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Competition between the gypsy moth, *Lymantria dispar*, and the northern tiger swallowtail, *Papilio canadensis*: interactions mediated by host plant chemistry, pathogens, and parasitoids

Abstract The gypsy moth, *Lymantria dispar*, and the northern tiger swallowtail, *Papilio canadensis*, overlap geographically as well as in their host ranges. Adult female swallowtails are incapable of distinguishing between damaged and undamaged leaves, and the opportunities for competition between these two species are numerous. We designed field and laboratory experiments to look for evidence of indirect competition between *P. canadensis* and *L. dispar* larvae. Swallowtail caterpillars were reared in the laboratory on leaves from gypsy-moth-defoliated and undefoliated trees to explore host-plant effects. We tested for pathogen-mediated interactions by rearing swallowtail larvae on both sterilized and unsterilized leaves from defoliated and undefoliated sources. In addition, we measured the effects of known gypsy moth pathogens, as well as gypsy moth body fluids, on the growth and survival of swallowtail larvae. Field experiments were designed to detect the presence of parasitoid-mediated competition, as well: we recorded parasitism of swallowtail caterpillars placed in the field either where there were no gypsy moth larvae present, or where we had artificially created dense gypsy moth populations. We found evidence that swallowtails were negatively affected by gypsy moths in several ways: defoliation by gypsy moths depressed swallowtail growth rate and survival, whether leaves were sterilized or not; sterilization significantly reduced the effect of defoliation, and gypsy moth body fluids proved lethal; and swallowtail caterpillars suffered significantly increased rates of parasitism when they were placed in the field near gypsy moth infestations.

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Introduction

In 1960, Hairston and co-workers asserted that herbivores could not possibly be limited by food given the overwhelming abundance of green plants on earth; defoliation, after all, seemed a relatively rare event (Hairston et al. 1960). Due in part to this influential paper, the importance of competition among herbivorous insects was for many years largely overlooked (McClure 1983; Denno et al. 1995) or discounted entirely (Lawton and Strong 1981). Moreover, most documented instances of competition between herbivorous species can be classified as "asymmetrical competition", in which only one species is affected negatively, leading Lawton and Hassell (1981) to argue that such interactions would take place only during insect outbreaks and thus occur so rarely as to be ecologically unimportant.

Many plant-herbivore ecologists have recently begun to reexamine interspecific competition among insect herbivores, which now appears to be far more common than once thought (Denno et al. 1995). However, it may yet, as Lawton and Hassell (1981) suggested, tend to be associated with introduced pests, free from their natural enemies and capable of devouring enormous amounts of vegetation (DeBach and Sundby 1963; Denno et al. 1995). Further, it probably involves indirect, or "apparent", competition more frequently than direct battles over food (Faeth 1985; Hawkins 1988; Karban et al. 1994; Denno et al. 1995). Typically, indirect competition between species occurs when the activity of one species induces a chemical response in its host plant, affecting other species feeding on the same plant (Niemela et al. 1984; Faeth 1985, 1986; West 1985; Harrison and Karban 1986; Gibberd et al. 1988; Neuvonen et al. 1988; Hunter 1990; Dankert et al. 1997).

Examples of indirect competition mediated by pathogens have been reported for a great many species, in-

cluding humans (Price et al. 1986), but not, as far as we know, for herbivorous insects. Few cases have been documented, but predators and parasitoids may also mediate indirect competition (McClure 1981; Karban et al. 1994). The attraction of polyphagous natural enemies to visual cues (Faeth 1990) or unknown factors associated with primary hosts (Settle and Wilson 1990) or host damage (Faeth 1986) can negatively affect neighboring herbivores. Environmental factors, in certain cases, may also change the outcome of competition: wind and rain (McClure and Price 1975, 1976), or temperature (Waloff 1968; Valle et al. 1989) may differentially affect herbivore species that vary in their tolerance of such factors, thus conferring an advantage on one competitor. A novel example of environmentally mediated competition occurs on oak trees, where an early-season leaf-chewer creates such large holes in leaves that a late-season leaf-rolling species is rendered incapable of creating structures airtight enough to maintain adequate humidity (Hunter and Willmer 1989).

As awareness of interspecific competition among insects increases, so does interest in its impact on the population dynamics, host use, and community organization of insect folivores. There is experimental evidence suggesting that the population dynamics of certain herbivore species can be driven both by changes in plant chemistry induced by competing species feeding on the same host, and by natural enemies associated with competitors. Karban (1986), for one, showed that competition between *Philaenus spumarius* (Homoptera: Cercopidae) and *Platyptilia williamsii* (Lepidoptera: Pterophoridae), presumably mediated in part by plant chemistry, negatively affected the abundance of *P. spumarius* on *Erigeron glaucus* (Compositae). Several years later, Karban et al. (1994) found that populations of the herbivorous *Tetranychus pacificus* (Acari: Tetranychidae) fluctuated in response to populations of a neighboring herbivore, *Eotetranychus willamettei* (Acari: Tetranychidae), and its associated predators on grapevines.

Further, a few researchers have shown that interspecific competition plays a part in shaping the host use and the community organization of folivores. For example, Ritchie and Tilman (1992) found that the relative portions of dicots and monocots in the diets of polyphagous grasshoppers were altered by the presence of indirect competition, and Karban (1989) found experimental evidence that interspecific competition helped to shape the community organization of folivores on *Erigeron glaucus*.

We investigated interspecific competition in a study system involving the northern tiger swallowtail and the gypsy moth, feeding on quaking aspen. The northern tiger swallowtail, *Papilio canadensis* (Lepidoptera: Papilionidae), is native to North America. Its range spans the United States and Canada north of about 44°N, extending from the east coast to Alaska (Hagen et al. 1991). It is distinguished from its more southerly sister species, *P. glaucus*, with which it frequently hybridizes, by the capacity to detoxify the phenolic glycosides that character-

ize salicaceous plants, which abound in northern latitudes (Lindroth and Scriber 1988; Scriber et al. 1989). *P. canadensis* is polyphagous, but it typically exhibits a strong preference for quaking aspen, *Populus tremuloides* (Salicaceae) (Scriber et al. 1991). Females of the univoltine *Papilio canadensis* generally oviposit on newly expanded leaves during the first few weeks of June, and larvae grow throughout the summer, pupating in mid- to late August.

Quaking aspen, which supports a large number of herbivores, is defended primarily by the phenolic glycosides salicortin and tremulacin, and secondarily by tannins (Clausen et al. 1989; Lindroth 1992). It grows indeterminately throughout the summer, even in the absence of defoliation, and increases its rate of growth when leaf tissue is removed (Hodson 1981). In some cases, refoliation replaces nearly 90% of damaged foliage (Heichel and Turner 1976) with leaves that tend to be rich in phenolic glycosides (Clausen et al. 1989). Damaged leaves themselves also tend to contain elevated levels of these compounds (Mattson and Palmer 1987).

The European gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) was brought to Massachusetts from France in 1868, and has since radiated steadily to the north, south, and west, taking over most of the eastern United States (Liebhold et al. 1997; Sharov et al. 1998). In the East, it prefers to feed on white oak and chestnut oak, and, in the Midwest, *Populus* species such as quaking aspen are favored (Wallner 1988). Gypsy moth outbreaks are ecologically dramatic events, and it is difficult to imagine that many species remain unaffected by the presence of such a voracious defoliator. During peak outbreak years, levels of stand defoliation by gypsy moths can reach nearly 100% in some areas (Cameron 1986; Hart 1990), opening the tree canopy and causing profound ecological changes, such as increased predation on bird nests (Thurber et al. 1994) and a reduction in the diversity of lepidopteran fauna (Sample et al. 1996). Gypsy moth defoliation affects the chemistry of primary host plants, such as quaking aspen (Lindroth 1992; Dankert et al. 1997), and gypsy moth outbreaks are associated with high densities of pathogens, predators, and parasitoids (Elkinton and Liebhold 1990). At least some of these natural enemies, e.g., *Compsilura concinnata* (Diptera: Tachinidae), are known to use alternative hosts (Leonard 1981).

Both the geographic range and the host range of *Papilio canadensis* overlap significantly with those of *L. dispar*. Therefore, it seemed likely to us that the tri- or sometimes biennial gypsy moth outbreaks on poplar in northern Michigan would influence *P. canadensis* in measurable ways. Given the scope of gypsy moth defoliation, we suspected that there would be direct competition between *L. dispar* and *P. canadensis*. There was no explicit evidence to support this contention, however, largely because direct competition for resources has been notoriously difficult to demonstrate for herbivorous insects (Strong et al. 1984). Given this fact, as well as the likelihood that indirect competition should be more prev-

alent than the relatively infrequent instances of direct competition during outbreaks, we investigated the possibility that indirect competition existed between these species, mediated by changes in host plant chemistry, shared pathogens, and generalist parasitoids.

Materials and methods

Other than the oviposition bioassay, laboratory experiments used foliage grown in a common garden as well as foliage gathered from natural stands within the ranges of both insect species studied. At the time of this study, 1993–1994, northern Michigan contained both gypsy-moth-infested and gypsy-moth-free areas within the geographic range of *P. canadensis*. Before collection, we determined that our sites had not been treated with aerial sprays of *Bacillus thuringiensis* (*Bt*) by the Michigan Department of Agriculture, and that uninfested sites were located in areas that had not yet reported gypsy moth infestation. Infested sites in the northeastern and north-central portions of the state, and uninfested sites in the northwest, were all within driving distance of our location at the University of Michigan Biological Field Station in Pellston, Michigan.

Oviposition

In 1993, to test the discriminatory ability of swallowtail adults, we performed a two-choice oviposition assay with 16 field-captured adult females, using partially eaten aspen sprigs from gypsy-moth-defoliated areas and undefoliated sprigs from undefoliated areas as oviposition substrates. No regrowth leaves were yet present to be assayed. Butterflies were tested separately in transparent plastic boxes with a sprig of each type of foliage in a water-filled tube placed against the wall in front of a light source (see Scriber 1993), with care taken to ensure that foliage sprigs from each treatment were roughly equal in size. We analyzed oviposition data with chi-squared contingency analysis (Sokal and Rohlf 1995). The eggs gathered in this bioassay, along with other eggs harvested from field-collected adult females, were incubated, and the larvae were used in the experiments described below.

Host plant quality

In 1993, we conducted a long-term growth trial to determine if defoliation by gypsy moths decreased the quality of quaking aspen leaves for *P. canadensis*. This assay consisted of 40 *P. canadensis* neonates on each of four treatments: (1) leaves from undefoliated stands, (2) leaves from resistant trees in defoliated stands, (3) regrowth leaves from defoliated stands, and (4) partially eaten leaves from defoliated stands. All leaves in all treatments were young, i.e., picked before full expansion.

"Defoliated" stands were defined, roughly, as suffering 50% defoliation or worse; "undefoliated" stands were located in sections of Michigan not yet reporting gypsy moth outbreaks and showing no evidence of gypsy moth presence or damage after twenty-minute inspections. "Resistant trees" were defined as trees that had suffered no discernible gypsy moth damage at the time of the study although they were surrounded entirely by defoliated trees, and "regrowth" was defined as new growth originating at the site of damage by gypsy moth larvae (Heichel and Turner 1976). "Partially eaten" leaves had at least 50% of their area removed, presumably by gypsy moth larvae. We harvested all leaves used in this bioassay, as well as in those described in the next sections, from infrequently traveled roadsides at the edges of mid-aged stands (consisting of trees 2–3 m in height), choosing exclusively young, sun-exposed, short-shoot growth from eye-level height in the canopy. In addition, no two larvae within one treatment received leaves from the same aspen stand, no stand was harvested more than once, and stands were at least 8 km apart.

Larvae were reared individually from hatching to pupation (approximately 5 weeks) at 24°C and 16 h light:8 h dark on detached leaves from each treatment in plastic cups that had been fitted with disks of moistened plaster of Paris to maintain high humidity and leaf turgor. Relative growth rates (RGR) were calculated for each caterpillar as the difference between the natural logarithm of final and initial (neonate) larval weights divided by time, according to Waldbauer (1968). RGR for this bioassay was calculated using the interval between hatching and the 11th day of growth, which was the longest interval available due to low survival in the defoliation treatments. RGR data were subjected to one-way analysis of variance (ANOVA), and Dunnett's one-tailed test was used to compare all treatments with a predefined "control" (in this case undefoliated leaves from uninfested sources) (JMP, SAS Institute 1999). We analyzed survival data with chi-squared contingency analysis, using individual chi-squared tests and the Dunn-äidák critical value for comparisons of individual treatments (PROC FREQ, SAS Institute 1990; Sokal and Rohlf 1995).

In 1994, we repeated this experiment using leaves from quaking aspen saplings planted between spring of 1993 and spring of 1994 in a common garden at the Dow Gardens research facility in Midland, Michigan. The experimental plots at Dow Gardens consisted of 36 *Populus tremuloides* saplings, watered every several days and fertilized minimally. These trees were randomly divided into two groups: "gypsy moth" and "control" (*n*=18). Both gypsy moth and control trees were covered with mesh bags. Bags covering treatment trees were filled with gypsy moth larvae collected from a natural infestation on quaking aspen, while bags covering control trees were left empty. We allowed the larvae to defoliate the experimental trees almost entirely before we removed them. Treatments in the subsequent bioassay included: (1) leaves from control trees, (2) partially eaten leaves from gypsy moth trees, and (3) regrowth leaves from gypsy moth trees (*n*=30 larvae). Data were analyzed as in the 1993 larval bioassay.

In 1995, we measured growth of swallowtail larvae on black cherry leaves (which contain no phenolic glycosides) that had been treated exogenously with known amounts of two phenolic glycosides at levels simulating those found in damaged foliage (Mattson and Palmer 1987). Freeze-dried, purified salicortin and tremulacin were dissolved in methanol and painted onto leaves with gloved fingers. Based on actual leaf weights and estimated water content (64.3%, from Scriber 1991), we applied: (1) tremulacin at 7% dry weight, (2) salicortin at 15% dry weight, (3) tremulacin+salicortin at 15% dry weight, and (4) methanol alone. *Papilio canadensis* fourth instars were weighed, placed singly on leaves, and weighed again after 4 days of feeding (*n*=22). Data were analyzed with one-way ANOVA (JMP, SAS Institute 1999).

Additional leaves were collected in 1994 concurrently with the Dow Gardens bioassay and with the leaf sterilization bioassay described below, for water and nitrogen analysis. From Dow Gardens, we harvested 15 regrowth leaves from 15 different defoliated trees, along with 15 partially eaten leaves. In the same manner, we also harvested 15 leaves from undefoliated trees. From the field, we took regrowth leaves from 15 trees growing in defoliated stands at least 24 km apart, as well as leaves from 15 trees growing in undefoliated stands separated by the same distance. Leaves were weighed and placed in a drying oven at 95°C. Several months later, they were weighed to determine water content, and subsamples were analyzed for nitrogen. The nitrogen content of 10-mg samples was determined by combustion using a Carlo Erba CHN analyzer, model NA 1500, following the method of Daun and DeClerq (1994). Data were analyzed with one-way ANOVA, and post hoc comparisons used Dunnett's method, with undefoliated trees serving as the control (JMP, SAS Institute 1999).

Gypsy moth pathogens

In 1994, we tested for the presence of pathogenic agents associated with gypsy moth-damaged foliage. *P. canadensis* neonates (*n*=25) were placed on the following treatments: (1) leaves from undefoliated stands, (2) surface-sterilized leaves from undefoliated stands, (3) regrowth leaves from defoliated stands, and (4) sur-

face-sterilized regrowth leaves from defoliated stands. Leaves were sterilized by soaking in 0.26% sodium hypochlorite solution for 5 min, followed by a 5-min rinse under running water and a spin through a lettuce-drier. Unsterilized leaves were soaked in water, rinsed, and dried in the same manner. The set-up followed those described previously. We tested for the main effects of sterilization and leaf source, and for interaction between the two factors, on RGR with two-way ANOVA; treatment×treatment comparisons were made with Tukey's HSD method (JMP, SAS Institute 1999). Survival was analyzed with chi-squared contingency analysis and the Dunn-äidák critical value for comparisons between treatments (PROC FREQ, SAS Institute 1990; Sokal and Rohlf 1995).

We also tested for the presence of pathogenic substances in gypsy moth body fluids themselves. In 1994, we collected the cadavers of gypsy moth larvae from an intensely defoliated quaking aspen stand on state forest land near Traverse City, Michigan after ascertaining that the area had never been sprayed with Bt. Dead gypsy moth larvae were typical of those found in diseased outbreak populations. We ground the cadavers with a mortar and pestle, diluted them with distilled water (10:1 water:larval homogenate), and painted approximately 1 ml of the resulting solution on quaking aspen leaves with gloved fingertips. Three additional treatments consisted of 1 ml of the following liquids painted on leaves in similar fashion: (2) water; (3) gypsy moth body fluids autoclaved for 30 min at 120°C and 380 kPa; and (4) nuclear polyhedrosis virus (NPV) spores in water solution at 3–5 times LD_{50} (which is approximately $7{\times}10^3$ polyhedral inclusion bodies ml^{-1}) for gypsy moth larvae. For all treatments, we painted both leaves from undefoliated areas and regrowth leaves from defoliated areas. Third and fourth instars ($n=20$) were weighed and reared on these treatments as described above; after seven days, final weights and survival were recorded. Dead swallowtail larvae were examined for signs of pathogen infection under a Nikon TMS inverted phase-contrast microscope. Due to low survival in the body fluid treatments, we were unable to calculate RGR. We analyzed survival data with chi-squared contingency analysis, using individual chi-squared tests and the Dunn-äidák critical value for comparisons of individual treatments (PROC FREQ, SAS Institute 1990; Sokal and Rohlf 1995).

In a separate experiment, we painted quaking aspen leaves as described above with either water or NPV solution (3–5 times gypsy moth LD_{50}), and reared 30 $P.$ $canadensis$ fifth instars on each treatment for 8 days before recording final weight and survival. We analyzed the resulting RGR data with one-way ANOVA (JMP, SAS Institute 1999).

Predators and parasitoids

In 1994, we set up a field experiment to test whether gypsy moth larvae attracted parasitoids that attacked $P.$ $canadensis$ larvae as well. Swallowtails were subjected to two treatments: quaking aspen stands artificially infested with gypsy moth larvae, and paired uninfested control stands. We chose eight sites, 3.2–6.4 km apart, of aspen saplings in the Pigeon River State Forest (Cheboygan County, Mich.), divided each site in two, and randomly assigned each half to one or the other of two treatments, control or gypsy-moth-infested, leaving approximately 50 m between treatments. On 20 trees within the experimental treatment at each site, we placed 30–50 fifth- to sixth-instar gypsy moths. Each of these trees was covered entirely with a large mesh bag to keep the larvae in place; 20 control trees at each site were bagged as well. We then interspersed $P.$ $canadensis$ third and fourth instars on aspen trees adjacent to the bagged trees in both treatments, with 23 swallowtail larvae per treatment per site, one to a tree. Their locations were marked with cryptic green twist-ties and recorded. We monitored survival every other day and then, after 15 days, brought the remaining swallowtail larvae back to the lab where we observed them for signs of parasitism. Dead larvae were dissected, and their parasitoids were preserved in alcohol and identified by the USDA-SEL laboratory in Beltsville, Maryland. Voucher specimens are housed at the Michigan State University Museum, East Lansing,

Mchigan. Multidimensional chi-squared analysis was used to estimate the effects of site, treatment, and site×treatment interaction on both survival and parasitism of swallowtail larvae (PROC CATMOD, SAS Institute 1990).

Aware of the danger of pseudoreplication, we nevertheless set up all of our field sites within a 32-km radius. This was necessary to avoid site-to-site variation in predation level and type, which we knew from previous experience to be quite high. We chose a forest that had been intensely defoliated by gypsy moths in 1993 but was completely devoid of them, as was much of northern Michigan, in 1994. Thus, our control treatments would be free of gypsy moth larvae, but natural enemy populations that had expanded in response to the previous year's infestation would theoretically still be present in both treatment and control plots.

Results

Oviposition

We found no evidence that females were able to discriminate between damaged and undamaged foliage; the mean number of eggs (±SE) laid on undefoliated aspen (29.63±7.26), was statistically indistinguishable from the mean number laid on partially eaten foliage (25.06±4.84) ($\chi^2=0.018$, $df=1$, $P=0.89$). Additionally, approximately as many females preferred damaged leaves (7) as undamaged leaves (9)

Host plant quality

In the 1993 growth trial, $P.$ $canadensis$ larvae grew significantly more slowly on leaves from resistant trees, regrowth leaves, and partially eaten leaves from gypsy moth-defoliated areas, than did larvae fed leaves from undefoliated areas ($F=21.735$; $df=3$, 39; $P=0.0001$; Dunnett's $P<0.05$) (Fig. 1A). The 1994 bioassay using trees from the experimental plots at Dow Gardens revealed no treatment effects on RGR ($F=0.595$; $df=2$, 29; $P>0.5$) (Fig. 1B).

All defoliation treatments severely reduced survival, whether we used leaves from naturally infested areas ($\chi^2=57.01$, $df=3$, $P<0.0001$) (Fig. 2A), or from Dow Gardens ($\chi^2=8.19$, $df=2$, $P=0.01$) (Fig. 2B). In both growth trials, all damaged-leaf and regrowth treatments differed significantly from the undefoliated control treatment (P-values ranged from 0.0001 to 0.05), but not from each other.

Exogenously applied phenolic glycosides did not affect either the growth or the survival of $P.$ $canadensis$ caterpillars. Growth rates (±SE) were as follows: 0.612(±0.132) for tremulacin, 0.556(±0.112) for solvent, 0.483(±0.082) for salicortin, and 0.370(±0.092) for salicortin and tremulacin together ($F=1.41$; $df=3$, 21; $P=0.2553$). Survival was roughly 50% on all treatments ($\chi^2=0.883$; $df=3$; $P=0.8296$).

Leaf water content was significantly affected by defoliation both in the field ($F=35.72$, $df=1$, $P<0.0001$) (Fig. 3A) and at Dow Gardens ($F=24.78$, $df=2$, $P<0.0001$) (Fig. 3B). Regrowth foliage contained a significantly
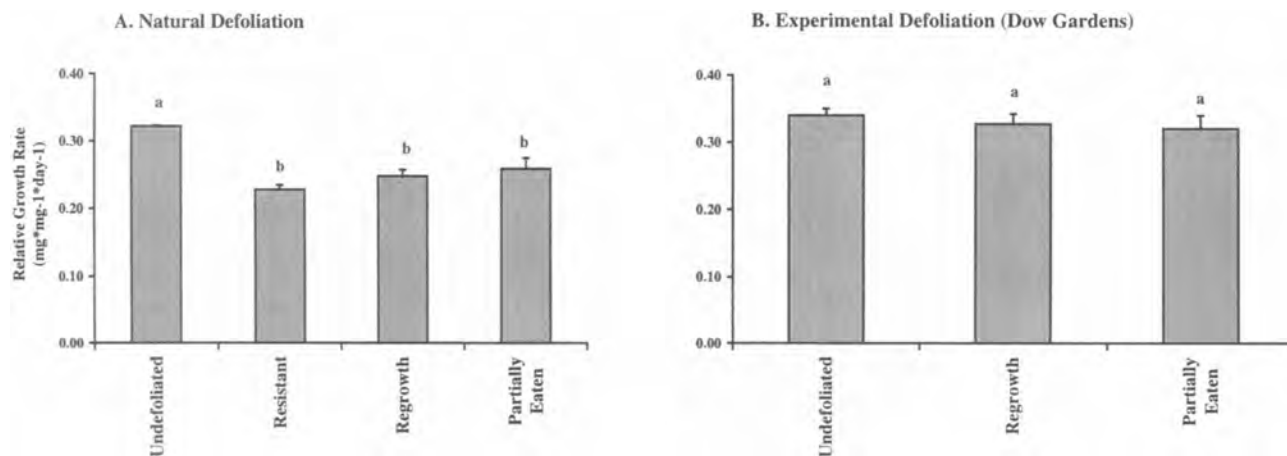
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Fig. 1 Mean (+SE) relative growth rates of *Papilio canadensis* larvae on leaves from various defoliation treatments, from **A** naturally and **B** experimentally defoliated trees. *Bars* with different *letters* are significantly different
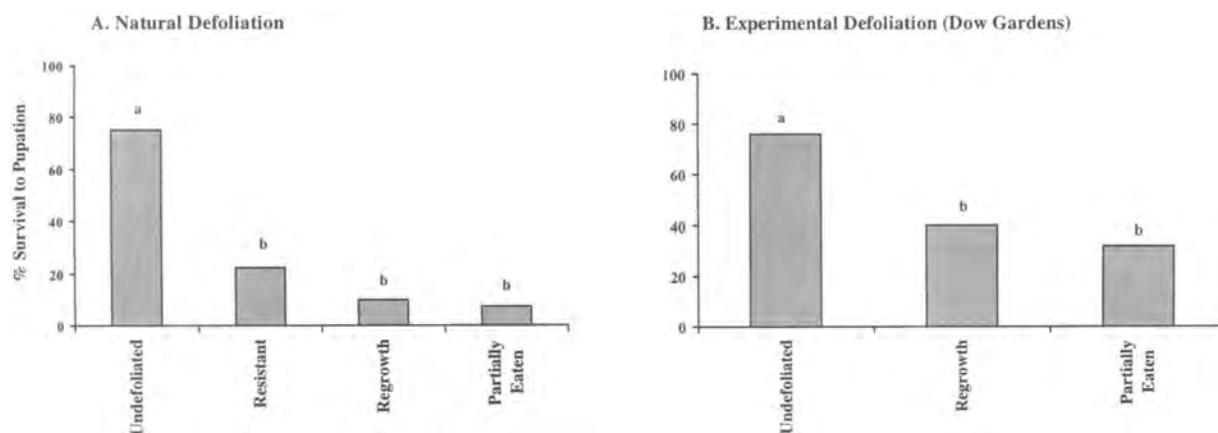

Fig. 2 Survival of *P. canadensis* to pupation on leaves from various defoliation treatments, from **A** naturally and **B** experimentally defoliated trees. *Bars* with different *letters* are significantly different

Fig. 3 Mean (+SE) water (%) and nitrogen (% of dry weight) content of leaves from various treatments, from **A** naturally and **B** experimentally defoliated trees. Within a category (water or nitrogen), *bars* with different *letters* are significantly different
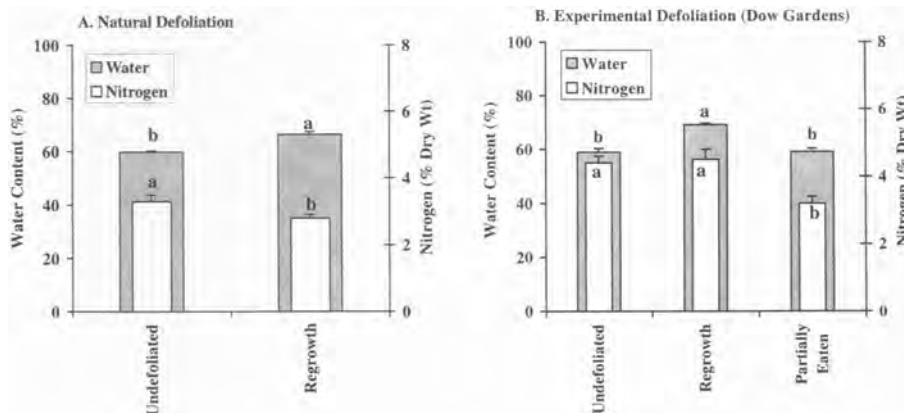
higher percentage of water than primary foliage in both field-grown and Dow Gardens (Dunnett's $P<0.05$) trees. Partially eaten leaves, gathered from Dow Gardens only, did not differ from primary foliage.

Nitrogen concentration was also affected by gypsy moth damage both in the field ($F=4.96$, $df=1$, $P=0.034$) (Fig. 3A) and at Dow Gardens ($F=7.91$, $df=2$, $P=0.001$) (Fig. 3B). Field-collected leaves from undefoliated areas contained significantly more N per milligram of dry weight than did regrowth leaves from defoliated stands. We saw a somewhat different pattern in the leaves from Dow Gardens, however, with regrowth leaves and leaves
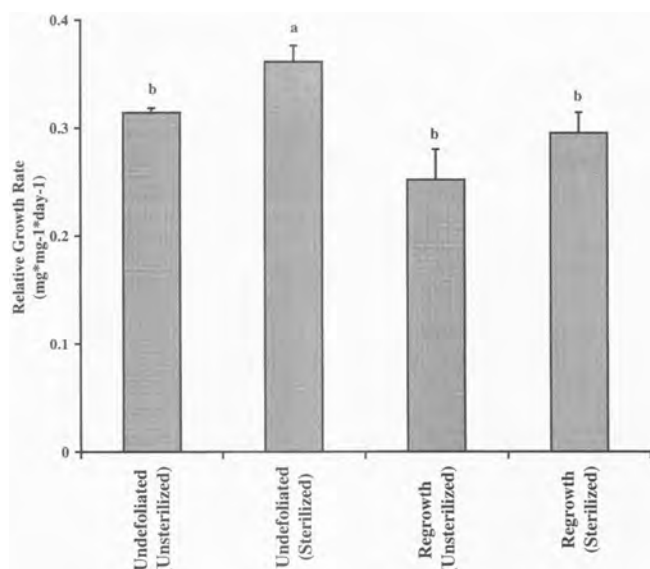
Fig. 4 Mean (+SE) relative growth rates of *P. canadensis* larvae on sterilized and unsterilized leaves from defoliated and undefoliated quaking aspen stands. *Bars* with different *letters* are significantly different

Fig. 5 Survival of *P. canadensis* to pupation on sterilized and unsterilized leaves from defoliated and undefoliated quaking aspen stands. *Bars* with different *letters* are significantly different

from undefoliated trees both showing high, statistically indistinguishable, concentrations of N, and partially eaten leaves containing a significantly lower concentration than leaves from undefoliated trees (Dunnett's $P<0.05$).

Gypsy moth pathogens

In the 1994 sterilization experiment, as before, the source of leaves significantly influenced RGR ($F=9.648$; $df=1$, 24; $P=0.003$), as did sterilization ($F=4.863$; $df=1$, 24; $P=0.03$) (Fig. 4). The interaction between sterilization and leaf source was not significant ($F=0.009$; $df=1$, 24; $P=0.92$). Individual treatment-comparisons revealed that sterilized leaves from undefoliated areas differed from all other treatments ($P<0.05$).

Swallowtail survival, overall, did not depend on sterilization ($\chi^2=1.21$, $df=1$, $P=0.27$), but it did depend on leaf source ($\chi^2=18.91$, $df=1$, $P<0.0001$), and interaction between sterilization and leaf source was significant ($\chi^2=3.84$, $df=1$, p=0.049) (Fig. 5). Survival on unsterilized leaves from defoliated areas differed from all other treatments ($P<0.05$), but no other treatments differed from one another, confirming that the interaction between main effects was due to increased survival when leaves from defoliated areas were sterilized, whereas sterilization of leaves from undefoliated stands had no effect on survival.

Leaves painted with gypsy moth body fluids and water resulted in 100% mortality of swallowtail caterpillars in a matter of hours, whether the leaves were taken from defoliated or undefoliated trees (Fig. 6). However, when we autoclaved the body fluid solution, the effect on survival nearly disappeared. NPV solution, in this same ex-
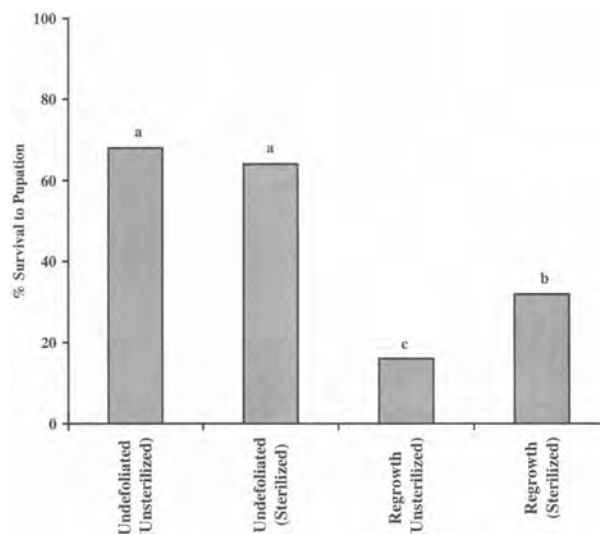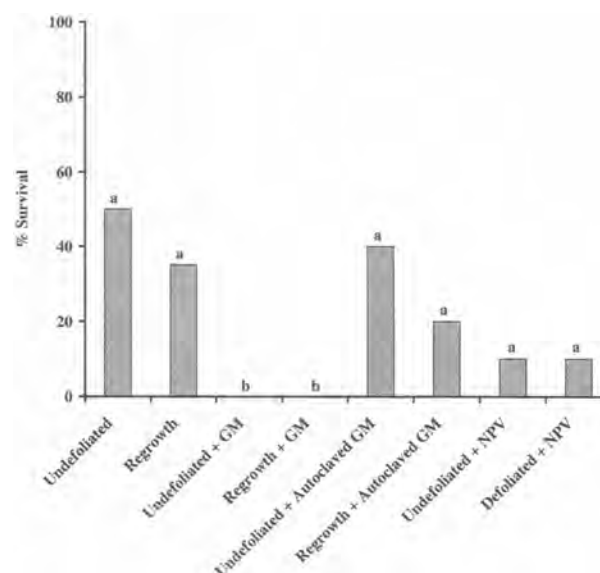

Fig. 6 Survival of *P. canadensis* larvae on regrowth or undefoliated quaking aspen leaves painted with gypsy moth body fluids (*GM*), autoclaved body fluids, nuclear polyhedrosis virus (*NPV*), or water. *Bars* with different *letters* are significantly different

periment, reduced survival to 10% on both types of foliage. Mortality was too high for growth measurements to be feasible, but the effect of treatment on survival was significant ($\chi^2=9.36$, $df=3$, $P=0.025$). The effect of leaf source was not significant ($\chi^2=0.000$, $df=1$, $P=0.99$), nor was the interaction between treatment and leaf source ($\chi^2=0.59$, $df=3$, $P=0.89$). Untreated gypsy moth body fluids, specifically, resulted in a significant increase in mortality ($P<0.05$). No other single treatment significantly affected *P. canadensis* survival.

In the separate NPV-painting experiment, we found no evidence that NPV reduced the survival of *P. can-*

Table 1 Survival and parasitism of *Papilio canadensis* larvae placed on quaking aspen saplings in the field with gypsy moth larvae present or absent

Gypsy moths present				Gypsy moths absent			
Site	% Returned to laboratory	% Parasitism of returned larvae	% Survival to emergence	Site	% Returned to laboratory	% Parasitism of returned larvae	% Survival to emergence
1	39.1	66.7	4.4	1	39.1	22.2	8.7
2	17.4	25.0	0	2	30.4	28.6	4.4
3	17.4	50.0	0	3	21.7	0	4.4
4	13.0	66.7	0	4	26.1	16.7	4.4
5	43.5	50.0	8.7	5	43.5	10.0	4.4
6	26.1	16.7	4.4	6	34.8	0	0
7	39.1	77.8	8.7	7	34.8	25.0	8.7
8	47.8	9.1	4.4	8	21.7	20	0
Total	30.4	*44.6	3.8	Total	31.5	15.5	4.3

* Number in the corresponding column of the opposite treatment is significantly different ($P \leq 0.05$)

adensis larvae (survival was 73.3% on the control and 76.7% on NPV), but it did depress RGR significantly from 0.098($\pm$0.010) to 0.079($\pm$0.006) (F=4.099; df=1, 43; P=0.049).

Predators and parasitoids

When we placed swallowtail caterpillars on trees in areas that had been artificially infested with gypsy moths, their overall survival did not differ from that of the controls (χ^2=1.82, df=1, P>0.10), but the incidence of parasitism increased significantly with the presence of gypsy moths (χ^2=12.66, df=1, P=0.0004) (Table 1). Neither site (χ^2=11.43, df=7, P=0.12) nor interaction between treatment and site (χ^2=6.44, df=7, P=0.49) proved to be significant effects. Parasitoids retrieved from swallowtails were primarily *Compsilura concinnata* and *Lespesia frenchii* (Diptera: Tachinidae).

Discussion

Host plant quality

Our data suggest that indirect competition between gypsy moths and tiger swallowtails can occur. Both natural and controlled gypsy moth-defoliation significantly depressed the quality of quaking aspen leaves for *Papilio* caterpillars, even when leaves were sterilized; thus, leaf chemistry appears to have reduced swallowtail performance. There have been examples of *Populus* specialists whose performance was reduced by high concentrations of phenolic glycosides (Bingaman and Hart 1993), but the results of our salicortin and tremulacin leaf-painting experiment did not support the hypothesis that the negative effects of defoliation on swallowtails were caused by these compounds. *P. canadensis* has strongly preferred quaking aspen in most previous oviposition assays (Scriber 1992), and it appears to have evolved a set of enzymes used solely to detoxify phenolic glycosides,

which comprise nearly the entire inducible defensive response in *Populus* (Lindroth 1992). However, the high variance and short duration of our phenolic glycoside bioassay leave room for further investigation.

Changes in the nutritional quality of leaves, to which even specialists are unlikely to be immune, are another common effect of defoliation. Nitrogen, phosphorous, and water, all of which can affect the growth and survival of caterpillars (Scriber and Slansky 1981), are frequently reduced in leaves following herbivore-attack (Mattson and Palmer 1987). In our experiments, although water content was somewhat higher or the same in leaves from defoliated sources, nitrogen was generally lower than it was in leaves from undefoliated trees. Nitrogen, the most limiting nutrient in the diet of folivores (Scriber and Slansky 1981), could have caused the differences in *P. canadensis* growth we witnessed. We were interested to note that the nitrogen content of regrowth leaves at Dow Gardens was not depressed, as it was in the field. This difference was probably due to the fertilization of the Dow plot, which produced relatively nitrogen-rich foliage in all treatments. Coincidentally, although Dow Gardens regrowth foliage reduced survival of *P. canadensis*, it failed to reduce RGR as field-collected regrowth leaves did.

Pathogens

During outbreaks of disease in dense gypsy moth populations, huge numbers of dead and dying caterpillars hang from leaves and branches by their prolegs, releasing dissolved body fluids onto foliage. The pathogen-painting and leaf sterilization experiments indicated that pathogens or other lethal agents associated with gypsy moth body fluids could affect swallowtail larvae negatively. Such agents, in natural settings, could potentially devastate wild tiger swallowtail populations. We observed 84% mortality in a very short period of time on unsterilized leaves gathered from infested aspen stands, and 100% mortality on leaves painted directly with gypsy moth body fluids.

Little research has been done on the susceptibility of *Papilio* to pathogens; it is not known whether common gypsy moth pathogens, such as *Entomophaga maimaiga*, NPV, or microsporidians associated with the gypsy moth, infect *P. canadensis*. NPV is thought to be highly specific to *L. dispar* (Barber et al. 1993), but sublethal effects, such as the reduction in growth reported here, have not been explored. We have considered the possibility that the NPV we used in our experiments was contaminated, but we feel that investigation is warranted. We have no definitive data to address the cause of mortality in the body fluid experiment, but the appearance of our larvae, the rapidity of death and liquefaction, and the absence of characteristic structures (e.g., polyhedral occlusion bodies, encysted nematodes) in swallowtail cadavers under microscopic examination, suggest bacteria and/or bacterial toxins as the most likely causal agents. Further research is required to sort through the possibilities, but regardless of the specific pathogen or compound responsible, the effect of gypsy moth body fluids on swallowtail survival stands to be profound under natural circumstances.

Predators and parasitoids

Although overall survival of *P. canadensis* did not decrease as a result of proximity to gypsy moths, parasitism rate was significantly altered. It is critical to note that the area in which we conducted this experiment supported a rather high ratio of predation, primarily by spiders, to parasitism (A.M. Redman, unpublished work). Parasitoids may well be more sensitive than predators to the specific volatile chemicals and other cues associated with the presence of gypsy moths and therefore more likely than predators such as spiders to orient toward dense populations of gypsy moth larvae when visual cues are obstructed. Thus, we might expect the differences between infested and uninfested sites to manifest most readily in the rate of parasitoid attack. In a different site with fewer predators and more parasitoids, the elevated rate of parasitism might have resulted in elevated mortality. Further, we cannot say how swallowtails or other herbivores might have fared within a more realistic time frame. The duration of this experiment was relatively short, and it most certainly reduced the rate of attack by parasitoids, which frequently will parasitize only one larval stage (Price 1975).

Because caterpillars remained in the field for such a brief period, natural enemy populations could not have increased through reproduction. Rather, elevated parasitism was due to the ability of resident parasitoids to detect and respond to cues associated with elevated gypsy moth populations, a phenomenon known as spatial, as opposed to temporal, density-dependence (Liebhold and Elkinton 1989; Ferguson et al. 1994). Dark mesh bags enclosed gypsy moth larvae and damaged foliage, so it is difficult to imagine that visual cues attracted parasitoids to infested sites; volatile infochemicals seem the most

likely alternative, given their prevalence in other systems (reviewed in Takabayashi and Dicke 1996).

Many plant species, when they are damaged by herbivores, release highly specific volatile chemicals that attract natural enemies, particularly parasitic wasps, which use odors to locate their prey (Turlings et al. 1990; Takabayashi and Dicke 1996). There is indirect evidence that tachinid parasitoids are also capable of responding to host-related volatile chemicals (Monteith 1964; Odell and Godwin 1979, 1984). In particular, *Compsilura concinnata*, which we harvested from our swallowtail caterpillars, has been shown to aggregate toward both artificially and naturally elevated gypsy moth populations (Liebhold and Elkinton 1989; Williams et al. 1992; Ferguson et al. 1994). The second tachinid we found, *Lespesia frenchii*, is another generalist parasitoid of the gypsy moth (Sabrosky and Reardon 1976). It has also been shown to aggregate toward outbreaks of at least one defoliator, the forest tent caterpillar (Parry et al. 1997).

Although we eliminated visual cues, we did not measure volatile release, and we cannot say conclusively whether damage-induced plant compounds, chemicals released from frass, odors given off by gypsy moth larvae themselves, or some combination of these were responsible for the attraction of parasitoids. However, damage-induced plant compounds appear to be the volatiles most commonly used by host-seeking parasitoids (Takabayashi and Dicke 1996). To the best of our knowledge, no one has yet shown elevated parasitism in the field due to the presence, or even the putative presence, of herbivore-related volatiles. Faeth (1986) speculated that the increase in parasitism of leaf-miners he observed in previously damaged foliage was due to the release of volatiles, but he was unable to control for larval duration, leaving open the possibility that leaf-miners on damaged plants were parasitized more heavily due simply to longer development time. De Moraes et al. (1998) showed attraction of parasitoids to damaged foliage on potted plants in the field, but did not demonstrate a corresponding increase in parasitism. In any case, our work represents the first real evidence that non-visual cues associated with damage affect herbivores by increasing parasitism rates.

Temporal, as well as spatial, density-dependent responses of parasitoids to gypsy moths are likely to work against native herbivores in outbreak zones. Williams et al. (1992) speculated that *C. concinnata* would remain numerous in gypsy moth-defoliated areas, even in non-peak years, due to its ability to parasitize alternative hosts. Although the gypsy moth population in our field site had collapsed, we found considerable levels of *C. concinnata* infestation, perhaps offering some support to this hypothesis. All told, the natural enemies associated with gypsy moth populations may have a significant impact on swallowtails and other native herbivores.

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Avoidance of competition

Ovipositing *P. canadensis* females did not demonstrate the ability to discriminate between damaged and undamaged foliage in our trials. We do recognize the limitations of our approach; in particular, our methods do not allow us to eliminate the possibility that ovipositing females avoid infested trees in the field by responding to cues unavailable in laboratory assays, e.g., long-range visual or olfactory cues. However, we have frequently observed swallowtail eggs in the field on trees damaged severely by gypsy moths (J.M. Scriber, unpublished work). We feel fairly confident in stating that, in *P. canadensis* populations that prefer quaking aspen, competition from the gypsy moth over the 12 or so years during which it has defoliated aspen in northern Michigan has apparently not resulted in selection for females to oviposit on undamaged foliage. We have noted, interestingly, that females from areas that have been infested by gypsy moths for a number of years tend to use white ash significantly more frequently in laboratory assays than do females from locations that have not yet been touched by gypsy moths (Scriber 1996). We have considered the possibility that competition with gypsy moths has selected for localized host shifts by *P. canadensis* from quaking aspen to white ash, but there have been other hypotheses advanced to explain this geographic pattern of host use (Scriber 1996).

Significance

Competition between species drives population fluctuations, species distributions, host use, and community organization. The mechanisms and impact of competition are well studied in many organisms, but their importance in insects, particularly in herbivorous insects, is unappreciated and poorly understood. We have uncovered several mechanisms driving competition between *P. canadensis* and *L. dispar*, mechanisms whose impact on the fitness of the many herbivores sharing hosts with the gypsy moth may be enormous. Further, the native forest tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae), has defoliated quaking aspen in northern Michigan for countless years. We were unable to find a resident population of *M. disstria* during the time of this study, so we do not know whether similar interactions take place between this insect and its neighbors, but we hope that further research (e.g., Parry et al. 1997) will examine the ecological impact of native defoliators.

In recent years, pest management decisions have incorporated knowledge drawn from research in insect biology, ecosystem-level effects, and, particularly, the non-target effects of pest control. As a result, much scientific effort of late has focused on the impact of various chemical and biological control agents on non-pest species (Melin and Cozzi 1990; Barber et al. 1993; McCarthy 1994). An equally pressing question, which has gone largely unanswered, is how non-target organisms are af-

fected by pest populations themselves. In the only such study that we know of, Sample et al. (1996) found evidence that gypsy moth outbreaks severely reduced the diversity of native Lepidoptera. Studies such as this and our own stand not only to illuminate the basic mechanisms and consequences of interspecific interactions but also to enhance our ability to manage pests responsibly.

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