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ISOLATION AND IDENTIFICATION OF VOLATILES IN THE FOLIAGE OF POTATO, *Solanum tuberosum,* A HOST PLANT OF THE COLORADO BEETLE, *Leptinotarsa decemlineata*

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Abstract—The volatile compounds of *Solanum tuberosum* L., a host plant of the Colorado beetle, *Leptinotarsa decemlineata* Say, were isolated by successive vacuum steam distillation, freeze concentration, and extraction. The main components are *trans*-2-hexen-1-ol, 1-hexanol, *cis*-3-hexen-1-ol, *trans*-2-hexenal, and linalool. The distribution of these compounds in a variety of plant families and their biosyntheses are reviewed. These leaf volatiles constitute a general green leaf volatile complex, being active in the olfactory orientation of the Colorado beetle and as such are probably of importance to various phytophagous insects.

Key Words—*Solanum tuberosum, trans*-2-hexen-1-ol, 1-hexanol, *cis*-3-hexen-1-ol, *trans*-2-hexenal, biosynthesis, host plant selection, olfactory orientation, *Leptinotarsa decemlineata,* Colorado beetle, Coleoptera, Chrysomelidae, potato.

INTRODUCTION

As contrasted with the well-studied actions of nonvolatile primary and secondary plant substances (Schoonhoven, 1968; Staedler, 1976), our knowledge is incomplete on the role of plant "odors" in host selection by phytophagous insects, in regard to host plant orientation, and the initiation and continuation of feeding. The reported information forms a range of possibilities concerning plant odors: (1) consisting of one or a group of chemically related, host-plant-specific "key" components, e.g., organic sulfur compounds to *Hylemya antiqua* (Matsumoto and Thorsteinson, 1968a,b) and isothiocyanates of cruciferous species to *Plutella maculipennis* (Gupta and

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Thorsteinson, 1960a,b); (2) being composed of substances less specific to host plants like the large chemical class of terpenes and their derivatives acting on a variety of forest pest insects (see, e.g., Werner, 1972; Staedler, 1974; Selander et al., 1974); (3) existing as a complex, a mixture of generally distributed unspecific components (Rodriguez et al., 1976). In this case, the total "essence" is required in performing the particular sequence of behavioral steps in host selection by phytophagous insects.

Visser and Nielsen (1977) have shown that adult Colorado beetles are attracted by the volatiles of their host plant, potato. Besides this, other members of the Solanaceae are attractive, while most of the nonsolanaceous plant species elicit neutral or repellent responses in Colorado beetles, except for *Apium graveolens* (de Wilde et al., 1969) and *Tropaeolum majus*, which enhance positive anemotaxis. Host plant selection by this oligophagous insect is a catenary process, in which the initial olfactory orientation confines this selection process mainly to solanaceous plant species. Eventually, when contact results, the aim is not achieved by a sole "odd" substance, but is attained by a combination of feeding incitants, feeding stimulants, feeding cofactors, and inhibitors (Ritter, 1967; Hsiao, 1969). Analogously, a complex of volatiles composing the attractive plant odor probably exists. The present study elucidates the chemical complexity of host plant odor acting in the initial attraction of Colorado beetles.

METHODS AND MATERIALS

The chemical analysis of potato plant odor started with the isolation of the volatile components in sufficient quantities to allow identification with a mass spectrometer. Extraction can be applied as a first-step procedure, using relatively large quantities of low-boiling organic solvents. The extraction process entails two major disadvantages: impurities from the solvent may accumulate in the aroma concentrate, and nonvolatile components are isolated along with the volatiles. Therefore, we preferred distillation as a first-step procedure for the isolation of all volatile material (see review of isolation procedures: Weurman, 1969). For the isolation of potato plant volatiles, a series of methods were employed: vacuum steam distillation followed by freeze concentration in order to reduce the amount of solvent used in the final extraction.

One kilogram of fully grown potato plants (cultivar Pimpernel), i.e., mainly leaves, stems, some flowers and fruits equivalent to the overground parts of two plants, were harvested from the field and homogenized in a mixer with 5 liters of demineralized water at 3°C. The resultant slurry was passed through glass wool, and the filtrate was steam distilled in two halves (Ahrenst-Larsen and Hansen, 1964) by the apparatus shown in Figure 1. Nitrogen was passed through the flask containing the potato plant filtrate for 4 min to minimize

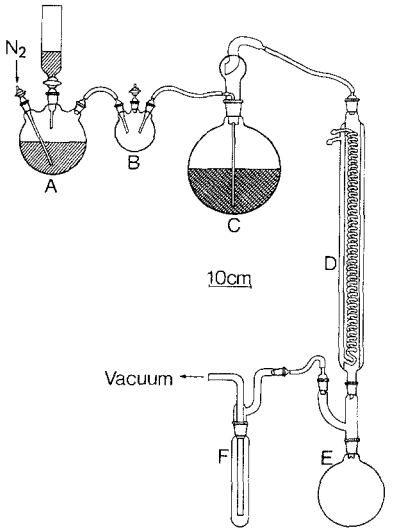

FIG. 1. Vacuum steam distillation apparatus. A: steam generator, filled with 1 liter of bidistilled water; B: steam drier; C: sample flask, containing 2.5 liters of potato plant filtrate; D: condenser; E: receiving flask, set in ice-water bath; F: cold trap, cooled in liquid nitrogen. Preceding the distillation, nitrogen was passed into the steam generator.

artifact formation during the distillation process (Nye and Spoehr, 1943). The steam distillation was carried out at reduced pressure (10–15 torr near the vacuum pump, 20–40 torr in the distillation system). At this reduced pressure, the water in the steam generator, set in a water bath kept at 42° C, was boiling, and the generated steam was bubbled through the potato plant filtrate, at a constant 39° C. The volatiles were transferred by the steam, condensed, and trapped into the receiving flask and a cold trap in liquid nitrogen. One liter of distillate was produced in one run. This amount was precooled to 2° C and transferred to the freeze concentration arrangement (see Figure 2). This technique had been reported to give high recoveries (>90%) after 20-fold concentration (Kepner et al., 1969). After a tenfold concentration the combined concentrates of two distillation runs (200 ml) were extracted three times with an equal volume of a mixture of diethylether and *n*-pentane, 1:2 by volume (Merck analytical grade, distilled before use). The extract was dried with sodium sulfate, followed by calcium sulfate at 4° C (Nursten and Williams, 1966). The solvents were carefully removed by distillation.

Analytical GLC separations were made on a Becker gas chromatograph (with flame ionization detector) fitted with packed polar (Carbowax 20M) and nonpolar (Apiezon L) columns. Mass spectra were recorded on the gas chromatograph (Varian 2700, fitted with a WCOT SP 2300 column)–mass

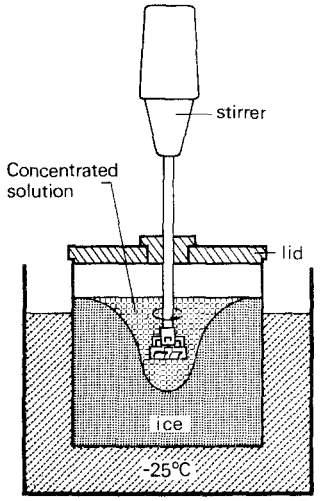

FIG. 2. Freeze concentration arrangement. A stainless-steel jar containing one liter of precooled distillate is inserted in a methanol bath of -25°C. While the mixture is cooled and stirred, the water is selectively frozen out, leaving the volatiles concentrated into a conical hole.

spectrometer (Varian MAT CH4) computer system (Varian Spectrosystem 100) of the Central Institute for Nutrition and Food Research TNO.

Authentic samples were obtained from commercial sources: the hexenols (98–99%) from Roth, *trans*-2-hexenal (99%) from Koch-Light Lab., linalool (99%) and 1-hexanol (99%) from Fluka.

RESULTS AND DISCUSSION

The main components of the oil (40 μl/kg)(Figure 3) were identified by coinjection with authentic samples on Carbowax 20M and Apiezon L columns, and by comparison of their mass spectra with those of authentic samples (Figures 4 and 5). The identity was further confirmed by analysis on the SP 2300 column. The mass spectra of *cis*-2- and *trans*-2-hexen-1-ol exhibited a high degree of similarity, as did *cis*-3- and *trans*-3-hexen-1-ol (Figure 4). However, GLC analyses of authentic samples showed consistent differences in their retention indices (Table 1) and allowed discrimination between geometrical isomers. The composition of the oil is shown in Figure 3, in decreasing order of magnitude: *trans*-2-hexen-1-ol, 1-hexanol, *cis*-3-hexen-1-ol, *trans*-2-hexenal, and linalool. At retention times >55 min only small quantities of compounds were detected. The most volatile components were lost in the final removal of the extractive solvents.

No evidence could be obtained that *cis*-2-hexen-1-ol, identified by Murray et al. (1972) as one of the components of *Solanum campylacanthum* oil, or *trans*-3-hexen-1-ol were present in the oil of potato plants. It is not clear to what extent the identification of *cis*-2-hexen-1-ol by Murray et al. (1972) had been based on mass spectral data only (see Table 1).

The main components of the potato plant oil are also present in other solanaceous plant species. They have been identified in *Solanum campylacanthum* leaves, potatoes, tomatoes, bell and tobasco peppers, and in the flowers of *Nicotiana alata* (see Table 2). These compounds are widely distributed in fresh foliage, vegetables, and fruits (Gildemeister and Hoffmann, 1960, 1963; Van Straten, 1977). The well-known leaf aldehyde 2-hexenal and the leaf alcohols 1-hexanol, 2-hexen-1-ol, and 3-hexen-1-ol have been reported as volatile components of numerous plant species belonging to a variety of plant families (Table 3).

The straight-chain, saturated and unsaturated aldehydes and alcohols are formed by oxidative degradation of plant lipids, as illustrated in Figure 6. Lipolytic acyl hydrolases liberate free fatty acids from the endogenous membrane lipids. The polyunsaturated fatty acids, linoleic and linolenic acid, are oxidized by the action of lipoxygenase to, respectively, hexanal and *cis*-3-hexenal.

Alcohol dehydrogenase converts hexanal to 1-hexanol, whereas *cis*-3-hexenal easily isomerizes to *trans*-2-hexenal and is converted to *cis*-3-hexen-1-ol. *Trans*-2-hexen-1-ol is formed from *trans*-2-hexenal. Possibly *trans*-3-hexen-1-ol and *cis*-2-hexen-1-ol originate from isomerization during processing and storage of plant products. These biosyntheses are operative in several

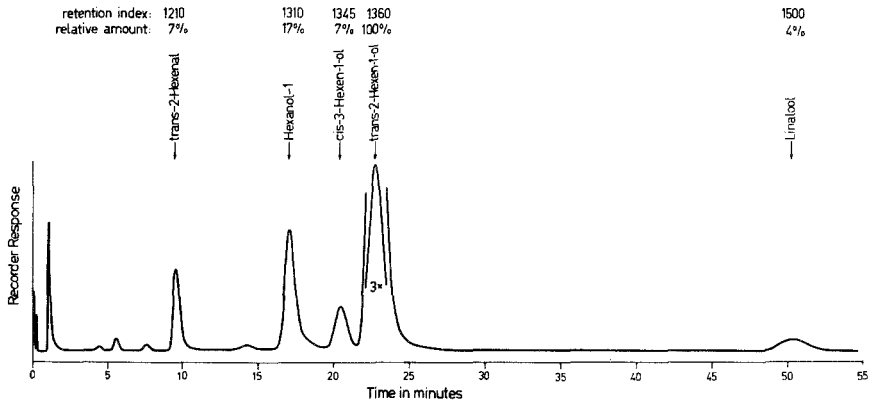

FIG. 3. Gas chromatogram of the potato plant oil: 0.1 μl of oil injected on a stainless-steel column, 3 m long and 4.4 mm ID, filled with 10% Carbowax 20M on Chromosorb P-AW-DMCS, 60–80 mesh. Chromatogram run isothermally at 100°C, carrier gas nitrogen at 30 ml/min. Retention indices were calculated according to Kováts (1961).

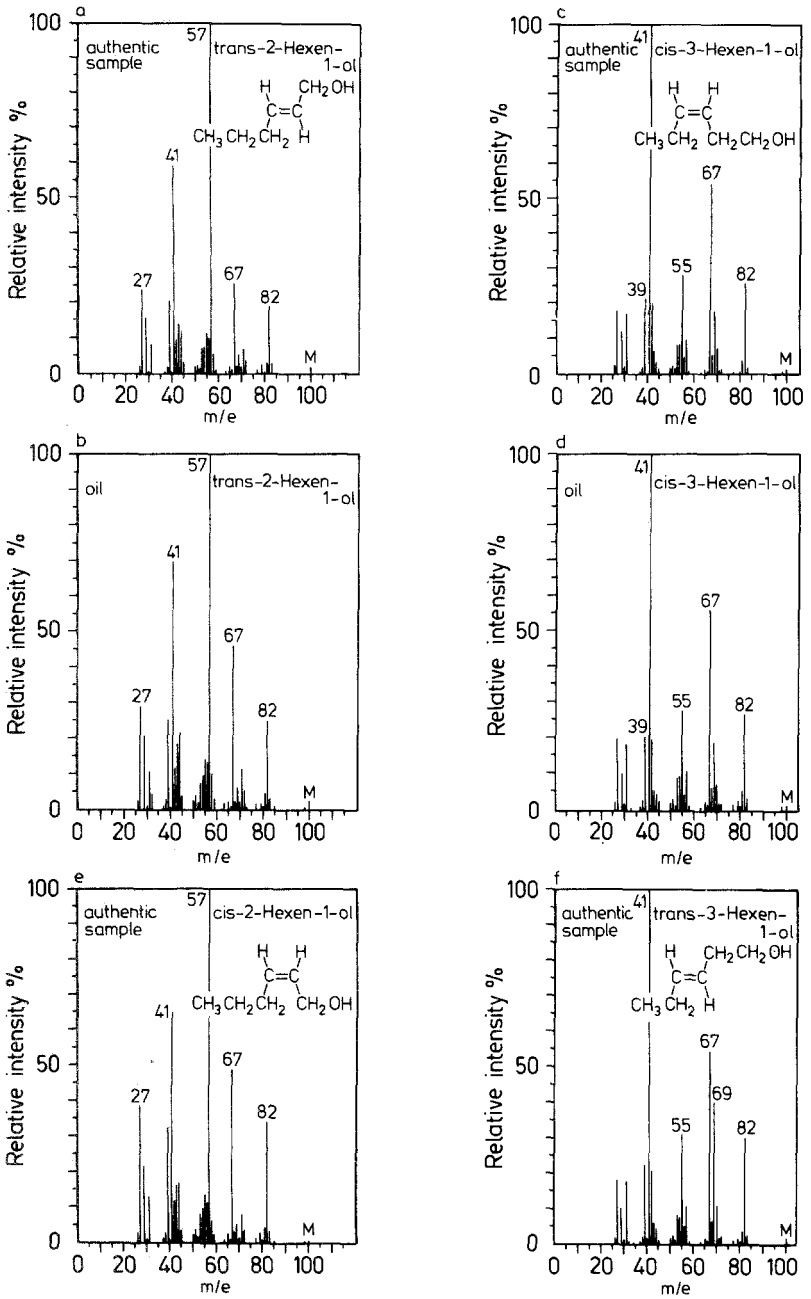

FIG. 4. Mass spectra of the main volatiles and of authentic samples.

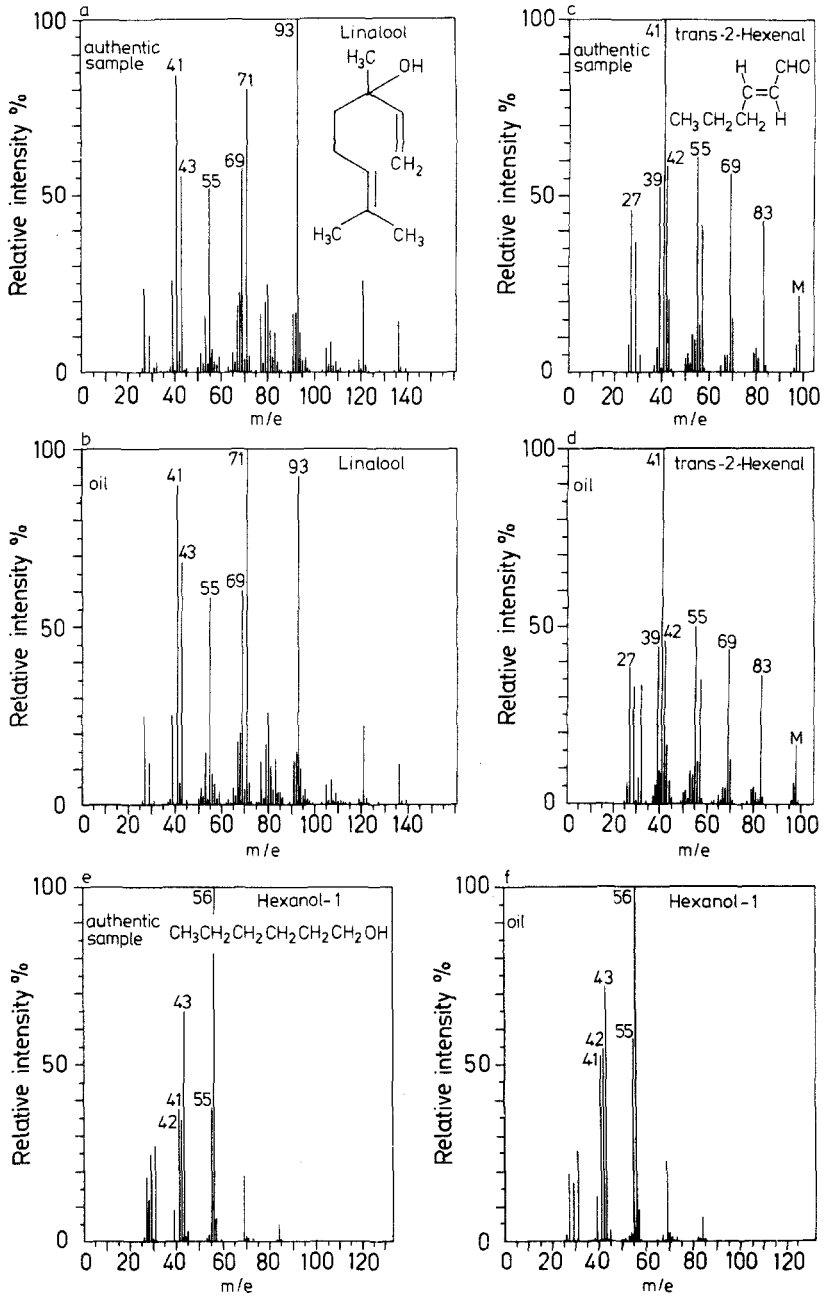

FIG. 5. Mass spectra of the main volatiles and of authentic samples.

TABLE 1. RETENTION INDICES[a]

	Present investigation 10% Carbowax 20M[b]		Murray et al. (1972) 8% Carbowax
	Authentic samples	Potato plant oil	*Solanum campylacanthum* oil
trans-2-Hexenal	1210	1210	1200
1-Hexanol	1310	1310	1312
trans-3-Hexen-1-ol	1320		
cis-3-Hexen-1-ol	1345	1345	1343
trans-2-Hexen-1-ol	1360	1360	
cis-2-Hexen-1-ol	1370		1360
Linalool	1500	1500	1500

[a] Retention indices were calculated according to Kováts (1961)
[b] See legend of Figure 3 for GLC conditions.

TABLE 2. DISTRIBUTIONS OF IDENTICAL COMPOUNDS IN THE OIL OF SOLANACEOUS PLANT SPECIES

Capsicum annuum
Bell peppers: *trans*-2-Hexenal,[1,21] *cis*-3-hexen-1-ol,[1,21] linalool[1,21]

Capsicum frutescens
Tobasco peppers: 1-Hexanol,[9] *cis*-3-hexen-1-ol[9,21]

Solanum campylacanthum
Leaves[12]: 1-Hexanol, 2-hexenal, *cis*-2-hexen-1-ol, *cis*-3-hexen-1-ol, linalool

Solanum lycopersicum
Tomatoes: Hexanol,[2,19,21] 1-hexanol,[4,5,7,11,13,14,17,22–24] 2-hexenal,[7,15,16] *trans*-2-hexenal,[2,6,11,14,18,21–24] *trans*-2-hexen-1-ol,[19,22] 3-hexen-1-ol,[20] *cis*-3-hexen-1-ol,[2,10,11,14,18,21–24] linalool[2,11,21,23]

Solanum tuberosum
Potatoes: 2-Hexenal,[8] *trans*-2-hexenal,[21] 2-hexenol[15]; Leaves[25]: 1-Hexanol, *trans*-2-hexenal, *trans*-2-hexen-1-ol, *cis*-3-hexen-1-ol, linalool

Nicotiana alata
Flowers[3]: 1-Hexanol, linalool

[1]Buttery et al., 1969; [2]Buttery et al., 1971; [3]Chang and Collins, 1972; [4]Dalal et al., 1967; [5]Dalal et al., 1968; [6]Galliard and Mattew, 1977; [7]Grosch, 1963; [8]Grosch et al., 1976; [9]Haymon and Aurand, 1971; [10]Johnson et al., 1968; [11]Kazeniac and Hall, 1970; [12]Murray et al., 1972; [13]Nelson and Hoff, 1969; [14]Pyne and Wick, 1965; [15]Ryder, 1966; [16]Schormüller and Grosch, 1962; [17]Schormüller and Grosch, 1964; [18]Schormüller and Kochmann, 1969; [19]Seck and Crouzet, 1973; [20]Shah et al., 1969; [21]Shankaranarayana et al., 1975; [22]Sieso et al., 1976; [23]Viani et al., 1969; [24]Wick, 1965; [25]present investigation.

TABLE 3. DISTRIBUTIONS OF LEAF ALDEHYDE 2-HEXENAL AND LEAF ALCOHOLS 1-HEXANOL, 2-HEXEN-1-OL, AND 3-HEXEN-1-OL IN VARIOUS PLANT FAMILIES

2-Hexenal:	*Polypodiaceae*[a] *Lauraceae*[a] *Piperaceae*[b] *Saxifragaceae*[b] *Rosaceae*[a,b] *Mimosaceae*[a] *Papilionaceae*[a,b] *Theaceae*[a,b] *Betulaceae*[a] *Fagaceae*[a] *Ulmaceae*[a] *Polygonaceae*[a] *Moraceae*[a] *Cruciferae*[a,b] *Myrtaceae*[b] *Umbelliferae*[a,b] *Caprifoliaceae*[a] *Oleaceae*[a,b] *Apocynaceae*[a] *Rutaceae*[a,b] *Aceraceae*[a] *Hippocastanaceae*[a] *Ericaceae*[b] *Vitaceae*[a,b] *Cucurbitaceae*[b] *Solanaceae*[b] *Labiatae*[a,b] *Salicaceae*[a] *Juglandaceae*[a] *Musaceae*[b]
1-Hexanol:	*Lauraceae*[a] *Saxifragaceae*[b] *Rosaceae*[a,b] *Papilionaceae*[b] *Theaceae*[a,b] *Violaceae*[a] *Passifloraceae*[b] *Caricaceae*[b] *Cannabinaceae*[b] *Cruciferae*[b] *Myrtaceae*[b] *Umbelliferae*[b] *Oleaceae*[b] *Rubiaceae*[b] *Geraniaceae*[a] *Rutaceae*[a,b] *Ericaceae*[b] *Vitaceae*[b] *Cucurbitaceae*[b] *Buettneriaceae*[b] *Solanaceae*[b] *Labiatae*[a,b] *Musaceae*[b] *Palmae*[b]
2-Hexen-1-ol:	*Saxifragaceae*[b] *Rosaceae*[a,b] *Papilionaceae*[b] *Theaceae*[b] *Cannabinaceae*[b] *Umbelliferae*[b] *Oleaceae*[b] *Rutaceae*[b] *Ericaceae*[b] *Vitaceae*[b] *Solanaceae*[b] *Labiatae*[b] *Musaceae*[b]
3-Hexen-1-ol:	*Piperaceae*[b] *Saxifragaceae*[b] *Rosaceae*[a,b] *Mimosaceae*[a] *Papilionaceae*[a,b] *Theaceae*[a,b] *Violaceae*[a] *Passifloraceae*[b] *Betulaceae*[a] *Fagaceae*[a] *Moraceae*[a] *Cannabinaceae*[b] *Cruciferae*[a,b] *Myrtaceae*[b] *Umbelliferae*[b] *Oleaceae*[b] *Geraniaceae*[a] *Rutaceae*[a,b] *Ericaceae*[a,b] *Vitaceae*[a,b] *Cucurbitaceae*[b] *Solanaceae*[b] *Labiatae*[a,b] *Gramineae*[a] *Musaceae*[b]

[a]Gildemeister and Hoffmann (1960, 1963).
[b]Van Straten (1977).

plant species: potatoes (Grosch et al., 1976), tomatoes (Galliard and Mattew, 1977; Kazeniac and Hall, 1970; Sieso et al., 1976), tea leaves (Hatanaka and Harada, 1973; Hatanaka et al., 1976a), peas (Grosch, 1968, 1969), apples and other fruits and leaves (Drawert et al., 1965, 1966), legumes like soybeans, and some cereal grains (Tappel, 1961), and are regarded as widely distributed.

Because enzyme inhibitors were not employed except for nitrogen in the present study, these products might be formed during the steam distillation of potato plant leaves and for that reason be regarded as biologically insignificant. However, vapor sampling of the air over potato plant leaves showed that these leaf alcohols and aldehydes are present (Visser and Schaefer, unpublished data).

These compounds are smelled by man as a grass-like odor. However, the ratio between the several products of this biosynthesis—the relative proportions of the different components—varies in and over different plant species. Within the same plant species, the proportions are modified seasonally (Hatanaka et al., 1976b) as caused by the expressions and/or the shift in the expressions of the several enzymes involved, owing to plant aging and injury (Buttery et al., 1971; Kazeniac and Hall, 1970; Sayo and Takeo, 1975). Consequently, unbalanced mixtures containing overdoses of one or more com-

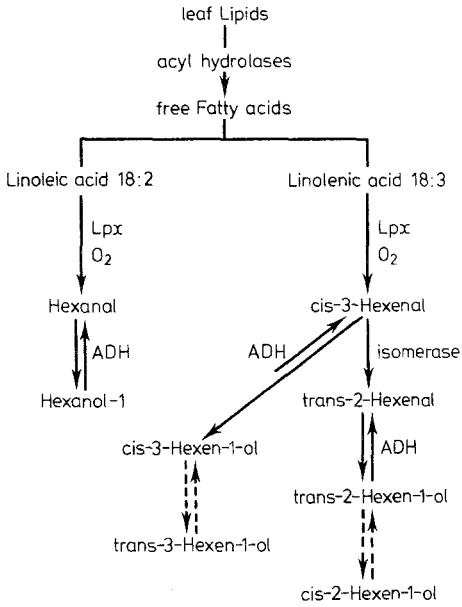

FIG. 6. The biosyntheses of the leaf aldehydes and alcohols, constituting a general green leaf volatile complex. Lpx: lipoxygenase (linoleate: oxygen oxidoreductase; EC 1.13.1.13); ADH: alcohol dehydrogenase (Alcohol: NAD oxidoreductase; EC 1.1.1.1). (According to: Drawert et al., 1966; Galliard and Mattew, 1977; Grosch, 1968, 1969; Hatanaka and Harada, 1973; Hatanaka et al., 1976a; Kazeniac and Hall, 1970; Sieso et al., 1976; Wardale and Galliard, 1977).

ponents, give an off flavor to the human sense, the haylike odors of several food products like deteriorated beans and peas (Whitaker, 1972).

In the same way, these leaf aldehydes and alcohols, constituting a general green leaf volatile complex, act in the olfactory orientation of the adult Colorado beetle. Electroantennogram recordings show the olfactory sensilla of the Colorado beetle to be mainly responsive to these types of compounds (Visser, 1979). In behavior tests none of these components, when applied singly, are attractive, whereas some of them, in minute quantities with potted potato plants, mask the attractive host plant vapors; that is, the beetles no longer react with an odor-conditioned positive anemotaxis (Visser and Avé, 1978).

The natural potato plant odor, attractive to Colorado beetles, appears to be the result of complex interactions between these leaf components. Detailed information of this system, probably operative to a variety of phytophagous insects, will be presented in subsequent papers.

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