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Chemical barriers to adaptation by a specialist herbivore

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Summary. *Depressaria pastinacella,* the parsnip webworm (Lepidoptera: Oecophoridae), feeds throughout eastern North America on *Pastinaca sativa* (wild parsnip) and few other species. The assumption that specialist herbivores such as the parsnip webworm are adapted to hostplant chemistry, and are therefore unaffected by chemical variation in hostplants, was tested. Flower buds from plants grown first in the greenhouse and then in the field were fed to ultimate instar webworms. Plant phenotype had a significant effect on virtually all webworm food utilization parameters. While nutritional factors (i.e., nitrogen content) were correlated with approximate digestibility, two constituents of the flowers – bergapten and xanthotoxin, both linear furanocoumarins – independently accounted for a significant amount of variation in food utilization indicies. The physiological effects of these furanocoumarins were confirmed in artificial diet experiments. Despite the fact that the two most important furanocoumarins in parsnip flowers relative to webworm feeding and growth are isomers, differing only in the positioning of a methoxy substituent, they have different physiological effects; while xanthotoxin in general has no effect on growth, bergapten decreases growth and digestibility of the diet. These results underscore the need in studies of plant-animal interactions to examine individual chemical components rather than classes of compounds.

Key words: Plant-insect interactions – Furanocoumarins – Parsnip webworm – Wild parsnip

Although plant chemicals have been implicated in insect resistance in crop systems (e.g., Guthrie et al. 1986; Maxwell and Jennings 1980), they have only rarely been examined in the context of wild populations of interacting herbivores and hostplants. Particularly for oligophagous species, plant chemicals elucidating behaviors involving host finding, feeding, or oviposition have been identified (Metcalf et al. 1982; Ikeshoji et al. 1982; Mitchell 1977; Bowers 1983; Rowell-Rahier and Pasteels 1982), but the role of plant chemicals in resistance to oligophagous herbivores is less widely recognized (but see Rogers et al. 1987; Blust and Hopkins 1987). The assumption is frequently made that specialists are adapted to characteristic hostplant chemistry and thus are unaffected by variation in chemical content and composition (Fox 1981). Even in studies in which plant chemistry is associated with resistance to herbivory by a specialist insect, the relationship demonstrated is often only correlative and the actual behavioral or physiological effects of the resistance chemicals are not elucidated (Dolinger et al. 1973; Edmunds and Alstad 1978; Sturgeon 1979). Because nutritional factors can covary with chemical content, correlative relationships between plant chemistry and herbivory may reflect nutritional unsuitability or nutrient-allelochemical interactions rather than toxicity per se (Kraft and Denno 1982; Wisdom 1985; Hare 1987; Cates et al. 1987). Therefore, such correlations have not proved particularly useful in determining coevolutionary trajectories in plant-insect interactions. As a result, the importance of chemistry in mediating plant-insect interactions has been subject to considerable criticism (Bernays and Graham 1988; Jermy 1984).

One such correlation between plant chemistry and patterns of herbivory involves the interaction between wild parsnip (*Pastinaca sativa*) and the parsnip webworm (*Depressaria pastinacella*). Wild parsnip is a biennial road-side weed introduced from Europe over 300 years ago (Schery 1974). Partly due to the economic importance of cultivated parsnips, the chemistry of *P. sativa* has been thoroughly characterized and over 50 compounds have been identified from aerial parts of the plant (Berenbaum 1985). Of these, furanocoumarins are known to possess a variety of toxic properties and in pure form in laboratory experiments are lethal to fungi, bacteria, nematodes, insects and other potential plant enemies (Murray et al. 1982). Although in general very few insect species attack wild parsnip in eastern North America (Berenbaum 1981), throughout its range it suffers considerable damage from *D. pastinacella,* an oecophorid caterpillar restricted to feeding on reproductive parts of wild parsnip and a few closely related plants in the family Umbelliferae (Hodges 1974; Gorder and Mertins 1987). Berenbaum et al. (1986) demonstrated that seed production in the presence of parsnip webworms is positively correlated with amounts of two furanocoumarins in seeds. However, the effects of these furanocoumarins on parsnip webworm behavior and physiology were not determined, nor was potential covariation in nutritional parameters that could also render plant tissue more or less suitable for webworm growth. In this study, we examined the effects of variation in both nutritional and furanocoumarin content of *P. sativa* flower buds on growth and development of *D. pastinacella.*

Materials and methods

Seeds of wild parsnip were collected from twenty plants in a population approximately 6 km northeast of the cam-

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pus (viz., Berenbaum et al. 1986). Seeds were sown in cardboard milk cartons filled with approximately 0.8 L of soil. At least 10 cartons were prepared for each of the twenty source plants. Plants were grown in a greenhouse on the UIUC campus in fall 1986 until February 1987, when all plants were transported to the University of Illinois Phillips Tract natural research area to facilitate vernalization under field conditions (Baskin and Baskin 1979). Pots were placed on the ground in a plot at Phillips Tract. Flowering commenced in early July. Secondary umbels in the same developmental stage, that is, just prior to bud burst, were collected at the same time from six different plants in the experimental plot. Sixth (ultimate) instar *D. pastinacella* were collected from other individuals in the experimental plot.

Umbellets and larvae were brought into the laboratory to conduct feeding trials. All larvae to be tested were starved for two hours. Five larvae were weighed, oven-dried at 60° C for 48 h, and weighed again to obtain a wet weight to dry weight conversion factor. Another 36 larvae were starved for two h, weighed and used in the feeding experiment. Umbellets from the secondary umbels were weighed and placed in 15 mm × 55 mm plastic petri dishes with moistened filter paper. Six replicate umbellets were prepared in this manner for each plant. Additional umbellets were weighed, oven-dried at 60° C for 48 h, and weighed again to obtain values of specific water content (mg H_2O/mg dry leaf) as well as wet weight to dry weight conversions for the plant material. These dried umbellets were subsequently analyzed for furanocoumarin and nitrogen content. The preweighed larvae were randomly assigned one per dish to each of the 36 dishes. Larvae were allowed to feed for 24 h, after which larvae, frass, and remaining plant material were removed, oven-dried and weighed. Relative growth rate (RGR), relative consumption rate (RCR), efficiency of conversion of ingested material (ECI), efficiency of conversion of digested material (ECD) and approximate digestibility (AD) were calculated according to Waldbauer (1968):

$$\mathrm{RGR} = \frac{\text{larval dry weight gain}}{\text{mean larval dry weight} \times \text{time}}$$

$$\mathrm{RCR} = \frac{\text{dry weight of plant material eaten}}{\text{mean larval dry weight} \times \text{time}}$$

$$\mathrm{ECI} = \frac{\text{larval dry weight gain}}{\text{dry weight of plant material eaten}} \times 100$$

$$\mathrm{ECD} = \frac{\text{larval dry weight gain}}{\text{dry weight of plant material eaten} - \text{dry weight of frass}} \times 100$$

$$\mathrm{AD} = \frac{\text{dry weight of plant material eaten} - \text{dry weight of frass}}{\text{dry weight of plant material eaten}} \times 100$$

The dried umbellet samples from each plant were ground to a fine powder. Part of the powdered material was weighed, placed into test tubes containing sulfuric acid-hydrogen peroxide digesting solution (Allen 1974), heated until the solution turned clear and then analyzed by the Nessler method for total nitrogen (Allen 1974). The remaining powder was weighed, extracted in hot ethyl ether for 2 min, evaporated to dryness, redissolved in ethyl acetate and injected into a high pressure liquid chromatograph (Waters, Milford, Massachusetts) as described in Berenbaum et al. (1984). The six furanocoumarins found in *P. sativa* – imperatorin, bergapten, isopimpinellin, xanthotoxin, sphondin, and psoralen – were quantified by ultraviolet absorbance detection at 254 nm.

The effect of plant phenotype on each feeding parameter was examined by one-way analysis of variance. Multiple regression of each feeding parameter against potentially correlated chemical and nutritional characters was performed to determine the relative influence of each character on insect feeding and growth. Feeding parameters were regressed against the concentration of each furanocoumarin, specific water content and nitrogen concentration.

Chemicals identified by ANOVA as having a significant effect on growth and development of webworms were then tested in artificial diet. Newly molted sixth instar parsnip webworms were obtained from a laboratory culture reared on artificial diet (Nitao and Berenbaum 1988). Parental individuals were collected as pupae in July, 1987 from wild parsnip stalks at two sites in Champaign County, Illinois. Xanthotoxin and bergapten, purchased from Aldrich Chemical Co. (Milwaukee, WI), were dissolved in ether and added directly to liquid diets, and vigorously mixed in a water bath (60° C) to evaporate the solvent. The final concentration of furanocoumarins was 0.15% wet weight, which corresponds to levels measured in natural hostplant populations (Berenbaum et al. 1984, 1986). The liquid diet was poured into plastic frames, solidified and cut into small cubes (each cube ca. 2 g after it solidified). Each larva was placed in a one oz. plastic cup with each diet cube and the cup was capped with a plastic petri dish cover to allow transmission of UVA radiation. In order to take into account photoactivation of furanocoumarins, which can greatly enhance toxicity to insects (Berenbaum 1978), for each chemical 15 larvae were exposed to a sunlight-simulated spectrum (BLB and cool-white bulbs, UVA intensity of 250 $\mu W/cm^2$, 16L:8D photoperiod) and another 15 larvae were protected from UV light with a UV-opaque filter. All the larvae were allowed to feed until they pupated. Larvae that finished feeding tended to crawl up to the cover, shrink in size, and spin silk around their bodies. This prepupal behavior was considered a criterion for cessation of feeding; larvae were checked every 8 h for prepupation. Pupae, diet, and frass plus silks were weighed after drying at 60° C for 6 days. Food utilization indices (RGR, RCR, ECI, ECD, AD) were calculated on a dry weight basis as previously described (Waldbauer 1968). Each furanocoumarin and the control were compared by two-way fixed effect ANOVA, with diet composition (with or without furanocoumarin) and light regime (with and without UV) as main effects.

Results

All plant characters measured differed significantly among phenotypes with the exception of nitrogen, which was marginally nonsignificant ($P = 0.067$) (Table 1). Concentrations of individual furanocoumarins varied up to ten-fold (Table 2). Plant identity had a significant effect upon all larval feeding parameters except relative consumption rate, which was marginally non-significant (Table 3).

Nutritional characters were correlated with furanocoumarins. Nitrogen was negatively correlated with three furanocoumarins, namely xanthotoxin, sphondin, and psoralen, and water content was positively correlated with sphondin and psoralen (Table 4). Multiple regression analysis revealed that both furanocoumarin and nutritional characters

Table 1. Analysis of variance of specific water content, nitrogen concentration and furanocoumarin concentration among different phenotypes of wild parsnip

Character	Source	d.f.	MS	F	*P*
Specific H_2O content	Plant	5	0.1298	7.536	<0.001
	Error	30	0.0172		
Nitrogen	Plant	5	23.0453	2.798	0.067
	Error	12	8.2378		
Imperatorin	Plant	5	1643 927.3372	36.4476	<0.001
	Error	30	45 103.8814		
Bergapten	Plant	5	356 065.4589	46.6826	<0.001
	Error	30	7627.3705		
Isopimpinellin	Plant	5	26 779.6631	14.1868	<0.001
	Error	30	1887.6521		
Xanthotoxin	Plant	5	1901 019.0023	72.0060	<0.001
	Error	30	26 400.8346		
Sphondin	Plant	5	3502.4198	28.2043	<0.001
	Error	30	124.1803		
Psoralen	Plant	5	96 026.6476	45.5721	<0.001
	Error	30	2107.1391		
Total furanocoumarin	Plant	5	10056 002.0000	48.5740	<0.001
	Error	30	207 024.0000		

Table 2. Means of insect feeding characters and plant nutrient and allelochemical characters associated with each of six phenotypes of wild parsnip. Standard deviations are in parentheses

Character[a]	Plants					
	1	2	3	4	5	6
RGR, mg $mg^{-1}d^{-1}$	0.42	0.48	0.32	0.28	0.52	0.45
	(0.144)	(0.172)	(0.138)	(0.115)	(0.055)	(0.055)
RCR, mg $mg^{-1}d^{-1}$	2.61	2.43	1.95	2.36	2.84	2.89
	(0.886)	(0.729)	(0.450)	(0.317)	(0.280)	(0.260)
ECI, %	16.0	20.4	15.9	11.7	18.5	15.5
	(2.70)	(7.34)	(5.26)	(3.58)	(2.02)	(2.53)
ECD, %	45.5	59.2	48.9	30.3	43.9	40.2
	(10.25)	(26.29)	(16.10)	(7.12)	(4.40)	(3.73)
AD, %	36.3	35.5	32.6	38.4	42.2	38.5
	(7.44)	(5.60)	(3.53)	(4.07)	(4.18)	(3.89)
Specific H_2O, mg/mg	3.47	3.53	3.15	3.43	3.52	3.53
	(0.05)	(0.15)	(0.14)	(0.12)	(0.16)	(0.14)
Nitrogen, μg/mg	36.00	35.9	37.1	42.4	38.3	34.6
	(1.96)	(3.38)	(1.85)	(3.35)	(2.86)	(3.36)
Imperatorin, μg/mg	0.12	0.22	1.10	0.16	1.18	1.40
	(0.042)	(0.056)	(0.358)	(0.076)	(0.265)	(0.249)
Bergapten, μg/mg	0.07	0.41	0.35	0.28	0.31	0.81
	(0.018)	(0.069)	(0.103)	(0.057)	(0.095)	(0.133)
Isopimpinellin, μg/mg	0.06	0.000	0.08	0.14	0.01	0.16
	(0.011)		(0.037)	(0.042)	(0.018)	(0.088)
Xanthotoxin, μg/mg	0.21	0.78	0.49	0.48	0.67	1.82
	(0.048)	(0.151)	(0.134)	(0.133)	(0.171)	(0.261)
Sphondin, μg/mg	0.04	0.07	0.02	0.01	0.07	0.05
	(0.009)	(0.014)	(0.007)	(0.003)	(0.017)	(0.010)
Psoralen, μg/mg	0.000	0.31	0.000	0.01	0.11	0.19
		(0.036)		(0.011)	(0.052)	(0.092)
Total furanocoumarin, μg/mg	0.59	1.78	2.03	1.43	2.35	4.43
	(0.082)	(0.316)	(0.617)	(0.266)	(0.576)	(0.592)

[a] Sample size for all means except nitrogen was 6. Sample size for nitrogen was 3

accounted for significant amounts of the variation in relative growth rate (RGR) and approximate digestibility (AD), accounting overall for 45.9% and 41.4% of the variance respectively (Table 5). A marginally non-significant regression for efficiency of conversion of ingested material (ECI) was also found ($P=0.055$). Growth was positively associated with increased xanthotoxin; for each standard deviation increase in xanthotoxin there was an associated 2.715 standard deviation increase in larval growth rate (Table 5). Approximate digestibility, the amount of plant material absorbed relative to the amount eaten, was enhanced by both xanthotoxin and nitrogen but was negatively associated

Table 3. Analysis of variance of insect feeding and growth by the parsnip webworm feeding on different plant phenotypes of wild parsnip

Character	Source	d.f.	Mean square	F	*P*
RGR	Plant	5	0.0518	3.504	0.013
	Error	30	0.0148		
RCR	Plant	5	0.7154	2.4253	0.058
	Error	30	0.2950		
ECI	Plant	5	52.3663	2.8036	0.034
	Error	30	18.674		
ECD	Plant	5	547.6564	2.8841	0.030
	Error	30	189.8907		
AD	Plant	5	62.2538	2.6420	0.0429
	Error	30	24.6989		

with bergapten content (Table 5). Thus, phenotypically negatively correlated characters – e.g. xanthotoxin and nitrogen – are independently positively associated with growth. These results suggest that furanocoumarins independent of nutritional characters account for a significant portion of the variation in webworm feeding parameters.

The results of the artificial diet experiment confirm the importance of furanocoumarin variation in resistance of parsnips to parsnip webworm (Table 6). Bergapten significantly lowered both relative growth rate and approximate digestibility, the same digestive parameters which earlier regression analysis indicated were affected by bergapten in umbellets. Moreover, these laboratory findings are consistent with earlier field studies in which bergapten concentrations in seeds alone accounted for 36% of the variation

Table 4. Phenotypic correlations between allelochemical and nutritional characters

	nit	wat	imp	ber	iso	xan	sph	pso
Nitrogen	1.000	−0.201	−0.113	−0.039	0.145	−0.475*	−0.617*	−0.497*
Water content		1.000	−0.122	0.143	−0.041	0.293	0.428*	0.411*
Imperatorin			1.000	0.658*	0.285	0.625*	0.112	0.039
Bergapten				1.000	0.412*	0.966*	0.351*	0.545*
Isopimpinellin					1.000	0.423*	−0.453*	−0.372*
Xanthotoxin						1.000	0.415*	0.553*
Sphondin							1.000	0.771*
Psoralen								1.000

* $P<0.05$

Table 5. Multiple regression of insect growth and feeding characters on plant nitrogen, specific water content and furanocoumarin concentration

Character	Source	d.f.	SS	F	*P*	% Variation
RGR	Regression	8	0.3230	2.872	0.019	45.9
	Residual	27	0.0380			
RCR	Regression	8	4.3007	1.786	0.124	34.6
	Residual	27	8.1256			
ECI	Regression	8	329.2407	2.254	0.055	40.0
	Residual	27	492.9428			
ECD	Regression	8	2688.3975	1.579	0.178	31.9
	Residual	27	5746.6047			
AD	Regression	8	441.5403	2.382	0.044	41.4
	Residual	27	625.8877			

Standardized regression coefficients for regressions

Independent variable	Dependent variables				
	RGR	RCR	ECI	ECD	AD
Specific water content	−0.329	−0.272	−0.176	0.025	−0.420
Nitrogen	0.268	0.283	0.060	−0.301	0.882**
Imperatorin	[a]	−0.396	−0.394	−0.245	−0.295
Bergapten	−1.300	−2.018*	0.014	0.869	−2.015*
Isopimpinellin	−0.764	−0.255	−0.738	−0.414	−1.191
Xanthotoxin	2.715*	2.877*	0.778	−0.650	3.118**
Sphondin	0.533	0.354	0.327	0.058	0.521
Psoralen	−0.727	−0.505	−0.406	−0.105	−0.535

[a] exceeded tolerance limit, dropped from procedure
* $p<0.05$; ** $P<0.01$

Table 6. Means and standard deviations of larval growth, consumption and feeding efficiency of parsnip webworms fed diets containing bergapten and xanthotoxin in the presence and absence of UV light

Index	Diet composition	Light level		*P*		
		UV+	UV−	Diet	Light	Interaction
RGR	Bergapten	0.244±0.025	0.245±0.020	0.047	0.359	0.311
	Xanthotoxin	0.250±0.030	0.260±0.027	0.652	0.844	0.120
	Control	0.265±0.028	0.252±0.030			
RCR	Bergapten	3.28±0.49	2.98±0.34	0.006	0.003	0.599
	Xanthotoxin	3.35±0.32	3.39±0.33	0.337	0.075	0.038
	Control	3.69±0.56	3.26±0.42			
ECI	Bergapten	7.59±1.28	8.28±0.95	0.121	0.031	0.686
	Xanthotoxin	7.48±0.92	7.72±0.85	0.739	0.125	0.613
	Control	7.29±0.99	7.76±0.77			
ECD	Bergapten	10.77±2.26	11.71±1.75	0.058	0.083	0.803
	Xanthotoxin	10.24±1.66	10.79±1.48	0.653	0.126	0.851
	Control	9.98±1.82	10.69±1.26			
AD	Bergapten	71.02±3.45	71.09±3.70	0.017	0.642	0.587
	Xanthotoxin	73.44±3.33	71.97±3.01	0.607	0.143	0.692
	Control	73.53±3.33	72.69±2.27			

* Effects of bergapten or xanthotoxin were compared to control; diet, UV and interaction effects that were not significant ($P<0.05$) are not shown

in resistance to seed removal by parsnip webworms (Berenbaum et al. 1986). In contrast, xanthotoxin had no negative main effects on any of the digestive parameters measured. This lack of negative effects is also consistent with the lack of a correlative association between xanthotoxin and resistance in field populations.

Discussion

More than ten years ago, Feeny (1976) wrote that "At the present time, it seems reasonable to suppose that although an insect species may possess some general adaptation to tolerate an entire class of chemical compounds, such as the glucosinolates, it may be better adapted to tolerating certain compounds within this class than others." Such is indeed the case for the oligophagous parsnip webworm. Despite the fact that it is capable of metabolizing xanthotoxin with efficiencies 10 to 100 times greater than other more generalized feeders (Nitao 1989), it is not necessarily immune to the effects of ingesting all furanocoumarins in its hostplant.

Curiously, the two furanocoumarins with the most pronounced physiological effects in the multiple regression – xanthotoxin with its positive effects on growth and bergapten with its negative effects – are isomeric, differing only in the positioning of a methoxy substituent. The mechanism by which bergapten is less well metabolized or tolerated is not known. The seemingly minor difference in structure (8-methoxy substitution in the case of xanthotoxin and 5-methoxy substitution in the case of bergapten) does have profound biochemical effects. The two isomers, for example, differ in the degree to which they interact with DNA. The apparent association constant of bergapten for double helical DNA is approximately half that for xanthotoxin and the number of apparent binding sites is also approximately half that for xanthotoxin (Sasaki et al. 1987). Evidently, the pyrone ring hinders the methoxy group in the five position and not in the eight position; such steric hindrance may protect bergapten from detoxification by the cytochrome P450 monooxygenases known to play a role in xanthotoxin metabolism. Yet another difference between the two isomers is reactivity toward ground state oxygen – quantum yield of singlet oxygen generation at 365 nm is almost three times greater for xanthotoxin than for bergapten (Blan and Grossweiner 1987).

These experiments greatly emphasize the utility of identifying variation in individual components of a biosynthetically related class of allelochemicals (Lindroth and Peterson 1988). Measurement of total amounts (e.g., "total phenolics," "total alkaloids," "total resins," etc.) may obscure subtle ecological relationships unique to individual chemicals. The current disaffection with plant chemistry as a principal factor leading to host specialization in herbivorous insects may actually derive not from a lack of evidence, as is frequently cited, but rather from a lack of appropriate hypothesis testing, which further experimental investigation can remedy.

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