Effects of Condensed Tannins and Catalpol on Growth and Development of *Compsilura concinnata* (Diptera: Tachinidae) Reared in Gypsy Moth (Lepidoptera: Lymantriidae)[1]

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ABSTRACT Condensed tannin is generally considered an example of a quantitative plant allelochemical defense, and catalpol an example of a qualitative chemical defense. The effects of these compounds on the growth and survival of a tachinid parasitoid, *Compsilura concinnata* (Meigen), reared in the gypsy moth, *Lymantria dispar* (L.), were compared. Each chemical was incorporated into synthetic diets in a range of ecologically relevant doses and fed to host larvae. Larvae were fed in each of two ways: immediately after parasitization (one day after fourth instar molt), and from egg hatch onward. Growth and survival of unparasitized gypsy moth larvae on test diets were also monitored. No significant effect of either catalpol or condensed tannin on *C. concinnata* growth or puparial survival was observed. Tannin did lengthen development time of unparasitized host larvae from fourth stadium onward, and lowered pupal weights of larvae fed tannin from egg hatch onward. Catalpol had no significant impact on overall gypsy moth larval development, indicating that this insect is able to compensate for the reduction in weight gain reported to be caused by catalpol in younger larvae. Mortality in all experiments was insignificant. It appears that these phytochemicals are more similar in their effects on the parasitoid than was predicted based on their roles as toxins and digestibility-reducers in herbivores. The data also suggest that generalist tachinid parasitoids such as *C. concinnata* may be more tolerant of allelochemicals in their host's diet, than their hymenopteran counterparts.

KEY WORDS Tachinidae, parasitoid, *Lymantria dispar,* plant allelochemicals, host suitability, tri-trophic level interactions.

Plant-derived chemicals have been intensely investigated for the better part of this century with respect to their role as defenses against herbivorous insects and in the coevolution of plants and phytophagous insects (Cates 1980, Futuyma 1983, Spencer 1988). Until recently, however, little consideration has been given to the influence of plant compounds on the natural enemies that feed upon the herbivore itself. Further research, within a tritrophic-level context, is required

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in order to develop realistic predictions about the effects of plant-derived compounds on natural enemies such as parasitoids. One of the cornerstones of research on insect-plant interactions has been Feeny's (1976) theory, which grouped plant chemical defenses by their "mode of action". Feeny suggested that such chemicals acted either qualitatively (i.e., were directly toxic in small doses), or quantitatively (i.e., acted indirectly by reducing plant nutrient quality, often in a dose-dependent manner). We recognize that these terms have been the subject of debate since compounds have been identified that are toxic and also act in a dose-dependent way (Bernays 1978, Barbosa and Krischik 1987). Nevertheless, they do describe a dichotomy in the effects of many plant allelochemicals and have been widely used in the literature in the absence of an accepted alternative (Barbosa 1988). Our objective in this study was to examine whether the "qualitative-quantitative" dichotomy is of relevance to host suitability for tachinid parasitoids.

The gypsy moth, *Lymantria dispar* (L.), is a polyphagous pest of forest trees throughout northeastern America and Canada (Northnagle and Schultz 1987). Most of its host plants are woody deciduous trees. However, in no-choice feeding trials, larvae will feed and even develop (albeit poorly), on various shrubs and Phorbaceae (Barbosa and Krischik 1987, Miller and Hanson 1989). Thus, the gypsy moth is relatively well-adapted to trees which typically contain high levels of tannins, but does feed on plants containing other types of secondary metabolites, such as alkaloids and iridoids. Thus, among the allelochemicals the gypsy moth encounters in its food plants are condensed tannin (a "quantitative" allelochemical), and catalpol, an iridoid glycoside (a "qualitative" defense).

The parasitoid, *Compsilura concinnata* (Meigen), is also highly polyphagous, with over 200 recorded host species, among which are larvae of several Lepidoptera (Clausen 1978). Recorded parasitization rates in outbreak populations of gypsy moths in North America are highly variable. Parasitization rates have been observed to be low (Williams et al. 1992), but in other studies it has been recorded as a dominant parasitoid (Barbosa et al. 1975). Field studies with artificially-elevated populations of gypsy moth larvae have shown a positive spatial density-dependent response by *C. concinnata* (Gould et al. 1990). There is some evidence that the uneven impact of *C. concinnata* on the gypsy moth could be at least partially explicable by a negative effect of tannin. When fed to host larvae in artificial diet, tannic acid, a hydrolyzable tannin, does reduce *C. concinnata* puparial weights (Bourchier 1991).

Compsilura concinnata is a unique choice for this research simply because it is a tachinid. Parasitoids in this family have been studied to far lesser extent than have hymenopteran ones, in the context of tritrophic level interactions. Only one other worker (Bourchier 1991) has studied a tachinid (*C. concinnata*) with regard to the effects of specific host plant allelochemicals. Our study is the first attempt to simultaneously compare how two distinctly different plant chemical defenses affect the physiological performance of a parasitoid.

Thus, the specific question addressed by our experiments was "Is the development and survival of *C. concinnata* influenced differently by the presence of condense tannin versus catalpol in the host's diet?" Gypsy moth fitness would be enhanced if they were unaffected by compounds in their diet and if the same chemicals were detrimental to their natural enemies. Since the gypsy moth prefers plants containing condensed tannin rather than catalpol, we hypothesized

that the iridoid should have a more deleterious effect on *C. coninnata* than the tannin.

Materials and Methods

Insect rearing. *Compsilura concinnata* adults were kept in a large steel-mesh cage (240 cm^3) supplied with honey and water, in a walk-in environmental chamber set at 22°C, 60% RH, and a 16:8 light:dark cycle. Flies used to start the colony were supplied by Dr. Vicente Sanchez (USDA Forest Service, Hamden, CT). For colony propagation, mid-fourth to early fifth-instar gypsy moths were presented to fecund *C. concinnata* females. Larvae were grouped on the basis of similarity of size and placed overnight in the cage in batches of 12. This allowed for parasitization of sufficient numbers of hosts while minimizing the chance of excessive superparasitism of smaller individuals, which might produce abnormally small progeny. Parasitized hosts were kept in groups of 8 in 180-ml plastic cups. Synthetic diet was given to larvae and changed every 2 to 3 days.

Gypsy moth egg masses (NJSS strain) were supplied by the USDA/APHIS rearing facilities at Otis ANGB, MA. Egg masses were surface sterilized for 20 min in a 10% formalin solution. Larvae were maintained on a synthetic wheat-germ based diet modified from that of Bell et al. (1981) and reared in the same walk-in chamber as the flies.

Allelochemicals. Quebracho tannin was purchased from Trask Co. (Georgia) as a crude mixture of spray-dried phenolic substances. This extract was semi-purified using a modified version of Asquith and Butler's (1985) protocol for purifying condensed tannin. This procedure yields a mixture of high (>2000 MW) molecular weight polyphenolic compounds, more reflective of the polymeric condensed tannin content of oak leaves than the crude quebracho mixture. Purified catalpol was synthesized according to methods based on those of Roby and Stermitz (1984).

Both condensed tannins and catalpol were incorporated into gypsy moth synthetic diet on a percent dry weight (% d.w.) basis. A bulk nonnutritive diet component, alphacellulose, was removed to compensate for the increased weight of the allelochemical. Casein was removed from the diets to eliminate the possibility of the tannin becoming insolubly bound with the protein (Dr. H. Appel, unpublished data). Doses used for condensed tannin reflected the reported range of concentrations found in oak (*Quercus* spp.) leaves (Montgomery 1986), 1.3% d.w. to 4.2% d.w. Doses selected for this study were 2%, 3% and 4% d.w. The reported range of catalpol concentrations in Catalpa tree (*Catalpa speciosa*) leaves, 0.1% d. w. to 0.7% d. w. (Dr. M. D. Bowers, University of Colorado, unpublished data) were used to establish the treatments with catalpol; 0.2% 0.3%, 0.5% and 0.7% d.w. Standard gypsy moth artificial diet (minus casein) was used as the control (0% d. w.) treatment in all experiments.

Feeding regimes and parasitisation procedure. Studies have suggested that parasitoids might be repelled by plant-derived compounds or odors, emanating from host herbivores (Bureleigh et al. 1973, Shahjahan and Streams 1973). To avoid any confounding effects this might create, our experiments were first conducted with host larvae fed test diets immediately after parasitization. However, this feeding regime reduced considerably the time the insects were exposed to the allelochemicals, since gypsy moths are halfway through their larval lifespan by

the fourth stadium (Leonard 1981). Thus, a second approach was undertaken, using hosts that had been reared on the various doses of each compound from egg hatch onward. This ensured that the insects would experience the maximum possible anti-nutritional (or toxic) impact of each chemical, albeit at the risk of biasing the larviposition of parasitoid females. For all experiments, host larvae were presented individually to parasitoid females one day after molting to the fourth instar, the preferred stage for *C. concinnata* (Weseloh 1980). Since *C. concinnata* can larviposit multiple progeny in one attack, host larvae were removed after a single distinct abdominal contact by the fly was observed. This minimized the number of maggots injected into a single host.

Parameters measured. For the first feeding regime, host larvae were placed individually in 180-ml plastic cups and randomly assigned to each experimental treatment. In experiments using the second feeding regime, larvae were returned (in individual cups) to the treatment they had been reared on from egg hatch onward. Larval weights were recorded for host larvae at this point. In all cases, a completely randomized experimental design was used.

Cups were checked daily for parasitoid emergence and the number of emerged parasitoids per host was recorded. Parasitoid larval and puparial development times also were recorded. Puparial weights were recorded one day after emergence of larvae from hosts, as were adult dry weights and the gender of eclosed flies. Puparial mortality, i.e., the number of puparia failing to produce adults, also was recorded on a per host basis. Host larvae were almost completely destroyed by parasitoid larvae by the time the maggots emerged. Tissue necrosis and decay was so extensive by this point that identification of unemerged parasitoid larvae was impossible. As a result, larval mortality could not be quantified.

Dose-response experiments. Separate experiments using the same allelochemical dosages also were conducted to monitor the effects of each compound on unparasitized host larvae. As in experiments with parasitized larvae, experiments were performed with both feeding regimes, using a completely randomized design. All larvae were weighed before assignment to treatments. Larvae were checked daily for mortality, and larval development time (days to pupation) and pupal weights were recorded.

Statistical methods. Error residuals of all weight and development time data were checked for homogeneity of variances using Levene's test, and for normality using Shapiro-Wilk's test (Milliken and Johnson 1984). If heterogeneity of variances or non-normality was detected, data were transformed to meet the assumptions of ANOVA. All continuous data were analysed using regression (Proc GLM in SAS, SAS Institute 1988). Analysis of covariance was used to examine the influence of host weight, measured at the time of parasitization, on the response of the parasitoid. This also was done for data from the dose-response experiments.

Parasitoid gender frequency and puparial mortality were analysed using Fisher's exact test, a contingency table analysis. This approach also was used to assess the influence of allelochemical dosage on mortality of gypsy moth larvae in the dose-response experiments. For these studies, the number of hosts successfully pupating versus the number dying before pupation was analyzed using Fisher's test.

Results

None of the development time or weight data for *C.concinnata* showed any statistically significant differences between treatments, for either allelochemical. This was the case no matter which feeding regime was used. Data and analyses for the tannin experiments are summarized in Table 1; those from the catalpol experiments are presented in Table 2. Analysis of covariance showed no significant covariance of any of these variables with initial host larval weight.

The analysis of puparial mortality frequency showed no statistically significant influence of either allelochemical ($P > 0.5$, all datasets). Parasitoid gender frequency also appeared uninfluenced by dosage of either catalpol or condensed tannins ($P > 0.45$, all experiments).

The regression results of the tannin dose-response experiments with unparasitized gypsy moth larvae were different for each feeding regime (Table 3). For larvae fed tannins from fourth instar onward, there was a significant regression of development time on tannin dose ($y = 35.3 + 1.04x$), indicating a longer time to pupation on tannin diets. Pupal weight, however, was not significantly affected by tannin dosage. For larvae fed tannins from egg hatch onward, development time was not influenced by tannin dosage, but pupal weights showed a significant negative regression on tannin dose ($y = 1499 - 201x$). In dose-response experiments with catalpol (Table 4), neither development time nor pupal weights were significantly influenced by catalpol dose, regardless of the feeding regime used.

Discussion

Compsilura concinnata appears unaffected by either allelochemical at any of the doses used in this study, regardless of the feeding regime used. Therefore, the hypothesis that the qualitative chemical defense, catalpol, has a greater deleterious effect (when fed either after parasitization or from egg hatch onward) than the quantitative one, tannin, must be rejected. Nevertheless, even these statistically "negative" results do provide some interesting implications for theory on the role of host plant chemistry in insect/plant interactions.

One prediction that has been made based on the quantitative/qualitative theory is the "slow growth/high mortality" hypothesis. This suggests that since quantitative chemical defenses act by reducing nutrient availability, they may slow herbivore development. This, in turn, may expose herbivores to mortality factors such as parasitoids for a longer time than they would endure on plants which allowed faster growth (Price et al. 1980, Rhoades 1983, Feeny et al. 1985). However, if parasitoids themselves are also negatively affected by quantitative defenses, the assumption that such natural enemies are unaffected by these chemicals would be invalidated. A sublethal negative effect of such allelochemicals on parasitoid larvae might translate into lowered fitness of the resulting adult parasitoids, and thus reduce long-term natural enemy impact on the herbivore.

Table 1. Mean puparial weights, adult dry weights, and development time of flies produced from host larvae fed diets supplemented with condensed tannin from fourth instar (FI) or egg hatch (EH) onward. Regression analysis results are shown below the data.

Tannin level	Puparial wt (mg) (± SE)		Adult wt (mg) (± SE)		Larval development (days) (± SE)		Puparial development (days) (± SE)	
	FI	EH	FI	EH	FI	EH	FI	EH
0%	33.0 (± 2.41)	34.1 (± 2.73)	5.7 (± 0.44)	5.1 (± 0.57)	11 (± 1.1)	14 (± 1.1)	9 (± 0.8)	10 (± 0.6)
n	17	13	12	10	17	13	12	10
2%	35.3 (± 2.30)	37.6 (± 3.08)	5.9 (± 0.41)	5.6 (± 0.54)	13 (± 1.1)	13 (± 1.2)	10 (± 0.8)	12 (± 0.7)
n	15	13	11	11	15	13	11	11
3%	33.5 (± 2.41)	32.4 (± 3.86)	6.2 (± 0.41)	4.4 (± 0.73)	12 (± 1.1)	12 (± 1.6)	10 (± 0.8)	11 (± 0.8)
n	15	10	10	7	15	10	10	7
4%	30.5 (± 2.41)	42.5 (± 4.17)	5.3 (± 0.38)	7.1 (± 1.03)	12 (± 1.0	13 (± 1.7)	10 (± 0.7	13 (± 1.1)
n	16	10	13	9	16	10	13	9
r^2	0.04	0.11	0.05	0.02	0.01	0.06	0.02	0.17
F	0.41	1.35	0.20	0.69	0.19	0.80	0.81	2.17
P	0.295	0.275	0.655	0.414	0.663	0.501	0.374	0.111

Note: n = number of individual parasitoids observed.

Table 2. Mean puparial weights, adult dry weights, and development time of flies produced from host larvae fed artificial diets supplemented with catalpol from fourth instar (FI) or egg hatch (EH) onward. Regression analysis results are shown below the data.

Catalpol level	Puparial wt (mg) (± SE)		Adult wt (mg) (± SE)		Larval development (days) (± SE)		Puparial development (days) (± SE)	
	FI	EH	FI	EH	FI	EH	FI	EH
0%	40.0 (± 2.22)	34.1 (± 2.51)	6.4 (± 0.52)	5.1 (± 0.58)	12 (± 0.7)	14 (± 1.2)	10 (± 0.6)	8 (± 1.6)
n	12	10	11	8	12	10	11	8
0.2%	38.2 (± 2.32)	31.7 (± 3.17)	6.5 (± 0.54)	5.4 (± 0.69)	10 (± 0.8)	12 (± 1.6)	10 (± 0.6)	9 (± 1.5)
n	11	11	10	9	11	11	10	9
0.3%	36.0 (± 2.32)	43.2 (± 3.88)	6.6 (± 0.54)	6.3 (± 0.75	13 (± 0.8)	15 (± 1.9)	10 (± 0.6)	11 (± 1.3)
n	11	12	10	9	11	12	10	9
0.5%	34.6 (± 2.43)	37.8 (± 3.88)	6.6 (± 0.54)	6.6 (± 0.75)	11 (± 0.8)	14 (± 1.9)	11 (± 0.6	11 (± 1.1)
n	10	12	10	9	10	12	10	9
0.7%	36.8 (± 2.43)	28.7 (± 3.17)	7.0 (± 0.57)	(5.1) (± 0.61)	10 (± 0.8)	13 (± 1.6)	13 (± 0.6)	10 (± 1.8)
n	11	11	9	9	11	11	9	9
r^2	0.05	0.09	0.03	0.02	0.02	0.01	0.11	0.09
F	1.78	2.47	0.13	0.08	1.15	0.30	0.78	3.66
P	0.188	0.124	0.725	0.785	0.288	0.582	0.495	0.06

Note: *n* = number of individual parasitoids observed.

Table 3. Mean development time and pupal weights of gypsy moth larvae reared on various doses of condensed tannin from (1) fourth instar onward ("feeding regime 1"), or (2) egg hatch onward ("feeding regime 2"). Regression analysis results are shown below the data.

	Feeding regime 1		Feeding regime 2	
Tannin level	Days to pupation (± SE)	Pupal wt (mg) (± SE)	Days to pupation (± SE)	Puparial wt (mg) (± SE)
0%	35.3 (± 1.12)	732 (± 68)	32.4 (± 0.91)	1670 (± 182)
n	17	17	10	10
2%	38.9 (± 1.24)	752 (± 75)	34.3 (± 1.09)	736 (± 235)
n	14	14	7	7
3%	35.9 (± 1.20)	699 (± 73)	33.6 (± 1.02)	543 (± 218)
n	15	15	9	9
4%	40.8 (± 1.24)	598 (± 75)	32.9 (± 1.02)	1119 (± 218)
n	14	14	8	9
r^2	0.20	0.02	0.01	0.40
F	6.37	1.44	0.30	7.11
P	0.014	0.235	0.586	0.013

Note: n = number of individual parasitoids observed.

Table 4. Mean development time and pupal weights of gypsy moth larvae reared on various doses of catalpol from (1) fourth instar onward ("feeding regime 1"), or (2) egg hatch onward ("feeding regime 2"). Regression analysis results are shown below the data.

Tannin level	Feeding regime 1		Feeding regime 2	
	Days to pupation (± SE)	Pupal wt (mg) (± SE)	Days to pupation (± SE)	Puparial wt (mg) (± SE)
0%	35.4 (± 0.92)	1410 (± 156)	32.4 (± 0.68)	1670 (± 242)
n	12	12	10	10
0.2%	35.7 (± 1.12)	1250 (± 162)	35.5 (± 0.98)	1520 (± 210)
n	12	12	10	10
0.3%	34.0 (± 0.63)	880 (± 142)	32.3 (± 0.92)	1560 (± 226)
n	12	12	10	10
0.5%	35.6 (± 0.77)	1080 (± 134)	31.5 (± 0.99)	1440 (± 240)
n	12	12	10	10
0.7%	36.4 (± 0.92)	1130 (± 126)	31.5 (± 0.82)	1290 (± 244)
n	12	12	10	10
r^2	0.01	0.03	0.02	0.03
F	6.73	1.83	1.06	1.48
P	0.398	0.182	0.308	0.230

Note: *n* = number of individual larvae observed.

The finding that a condensed tannin affects the growth of a host herbivore without negatively affecting its suitability as a nutritional resource for its parasitoid lends support to the slow growth/high herbivore mortality hypothesis. However, the same cannot necessarily be said for all types of quantitative defense compounds. Tannic acid, a hydrolyzable tannin, does reduce *C. concinnata* puparial weight and lengthen gypsy moth development time (Bourchier 1991). Interestingly, although condensed tannin has no impact on the parasitoid, it too slows gypsy moth development when fed from fourth instar onwards, and reduces pupal weights when fed from egg hatch onward. This difference in effect may be due to the structural differences between these two types of tannins. Condensed tannin may be too large to pass beyond the peritrophic membrane. Tannic acid, on the other hand, is a smaller molecule and did appear to be present in the midgut lumen, where *C. concinnata* feeds (Bourchier 1991). No reliable stain specific for condensed tannin exists (Hagerman, pers. comm.), so this possibility could not be verified in our experiments.

The results for the experiments with catalpol are puzzling in light of the findings of previous workers that catalpol has a significant negative effect on gypsy moth growth (Bowers and Puttick 1988). One explanation may be the fact that in those earlier studies gypsy moth larvae were reared on catalpol-augmented diets immediately upon hatching. Furthermore, they were followed only for the first 15 days of development (Bowers and Puttick 1988). It is possible that larvae become more tolerant of catalpol beyond this point, which is roughly when larvae enter the fourth instar. The results of the dose-response experiments with larvae fed catalpol from egg hatch onward support the possibility that gypsy moth larvae are somehow able to compensate for any initial effects of the iridoid, and reach normal pupal weights in an average development time identical to control larvae. Nevertheless, the results of these experiments do suggest that, despite their very different chemical structures and botanical occurrence, catalpol and condensed tannin appear to be similar in their lack of effects on the parasitoid, *C. concinnata*. Therefore, the assignment of catalpol as a qualitative allelochemical, in the context of its effects on the third trophic level in this system, appears untenable.

Previous studies with other generalist parasitoids (El-Heneidy et al. 1988, Campbell and Duffey 1981) have shown more severe detrimental effects of plant compounds than have studies with specialist parasitoids (Thorpe and Barbosa 1986). These findings have led to the suggestion that generalist parasitoids may be more severely affected by plant allelochemicals than specialists (Barbosa 1988). However, all these studies have focused on hymenopteran parasitoids. Our results suggest that generalist tachinid parasitoids such as *C. concinnata* may not be as sensitive as their hymenopteran counterparts to the toxic or antinutritive effects of plant-derived compounds in their hosts' diet. This ability to feed and develop, unaffected by host-ingested plant allelochemicals, may be one reason *C. concinnata* is able to successfully exploit over 200 host species, in what must undoubtedly be a variety of host-plant habitats.

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