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Epicuticular Lipids from Azalea (*Rhododendron* spp.) and Their Potential Role in Host Plant Acceptance by Azalea Lace Bug, *Stephanitis pyrioides* (Heteroptera: Tingidae)

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Abstract—Epicuticular lipids of the foliage of four evergreen azalea hybrids (*Rhododendron* spp.) and one deciduous species, *R. canescens* (Michaux) Sweet, were extracted and characterized by gas chromatography–mass spectrometry. Each azalea hybrid and the deciduous species had a distinct epicuticular lipid composition. The most dominant epicuticular lipid components were triterpenoids, comprising 19–47% of the surface lipids for the five azaleas. For each cultivar and for *R. canescens*, the major triterpenoid was ursolic acid (11–30% of total epicuticular lipids). Two triterpenoid components, α- and β-amyrin, previously implicated as insect feeding and/or oviposition deterrents, were present in lower levels in cultivars more susceptible to damage by the azalea lace bug (*Stephanitis pyrioides*), a herbivorous pest of evergreen and deciduous azaleas. Scanning electron microscopy revealed distinct differences between the adaxial and abaxial surfaces of azalea leaves. Wax crystals were only seen on the lower surface of the leaves of 'Hino Crimson', the cultivar most susceptible to the azalea lace bug.

Introduction

Azaleas (*Rhododendron* spp.) are commonly cultivated ericaceous evergreen and deciduous shrubs. Evergreen azalea cultivars are classified first upon general physical similarities, and then by geographical origin. Within these groups, physical characteristics such as leaf texture or flower colour are quite variable (Galle, 1985).

Relatively few insects attack azaleas and most of these feed on foliage or on plant sap obtained by piercing the leaves (Galle, 1985). The major insect pest of evergreen azaleas in the United States is the azalea lace bug, *Stephanitis pyrioides* (Scott) (Heteroptera: Tingidae) (Neal and Douglass, 1988). Feeding by the azalea lace bug on plant sap causes chlorotic spots to develop on the leaves; bleached leaves are indicative of severe infestations (Lee, 1980). Evergreen azalea cultivars vary in their susceptibility to this insect pest (Schultz, 1993), but they generally suffer greater damage than do deciduous azaleas (Braman and Pendley, 1992). Preference for certain azalea cultivars by this herbivorous pest may be influenced by secondary plant products on the leaf surface.

The aerial surface of all plants is covered with a protective cuticle composed of a lipid polymer and a mixture of epicuticular lipids (Baker, 1982; Walton, 1990). These surface lipids serve primarily to protect the plant from water loss, but they also affect the behavior of many insects (Southwood, 1986; Eigenbrode and Espelie, 1995). Epicuticular lipids may cause herbivorous insects to accept or reject a plant and they may also serve as recognition cues for oviposition sites (Woodhead and Chapman, 1986; Städler, 1986; Chapman and Bernays, 1989; Espelie *et al.*, 1991).

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Epicuticular lipid composition varies among closely related plants and even from one surface to another in different areas within an individual plant (Holloway *et al.*, 1977; Yang *et al.*, 1993b; Eigenbrode and Espelie, 1995). In the present study, the foliar epicuticular lipids from four evergreen azalea hybrids and from one deciduous species were chemically characterized and the leaf surfaces were examined by scanning electron microscopy.

Materials and Methods

Azaleas. Liners of four evergreen azalea hybrid cultivars, 'Delaware Valley White', 'Hino Crimson', 'President Clay', and 'Higasa', were transplanted into 11.2 cm x 11.2 cm plastic containers during October, 1992, and placed in a greenhouse at the Georgia Station in Griffin, Georgia, with a 14:10 h (L:D) photoperiod. Overhead irrigation was applied twice a week and plants were fertilized once a week with Peters' 20:20:20 fertilizer. Plants were moved outdoors to a screenhouse in April, 1993. Leaf samples were collected in mid-September, 1994 from four plants per cultivar. At least 10 leaves, with no evidence of azalea lace bug damage, were collected from the upper part of each plant. Leaves were also collected from the upper part of four plants of a deciduous azalea, *Rhododendron canescens*, grown outdoors in a screenhouse at the Georgia Station. Leaves from each plant were placed in clean, separate glass containers and returned to the laboratory in Athens, GA where the leaves were allowed to dry at room temperature (20°C).

Epicuticular lipid analysis. Dried foliage (320 mg) from each of the four samples from each cultivar and the deciduous azalea was immersed in redistilled chloroform for approximately 1 min at room temp. Extracts were taken to dryness under a stream of N_2, derivatized with *N,O-bis*(trimethylsilyl)acetamide at 110°C for 10 min and dried with N_2. The derivatized extracts were dissolved in redistilled hexane and aliquots (approximately 10%) were analyzed by combined gas chromatography–mass spectrometry (Hewlett Packard 5890A/5970A). The capillary column, 25 m cross-linked methyl silicone HP-1, was held at 55°C for 3 min after injection, then the oven temperature was increased to 305°C at a rate of 15°C min^{-1} and held at this temperature for 36 min, for a total of 60 min for each analysis. The column was connected to a mass spectrometer and electron impact mass spectra were recorded at 70 eV at intervals of 0.8 s. Individual components were characterized by their mass spectra, which were compared to those of standards, and were matched by computer search with an IBM-PC version of the NIST/EPA/NIH Mass Spectral Database (Yang *et al.*, 1992; Smith and Severson, 1992). Quantitation was based upon the integration of total ion chromatograms (Yang *et al.*, 1993a).

Microstructural analysis. Leaf samples (1 cm^2) excised from *R. canescens* and the azalea hybrid cultivars 'Delaware Valley White' and 'Hino Crimson' were fixed overnight in 2% glutaraldehyde in 0.2M cacodylate, washed in 0.1M cacodylate buffer with 5% sucrose for 3 min, postfixed in 1% osmium tetroxide for 1 h, washed again in 0.1M 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. Samples were then mounted on aluminum stubs and a 50 nm layer of gold/palladium applied to each sample with a Hummer x Sputter Coater (Anatech) in preparation for scanning electron microscopy. Samples were viewed and photographed with a Phillips 505 Scanning Electron Microscope operated at 20 keV. Adaxial leaf surfaces were examined at 500 x and 1000 x. Abaxial leaf surfaces were viewed at 500 x, 1000 x, 5000 x, and 10,000 x.

Results

The four azalea cultivars and the deciduous azalea, *R. canescens*, each had a distinct epicuticular lipid composition (Table 1). Triterpenoids were major components in the surface lipids of each of the azaleas. Ursolic acid was the most prevalent of the triterpenoids, ranging from 10.6% of the epicuticular lipids in 'Delaware Valley White' to 30.2% in *R. canescens*. Oleanolic acid, α-amyrin, and β-amyrin were also present in each of the epicuticular lipids, but the proportions of these components varied for the foliar lipids of the different azaleas (Table 1). α-Amyrin was present in greater quantities than β-amyrin, except in the 'President Clay' cultivar in which the proportion of β-amyrin (3.8%) was slightly more than that of α-amyrin (3.3%). The lowest levels of β-amyrin were found in the epicuticular lipids of 'Hino Crimson' (1.1%), and the leaves of this cultivar also had the lowest levels of α-amyrin (2.0%) (Table 1).

The principle *n*-alkane in the epicuticular lipids of each of the azaleas was *n*-hentriacontane (1.0–13% of total surface lipids) (Table 1). In the epicuticular lipids of the leaves of 'Hino', 'Delaware Valley White', and 'President Clay', and *R. canescens*,

TABLE 1. AVERAGE PERCENTAGE COMPOSITION* OF EPICUTICULAR LIPIDS RECOVERED FROM THE FOLIAGE OF FOUR EVERGREEN AZALEA HYBRID CULTIVARS AND A DECIDUOUS AZALEA, *RHODODENDRON CANESCENS*

Peak†	R.T.‡	Component	'Hino Crimson'	'Delaware Valley White'	'Higasa'	'President Clay'	R. canescens
1	17.71	Hexadecanoic acid	11.0	5.5	2.9	8.5	1.5
2	18.49	Octadecanol	1.0	0.6	0.2	0.5	0.1
3	18.83	Octadecenoic acid	5.3	1.6	0.8	1.5	0.3
4	19.00	Octadecanoic acid	5.7	1.6	0.7	3.0	1.0
5	20.20	Eicosanoic acid	2.1	1.6	1.4	1.4	1.1
6	20.61	n-Pentacosane	1.1	0.7	0.5	1.5	0.5
7	21.50	Docosanoic acid	0.8	0.9	1.1	0.9	1.5
8	22.01	n-Heptacosane	0.6	0.9	0.5	1.9	1.8
9	22.23	Unknown	8.8	0.0	0.0	0.0	2.1
10	22.37	Tetracosanol	0.3	0.3	0.1	0.1	3.6
11	23.82	n-Nonacosane	0.9	9.7	1.9	5.2	14.9
12	24.14	Unknown	0.0	8.2	0.0	0.3	0.0
13	24.27	Hexacosanol	1.0	1.8	0.1	0.4	1.9
14	24.91	n-Triacontane	0.1	0.8	0.6	0.8	0.5
15	25.25	Hexacosanoic acid	0.1	0.1	0.3	0.1	0.7
16	26.28	n-Hentriacontane	1.0	13.2	7.6	12.2	4.2
17	26.88	Octacosanol	0.8	1.5	0.3	1.5	1.4
18	27.79	n-Dotriacontane	0.1	0.8	1.3	0.7	0.0
19	28.25	Octacosanoic acid	0.1	0.1	0.1	0.1	1.1
20	28.55	Nonacosanol	0.1	0.2	0.1	0.2	0.3
21	29.68	n-Tritriacontane	0.2	3.1	6.5	2.9	0.2
22	30.03	Unknown	2.4	8.8	0.1	9.9	0.2
23	30.56	Triacontanol	0.8	2.9	0.5	3.7	0.6
24	32.07	β-Amyrin	1.1	2.8	6.6	3.8	2.7
25	32.30	Unknown	0.5	0.8	2.6	0.8	0.5
26	32.83	α-Amyrin	2.0	3.4	12.5	3.3	4.8
27	35.10	Unknown	0.5	1.4	1.1	2.1	0.0
28	35.60	Unknown	0.7	0.6	4.5	0.7	0.0
29	35.87	Dotriacontanol	0.8	1.7	8.6	4.9	0.9
30	36.91	Unknown	0.3	0.3	1.1	0.2	3.0
31	37.82	Oleanolic acid	3.9	2.6	3.4	3.2	8.8
32	38.73	Unknown	0.6	0.7	0.5	0.5	1.4
33	39.37	Ursolic acid	20.5	10.6	11.8	11.5	30.2

*N = 4.

†Peak numbers correspond to those listed in Fig. 1.

‡Retention time.

Components are listed only if they were identified by their mass spectra.

n-nonacosane was the second most prevalent n-alkane (0.9–14.9%), but the surface lipids of 'Higasa' had the most distinct n-alkane profile with low levels of n-nonacosane (1.9%) and the highest proportion of n-tritriacontane (6.5%).

The proportion of alkanes varied from 4.0% of the total lipids in the azalea cultivar 'Hino Crimson' to 29.4% in 'Delaware Valley White' (Fig. 1). There was relatively little variation in the proportions of fatty alcohols from the evergreen cultivars and the deciduous species (4.8–11.3% of total surface lipids) (Table 2). There was a great deal of variation in chain length of the fatty alcohols for the different azaleas: n-dotriacontanol was the major fatty alcohol in the surface lipids of 'Higasa' and 'President Clay'; n-triacontanol was the most prevalent fatty alcohol in 'Delaware Valley White'; n-hexacosanol was the major fatty alcohol in 'Hino Crimson'; and n-tetracosanol was the dominant fatty alcohol in the epicuticular lipids of R. canescens (Table 1).

Scanning electron microscopy showed that the adaxial leaf surface of R. canescens had a striated cuticle with no distinct surface wax morphology (Fig. 2A). The adaxial leaf surface of the cultivar 'Delaware Valley White' had a similar
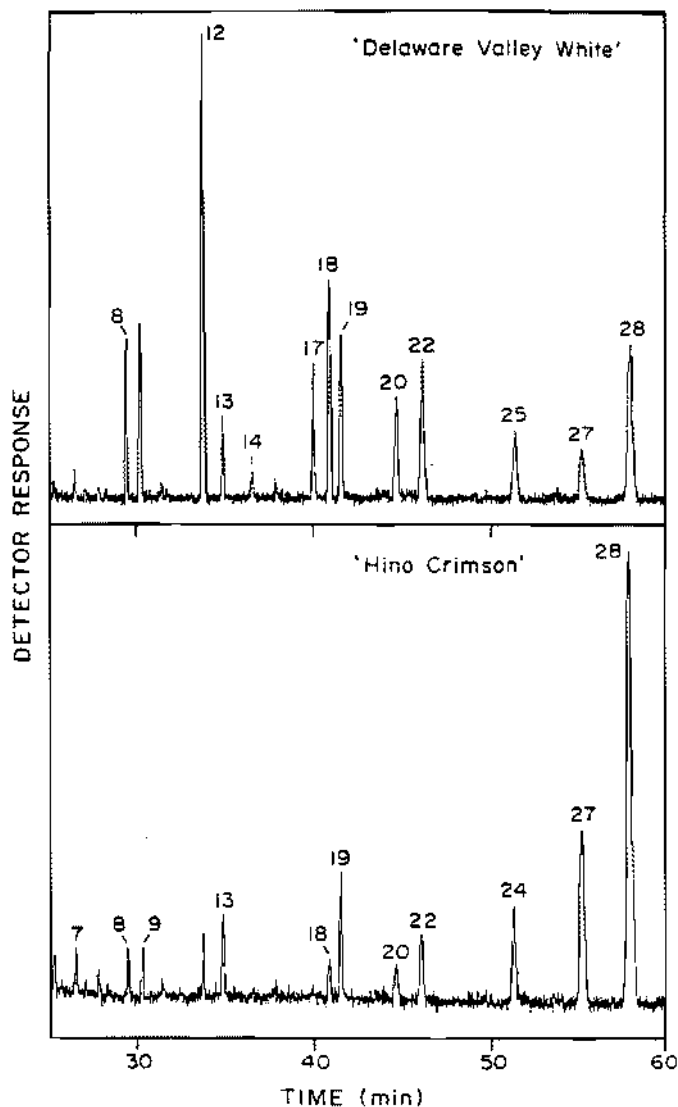
FIG. 1. TOTAL ION CHROMATOGRAMS OF THE DERIVATIZED EPICUTICULAR LIPIDS EXTRACTED FROM THE AZALEA CULTIVARS 'DELAWARE VALLEY WHITE' (TOP) AND 'HINO CRIMSON' (BOTTOM). Numbered components were identified by their mass spectra and are listed in Table 1.

TABLE 2. COMPOSITION (%) BY CLASS OF EPICUTICULAR LIPIDS OF THE FOLIAGE OF FOUR EVERGREEN AZALEA HYBRID CULTIVARS AND A DECIDUOUS AZALEA, *RHODODENDRON CANESCENS* (±standard errors)

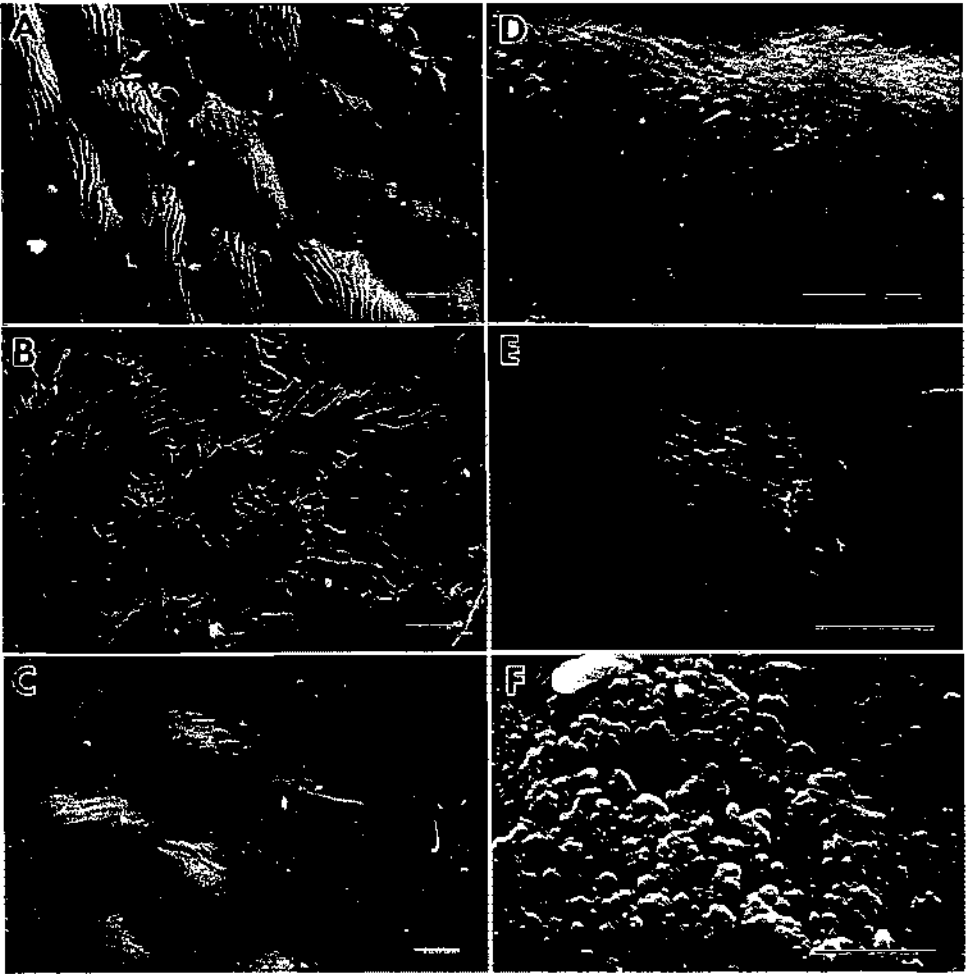| Class of Component (Chain Length)	'Hino Crimson'	'Delaware Valley White'	'Higasa'	'President Clay'	*R. canescens*
n-Alkanes (C_{25}-C_{33})	4.0±0.3	29.4±2.7	18.7±1.5	25.2±1.5	22.0±1.3
n-1-Alkanols (C_{18}-C_{32})	4.8±0.5	9.0±0.9	9.9±0.6	11.3±0.5	8.8±1.9
n-Alkanoic acids (C_{16}-C_{28})	25.1±3.5	11.4±2.0	7.2±0.5	15.4±0.1	7.3±1.4
Triterpenoids	27.8±3.8	19.3±4.7	34.1±0.9	21.8±1.3	46.5±6.3

FIG. 2. SCANNING ELECTRON MICROGRAPHS OF THE ADAXIAL SURFACE OF AZALEA LEAVES. (A) *Rhododendron canescens*; (B) 'Delaware Valley White'; and (C) 'Hino Crimson'. Abaxial surface of azalea leaves: (D) *R. canescens*; (E) 'Delaware Valley White'; and (F) 'Hino Crimson'. Scale bars in A-C 10 μm; scale bars in D-F, 5 μm.

appearance (Fig. 2B). The adaxial side of the leaves of the azalea cultivar 'Hino Crimson' had a much different appearance, with very few striations and a smooth, amorphous surface (Fig. 2C). The abaxial leaf surfaces of both *R. canescens* and 'Delaware Valley White' had a smooth, amorphous appearance with no crystal structures (Fig. 2D and E). In contrast, the abaxial side of 'Hino Crimson' leaves had a very distinct appearance, with irregularly-shaped, globular crystals covering the surface (Fig. 2F).

Discussion

The epicuticular lipid compositions of the four azalea cultivars and the deciduous azalea, *R. canescens*, are similar to compositions previously reported for other members of the Ericaceae. As with 'Hino Crimson' and *R. canescens* (Table 1), ursolic acid and oleanolic acid were the major components in the surface lipids of cranberry, *Vaccinium macrocarpon* (Croteau and Fagerson, 1971). The dominant *n*-alkane in the epicuticular lipids of *V. myrtillus*, *V. uliginosum*, and *V. vitis-idaea* was *n*-hentriacontane (Stránský *et al.*, 1967), which is the same hydrocarbon which was most prevalent in the foliar wax of each of the azaleas (Table 1).

An investigation of the role of leaf pubescence and bloom colour on host plant acceptance by the azalea lace bug revealed that although 'Hino Crimson' was more susceptible to azalea lace bug damage than 'Delaware Valley White', it was not these physical traits that were influencing host plant acceptance by the lace bug (Schultz, 1993). Previously, results of bioassays indicated that the 'Delaware Valley White' cultivar, in turn, was more susceptible to azalea lace bug activities than the deciduous species, *R. canescens* (Braman and Pendley, 1992). The deciduous habit of this native species is not optimal for overwintering lace bug eggs and may partially explain reduced populations on the deciduous azaleas as a whole, compared to evergreen hybrids.

The triterpenols, α- and β-amyrin, structurally similar to sterols and found in relatively high proportions in the epicuticular lipids of the deciduous and evergreen azaleas, may deter feeding and/or oviposition on plants by herbivorous insects. These compounds inhibit feeding by the migratory locust, *Locusta migratoria* (Chapman, 1977), and the palmitate ester of α-amyrin inhibits growth of several species of lepidopteran larvae (Shankaranarayana *et al.*, 1980). Yang *et al.* (1993b) found that corn genotypes susceptible to feeding damage by fall armyworm, *Spodoptera frugiperda*, had lower levels of α- and β-amyrins than insect-resistant corn genotypes. Chemical changes in the epicuticular lipids of a cabbage variety were shown to provide resistance to feeding by larvae of the diamondback moth, *Plutella xylostella* (Eigenbrode *et al.*, 1991). The presence of α- and β-amyrin in the surface lipids of the resistant cabbage, and the absence of these compounds in a susceptible cabbage, suggested that they may be important in providing resistance to insect herbivory. Discriminant analysis of the epicuticular lipids of several raspberry cultivars suggested that high levels of β-amyrin provided resistance to the raspberry aphid, *Amphorophora idaea* (Robertson *et al.*, 1991). Interestingly, the cultivar, 'Hino Crimson', which had the lowest levels of α- and β-amyrin of the azaleas examined in this study (Table 1), is the most susceptible to the azalea lace bug (Schultz, 1993). However, high levels of α- and β-amyrin do not always provide resistance to insect herbivory; in a comparison of several peanut species (*Arachis* spp.), the species most susceptible to insect damage had the highest levels of these triterpenols (Yang *et al.*, 1993a).

The crystalline structure of plant waxes is determined by the chemical composition of the waxes (Baker, 1982; Jeffree, 1986). The distinct difference between the microstructural appearance of the adaxial and abaxial surfaces of the azalea leaves (Fig. 2) supports previous studies that have shown distinct differences between the upper and lower sides of the same leaf (Carver *et al.*, 1990; Gülz *et al.*, 1992; Yang *et*

al., 1993b). Since the primary feeding site of the azalea lace bug is on the abaxial surface of the leaf (Braman and Pendley, 1992), it is interesting that the abaxial leaf surface of the cultivar most susceptible to the azalea lace bug, 'Hino Crimson', had a distinct surface morphology with globular crystals (Fig. 2F). Leaf surfaces with high proportions of triterpenoids often have an amorphous appearance under the scanning electron microscope (Jeffree, 1986). Gülz et al. (1992, 1993) have suggested that wax crystals will form on a plant surface only when the major class of lipids equals 40% or more of the lipids, and when one compound comprises 80% or more of that class. The azalea cultivar that comes closest to meeting these criteria is 'Hino Crimson' with ursolic acid as a dominant component of the surface lipids (Table 1), and the difference between the adaxial and abaxial surfaces (Fig. 2C and F) suggest that the proportion of this triterpenoid may be higher on the lower leaf surface.

Preference of the azalea lace bug for certain azalea cultivars is most likely influenced by a combination of factors including the surface chemistry of the host plant, as well as physical and physiological characteristics. Our findings suggest that there may be a chemical basis for the variation in host plant acceptance of azalea cultivars. However, it will be necessary to develop laboratory and field bioassays in order to determine the influence that individual components in the epicuticular lipids of azalea have upon the feeding behavior of the azalea lace bug.

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