	High[a]
Protein-binding capacity (mg TAE)	8.85 (0.28)[B]	4.54 (1.24)[C]	9.95 (0.23)[A]	6.30 (0.82)[C]	9.41 (1.24)[A]	6.66 (0.98)[B]	10.84 (0.47)[A]	5.91 (1.78)[B]
Nitrogen (% dry mass)	1.79 (0.16)[B]	2.04 (0.20)[AB]	1.76 (0.04)[B]	2.10 0.07)[A]	1.46 (0.15)	1.73 (0.12)	1.63 (0.19)	1.48 (0.12)
Water (% fresh weight)	60 (2)[C]	65 (2)[A]	60 (1)[C]	62 (1)[B]	54 (1)[C]	56 (1)[AB]	57 (1)[A]	55 (1)[AB]
N/PBC[b]	0.20 (0.01)[B]	0.49 (0.20)[A]	0.18 (0.01)[B]	0.34 (0.04)[A]	0.16 (0.01)[B]	0.26 (0.02)[A]	0.15 (0.02)[B]	0.27 (0.08)[A]
Total Phenolics	0.068	0.076	0.085	0.059	0.076	0.048	0.057	0.062
Condensed tannins	0.129	0.081	0.071	0.089	0.126	0.104	0.093	0.160
Hydrolyzable tannins	0.664	0.592	0.710	0.480	0.609	0.330	0.460	0.456

[a] Low or high leaf-quality treatment
[b] Tree leaf quality estimated as mean percentage nitrogen/mean protein binding capacity
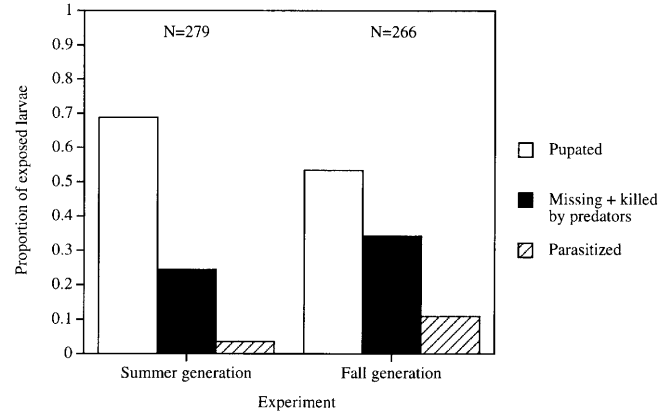
Fig. 1 Fates of exposed *Psilocorsis quercicella* larvae in the two experiments. (N total number of exposed larvae placed in the field during each experiment)

Mortality

A total of 451 and 360 larvae were placed in individual leaf ties during E1 and E2, respectively. At the end of the 14-day exposure period, the mean (±SE) instar of the larvae was 4.07±0.05 (E1) and 3.28±0.04 (E2). At the time of collection, 88% (E1) and 80% (E2) of the leaf ties showed some feeding damage, indicating that the majority of larvae succeeded in establishing in the ties. The largest source of mortality was missing caterpillars: 20.2% in E1 and 34.4% in E2. Caterpillars missing from the experimental leaf ties were presumed dead, since a search of the trees at the time of collection revealed no caterpillars in non-experimental ties (i.e., there was no evidence of movement within the trees or of caterpillars escaping from the bags). Detecting dead caterpillars was difficult given the extremely small size of the neonate larvae (0.2 mm wide×1.5 mm long). Several instances of predation by lacewing larvae were observed in exposed leaf ties only. Parasitism rates of exposed larvae were 3.6% in E1 and 10.9% in E2 (Fig. 1). Parasitoid species reared included *Diadegma psilocorsis, Bassus calcarata, Lestodiplosis venusta*, and an unidentified species of Eulophidae. Pathogens were not an obvious source of mortality in either the field or the laboratory.

Significant logistic regression models were fitted for larval mortality during both E1 [chi-square for covariates (χ^2_{cov})=26.52, df=4, P=0.0001 using the $-2 \log L$ criterion (reported hereafter for all logistic regression models); Stokes et al. 1995] and E2 (χ^2_{cov}=8.21, df=3, P=0.042). During the summer generation experiment, a larva in the high-quality treatment was half as likely to die before pupating as a larva in the low-quality treatment (Wald chi-square [U_W]=5.43, df=1, P=0.020), based on the conditional odds ratios (hereafter used for all treatment comparisons). To examine the source of this effect, we subtracted the percentage mortality experienced in the bagged treatment (due to host plant effects) from the mortality experienced in the exposed treatment (due to the combination of host plant effects and the third

Table 2 Results of ANOVA for development time and pupal mass of *P. quercicella* larvae in the summer and fall generation experiments

|	Development time[a]				Pupal mass[b]			
	Summer		Fall		Summer		Fall	
Source of variation	*df*	*F*	*df*	*F*	*df*	*F*	*df*	*F*
1. Leaf quality (LQ)	1,10.1	1.11	1,13.3	2.56	1,9.6	22.24***	1,10.2	1.23
2. Block	1, 7.5	12.26**	1, 8.2	0.27	1, 7.5	2.37	1,13.4	3.05
3. Sex	1,304	79.92***	1,185	1.77	1,296	268.32***	1,184	89.55***
4. Bagging[c]	1,304	12.13***	(1,23.1)	(0.25)	1,8.6	0.01	(1,145)	(0.75)
5. Family (Block)	7,7.1	5.29*	7,7	5.00*	7,6.3	1.41	7,7	0.58
6. LQ×Block	1,10.1	9.67*	1,13.9	3.45	1,9.7	30.71***	1,10.5	0.37
7. LQ×Family (Block)	7,304	0.65	7,185	1.10	7,296	0.84	7,184	2.15*
8. Bagging×Family (Block)	–	–	–	–	8,296	2.60**	(5,145)	(1.13)
9. Error	304		185		296		184	

*P<0.05, **P<0.01, ***P<0.001
[a] Denominator mean squares used in mixed-model ANOVA *F*-tests were as follows: sources 1, 5, and 6 were tested over source 7; source 2 was tested over source 5; sources 3, 4, and 7 were tested over source 9
[b] Denominator mean squares used in mixed-model ANOVA *F*-tests were as follows: sources 1, 5 and 6 were tested over source 7; source 2 was tested over source 5; source 4 was tested over source 8; sources 3, 7, and 8 were tested over source 9
[c] The bagging treatment could not be included in the full model for the fall generation experiment because not all of the families had enough individuals to include a bagging treatment. The values in parentheses are from a model containing only the six families with bagging treatments
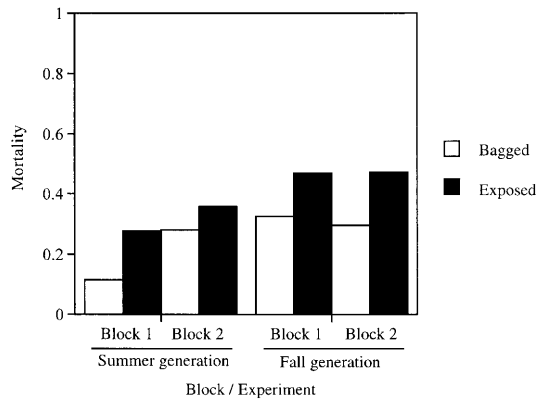
Fig. 2 Mortality of bagged and exposed *P. quercicella* larvae in each block during both experiments. Plotted values are unadjusted for other factors

trophic level) for each leaf-quality treatment separately. Assuming bagging effects to be minimal, this difference represents the effect of the third trophic level alone. For E1, the third trophic level accounted for 7.4% mortality in the low-quality treatment and 9.5% mortality in the high-quality treatment. Thus, the overall higher survivorship of larvae in the high-quality treatment appears to be due entirely to first trophic level effects rather than decreased attack by the third trophic level. Block was also significant (U_W=14.13, *df*=1, *P*=0.0002), with a larva in block 2 experiencing almost 5 times the mortality of a larva in block 1. A larva in an exposed leaf tie was on average three times more likely to die than a larva in a bagged leaf tie (U_W=8.71, *df*=1, *P*=0.003; Fig. 2). There was also a significant block×bagging interaction (U_W=5.62, *df*=1, *P*=0.018): bagging was 3 times more effective in decreasing larval mortality in block 1 than in block 2. During the fall generation experiment (E2), a

larva in an exposed leaf tie was twice as likely to die before pupating as a larva in a bagged leaf tie (U_W=6.97, *df*=1, *P*=0.008; Fig. 2). Leaf quality, block, and all interactions were not significant predictors of mortality in E2. Overall, predation and parasitism were significant sources of mortality in both E1 and E2, but were unaffected by leaf-quality treatment.

Development time

Despite the fact that leaf quality affected the risk of mortality in E1, development time was not significantly affected by the leaf-quality treatment in either E1 or E2 (Table 2). There were also no significant relationships between the concentrations of total phenolics, condensed tannins, or hydrolyzable tannins, and development time for either E1 or E2 (*P*»0.05 for all regressions). Block was highly significant in E1, with larvae in block 1 completing development an average of 1.6 days (7%) faster than larvae in block 2. Sex was also a highly significant predictor of development time during E1, with males (mean development time (±SE) 22.36±0.17 days) developing more quickly than females (24.51±0.17 days); however, this sexual dimorphism was not significant in E2. Bagging decreased development time by 0.8 days (3.3%) during E1 (possibly due to increased temperature/humidity inside the bags), but had no effect during E2.

The family component to the study was significant in both E1 and E2, indicating that over and above the effect of the treatments, mean development time of full-sib families differed significantly. The range in mean family development time was 22.2–25.2 days in E1 and 32.8–36.8 days in E2. There was also a significant block×leaf quality interaction in E1, with larvae in block 1 developing more quickly on the low-quality tree compared with the high-quality tree, while larvae in

Summer generation experiment (E1)

(a)
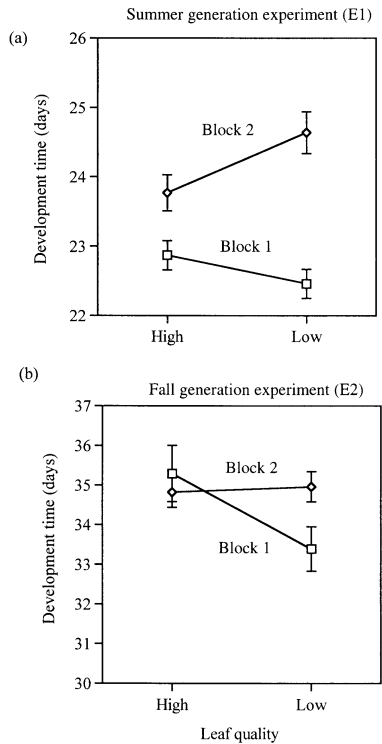
Block 2

Block 1

Fig. 3 Least square mean development time (±1 SE) of *P. quercicella* larvae reared on high- and low-quality foliage in two blocks during a the summer generation and b the fall generation. The interaction between leaf quality and block was significant in the summer generation ($P=0.011$) and approached significance in the fall generation ($P=0.08$)

block 2 showed the opposite pattern (Fig. 3a). This inter-action was also marginally significant in E2 (Fig. 3b). Only one of the four blocks examined (E1, block 2) showed the predicted positive relationship between leaf quality and development time (Fig. 3a). The mean devel-opment time of larvae in E1 and E2 differed significantly (two-tailed $t_s=47.3$, $df=531$, $P<0.0001$), with the average larva in E2 (the fall generation) requiring 12 days longer than the average larva in E1 (the summer generation) to complete development, an increase of approximately 50%. The longer development time observed for fall generation larvae was associated with increased mortality from natural enemies (Fig. 1).

Pupal mass

Leaf quality significantly affected pupal mass in E1 (Table 2); larvae in the high-quality treatment were on average 8% heavier than larvae in the low-quality treat-ment (Fig. 4). Leaf quality did not significantly affect pupal mass in E2 (Table 2), but the trend was toward greater pupal mass in the high-quality treatment (Fig. 4). For both E1 and E2, the concentrations of both total phenolics and hydrolyzable tannins were negatively related to mean pupal mass, although the regressions only indicated non-significant trends (Fig. 5). In contrast,
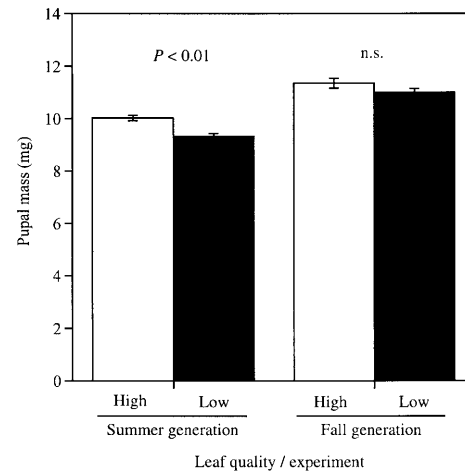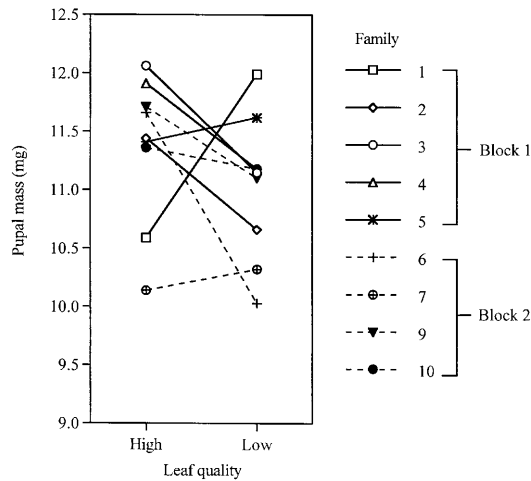

Fig. 4 Least square mean pupal mass (±1 SE) of *P. quercicella* reared on high- and low-quality foliage in the two experiments
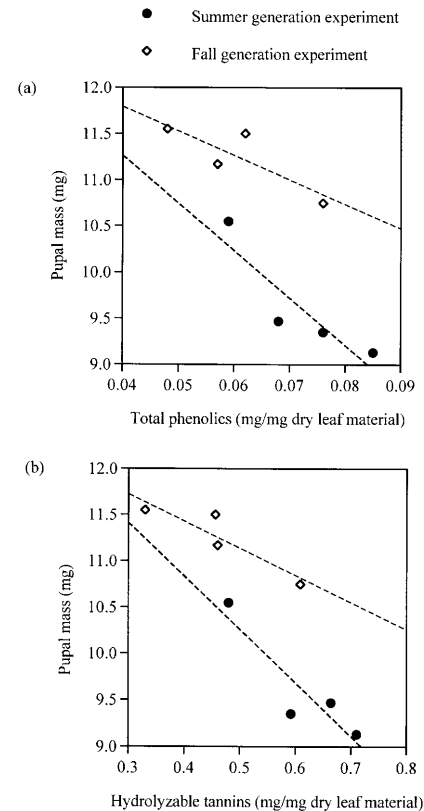
Fig. 5 Relationship between two leaf-quality measures: a total phenolics, and b hydrolyzable tannins, and mean pupal mass of *P. quercicella* reared during experiment 1 (E1, summer generation) [$r^2=0.81$, $F=8.40$, $P=0.10$ (total phenolics) and $r^2=0.83$, $F=9.71$, $P=0.09$ (hydrolyzable tannins)], and experiment 2 (E2, fall genera-tion) [$r^2=0.70$, $F=4.66$, $P=0.16$ (total phenolics) and $r^2=0.82$, $F=9.09$, $P=0.10$ (hydrolyzable tannins)]. Each *symbol* represents one white oak tree ($n=4$)

mean pupal mass and condensed tannin concentration were not significantly related in either E1 ($P=0.90$) or E2 ($P=0.87$). Pupal mass was highly sexually dimorphic in both E1 and E2, with female pupae averaging 30% (E1)

Fig. 6 Reaction norms plot of the least square mean pupal mass of full-sib families of *P. quercicella* in each leaf-quality treatment in the fall generation experiment (E2)

and 19% (E2) heavier than male pupae. Additionally, E2 pupae were an average of 18% heavier than E1 pupae (two-tailed t_s=10.75, df=528, P<0.0001). Block, bagging, and family(block) were not significant predictors of pupal mass in either E1 or E2 (Table 2). As with development time, there was a significant block×leaf quality interaction in E1; decreased leaf quality negatively affected pupal mass in block 2, but had no effect in block 1. Even though there was no main effect of bagging on pupal mass (Table 2), there was a significant bag×family interaction effect on pupal mass in E1. In E2, there was also a significant leaf quality×family interaction effect on pupal mass (Fig. 6).

Slow-growth-high-mortality hypothesis

There was no relationship between a family's mean development time in the protected treatment and its percentage mortality in the exposed treatment. This was true for both experiments and for both total mortality [P=0.63 (E1); P=0.32 (E2)] and mortality due only to parasitoids [P=0.37 (E1); P=0.87 (E2)]. Additionally, mean family development time was not a significant positive predictor of mean family fitness (after adjusting the alpha-level) in either the bagged or exposed treatments, providing no evidence of selection by natural enemies on this trait.

Discussion

Mortality

The significant reduction in mortality resulting from bagging during both experiments indicates that natural enemies were an important source of mortality for *P. quercicella*, accounting for a minimum of 9–15% of the total mortality in a given experiment (pooling across leaf-quality treatments). The increased mortality observed for larvae in the low-quality treatment during E1 was found to result largely from first trophic level effects, suggesting that low leaf quality can be lethal for at least some *P. quercicella* larvae.

The significant effect of block on mortality in the first experiment (E1) indicates that larvae on one pair of trees (block 2) had much lower survivorship than on the other (block 1). It appears that in the understory, the risk of mortality from natural enemies varies spatially, due to unknown factors. Natural enemy density (including spiders, insect predators, and parasitoids) for individual trees at the study site ranges from 1.2 to 19.6 predators per 100 leaves on *Q. alba* (J. Lill and R. Marquis, unpublished work). In addition, the density of alternative prey (e.g., other caterpillars) for generalist predators on the experimental trees was not recorded in this study, and may have influenced the local density of natural enemies.

Development time

Leaf quality (N/PBC) generally was a poor predictor of development time for *P. quercicella*. With the exception of block 2 in E1, larvae were little affected by the nitrogen availability of the leaves on which they were reared. In addition, none of the three additional measures of leaf quality was predictive of development time. These negative results also must be viewed within a broader context; individual herbivore species show variable responses to different mixes of tannins (Ayres et al. 1997), and different herbivore species show variable responses to particular phenolic compounds (Martin et al. 1987; Lindroth and Peterson 1988; Karowe 1989; Scriber et al. 1989; Auerbach and Alberts 1992; Hemming and Lindroth 1995). During E1, the two "low"-quality trees differed considerably in their effects on development time, even though their leaves both had relatively low nitrogen availability. These two trees may have differed considerably in the concentration of particular phenolic compounds affecting development time in *P. quercicella*. Laboratory experiments in which the concentrations of particular phenolic compounds (as well as different combinations of compounds) are varied systematically using artificial diets (see Karowe 1989; Ayres et al. 1997) are needed to determine their influence on development time.

Significant family-level variation for development time in both E1 and E2 was found, with some families developing more quickly than others, irrespective of leaf quality. To the extent that this among-family variance represents genetically based differences in development time (maternal environmental effects may also contribute to full-sib family traits), this trait has the potential to respond to selection. However, the responses of individual families within a block to the leaf-quality treatments did not differ significantly (i.e., no G×E effects occurred), indicating no apparent genetically based tradeoffs in development time in the two environments.

Pupal mass

In contrast to development time, we detected an effect of leaf quality on pupal mass. This effect was significant in E1, with larvae in the high-quality treatment producing heavier pupae than larvae in the low-quality treatment. Pupal mass is a commonly used fitness measure for insects, since female fecundity has often been shown to be size-related (Roff 1992). This is true for *P. quercicella*, where female pupal mass is a significant positive predictor of the number of F1 larvae surviving to pupation in the laboratory (Lill 1999b). Using this relationship, the average female in the E1 low-quality treatment would suffer an 18% decrease in fecundity relative to the average female in the high-quality treatment. This main effect was driven in large part by the response of pupal mass in block 2 to the leaf-quality treatments. As in the analysis of development time, the trees in block 2 elicited a strong phenotypic response, whereas block 1 individuals showed little or no response to the two leaf-quality treatments. In addition, the marginally significant negative relationships between two additional leaf-quality measures (total phenolics and hydrolyzable tannins) and pupal mass in both E1 and E2 suggest that as defensive traits, these classes of phenolics may have a greater impact on herbivore fecundity than survivorship.

We suggest that the effect of low leaf-quality on pupal mass may reduce herbivory directly over time by decreasing the average clutch size of herbivores. For individual plants, the effect of reducing herbivore fecundity may, over time, locally reduce the load of herbivores possessing limited dispersal capabilities (e.g., scales and microlepidopterans: Hanks and Denno 1994; Mopper and Simberloff 1995). Given that microlepidopterans dominate the herbivore community of *Q. alba* in Missouri (Le Corff and Marquis 1999), leaf-quality traits that reduce the local abundance of these herbivore species could have substantial effects on subsequent levels of herbivory encountered by individual plants or small stands of trees.

The influence of G×E effects on pupal mass was detected in E2, where families differed in both the magnitude and the direction of their response to the leaf-quality treatments (Fig. 6). While most families had decreased pupal mass in the low-quality treatment, some families (e.g., families 5 and 7) had slightly higher mean pupal mass in the low-quality treatment and one family (family 1) appeared to perform substantially better on the low-quality foliage. Thus, not only do individual herbivore species vary in their response to particular leaf-quality traits (e.g., phenolic compounds, which can act as either feeding deterrents or stimulants; Ayres et al. 1997), but these data suggest that individual insect herbivore populations may consist of a mix of genotypes that show differential responses to these traits.

Slow-growth-high-mortality hypothesis

For *P. quercicella*, the only line of evidence supporting the SG-HM hypothesis is the increase in predation and parasitism from the summer to the fall generation, which is correlated with a sharp increase in the mean duration of development (fall generation larvae develop 50% slower than summer generation larvae). Since leaf quality has generally been shown to decline over the growing season as leaves age (Feeny 1970; Scriber 1977; Mattson 1980; Bryant et al. 1983; Coley 1983; Rossiter et al. 1988; Mauffette and Oechel 1989; this study) due to increasing tannin and lignin content and decreasing water and nitrogen content, we might predict a priori that herbivores feeding early vs. late in the season would suffer differential attack from natural enemies due to diet-related differences in development time. However, several studies have shown that natural enemy populations can increase over the season (Root 1973; Myers 1981; DeLoach 1983), confounding such comparisons.

The more rigorous test of the SG-HM hypothesis, examining the results of E1 and E2 separately, failed to support its predictions. Mean development times of full-sib families varied significantly in both experiments, but there was no significant relationship between development time in the absence of enemies and mortality in the presence of enemies. Moreover, family mean development time was not a significant predictor of mean family fitness in either the presence or absence of natural enemies. While it is possible that individual natural enemy species may respond differentially to variation in host development time, no net effects were detected in this study indicating that leaf-quality traits that prolong *P. quercicella* development are unlikely to act as a defense via increased attack by the third trophic level.

Results have been mixed from the other studies examining the SG-HM hypothesis for herbivores feeding on a single host plant species. The laboratory experiments conducted by Benrey and Denno (1997) demonstrated that for each of four different host plant species, *Pieris rapae* larvae with delayed development (i.e., wider windows of vulnerability) suffered increased mortality from the parasitoid *Cotesia glomerata*; however, the results of a field experiment involving all four host plant species indicated that the direct effects of host plant traits on parasitoid foraging overwhelmed their ability to detect the indirect effects demonstrated in the laboratory. In the three field studies that have found the strongest support for the SG-HM hypothesis (Bouton 1984; Häggström and Larsson 1995; Parry et al. 1998), the natural enemies consisted solely of generalist predators (pentatomid bugs, spiders, and other Heteroptera). In contrast, field studies involving specialist parasitoids (Clancy and Price 1987; Craig et al. 1990), or a mix of parasitoids and generalist predators (Loader and Damman 1991; this study) have been much less supportive of the hypothesis. Plant traits that slow the development of herbivores primarily attacked by generalist predators might be expected to be more effective in reducing herbivory than traits that slow the development of herbivores attacked by parasitoids, since many parasitoids (particularly specialist parasitoids) do not kill their hosts until they have completed development and done their

damage (Loader and Damman 1991; Mills 1992). Additional studies are needed to examine the relative importance of direct versus indirect effects of host plant quality, on the one hand, and the degree of specificity of the natural enemies, on the other.

Conclusion

These two experiments demonstrate that development time in *P. quercicella* is largely determined by herbivore family and is little affected by intraspecific variation in host plant quality. In contrast, the direct effect of leaf quality on pupal mass was more substantial and varied among families in the second generation. Total phenolics and/or hydrolyzable tannin concentrations were negatively related to pupal mass and thus are likely to be important bottom-up determinants of herbivore fitness in this system. The third trophic level was a significant source of mortality in both experiments, but as a whole showed little response to family-based differences in development time. Thus, from the perspective of *P. quercicella*, plant quality appears to serve as a defense more through its direct effect on herbivore fecundity and survival than through an indirect effect on predation via changes in herbivore development. Studies involving other long-lived plant species commonly attacked by herbivores with limited dispersal capabilities are needed in order to test the generality of these results.

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