Characterization of Cuticular Lipids from Cultivated and Wild Peanut Species and Their Effect on Feeding by Fall Armyworm (Lepidoptera: Noctuidae)[1]

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ABSTRACT

The cuticular lipids from the adaxial and abaxial leaf surfaces of two peanut cultivars and four wild peanut species were isolated individually and characterized by combined gas chromatography-mass spectrometry. The two *Arachis hypogaea* peanut cultivars, Florunner and Southern Runner, and three of the wild peanut species *A. ipaensis*, *A. paraguariensis*, and *A. diogoi* had higher proportions of fatty alcohols on the adaxial leaf surface (17-37%) than on the abaxial surface (11-14%) and a higher percentage of *n*-alkanes on the abaxial surface (23-66%) than on the adaxial surface (15-30%). The wild peanut species *A. villosulicarpa* had high proportions of *n*-alkanes on both the adaxial and abaxial leaf surfaces. Scanning electron microscopy showed that leaf surfaces with high fatty alcohol content had a dense array of wax crystals while those with larger amounts of *n*-alkanes had an amorphous appearance. Fall armyworm, *Spodoptera frugiperda* (J. E. Smith), larvae were reared on meridic diet containing foliage from each of the peanut entries, diet with foliage from which the cuticular lipids had been extracted, and diet containing cuticular lipid extracts. Fall armyworm growth was enhanced when larvae were fed diet with *A. ipaensis* foliage from which the surface lipids had been removed.

Key Words: *Arachis*, *Spodoptera frugiperda*, cuticular lipids, host plant resistance, scanning electron microscopy, wild species.

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith), is one of the major defoliating pests of peanut in the Southeastern United States (Todd *et al.*, 1991). The development of sources of resistance to fall armyworm in peanut is an economically and environmentally acceptable method to control this important insect pest. Some peanut cultivars and wild peanut species have demonstrated resistance to fall armyworm feeding (Leuck and Skinner, 1971; Todd *et al.*, 1991; Stevenson *et al.*, 1993; Yang *et al.*, 1993a). Identification of the reason for insect resistance both in the wild and cultivated species of peanut will allow for a more efficient peanut breeding program where multiple pest resistance is a priority.

The plant surface, 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 bases of the chemical and ultrastructural characteristics of the plant surface (Woodhead and Chapman, 1986; Chapman and Bernays, 1989; Espelie *et al.*, 1991; Eigenbrode and Espelie, 1995). Certain plant cuticular lipids can contribute to insect resistance by affecting insect feeding behavior (Bernays *et al.*, 1976; Chapman, 1977; Eigenbrode *et al.*, 1991). In this study our objectives were to characterize the chemical and ultrastructural nature of the cuticular lipids from two peanut cultivars and four wild peanut species, and to examine the effect that these lipids have on the development of fall armyworm.

Materials and Methods

Plant Material. Two *Arachis hypogaea* L. cultivars, Florunner and Southern Runner, and four wild peanut species—*A. ipaensis* Krapov. and W.C. Gregory (PI 468322), *A. paraguariensis* Chod. et Hassl. (PI 468362), *A. diogoi* Krapov. and W.C. Gregory (previously called *A. chacoensis*) (PI 276235), and *A. villosulicarpa* Hoehne (PI 336985)—were planted in the field near Tifton, GA in the summer of 1992. Peanut plants were grown using standard agronomic practices with irrigation as needed. No insecticide applications were made prior to, or during, the period when peanut foliage was collected for the cuticular lipid analysis and for the fall armyworm laboratory bioassays.

Fall Armyworm. Larvae of the fall armyworm were obtained from a colony maintained at the Insect Biology and Population Management Research Laboratory, USDA-ARS, Tifton, GA (Burton and Perkins, 1989).

Cuticular Lipid Extraction. Fresh and clean branches of peanut plants were excised about 10 cm from the branch tip from 4-mo-old field-grown plants. Plant materials were placed into plastic bags and cooled in an ice chest prior to being transported to the laboratory. Peanut foliage was air-dried at room temperature for a week. The adaxial (upper) and abaxial (lower) surfaces of individual, fully expanded leaves (5 g, dry weight) were washed separately with a fine stream of redistilled chloroform for 5 sec at room temperature. This very brief extraction time was used in order to prevent cross-contamination between the lipid extracts from the upper and lower leaf surfaces (Premachandra *et al.*, 1993). Chloroform extracts were concentrated to a volume of 2 mL with a rotary evaporator at 40 C and stored at -20 C for chemical analysis.

Chemical Analysis. Aliquots (equivalent to 10% of each extract) 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 a N_2 stream, and the derivatized extract was resuspended in 0.1 mL redistilled hexane. Aliquots (1%) were analyzed by combined gas chromatography-mass spectrometry (Hewlett-

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Packard 5890A/5970). The capillary column (25 m cross-linked methyl silicone, 0.2 mm internal diameter, 0.33 μm film thickness, 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-sec intervals. Individual components were identified by their mass spectra which were compared to those of standards, and were matched by computer search with the National Bureau of Standards Mass Spectral Library (Walton, 1990). 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 (Yang *et al.*, 1992).

Scanning Electron Microscopy. The second fully-expanded leaf was harvested from the branch tip of field-grown peanut plants. The middle region next to the midrib of the first leaflet was cut into small sections (0.6 x 0.6 cm), fixed overnight in 2% glutaraldehyde in 0.2 M cacodylate, washed in 0.1 M cacodylate buffer with 5% sucrose for 2-3 min, post-fixed in 1% osmium tetroxide for 1 hr, washed again in 0.1 M cacodylate buffer with 5% sucrose, dehydrated sequentially in 30, 50, 70, 80, 95, and 100% ethanol (each for 10 min), rinsed twice in 100% ethanol, and critical-point dried. Leaf samples were then mounted on aluminum stubs with double-sided sticky tape and silver paint, coated with gold-palladium (40 nm thickness) with a Hummer X Sputter Coater, and examined with a Phillips 505 scanning electron microscope located at the Center for Advanced Ultrastructure Research, Univ. of Georgia, Athens. Both the adaxial and abaxial leaf surfaces were examined for each peanut species.

Fall Armyworm Bioassay. Peanut branches were excised about 20 cm from the branch tip from 4-mo-old field-grown plants. Fresh foliage was collected and divided into two equal fractions. One fraction of foliage (100 g) was dipped in redistilled chloroform (500 mL) for 1 min at room temperature to remove the cuticular lipids, and the extracted foliage was then air-dried in a hood for 1 hr. A brief extraction time was used to minimize the extraction of internal lipids (Espelie *et al.*, 1980). The chloroform extract was reduced to a volume of 2 mL on a rotary evaporator at 40 C, mixed with Celufil (1 g), and then air-dried for 12 hr. The other foliage fraction was not treated. Each foliage fraction (either extracted or unextracted) was blended with 250 mL pinto bean diet plus 50 mL distilled water and distributed into 30 plastic diet cups (30 mL). Similar diets were prepared by blending the entire extract in Celufil with pinto bean diet and water as described above. Each diet cup was infested with a single neonate fall armyworm larva and maintained at 28 C in an environmentally controlled chamber. Tests were arranged as a split-block design with 30 replicates. The following fall armyworm developmental parameters were recorded: 7- and 10-d larval weights, pupal weight, days to pupation, and days to adult emergence. All data were analyzed by ANOVA and means were separated by Fisher's protected least significant difference (LSD) at $P \leq 0.05$ level (Ott, 1988).

Results

Chemical Composition of Cuticular Lipids of Adaxial and Abaxial Leaf Surfaces. The cuticular lipid compositions of the adaxial and abaxial leaf surfaces of six peanut entries were determined by combined gas chromatography-mass spectrometry. The major classes of components were *n*-alkanes, free fatty acids, fatty alcohols, aldehydes, and triterpenols (Table 1). There were several differences between the cuticular lipid compositions of the upper and lower leaf surfaces as indicated by the ion chromatograms of *A. ipaensis* (Fig. 1). The adaxial leaf surface of Florunner, Southern Runner, *A. ipaensis*, *A. paraquariensis*, and *A. diogoi* had higher proportions of fatty alcohols than did the abaxial surface (Table 1). The abaxial surface of these species had larger amounts of *n*-alkanes (23-66%) than the adaxial surface (15-30%). There were only minor differences between the cuticular lipid compositions of the adaxial and abaxial leaf surfaces of *A. villosulicarpa*. Triterpenols were major components on the adaxial and abaxial leaf surfaces of *A. hypogaea* cultivars Florunner and Southern Runner but these compounds comprised less than 10% of the surface lipids of the wild peanut species.

Ultrastructure of Adaxial and Abaxial Leaf Surfaces. Scanning electron micrographs taken at low magnification of the adaxial leaf surface of *A. hypogaea* (Florunner) revealed a dense array of crystals (Fig. 2A). In contrast, the abaxial surface of Florunner leaves had large trichomes, but very few crystals (Fig. 2B). The adaxial surface of *A. ipaensis* had a crystalline appearance (Fig. 2C), whereas the abaxial surface had very few crystals and large trichomes (Fig. 2D). The adaxial surface of *A. paraquariensis* leaves also exhibited a crystalline appearance (Fig. 2E), but the abaxial surface had

Table 1. Composition by class of cuticular lipid components from adaxial and abaxial leaf surfaces of cultivated and wild *Arachis* species.

Species	Leaf surface	Class of component				
		n-Alkanes	Alcohols	Aldehydes	Fatty acids	Triterpenols
		%				
A. hypogaea	Adaxial	15.0	20.6	0.6	24.5	34.4
cv. Florunner	Abaxial	23.0	12.2	2.5	31.4	26.3
A. hypogaea	Adaxial	17.2	23.5	1.0	23.8	29.5
cv. Southern Runner	Abaxial	24.2	14.3	3.9	33.2	19.5
A. ipaensis	Adaxial	29.6	37.1	2.2	18.5	7.9
	Abaxial	49.5	14.0	1.8	24.9	5.0
A. paraguariensis	Adaxial	31.1	16.8	0.8	48.1	0.8
	Abaxial	33.1	10.9	0.8	50.2	0.0
A. diogoi	Adaxial	22.0	23.5	0.0	45.3	4.3
	Abaxial	66.4	12.9	0.0	13.8	2.3
A. villosulicarpa	Adaxial	70.0	9.8	0.7	12.3	1.6
	Abaxial	64.8	11.0	1.1	17.2	0.7

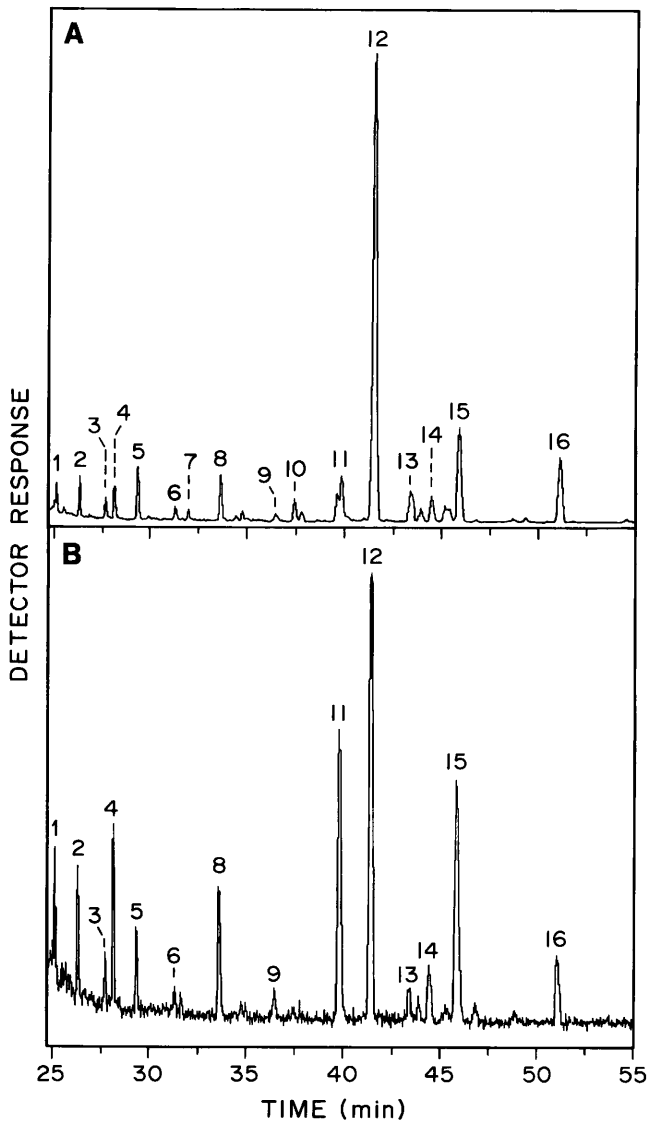

Fig. 1. Total ion chromatograms of the derivatized cuticular lipids recovered from the adaxial (A) and abaxial (B) surfaces of leaves of the peanut species *A. ipaensis*. Numbered peaks were identified by their mass spectra. *n*-Alkanes: 1, C_{26}; 2, C_{27}; 3, C_{28}; 5, C_{29}; 6, C_{30}; 8, C_{31}; 9, C_{32}; 11, C_{33}. Squalene: 4. Fatty acids: 7, C_{26}. Aldehydes: 10, C_{30}. Fatty alcohols: 12, C_{30}; 16, C_{32}. Terpenols: 13, β-amyrin; 14, α-amyrin.

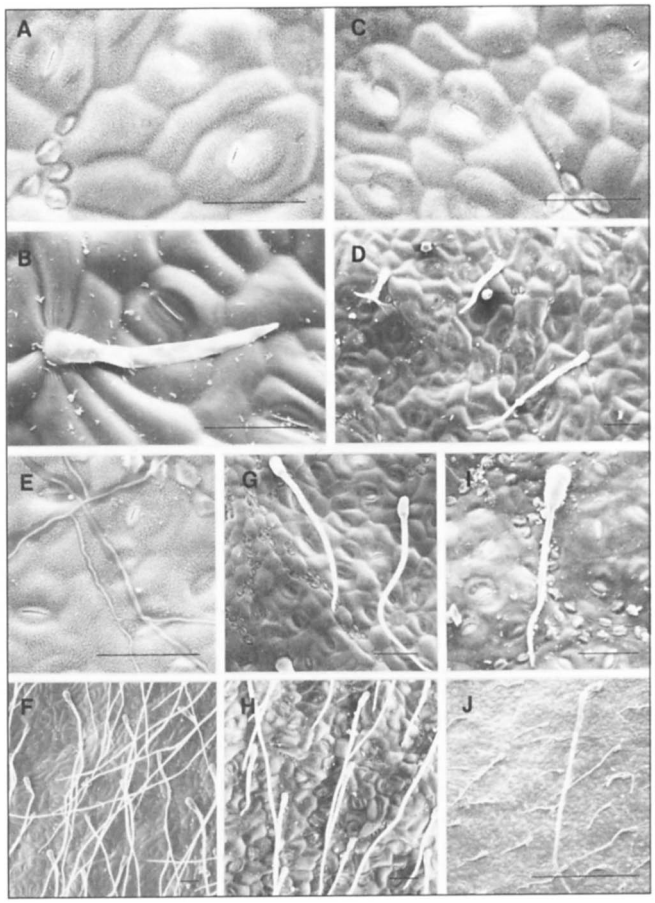

Fig. 2. Scanning electron micrographs of peanut foliage from the adaxial (A) and abaxial (B) leaf surfaces of *A. hypogaea* (Florunner); the adaxial (C) and abaxial (D) leaf surfaces of *A. ipaensis*; the adaxial (E) and abaxial (F) leaf surfaces of *A. paraguariensis*; the adaxial (G) and abaxial (H) leaf surfaces of *A. diogoi*; and the adaxial (I) and abaxial (J) leaf surfaces of *A. villosulicarpa*. The bar in the lower right corner of each micrograph equals 50 μm.

a dense array of fine trichomes (Fig. 2F). Both the upper (Fig. 2G) and the lower (Fig. 2H) surfaces of *A. diogoi* leaves had trichomes, although they were more prevalent on the abaxial surface. The adaxial surface of *A. villosulicarpa* leaves had large trichomes and no crystals (Fig. 2I), whereas the abaxial surface of the leaves of this species had both large and small trichomes (Fig. 2J).

At higher magnification, scanning electron micrographs revealed a dense pattern of plate-like crystals on the adaxial surface of leaves of Florunner (Fig. 3A), *A. ipaensis* (Fig. 3C), *A. paraguariensis* (Fig. 3E), and *A. diogoi* (Fig. 3G). The adaxial surface of *A. villosulicarpa* leaves (Fig. 3I) showed an amorphous appearance as did the abaxial surface of the five *Arachis* species (Fig. 3B,D,F,H,J). The upper and lower surfaces of *A. villosulicarpa* leaves were very similar in appearance (Fig. 3I,J).

Fall Armyworm Growth on Diet Containing Peanut Foliage, Extracted Foliage, or Foliage Extracts. Fall armyworm development was significantly affected when larvae were fed meridic diet containing untreated peanut foliage (Table 2). For each peanut species, fall armyworm weighed less at 7 and 10 d, took longer to pupate, weighed less at pupation, and took longer to emerge than insects fed the control diet. Larvae that were fed the diet containing peanut foliage from which the cuticular lipids had been extracted also weighed less as larvae and pupae, and took longer to pupate and emerge, than individuals reared on control diet. Nonsignificant differences were observed in weight among larvae fed a meridic diet or one containing foliage from Southern Runner or the wild peanut species. However, a consistent trend for insects to weigh less when fed peanut foliage was observed as compared to the control diet. There was a significant increase in larval weight and a significant difference in times to pupation and adult emergence when larvae were fed a diet with *A. ipaensis*

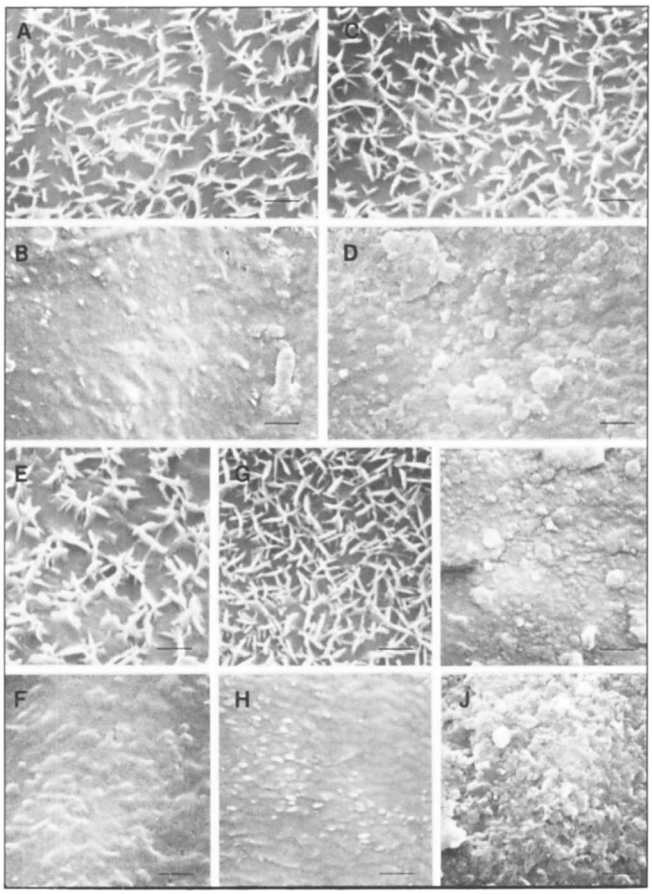

Fig. 3. Scanning electron micrographs of peanut foliage from the adaxial (A) and abaxial (B) leaf surfaces of *A. hypogaea* (Florunner); the adaxial (C) and abaxial (D) leaf surfaces of *A. ipaensis*; the adaxial (E) and abaxial (F) leaf surfaces of *A. paraguariensis*; the adaxial (G) and abaxial (H) leaf surfaces of *A. diogoi*; and the adaxial (I) and abaxial (J) leaf surfaces of *A. villosulicarpa*. The bar in the lower right corner of each micrograph equals 1 μm.

foliage from which the cuticular lipids had been removed compared to when individuals were fed untreated foliage of this wild species (Table 2).

Table 2. Fall armyworm development on meridic diet containing foliage, chloroform-extracted foliage, and extracts of cultivated and wild *Arachis* species.[a]

Meridic diet + plant source	Foliage	Extracted foliage	Foliage extract
	7-d weight of larvae (mg)		
Florunner	23.6±9.1bY	29.2±13.2cY	63.0± 22.9aX
Southern Runner	16.0±6.7cY	17.0±9.5dY	47.6±21.5aX
A. ipaensis	7.9±5.1dZ	38.2±13.7bY	47.8±24.8aX
A. paraguariensis	20.3±11.3bcY	22.6±10.7dY	45.6±21.6aX
A. diogoi	21.2±10.0bcY	17.6±10.0dY	48.7±22.4aX
A. villosulicarpa	24.2±13.1bY	23.0±9.4cdY	49.8±23.3aX
Diet only	54.7±20.8a	54.7±20.8a	54.7±20.8a
	10-d weight of larvae (mg)		
Florunner	132±42bcY	148±45bY	391±113aX
Southern Runner	103±46cY	102±54cY	310±144aX
A. ipaensis	47±35dZ	175±52bY	309±154aX
A. paraguariensis	126±52bcY	144±53bY	290±139aX
A. diogoi	126±46bcY	102±46cY	326±119aX
A. villosulicarpa	139±46bY	143±49bY	309±128aX
Diet only	348±139a	348±139a	348±139a
	Pupation (d)		
Florunner	17.0±1.2cX	16.9±1.6bX	13.9±0.8aY
Southern Runner	18.1±2.0bX	18.2±1.7aX	14.4±0.9aY
A. ipaensis	19.5±1.9aX	16.1±1.7cY	14.3±1.3aZ
A. paraguariensis	17.0±1.5cX	16.9±1.5bX	14.8±1.5aY
A. diogoi	17.2±1.4cX	17.9±1.3aX	14.4±0.8aY
A. villosulicarpa	16.7±1.7cX	16.7±1.1bcX	14.9±1.9aY
Diet only	14.3±0.9d	14.3±0.9d	14.3±0.9a
	Pupal weight (mg)		
Florunner	243±28cY	251±30bY	278±20aX
Southern Runner	247±35bcY	255±23bY	282±17aX
A. ipaensis	235±25cY	236±34cY	267±34aX
A. paraguariensis	261±25bXY	249±29bcY	265±19aX
A. diogoi	248±19bcY	244±19bcY	277±29aX
A. villosulicarpa	250±32bcY	254±26bXY	266±31aX
Diet only	278±25a	278±25a	278±25a
	Adult emergence (d)		
Florunner	26.6±1.8bX	26.3±1.5bX	23.3±1.0aY
Southern Runner	27.1±2.2bX	27.7±1.7aX	24.0±1.6aY
A. ipaensis	28.8±2.4aX	25.2±1.5cY	23.5±1.5aZ
A. paraguariensis	26.4±1.7bcX	26.6±1.9bX	24.4±1.7aY
A. diogoi	26.3±1.1bcX	26.9±1.5abX	23.7±1.3aY
A. villosulicarpa	25.7±1.6cX	26.1±1.4bX	24.4±2.0aY
Diet only	23.4±1.0d	23.4±1.0d	23.4±1.0a

[a]Means (± SD, N = 30) followed by the same letter in a column (a, b, c, or d) are not significantly different; and means followed by the same letter in a row (X, Y, or Z) are not significantly different ($P < 0.05$; Fisher's protected least significant difference) (Ott, 1988).

Discussion

The differences between the chemical composition of the cuticular lipids from the adaxial and abaxial surfaces of peanut leaves found by gas-chromatography/mass spectrometry (Table 1) were supported by the scanning electron microscopy results. The high proportion of fatty alcohols found on the adaxial surfaces of *A. hypogaea*, *A. ipaensis*, *A. paraquariensis*, and *A. diogoi* resulted in a crystalline appearance (Fig. 3A,C,E,G), whereas the higher percentage of *n*-alkanes found on the abaxial side of the leaves caused these surfaces to have an amorphous appearance (Fig. 3B,D,F,H). Variations in cuticular lipid chemical composition have been shown to affect the ultrastructural appearance of the leaf cuticle (Baker, 1982; Jeffree, 1986). Leaf surfaces with cuticular lipids rich in fatty alcohols have plate-like crystals, whereas surfaces with high proportions of *n*-alkanes usually have an amorphous appearance (Baker, 1982; Yang *et al.*, 1993d).

The cuticular lipid compositions of the adaxial and abaxial leaf surfaces have been examined for only a few plant species. The dominance of fatty alcohols on the adaxial surfaces and of *n*-alkanes on the abaxial surfaces of peanut leaves (Fig. 1) is analogous to the results of previous studies. Holloway *et al.* (1977) found that fatty alcohols comprised 70% of the cuticular lipids on the adaxial surface of pea leaves, whereas *n*-alkanes were the dominant components (86%) of the abaxial surface lipids. The surface lipids on the upper surface of peach leaves were dominated by fatty alcohols and wax esters and the lower surface had higher amounts of *n*-alkanes and triterpenols (Bukovac *et al.*, 1979).

Variation in foliar cuticular lipid composition has been shown to affect movement rates of lepidopteran larvae

(Eigenbrode *et al.*, 1991; Eigenbrode and Espelie, 1995). In both laboratory and field studies, fall armyworm larvae moved more rapidly on corn leaves with high proportions of *n*-alkanes in the surface lipids than on leaves with a high percentage of fatty alcohols (Yang *et al.*, 1993b,c). Yang *et al.* (1993b) showed that fall armyworm larvae moved more rapidly on the abaxial leaf surface of corn leaves than on the adaxial surface. Consequently, because of the large difference in the cuticular lipid chemistry (Table 1), fall armyworm larvae would be expected to behave differently on the adaxial leaf surface than on the abaxial surface of peanut foliage. The variation in trichome density observed between adaxial and abaxial surfaces of the same peanut species and between different species might also be expected to affect the behavior of fall armyworm larvae (Fig. 2). On some plants, trichomes have been shown to affect insect behaviors such as oviposition and settling (Campbell *et al.*, 1976; Duffey, 1986; Lambert *et al.*, 1992).

Several studies have indicated that ingestion of cuticular lipids has an adverse effect on the development of fall armyworm (Quisenberry *et al.*, 1988; Yang *et al.*, 1991, 1992, 1993d). Fall armyworm that were fed a diet containing foliage of *A. ipaensis* from which the cuticular lipids had been extracted had increased larval weights and earlier pupation and adult emergence compared with individuals reared on diet with unextracted foliage (Table 2). Fall armyworm development was significantly better on the control diet than it was on a meridic diet containing peanut foliage, supporting previous results of Wiseman and Davis (1979). The developmental parameters of fall armyworm that were fed a diet containing the lipids that had been extracted from the foliage of *A. ipaensis* did not differ from those of insects fed control diet. We did not have sufficient plant material to compare the development of fall armyworm larvae fed a diet containing cuticular lipids separately extracted from the abaxial and the adaxial surfaces of peanut leaves. Since fall armyworm larvae consume both surfaces of peanut leaves (J. W. Todd, unpubl. data, 1984), it is probable that the difference in the chemical composition of the abaxial and adaxial cuticular lipids does not have a nutritional effect on the development of these insects. Several other factors, including a variety of allelochemicals, may play a role in the increased resistance of wild peanut varieties to fall armyworm.

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