A Major Gene for Time of Flowering in Chickpea

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A major gene for the number of days from sowing to appearance of the first flower (time of flowering) was identified in a cross between an extrashort duration chickpea (*Cicer arietinum* L.) variety, ICCV 2, and a medium duration variety, JG 62. The F_2 population was advanced through the single-seed-descent method to develop random recombinant inbred lines (RILs). Time of flowering was recorded for the parents and 66 F_6 RILs from this cross that were grown in a Vertisol field in the post-rainy season of 1996–1997. Similarly the parents, F_1, and F_{10} RILs were evaluated in 1997–1998. The F_1 flowered along with JG 62. The time of flowering for the two sets of RILs showed bimodal distributions with nearly equal peaks. One peak corresponded with ICCV 2 and the other with JG 62. This suggests that a single gene controls the difference for the time of flowering between ICCV 2 and JG 62 and the allele carried by the latter parent is dominant. To our knowledge no gene has been identified for the time of flowering in chickpea. Therefore the allele carried by JG 62 is designated as *Efl-1* and that by ICCV 2 as *efl-1*. The proposed genotype for ICCV 2 *is efl-1 efl-1* and for JG 62 is *Efl-1 Efl-1.* The genotype *efl-1 efl-1* reduces the time of flowering at ICRISAT by nearly 3 weeks. The significance of this gene for breeding for early maturity and genome mapping has been discussed.

Chickpea (*Cicer arietinum* L.) is an important legume crop especially for rain-fed agriculture. Ninety percent of the world chickpea production is on conserved receding soil moisture. Therefore crop productivity is largely dependent on efficient utilization of available soil moisture. In peas (*Pisum sativum*), at least six genes for time of flowering influence maturity and crop yield through their effects on the onset of reproduction and the duration of the reproductive phase (Murfet and Reid 1985). A genome map of *Cicer* published recently shows about 40% synteny with the map of *Pisum* (Simon and Muehlbauer 1997). There are differences in time of flowering among the world chickpea germplasm accessions (Pundir et al. 1988). To our knowledge, so far no gene has been identified for the time of flowering in chickpea. A study was undertaken to investigate the inheritance of this trait in chickpea.

Materials and Methods

ICCV 2, an extrashort duration chickpea variety was crossed in 1993 with JG 62, a medium duration variety. ICCV 2 flowers in about 35 days and JG 62 in 55 days at ICRISAT Center Patancheru (latitude 17.6°N, altitude 550 m), Andhra Pradesh, India. The F_1 seed was planted in the summer season of 1993 to produce the F_2 generation. The F_2 seed from a single F_1 plant was advanced through the single-seed-descent method in a glasshouse with extended photoperiod to produce F_6 RILs in 1995–1996 and F_{10} RILs in 1996–1997.

The parents and 66 F_6 RILs were evaluated on conserved moisture in a deep Vertisol field during the post-rainy season of 1996–1997. For parents and each RIL, the plot size was one row 4 m long, placed 60 cm apart, with 20 cm between plants. These were sown in a randomized complete block design with two replications on 1 November 1996. The following year, parents, F_1, and 66 F_{10} RILs were planted in an incomplete block design with three replications on 3 November 1997. Recommended cultural and plant protection measures were undertaken at appropriate times.

Data on number of days to first flower (time of flowering) were recorded when the first fully open flower was noticed in a plot or on each single plant in the parental and F_1 generations. Standard statistical analyses were done to test for differences.

Results and Discussion

The time of flowering for parental, F_1, F_6, and F_{10} generations of the cross ICCV 2 × JG 62 was plotted. The two parents, ICCV 2 and JG 62, showed a difference of 18 days in 1996 (Figure 1) and 20 days in 1997 (Figure 2). The F_1 was not available in 1996, but it flowered in about the same number of days as JG 62 in 1997.

The distribution for time of flowering for the F_6 generation was bimodal. There is a clear break between the two peaks, one corresponding to ICCV 2 and the other to JG 62. The area under the two peaks is about equal. This strongly suggests that the difference for the time of flowering of ICCV 2 and JG 62 is controlled by a single locus. Since the F_1 flowered at about the same time as JG 62, the gene for delayed flowering is dominant to that for early flowering. To our knowledge a locus for time of flowering has not been named in chickpea. Therefore we propose that the single recessive gene for time of flowering be designated *efl-1.* Therefore the genotype for the parent ICCV 2 is *efl-1 efl-1* and that for JG 62 is *Efl-1 Efl-1.*

These results are supported by the seg-

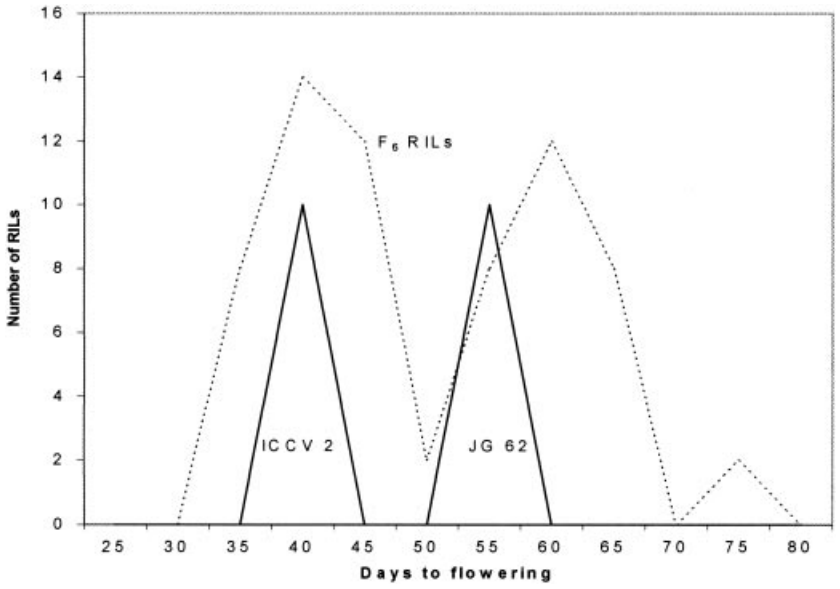

Figure 1. Distribution of time of flowering for parents and F_6 generation RILs of the chickpea cross ICCV 2 × JG 62 at ICRISAT Center, 1996–1997.

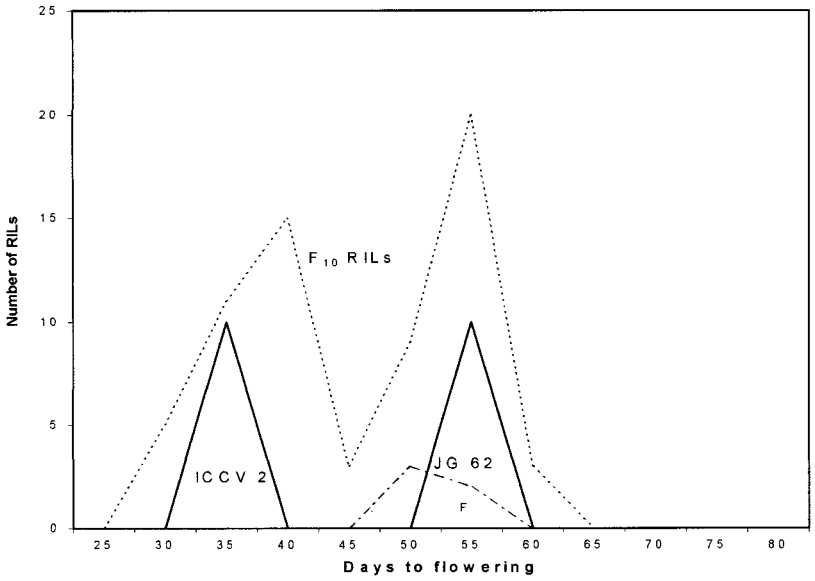

Figure 2. Distribution of time of flowering for parents, F_1, and F_{10} generation RILs of the chickpea cross ICCV 2 × JG 62 at ICRISAT Center, 1997–1998.

regation for this trait among the F_{10} RILs that also showed a bimodal distribution. As expected for the segregation of a single gene, the two peaks cover nearly equal areas.

Segregants were observed that flowered significantly earlier than ICCV 2 and later than JG 62. Although a major gene *efl-1* is operating for 18–20 days difference between ICCV 2 and JG 62, there are indications that other genes with relatively small effects are also operating in this cross. *Pisum* (*sativum*), a related genus, also has several genes for time of flowering (Murfet and Reid 1985). Parallel variation can be expected in chickpea as its genome shows about 40% synteny with that of pea (Simon and Muehlbauer 1997). Therefore several genes for this trait may also be operating in chickpea. Such an observation is also supported by the development of superearly genotypes ICCV 96029 and 96030 in crosses of ICCV 2 with other extrashort duration genotypes (Kumar and Rao 2000). Identification of a gene for time of flowering has much significance for early maturity. Genotypes carrying the *efl-1* allele in homozygous conditions escape end-of-season drought by nearly 3 weeks in receding soil moisture in environments represented by peninsular and central India, Myanmar, and Ethiopia. End-of-season drought is a major constraint to high productivity in such environments (Kumar et al. 1996). Cultivars carrying such alleles may also help extend chickpea adaptation to relatively shorter growing environments and facilitate their inclusion in new cropping patterns. ICCV 2 also possesses early growth vigor. Thus early flowering coupled with early growth vigor may help such varieties utilize the available soil moisture efficiently and produce relatively higher yields. This development may enhance and stabilize chickpea seed yields in rain-fed, short duration environments. This gene can be used for chickpea mapping studies, where much research is needed before a usable genetic map becomes available.

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Heritability Estimates for Octyl Acetate and Octyl Butyrate in the Mature Fruit of the Wild Parsnip

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The aliphatic esters octyl acetate and octyl butyrate occur as major components of essential oils in the vittae, or oil tubes, of the wild parsnip (*Pastinaca sativa*). We determined phenotypic variation and narrow-sense heritabilities of these octyl esters in wild parsnip fruits from 30 maternal families. The mean octyl acetate content was 1.56 μg/mg dry fruit (0.08–5.51 μg/mg dry fruit) and the mean octyl butyrate content was 4.28 μg/mg dry fruit (1.28–14.22 μg/mg dry fruit). Narrow-sense heritabilities for each ester's content were calculated by analysis of half-sib families (HS) and parent-offspring regression (OP). Heritabilities were 0.389 (HS) and 0.654 (OP) for octyl acetate and 0.670 (HS) and 0.626 (OP) for octyl butyrate. The amounts of the esters were phenotypically correlated with each other and with the linear furanocoumarins bergapten and xanthotoxin, phototoxic compounds that co-occur in the vittae with the esters. Ester amounts were not genetically correlated, indicating that these compounds could respond independently to selection pressures. These octyl esters may serve as carrier solvents that enhance penetration of these furanocoumarins into herbivore integuments and gut walls.

Despite the universality of aliphatic compounds in plants, specific compounds may be rare enough to be diagnostic for certain species. The aliphatic esters octyl acetate and octyl butyrate are compounds that are limited in taxonomic distribution among plant species as well as in anatomical distribution within the producing plant. An appreciable accumulation of octyl acetate or octyl butyrate is limited to a few related species within the Apiaceae. Both wild parsnip (*Pastinaca sativa*) and cow parsnip (*Heracleum sphondylium*) produce octyl esters as major components of their essential oils (Bicchi et al. 1990). The biosynthesis of the octyl esters is restricted to the developing oil tubes, or vittae, of reproductive tissues (Kubeczka and Stahl 1975, 1977). The appearance of the octyl esters in the reproductive tissues of wild parsnip follows a restricted and predictable ontogenetic pattern. No esters

are produced in the axillary meristems and only small amounts of octyl butyrate are produced in the buds. The content of both esters rapidly increases during the flowering stages to a maximum concentration and then tapers off slightly during the green fruit stage (Zangerl et al. 1997).

Considerable variation in octyl acetate and octyl butyrate content is also found both within and between populations of wild parsnip. Stahl and Kubeczka (1979) recognized the presence or absence of octyl and decyl aliphatic acetates (primarily octyl acetate) as one of two characteristics distinguishing four basic chemotypes of European parsnips. The loss of aliphatic acetate production was accompanied by an increase in octyl butyrate production. Plants lacking the aliphatic acetates had much higher levels of octyl butyrate than those with detectable acetate levels. All of the populations deficient in octyl acetate were cultivated varieties, whereas all wild populations had appreciable levels of octyl acetate and lower concentrations of octyl butyrate (Stahl and Kubeczka 1979). Whether this variation is under genetic control was not determined.

If phenotypic variation does exist in octyl acetate and octyl butyrate content, then it is of interest to determine what proportion of the variation is under genetic control and therefore available for selection. We measured the octyl acetate and octyl butyrate contents of mature fruits from different wild parsnip plants collected from a single location to obtain estimates of within-population phenotypic variation. Quantitative genetic estimates were then used to determine the amount of phenotypic variation in fruit octyl ester content attributable to additive genetic variation.

Interactions between wild parsnip and its herbivores may also be influenced by the co-occurrence of the octyl esters with furanocoumarins in the vittae. Furanocoumarins are phototoxic defense compounds that provide resistance against some parsnip herbivores, including the oligophagous parsnip webworm [*Depressaria pastinacella* (Lepidoptera: Oecophoridae)] (Berenbaum et al. 1986; Zangerl and Berenbaum 1993). Aliphatic esters have previously been assigned roles as enhancers of lipophilic toxins because they physically carry the toxin through a herbivore's integument (see Prestwich 1976). Because furanocoumarins are lipophilic compounds, the octyl esters could conceivably serve as carrier solvents to facilitate transport across a caterpillar's integument or gut wall. Therefore the furanocoumarin content of the mature fruits was also measured in order to evaluate quantitatively the phenotypic associations of octyl acetate, octyl butyrate, and furanocoumarins in wild parsnip fruits.

Materials and Methods

We determined the phenotypic variation of octyl acetate, octyl butyrate, and furanocoumarins in mature fruits by measuring the contents of seeds collected from different plants. Because the essential oil components are synthesized and stored in maternally derived tissue of the fruit, the oil constituent content measured for a fruit presumably reflects maternal genetics and the environment, and not the offspring's contribution (Zangerl et al. 1989). Seeds were collected from the primary umbel of 32 plants from a population at Phillips Tract, a university-owned natural area approximately 6 km northeast of Urbana, Illinois.

After setting seed aside to produce offspring plants for heritability studies, sufficient numbers of seeds remained for characterization of 31 plants. For each replicate, three seeds were weighed, cut in half across the vittae, and extracted in 2.0 ml of hexane augmented with a 0.02% hexadecane internal standard. Half of the supernatant was removed for gas chromatography (GC) analysis of the octyl ester content. The remaining solvent and seed material was dried and extracted with 1.5 ml ethyl acetate. One milliliter of the ethyl acetate layer was removed for high-pressure liquid chromatography (HPLC) analysis of furanocoumarins.

Estimates of heritability for octyl acetate and octyl butyrate contents were made by comparing the octyl ester content of mature seeds among the progeny of the maternal plants. Because the paternity of the seeds was not controlled in these collections, offspring from any one plant likely consisted of both half sibs and full sibs (Berenbaum et al. 1986). Because it is monocarpic, wild parsnip undergoes vegetative growth during its first summer and reproduces only once, usually during its second season. Wild parsnip plants require exposure to near-freezing temperatures (vernalization) before they can reproduce successfully (Baskin and Baskin 1979). Seeds from the maternal plants were sown in pots in a greenhouse during fall 1993. Resulting plants were transferred to a heated cold frame at Phillips Tract during February 1994. Later that spring the plants were transferred to an adjacent plot. The progeny plants were allowed to grow, flower, and produce seeds. The mature seeds of the progeny plants were then harvested from the primary umbel to characterize the offspring phenotype.

All chemical analyses were performed on fertilized seeds to avoid the chemical variation noted between fertilized and parthenocarpic seeds (Zangerl et al. 1991). Two offspring plants that did not produce sufficient numbers of fertilized seeds were excluded from the heritability analyses and thus heritability estimates were based on progeny of 30 plants. One set of five fruits was analyzed from each offspring. For each sample, the fruits were weighed, cut in half, and extracted with a 1.5 ml solution of hexane augmented with a 0.1% hexadecane internal standard. Extracts were analyzed for octyl acetate and octyl butyrate content by gas chromatography (Hewlett-Packard 5890 gas chromatograph). A 3 μl sample was autoinjected by a Hewlett-Packard 7673 automatic sampler and separated on an Alltech SE-30 column (30 mm × 0.32 mm ID). Standards for both esters were analyzed as well to provide calibration factors. Integrated sample peaks were quantified and amounts were adjusted for variation in injection volume by calibrating to variation in the amount of internal standard. The calculated amount of each ester was divided by seed mass to obtain octyl ester content values.

The furanocoumarin content of maternal plants was analyzed on a Waters high-pressure liquid chromatograph with a Model 440 absorbance (254 nm) detector. Samples were autoinjected and separated on an Alltech Adsorbosphere Silica 5 μm column (150 mm × 4.6 mm) with a 55:42:3 cyclohexane:isopropyl ether:butanol solvent mixture. The furanocoumarin content of the mature fruits was quantified by comparison of the integrated peaks against calibrated standards of bergapten (Sigma Chemical Company, St. Louis, MO), imperatorin (SERVA, Heidelberg, Germany), sphondin (Dr. William Wuff, University of Chicago), and xanthotoxin (Sigma Chemical Company).

To obtain a normal distribution of octyl acetate, octyl butyrate, and furanocoumarin contents, the data were transformed as $\log(C_o + 1)$, where C_o is the allelochemical seed content. All analyses, save descriptive statistics, were performed on transformed data. The octyl ester and furanocoumarin contents of mature fruits in the maternal plants were

Table 1. Chemical content (μg/mg dry fruit mass) of octyl esters and furanocoumarins in mature wild parsnip fruits (n = 31)

Characteristic	Mean	Standard error	Range
Octyl acetate	1.56	0.21	0.08–5.51
Octyl butyrate	4.28	0.35	1.28–14.22
Bergapten	1.85	0.13	0.80–3.92
Imperatorin	3.72	0.31	1.22–8.79
Sphondin	0.31	0.09	0.00–2.81
Xanthotoxin	4.02	0.34	1.35–11.08

Table 2. Estimates of phenotypic correlations between allelochemicals in mature wild parsnip fruits (n = 31)

	OA	OB	BER	IMP	SPH	XAN
Octyl acetate (OA)	1.000	0.432[b]	0.309[a]	0.451[b]	0.031	0.331[b]
Octyl butyrate (OB)		1.000	0.390[b]	0.482[b]	0.278[a]	0.366[b]
Bergapten (BER)			1.000	0.813[b]	0.268[a]	0.887[b]
Imperatorin (IMP)				1.000	0.311[a]	0.778[b]
Sphondin (SPH)					1.000	0.252[a]
Xanthotoxin (XAN)						1.000

[a] $P < .05$.

[b] $P < .01$.

examined for correlation by r values (SAS Institute 1990).

Estimates of narrow-sense heritability (h^2) were calculated for octyl acetate and octyl butyrate both by analysis of half-sib families and parent-offspring regression. Estimates of narrow-sense heritability were calculated by analysis of half-sib families as

$$h^2 = \frac{4\sigma_a^{\,2}}{\sigma_p^{\,2}}$$

where o_a^2, the additive genetic variance component, and o_p^2, the total phenotypic variance, were obtained from one-way analysis of variance (Falconer 1981). The standard error of the heritability estimate was calculated as

$$\mathrm{SE}(h^2) = 4[[2(1 - t)^2(1 + (k + 1)t)^2] \div [k(k - 1)(f - 1)]]^{1/2},$$

where $t = \frac{1}{4}h^2$, k is the family size, and f is number of families (Lynch and Walsh 1998). Due to variation in the family size, for purposes of estimating variance components, family size was calculated as

$$k = \left(N^2 - \sum_{i=1}^{f} n_i^{\,2}\right) \Big/ (N(f - 1)),$$

where N is the total number of individuals, n_i is the number of individuals in the fth family, and f is the number of families (Falconer 1981). To the extent that full as well as half sibs were included in the analysis, the heritability estimates may include dominance effects in addition to maternal effects.

Estimates of narrow-sense heritability were also calculated by parent-offspring regression as

$$h^2 = 2b_{\mathrm{op}},$$

where b_{op} is the regression coefficient between maternal parent and offspring. The standard error of the heritability estimate was calculated as twice the standard error of the parent-offspring regression (Falconer 1981; SPSS 1997).

Additive genetic correlation between octyl acetate and octyl butyrate contents was estimated by parent-offspring analysis as

$$r_a = \frac{\mathrm{cov}(z1x,\ z2y) + \mathrm{cov}(z2x,\ z1y)}{2\sqrt{\mathrm{cov}(z1x,\ z1y) \cdot \mathrm{cov}(z2x,\ z2y)}},$$

where $\mathrm{cov}(z_{1x}, z_{2y})$ is the covariance between maternal octyl acetate and offspring octyl butyrate, $\mathrm{cov}(z_{2x}, z_{1y})$ is the covariance between maternal octyl butyrate and offspring octyl acetate, $\mathrm{cov}(z_{2x}, z_{2y})$ is the covariance between maternal octyl acetate and offspring octyl acetate, and $\mathrm{cov}(z_{1x}, z_{1y})$ is the covariance between maternal octyl butyrate and offspring octyl butyrate (Lynch and Walsh 1998).

Results

Among the 31 maternal plants examined, the mean octyl acetate content was 1.56 μg/mg dry fruit (range 0.08–5.51 μg/mg dry fruit) and the mean octyl butyrate content was 4.28 μg/mg dry fruit (range 1.28–14.22 μg/mg dry fruit) (Table 1). The octyl butyrate content was more variable across maternal plants (as indicated by standard error) than the octyl acetate content. All significant phenotypic correlations between mature fruit characteristics were positive (Table 2). Both octyl acetate and octyl butyrate contents are significantly correlated with the linear furanocoumarins bergapten (r = 0.309 and 0.390, respectively, P = .0144 and .0017), imperatorin (r = 0.452 and 0.482, respectively, P = .0002 and $P < .0001$), and xanthotoxin (r = 0.331 and 0.366, respectively, P = .0086 and .0035). Octyl butyrate was significantly correlated with the angular furanocoumarin sphondin (r = 0.278, P = .0288), while octyl acetate was not significantly correlated with sphondin (r = 0.031, P = .8106). The octyl acetate and octyl butyrate contents of mature fruit displayed a significant phenotypic correlation (r = 0.432, P = .0005).

In contrast, the genetic correlation between octyl acetate and octyl butyrate contents was not significant (r_a = 0.108, regressions between traits were not significant, $P > .05$). The narrow-sense heritability estimates of octyl acetate were 0.389 by analysis of half-sib families and 0.654 by parent-offspring regression (Table 3), while the narrow-sense heritability estimates of octyl butyrate were 0.670 by analysis of half-sib families and 0.626 by parent-offspring regression (Table 4).

Discussion

Narrow-sense heritability estimates provide a measure of the amount of pheno-

Table 3. Narrow-sense heritabilities for octyl acetate content of mature fruits estimated from 30 maternal half-sib families of wild parsnip

Octyl acetate: Source	df	MS	F	P	(h^2 ± SE)
From analysis of half-sib families:					
Family	29	2.682	1.75	0.014	0.389 ± 0.249
Within family	194	10.234			
Total	223				
o_a^2 = 0.00537					
o_p^2 = 0.05537					
From regression of offspring on maternal parent:					
Regression	1	0.183	26.5	<.001	
Residual	28	0.007			
Independent variable:					
Regression coefficient		SE	(h^2 ± SE)		
0.327		0.064	0.654 ± 0.128		

Narrow-sense heritabilities and their standard errors were estimated according to Falconer (1981) and Lynch and Walsh (1998).

Table 4. Narrow-sense heritabilities for octyl butyrate content of mature fruits estimated from 30 maternal half-sib families of wild parsnip

Octyl butyrate: Source	df	MS	F	P	($h^2 \pm$ SE)
From analysis of half-sib families:					
Family	29	2.814	2.57	.001	0.670 ± 0.310
Within family	194	7.322			
Total	223				
$o_a^2 = 0.00805$					
$o_p^2 = 0.05805$					
From regression of offspring on maternal parent:					
Regression	1	0.137	13.00	<.001	
Residual	28	0.010			
Independent variable:					
Regression coefficient		SE	($h^2 \pm$ SE)		
0.313		0.087	0.626 ± 0.174		

Narrow-sense heritabilities and their standard errors were estimated according to Falconer (1981) and Lynch and Walsh (1998).

typic variation in a trait attributable to additive genetic effects (Berenbaum and Zangerl 1992). The narrow-sense heritability estimates of octyl acetate and octyl butyrate in mature fruits of wild parsnip indicate that a substantial amount of the variation observed for both compounds is under genetic control. The amounts of both compounds could respond to selection, such as might be exerted by a fruit-consuming herbivore such as the parsnip webworm. Other chemical and morphological features of wild parsnip seeds display genetic variation; significant heritabilities have previously been found for seed contents of the linear furanocoumarins, xanthotoxin and bergapten, and the angular furanocoumarin, sphondin, and for vittae area, vittae number, and the length of the seed (Zangerl et al. 1989).

Octyl acetate and octyl butyrate do not share a common genetic regulation of their production, as is evident by the lack of a significant correlation. The two are positively correlated phenotypically. This correlation appears to be due entirely to environmental effects, as there is no genetic correlation, in spite of their origin from a common biosynthetic pathway (Mann 1987). Presumably, the endpoint biosynthetic reactions responsible for the differences between octyl acetate and octyl butyrate are under separate genetic control. Such differences in genetic regulation would allow selection to operate independently on each octyl ester.

The octyl esters, as constituents of the essential oils of parsnip fruit, may be strongly correlated with linear furanocoumarins due to a functional rather than biosynthetic relationship. The octyl esters may serve in part as solvents for the furanocoumarins in the vittae. The function of octyl esters as solubility agents has been documented previously in a variety of insect defensive secretions. Octyl esters are used by some hemipterans as minor components of defensive or alarm sprays. The octyl esters do not display marked toxicity by themselves, nor do they show a specific synergism with their co-occurring toxins. Instead, the octyl esters of these hemipterans can carry and deliver more potent toxins to an enemy's target sites. Octyl acetate is a minor component of some coreid defensive secretions, while 2-octenyl acetate is a minor component of pentatomid defensive secretions (Prestwich 1976). The carabid *Helluomorphoides clairvillei* (Coleoptera) uses octyl acetate as an aliphatic constituent of its formic acid spray. The octyl acetate and other aliphatic spray components are thought to promote penetration of the formic acid into an enemy's integument (Attygalle et al. 1992).

Although a role as solubilizing agents has never before been suggested for octyl esters in plants, the results of this study are entirely consistent with such a function. These esters are anatomically restricted to vittae in fruits of parsnip, as are furanocoumarins, and their production is significantly correlated with furanocoumarin production. In wild parsnip tissues, the octyl esters may enhance the transfer of furanocoumarins onto herbivore surfaces after rupture of the oil tubes. Whether they themselves act as defensive compounds has not yet been demonstrated.

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