Cuticular Lipids from Wild and Cultivated Peanuts and the Relative Resistance of These Peanut Species to Fall Armyworm and Thrips

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Cuticular lipids were extracted from blooms and foliage of the peanut cultivar *Arachis hypogaea* L. (Southern Runner) and identified by gas chromatography–mass spectrometry. The major components of the bloom surface lipids were *n*-alkanes, aldehydes, and fatty acids, while fatty alcohols, fatty acids, and *n*-alkanes were the major components of the foliage lipids. Cuticular lipids of the foliage from five wild peanut species, *A. glandulifera*, *A. batizocoi*, *A. ipaensis*, *A. chacoense*, and *A. paraguariensis* differed in composition. Each wild peanut species was more resistant to fall armyworm, *Spodoptera frugiperda*, than the cultivar was, and each suffered less thrips damage than the cultivar did.

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith), is a major defoliating pest of peanut in the southeastern United States (Smith and Barfield, 1982; Todd et al., 1991). Tobacco thrips, *Frankliniella fusca* (Hinds), and western flower thrips, *F. occidentalis* Pergrande, cause damage to blooms and branch terminal buds of peanut and are also important vector species of the tomato spotted wilt virus (TSWV), which is a serious threat to peanut in the southeastern United States (Sakimura, 1962, 1963; Smith and Barfield, 1982; Hagan et al., 1990; Culbreath et al., 1991; Chamberlin et al., 1992). The development of sources of resistance to fall armyworm and thrips in peanut is an economically and environmentally acceptable method to control these important insect pests. Identification of the chemical bases of insect resistance in peanut will allow for a more efficient breeding program.

The plant cuticle, with which an insect pest first comes in contact, plays an important role in plant/insect interactions. Many herbivorous insects seem to select their host plants on the basis of the chemical characteristics of the plant surface (Woodhead and Chapman, 1986; Chapman and Bernays, 1989; Espelie et al., 1991). Certain plant cuticular lipids affect insect feeding behavior and contribute to insect resistance (Bernays et al., 1976, 1985; Chapman, 1977; Eigenbrode et al., 1991; Yang et al., 1993). The addition of cuticular lipids to the diet of lepidopteran insects inhibits larval growth, and specific or genotypic variation in these lipids may also play a role in host plant resistance (Quisenberry et al., 1988; Yang et al., 1991). In the present paper, we characterized the cuticular lipids from the cultivated peanut, *Arachis hypogaea* L. (Southern Runner), and from five wild peanut (*Arachis*) species. We investigated their relative resistance to feeding by fall armyworm larvae, and we compared the damage done by thrips in the field.

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MATERIALS AND METHODS

Peanut Plants. The peanut cultivar Southern Runner, *A. hypogaea* L. (PI 506419), and five wild peanut species, *A. glandulifera* Stalker (PI 468342), *A. batizocoi* Krap. et Greg. (PI 468329), *A. ipaensis* Krap. et Greg. *nom. nud.* (PI 468322), *A. chacoense* Krap. et Greg. *nom. nud.* (PI 276235), and *A. paraguariensis* Chod. et Hassl. (PI 262842), were planted in field nursery plots in Tifton and Attapulgus, GA, in April 1991. Peanut plants were grown using standard agronomic practices with irrigation as needed. No insecticide applications were made prior to, during, or after the period when peanut foliage was collected for the cuticular lipid analysis and for the fall armyworm laboratory bioassays.

Cuticular Lipid Isolation. Fresh and clean branches of peanut plants were excised at the base, and peanut blooms were hand-picked from 4-month-old field-grown plants. Plant materials were placed into plastic bags in a cooler and transported immediately to the laboratory. Branch terminal buds and base foliage (13 cm below the terminal buds) were separated for each peanut species. Samples of foliage (5 g) and blooms (1 g) were immersed in 100–150 mL of redistilled chloroform for 1 min at room temperature to remove the surface lipids. A brief extraction period was utilized to remove primarily cuticular lipids (Espelie et al., 1980; Misra and Ghosh, 1991). Chloroform extracts were concentrated to a volume of approximately 2 mL on a rotary evaporator at 40 °C and then stored at −20 °C.

Chemical Analysis. Aliquots (equivalent to the extract from 1 g of fresh foliage or 0.5 g of blooms) were dried under a stream of N_2 and then derivatized with *N,O*-bis(trimethylsilyl)acetamide at 110 °C for 10 min. Excess derivatizing reagent was removed under N_2, and the derivatized extract was dissolved in 0.1 mL of redistilled hexane. Aliquots (1%) were analyzed by combined gas chromatography–mass spectrometry (Hewlett-Packard 5890A/5970). The capillary column (25-m cross-linked methyl silicone) with helium as the carrier gas was held at 55 °C for 3 min, and then the oven temperature was raised to 305 °C at a rate of 15 °C/min. Mass spectra were recorded at 70 eV at 0.8-s intervals. Quantitation was based upon total ion chromatogram integrations which were corrected for response factors by utilizing a standard for each class of cuticular lipid component (Mattheis et al., 1991; Yang et al., 1992).

Fall Armyworm Bioassay. Fall armyworm larvae were obtained from laboratory colonies maintained on artificial diet at the Coastal Plain Experiment Station in Tifton, GA. Bioassays were initiated by placing 25 neonate larvae into individual, 9 cm diameter, plastic Petri dishes containing the terminal buds from mature field-grown plants of the six tested peanut species. The Petri dishes were lined with moistened filter paper to maintain

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Table I. Cuticular Lipid Composition (Percent) of Blooms and Branch Foliage of Cultivated and Wild *Arachis* Species

		A. hypogaea			branch terminal buds of wild *Arachis*				
peak[a]	component	BL[b]	BTB[c]	BBL[d]	*glandulifera*	*batizocoi*	*ipaensis*	*chacoense*	*paraguariensis*
16.31	tetradecanoic acid	2.5	1.0	1.7	13.0	4.9	1.4	2.5	0.5
16.97	*p*-coumaric acid		2.4				7.3	2.3	D[e]
17.04	pentadecanoic acid	1.1	1.8	1.7	2.7	2.4	1.5	2.1	0.6
17.58	hexadecenoic acid	1.4	0.9	1.6	4.7	4.8	2.5	2.6	1.2
17.73	hexadecanoic acid	10.5	9.9	9.0	15.9	13.5	12.2	12.1	4.4
17.98	ferulic acid		3.2	1.0			1.7	5.7	
18.06	heptadecyl acetate								1.6
18.32	octadecenol[f]								3.9
18.38	heptadecanoic acid[f]	1.0	0.4	1.2	1.3	1.1	1.4	1.6	1.1
18.51	octadecanol					1.0		1.5	4.9
18.57	octadecenyl acetate								13.3
18.72	octadecyl acetate								5.6
18.83	octadecadienoic acid[f]	4.9	14.0	11.1	1.9	3.0	17.6	4.4	3.2
18.89	octadecenoic acid[f]	4.9	6.5	1.7	5.7	3.0	8.0	8.1	2.9
19.01	octadecanoic acid	4.8	3.2	2.4	5.7	1.8	4.1	5.5	3.4
19.19	nonadecenyl acetate								1.4
19.41	*n*-tricosane	4.9	2.4	1.8	3.1	3.5	5.5	6.9	2.4
19.71	eicosanol								1.9
19.96	eicosyl acetate								2.8
20.01	*n*-tetracosane	3.4	1.5	1.7	2.9	6.1	2.9	8.1	
20.21	eicosanoic acid		0.7	0.4			1.1	1.5	0.8
20.65	*n*-pentacosane	6.0	3.0	3.5	4.2	5.6	3.9	5.3	3.9
20.95	docosanol		0.2	0.7	2.8	D		1.0	1.1
21.30	*n*-hexacosane	1.8	0.5	1.8	1.9	4.7	D	1.8	
21.46	tetracosanal	1.7							
21.53	docosanoic acid		0.5	0.4		D		1.3	0.5
22.08	*n*-heptacosane	13.6	2.2	3.2	4.1	15.5	2.0	3.2	2.0
22.41	tetracosanol		D	D	0.5	1.5	D		0.3
22.87	*n*-octacosane	1.5	1.1	3.0	1.4	1.9	D	D	0.9
23.11	hexacosanal	3.6							
23.19	tetracosanoic acid		0.5	0.6				1.0	1.5
23.89	*n*-nonacosane	6.8	4.6	7.6	7.9	3.7	2.1	2.4	4.3
24.29	hexacosanol			D	1.2	0.9		D	0.3
25.26	octacosanal	1.4				0.8			
25.30	hexacosanoic acid		D	0.5				0.5	0.8
26.24	*n*-hentriacontane	10.5	3.8	4.3	3.3	2.1	1.2	1.2	4.2
26.82	octacosanol		D	D	1.7	3.7	D	0.3	0.8
28.28	triacontanal		0.8	1.6			1.2		D
28.32	octacosanoic acid			D				0.5	2.0
29.64	*n*-tritriacontane	8.6	3.5	2.7	D	4.5	2.5	2.2	5.2
30.60	triacontanol		12.2	15.4	8.6	3.9	10.8	7.3	8.0
32.00	β-amyrin		4.8	2.1		D	D		
32.66	dotriacontanal								3.2
32.78	α-amyrin		11.0	10.1		D	3.1		D
35.80	dotriacontanol		2.2	3.5	0.9	1.5	1.6	1.5	3.2

[a] Retention time (minutes). Components are listed only if they were identified by mass spectra. [b] Blooms. [c] Branch terminal buds. [d] Branch base leaves. [e] Detectable, but less than 0.1%. [f] Estimated by selected ion chromatography.

Table II. Composition (Percent) by Class of Cuticular Lipid Component of Blooms and Branch Foliage from Cultivated and Wild *Arachis* Species

	A. hypogaea			branch terminal buds of wild *Arachis*				
class of component	BL[a]	BTB[b]	BBL[c]	*glandulifera*	*batizocoi*	*ipaensis*	*chacoense*	*paraguariensis*
n-alkanes (C_{23}–C_{33})	57.1	22.6	29.6	28.8	47.6	20.1	31.1	22.9
primary alcohols (C_{18}–C_{32})		14.6	19.6	15.7	12.5	12.4	11.6	24.4
aldehydes (C_{18}–C_{32})	6.7	0.8	1.6		0.8	1.2		3.2
fatty acids (C_{14}–C_{28})	31.1	39.4	32.3	50.9	34.5	49.8	43.7	22.9
alcohol acetates (C_{17}–C_{20})								24.7
phenolic acids		5.6	1.0			9.0	8.0	D[d]
triterpenols		15.8	12.2		D	3.1		D

[a] Blooms. [b] Branch terminal buds. [c] Branch base leaves. [d] Detectable, but less than 0.1%.

high moisture. Foliage was replaced at 48-h intervals. There were four replicates for each treatment. Petri dishes containing fall armyworm larvae and peanut foliage were held at 25 °C and 70% relative humidity with a 14:10 (L/D) photoperiod in an incubator. Percent larval mortality after 8 days, days to larval mortality, pupal weight, number of individuals that survived to adulthood, number of eggs laid by these adults, and number of these eggs that hatched were recorded.

Thrips Damage and Distribution. Field plots of the six peanut species were visually rated for thrips damage using a scale of 1–5, with 1 being the score for plants with no damage, in Tifton and Attapulgus, GA, in September 1991. All observations were made as a completely random design with 10 replicates for each peanut species. Twenty terminal buds and blooms were randomly selected from each wild peanut species in the field in Tifton and Attapulgus, GA, in July 1991. The terminal buds and blooms were placed in 70% alcohol and taken to the laboratory for thrips identification. Numbers of adult *Frankliniella* species *fusca*, *occidentalis*, *tritici*, and *bispinosa* were recorded for each peanut sample. The total number of thrips immatures were counted, but these insects were not identified to species due to a lack of adequate keys. Bioassay data were subjected to an analysis of variance (SAS Institute,

Table III. Effect on Fall Armyworm of Feeding on Branch Terminal Foliage of Cultivated and Wild *Arachis* Species[a]

peanut species	larval mortality after 8 days, %	days to larval mortality	pupal weight, mg	total no. of adults[b]	eggs[b] laid	eggs[b] hatched
A. hypogaea	17b	12.6a	180.1a	8	468	271
A. glandulifera	80a	7.9b		0	0	0
A. batizocoi	84a	7.4b	128.0a	3	0	0
A. ipaensis	79a	8.1b	151.5a	2	0	0
A. chacoense	91a	5.8b		0	0	0
A. paraguariensis	80a	7.6b	161.3a	1	0	0

[a] Means followed by the same letter in a column were not significantly different at $P > 0.05$ level (Waller and Duncan, 1969). [b] These numbers were not kept separately as replications and were not analyzed statistically.

1985), and means were separated by Waller–Duncan k-ratio t test (k ratio = 100, $P \leq 0.05$; Waller and Duncan, 1969).

RESULTS

The cuticular lipids from the blooms, branch terminal buds, and branch base leaves of the peanut cultivar, *A. hypogaea* (Southern Runner), were identified by combined gas chromatography–mass spectrometry. The major components of the surface lipids of the blooms were primarily n-alkanes, free fatty acids, and aldehydes (Table I). The composition of the cuticular lipids of the foliage of *A. hypogaea* was different from that of the blooms. The foliage lipids contained a series of fatty alcohols dominated by 1-triacontanol and lesser amounts of n-alkanes and aldehydes than did the blooms. The branch terminal buds and the branch base leaves of *A. hypogaea* had very similar cuticular lipid compositions, although the branch terminal buds had a higher proportion of phenolic acids than did the branch base leaves (Table II).

The cuticular lipids from the branch terminal buds of five wild peanut species, *A. glandulifera*, *A. batizocoi*, *A. ipaensis*, *A. chacoense*, and *A. paraguariensis*, were also identified by combined gas chromatography–mass spectrometry (Table I). n-Alkanes were major components of the cuticular lipids of the branch terminal buds from all six peanut species. The proportion of alkanes ranged from 20% of the total surface lipids in *A. ipaensis* to 48% in *A. batizocoi* (Table II). There was a great deal of variation in the chain lengths of the dominant alkanes for the six species. n-Nonacosane was the major alkane of the cuticular lipids of *A. hypogaea* and *A. glandulifera*, while n-heptacosane was the most prevalent alkane in the surface lipids of *A. batizocoi*. n-Tricosane was the major alkane in the cuticular lipid fraction of *A. ipaensis* and *A. chacoense*, but n-tritriacontane was the dominant hydrocarbon in the lipid fraction of *A. paraguariensis* (Table I).

Free fatty acids were also major components of the branch terminal bud cuticular lipids in each peanut species. The proportion of fatty acids ranged from 23% of the total lipids in *A. paraguariensis* to 51% in *A. glandulifera* (Table II). Hexadecanoic acid and octadecadienoic acid were the most prevalent components in this class of cuticular lipids (Table I). Primary alcohols comprised between 12% (*A. ipaensis* and *A. chacoense*) and 24% (*A. paraguariensis*) of the branch terminal bud cuticular lipids. The dominant primary fatty alcohol was triacontanol for the surface lipids of all six peanut species (Table I).

The cuticular lipid composition of the branch terminal buds of *A. paraguariensis* was distinct from that of the other peanut species. Several components, including heptadecyl, octadecenyl, octadecyl, nonadecenyl, and eicosyl acetates, were only found in the cuticular lipids of *A. paraguariensis* (Table I). Aldehydes comprised a higher percentage of the cuticular lipids of this species than they did for the lipids from the branch terminal buds of the other peanut species (Table II).

Table IV. Ratings of Damage to Cultivated and Wild *Arachis* Species Caused by *Frankliniiella* Species in the Field

peanut species	ratings[a] Tifton, GA	ratings[a] Attapulgus, GA
A. hypogaea	4.0a	4.0a
A. glandulifera	1.5c	1.0b
A. batizocoi	2.0b	1.3b
A. ipaensis	2.0b	1.0b
A. chacoense	1.0d	1.0b
A. paraguariensis	1.0d	1.0b

[a] Visual ratings for thrips damage on peanuts on a scale of 1–5 with 1 being no damage. Means followed by the same letter in a column were not significantly different at $P > 0.05$ level (Waller and Duncan, 1969).

p-Coumaric acid and ferulic acid were present in the cuticular lipids of branch terminal buds of *A. hypogaea* (2.4% and 3.2%, respectively), *A. ipaensis* (7.3% and 1.7%), and *A. chacoense* (2.3% and 5.7%) (Table I). The triterpenoids, β-amyrin and α-amyrin, comprised 16% of the surface lipids of the *A. hypogaea* branch terminal buds, but these compounds were present in much lower amounts (0–3%) in the cuticular lipids of the wild peanut species (Table II).

In feeding bioassays the five wild peanut species, *A. glandulifera*, *A. batizocoi*, *A. ipaensis*, *A. chacoense*, and *A. paraguariensis*, exhibited significantly greater resistance to the fall armyworm than did the cultivar Southern Runner, *A. hypogaea* (Table III). After 8 days, the fall armyworm larvae which were reared on the branch terminal buds of the five wild peanut species had 79–91% mortality compared to 17% mortality for larvae reared on foliage of the cultivated peanut. The average time to larval mortality ranged from 5.8 to 8.1 days when fall armyworm larvae were reared on the wild peanut species. However, when larvae were reared on the peanut cultivar, the average time to mortality was 12.6 days. None of the larvae feeding on either *A. glandulifera* or *A. chacoense* foliage survived through the pupal stage. There were no eggs laid by the fall armyworm adults that developed from larvae reared on the branch terminal buds of the wild peanut species.

The visual ratings of the damage caused by thrips (*Frankliniella* spp.) on the six peanut species in the field are listed in Table IV. The cultivar, *A. hypogaea*, suffered significantly ($P < 0.05$) more severe thrips damage than the five wild peanut species did in both Tifton and Attapulgus, GA. The distribution of *Frankliniella* species on the five wild *Arachis* species in the field is given in Table V. There were significantly more *F. fusca* adults found on the branch terminal buds of *A. ipaensis* than on *A. glandulifera*, *A. chacoense*, and *A. paraguariensis* grown in Tifton, GA. The blooms of *A. ipaensis* had the highest level of *F. fusca* adult infestation in both Tifton and Attapulgus, GA. There were more *F. fusca* adults on

Table V. Distribution of *Frankliniella* Species on Wild *Arachis* Species in the Field[a]

peanut species	terminal buds		blooms		
	F. fusca adults	total immatures	*F. fusca* adults	*F.* species adults[b]	total immatures
			Tifton, GA; July 23, 1991		
A. glandulifera	0.0c	0.5a	8.8a	0.8a	1.3a
A. batizocoi	1.3ab	1.3a	8.0a	0.3a	2.3a
A. ipaensis	2.0a	0.5a	15.3a	1.0a	0.5a
A. chacoense	0.8bc	1.5a	7.8a	1.8a	2.3a
A. paraguariensis	0.0c	0.5a	4.0a	0.8a	0.5a
			Attapulgus, GA; July 23, 1991		
A. glandulifera	1.5a	0.3a	18.8b	0.0a	1.3a
A. batizocoi	1.8a	0.8a	37.5ab	0.0a	2.5a
A. ipensis	1.8a	1.5a	43.8a	0.5a	1.3a
A. chacoense	3.0a	1.3a	26.8ab	0.8a	0.0a
A. paraguariensis	0.3a	1.5a	21.0b	0.0a	0.8a

[a] Mean number of *Frankliniella* spp. per 20 terminals or blooms. Means followoed by the same letter in a column were not significantly different at $P > 0.05$ level (Waller and Duncan, 1969). [b] Sum of *F. occidentalis*, *F. tritici*, and *F. bispinosa*.

the blooms than on the branch terminal buds for each wild peanut species in both Tifton and Attapulgus, GA.

DISCUSSION

Although the cuticular lipids of *A. hypogaea* foliage had previously been examined by thin-layer chromatography (Rao et al., 1981), the compositions reported here for the six *Arachis* species represent the first detailed chemical examination of the surface lipids of peanut foliage and blooms. It is not unusual for the composition of cuticular lipids from the same plant to vary from one plant part to another (Baker, 1982; Jeffree, 1986), and it has been suggested that such variations may influence herbivorous insect behavior (Espelie et al., 1991). Compositional differences between the cuticular lipids of the blooms and foliage might explain why the blooms of wild peanut had significantly higher numbers of thrips than did the terminal buds (Table V). This result is similar to previous studies that indicate that thrips prefer the blooms over the foliage of the cultivated peanut, *A. hypogaea* (Tappan, 1986a,b).

Ferulic acid and *p*-coumaric acid are not commonly found in plant cuticular lipids (Baker, 1982; Jeffree, 1986). Recently, ferulic and *p*-coumaric acids were found to play important roles for resistance to the maize weevil (*Sitophilus zeamais*), which is a severe preharvest and postharvest pest of maize grain (Classen et al., 1990). The absence of phenolic acids in the cuticular lipids of the blooms of *A. hypogaea* and the variation in the percentage that these acids comprised of the foliage of the six peanut species may be factors in the variable insect resistance that was observed (Tables III–V). Fatty alcohol acetates are also rare components in plant cuticular lipids (Baker, 1982). Acetates of C_{24}, C_{26}, and C_{28} fatty alcohols were characterized in the foliar cuticular lipids of *Chenopodium album* (Allebone et al., 1970) and *Tilia tomentosa* (Gülz et al., 1991). The acetates that were found in the cuticular lipids of *A. paraguariensis* had alcohols of shorter chain length (C_{17}–C_{20}) (Table I). The high proportion of acetates in the cuticular lipids of the foliage of *A. paraguariensis* is particularly interesting, because this peanut species has shown very high insect resistance (Todd, Culbreath, Pittman, and Demski, unpublished results).

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