Patterns of Furanocoumarin Production and Insect Herbivory in a Population of Wild Parsnip (*Pastinaca sativa* L.)

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Summary. Seasonal changes in the distribution and abundance of furanocoumarins in wild parsnip, *Pastinaca sativa* (Umbelliferae), were examined in a population of plants in Tompkins County, New York. Xanthotoxin, imperatorin and bergapten (linear furanocoumarins) occur in all above-ground parts of the plant; in addition, angelicin and sphondin (angular furanocoumarins) occur in umbels of some individuals. Total furanocoumarin content, as measured by percent dry weight, is greatest in reproductive parts, particularly buds and seeds; variation in concentrations between plants is greatest in vegetative structures (e.g., leaves).

Within the plant, the distribution of furanocoumarins is significantly correlated with nitrogen, as opposed to biomass, allocation. In that nitrogen is often a factor limiting the plant growth, furanocoumarins appear to be allocated in proportion to plant tissue value; reproductive structures, obvious contributors to plant fitness, contain over ten times the amount of nitrogen and furanocoumarin contained in vegetative structures such as senescent leaves.

Stepwise multiple regression analysis revealed that generalized insect herbivores tend to feed on plants or plant parts low in furanocoumarin content and, correspondingly, low in nitrogen content. Parsnip specialists, notably *Depressaria pastinacella* (Lepidoptera: Oecophoridae), feed exclusively on umbels, plant parts rich in nitrogen and furanocoumarins; furanocoumarin number and content in fact account for over 60% of the variance in number of umbel feeders. These patterns conform with previous determinations of the toxicological properties of furanocoumarins. Nitrogen is known to affect growth rate, fecundity, longevity and survivorship of insect herbivores; by tolerating or detoxifying furanocoumarins, *D. pastinacella* can consume plant tissues containing significantly greater amounts of nitrogen than tissues consumed by generalist feeders. That the presence of *D. pastinacella* on individual plants is correlated with the number of furanocoumarins present is consistent with the hypothesis that parsnip specialists use angular furanocoumarins as host recognition cues.

Introduction

Qualitative and quantitative variation in the production of secondary substances is known to occur in natural plant populations: alkaloids (Alston 1967; Dolinger et al. 1973), cyanogenic glycosides (Jones 1967, 1977; Cooper- Driver and Swain 1977), glucosinolates (Rodman 1974) and terpenes (von Rudloff 1975; Irving and Adams 1973) have all been shown to demonstrate such variation. Since secondary substances can affect insect behavior and hence hostplant choice (e.g., Metcalf et al. 1980; Nielsen et al. 1977, 1979; Chapman 1974; Boscher 1977; Jermy and Szentesi 1978), variation in secondary chemistry among members of a plant population, irrespective of the selective factors producing the variation, affects susceptibility to insect attack.

Although phytochemical variability has been correlated with a number of environmental variables (Flück 1963), it is widely assumed that insect herbivory is an important selective force in determining furanocoumarin content and distribution within a single-species population of plants. McKey (1979) identified four factors thought to influence the distribution of "defense chemicals" (secondary substances that affect the distribution and abundance of insects) within the individual plant:

1. cost of herbivory to different plant parts - that is, the relative value of different tissues as reflected by their potential contribution to fitness (McKey 1974)
2. probability of discovery and successful attack in the absence of chemical defense - a function of such factors as physiology, density or size (Feeny 1976)
3. physiological constraints - e.g., avoidance of autotoxicity (Fowden and Lea 1979)
4. distribution of other chemical defenses in the same plant (Janzen 1973).

Although several investigators have examined patterns of insect herbivory in relation to secondary chemistry within a plant population (Dolinger et al. 1973; Moore 1978; Hare and Futyma 1978; Sturgeon 1979), the studies have been largely correlational and hence inconclusive. Since there is considerable experimental evidence that furanocoumarins affect the feeding behavior and physiological development of insects (Yajima et al. 1977; Berenbaum 1978; Gebreyesus 1980; Berenbaum 1980 and in preparation), I conducted a three-part experiment, designed:

1. to determine patterns of variation in furanocoumarin production within a single-species population of plants;
2. to investigate the physiological and environmental correlates of the observed chemical patterns; and
3. to examine the relationship between variation in chemistry and susceptibility to insect herbivory.

For this investigation, I chose a population of *Pastinaca sativa* L. (Umbelliferae), wild parsnip. *P. sativa* is a widespread weed that grows primarily in disturbed areas, forming identifiable populations circumscribed by the area of disturbance. Throughout its range, wild parsnip has a limited and thus experi-
### Table 1. Growth stages of *Pastinaca sativa*

<table>
<thead>
<tr>
<th>Stage</th>
<th>Characteristics</th>
<th>Time of year</th>
<th>Number of plants analyzed chemically</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Rosette; 3–4 leaves present; roots less than 10 cm in length</td>
<td>June</td>
<td>5</td>
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<tr>
<td>2.</td>
<td>Rosette; 4–5 leaves present; roots 10–20 cm in length</td>
<td>July</td>
<td>5</td>
</tr>
<tr>
<td>3.</td>
<td>Rosette; 5–6 leaves present; roots 20–50 cm in length</td>
<td>August–September</td>
<td>2</td>
</tr>
<tr>
<td>4.</td>
<td>Stem 10–20 cm in height</td>
<td>May</td>
<td>3</td>
</tr>
<tr>
<td>5.</td>
<td>Stem 40–100 cm in height</td>
<td>June</td>
<td>4</td>
</tr>
<tr>
<td>6.</td>
<td>Buds present in terminal umbel</td>
<td>late June</td>
<td>5</td>
</tr>
<tr>
<td>7.</td>
<td>Flowers present in terminal umbel</td>
<td>July</td>
<td>2</td>
</tr>
<tr>
<td>8.</td>
<td>Unripe seeds present in terminal umbel</td>
<td>mid-July</td>
<td>2</td>
</tr>
<tr>
<td>9.</td>
<td>Half-ripe seeds present in terminal umbel</td>
<td>late July–August</td>
<td>2</td>
</tr>
<tr>
<td>10.</td>
<td>Ripe seeds – plants senescent</td>
<td>late August–September</td>
<td>3</td>
</tr>
</tbody>
</table>

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**Materials and Methods**

The parsnip, *Pastinaca sativa*, is a biennial herb in the family Umbelliferae, one of about 14 species in the genus. Native to the Mediterranean region, the parsnip has long been cultivated for its edible white taproot (Schery 1972). The parsnip was introduced to North America in 1609 for the purpose of cultivation and has since escaped and become widely naturalized (Schery 1972; Nuttall 1818; Fernald 1950). At present, wild parsnip characteristically grows in waste places, roadsides, and similar disturbed areas, primarily in the eastern half of North America (Fernald 1950).

The parsnip population studied grows on a hillside on the campus of Cornell University in Ithaca, Tompkins County, New York. Parsnip is the dominant species throughout most of the summer in area oldfield habitats. Seedlings first appear in late April and early May. In its first year of growth, parsnip forms a rosette with a long overwintering taproot. Whether or not flowering occurs in the following season depends on the size of the taproot at the onset of winter (Thompson 1978); thus, parsnip is a facultative biennial. In the year of flowering, shoots arising from overwintered taproots in mid-April elongate and terminate in yellow umbellate inflorescences that open in June. From leaf axils, secondary or lateral umbels can appear and can in turn produce tertiary and quaternary umbels. Umbels mature in sequence, from primary to tertiary and quaternary umbels (Hendrix 1979). Seeds mature through July, ripen and dislodge in August, at which time plants that have set seed senesce and die.

Fifty plants in the population were numbered and marked with surveyors' flags; at weekly and then four-day intervals, a plant was selected with a random numbers table and classified into one of ten

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**Fig. 1.** Representative parsnip plant; insects observed during sampling were recorded on the appropriate plant part. a, primary (terminal umbel); b, secondary (lateral umbel); c, tertiary (auxiliary umbel); d, leaves. Additional leaves and umbels were drawn in so as to conform with the architecture of the individual plant.

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**Fig. 2.** Furanocoumarins in *Pastinaca sativa*

- **Linear furanocoumarins:**
  - a, imperatorin R8 = OCH2CH = C(CH3)2;
  - b, bergapten R5 = OCH3;
  - c, xanthotoxin R8 = OCH3;
  - d, isopimpinellin R5 = R8 = OCH3.

- **Angular furanocoumarins:**
  - a, angelicin R5 = R6 = H;
  - b, sphondin R6 = OCH3.

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**Fig. 3.** Nonphenolic lactone fraction of umbel extracts of *Pastinaca sativa*. On the left is the extract of a plant infested with *Depressaria pastinacella*; on the right is the extract of a plant without *D. pastinacella*. a, angelicin; b, bergapten; s, sphondin; i, imperatorin; x, xanthotoxin.