

CHARACTERIZATION OF CHEMICALS MEDIATING
OVIPOSITIONAL HOST-PLANT FINDING BY
Amyelois transitella FEMALES

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Abstract—Ovipositional host-finding in the navel orangeworm, *Amyelois transitella* (Walker), is brought about by an in-flight response to host odors. Wind-tunnel studies of the response of gravid females to almonds showed that this response is mediated primarily by long-chain fatty acids, particularly oleic acid and linoleic acid. Evidence for the behavioral activity of fatty acids is based on the fact that: (1) behavioral activity of almond oil was concentrated in a single liquid chromatographic fraction whose composition was predominantly long-chain fatty acids, (2) behavioral activity was lost when either almond oil or the active fraction of that oil was treated with diazomethane, (3) full activity was elicited by a selective extraction of free fatty acids from crude almond oil, and (4) upwind response by females was elicited by a blend of synthetic oleic and linoleic acids, albeit at a level less than that elicited by almond oil. Five fatty acids identified from the almond oil were: myristic acid (1%), palmitic acid (16%), stearic acid (3%), oleic acid (58%), and linoleic (22%). Attraction to various combinations of synthetic acids was observed only when oleic acid was present, and oleic acid elicited upwind flights to the source when presented alone; however, short-range responses were enhanced by the addition of linoleic acid, which elicited no long-range

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orientation by itself. Despite significant levels of attraction to synthetic blends, the percentage of females flying to the source was lower than that flying to acidulated almond oil, the best natural attractant tested. Thus, although long-range response may be mediated primarily by a blend of oleic and linoleic acids, additional and as yet unidentified components must also play an important role. Long-range chemically modulated host finding in this and other generalist plant feeders is discussed with respect to current models of the evolution of host finding, and it is argued that suggestions that long-range host finding should be correlated with narrowness of host utilization are logically flawed and are not supported by our current understanding of specific examples of host finding.

Key Words—Host finding, *Amyelois transitella*, navel orangeworm, Lepidoptera, Pyralidae, flight behavior, chemoorientation, attraction, fatty acids, oleic, linoleic, palmitic

INTRODUCTION

Amyelois transitella (Walker), the navel orangeworm, was first detected in the United States in rotting fruit and its initial presence elicited little concern because of its apparent preference for fallen or diseased fruits (Wade, 1961); however, since that time, this insect has become the key pest of almonds, as well as a serious problem in pistachios and walnuts, causing nut growers in the western United States many millions of dollars in damage each year. Previous work based on field trapping suggested that host finding by the navel orangeworm was mediated by odors of almond nuts and/or volatiles from frass of navel orangeworm larvae (Curtis and Clark, 1979; Andrews and Barnes, 1982; Rice et al., 1984). A long-range response to almond odors was confirmed by Phelan and Baker (1987) in studies of flight by navel orangeworm females in a laboratory wind tunnel. This work demonstrated that mated females, but not males or virgin females could be induced to take off and fly more than 1.5 m up an odor plume of almond by-products. Unrefined oil from almonds was determined to be the most potent source of flight activity on a per-weight basis, with 100 mg of this oil eliciting a response several times greater than mummified almonds, the preferred sites of oviposition in the field. Recently, the zigzagging flight track of navel orangeworm females flying to host odors was analyzed in further detail by Haynes and Baker (1989), who describe track angles for females in contact with a host-odor plume and after loss of the odor plume. Comparison of various angular and velocity components of the flight pattern revealed a counterturning program very similar to that of navel orangeworm males flying to female sex pheromone.

In the present study, we examined the chemical basis of host finding in navel orangeworm females with the objective of characterizing the constituents of almond odor that are responsible for ovipositional attraction.

METHODS AND MATERIALS

Navel orangeworm larvae were reared on a honey-bran-glycerol diet according to the methods of Strong et al. (1968). Pupae were collected from rearing containers and were placed in cups with moist vermiculite held in mating cages. The behavioral characterization of almond-odor components responsible for ovipositional attraction of navel orangeworm females was carried out in wind tunnels at both institutions. The construction of the Riverside tunnel, which measured $0.6 \times 0.6 \times 1.8$ m, has been described previously (Willis and Baker, 1984). The tunnel at the OARDC is similar in operation although somewhat larger. The working portion of this tunnel measured 2.5 m long \times 1 m wide \times 0.5 m high and was constructed of 6-mm Plexiglas. Airflow was generated by a 3/4-horsepower Dayton model 3C152 fan with a 64-cm-diam. six-wing blade and was made laminar as it was forced through three muslin screens spaced 10 cm apart. The wind speed was maintained at 0.4 m/sec by a 61 \times 61-cm adjustable-louver box mounted on the upwind side of the fan box, which was equipped with standard fiberglass furnace filters to reduce the ambient dust reaching the muslin screens. The odor plume was exhausted from the downwind end of the wind tunnel and was directed outside the building by a 30-cm-diam. flexible exhaust duct and a 25-cm-diam. 1/15-horsepower exhaust fan. The tunnel was illuminated by three 60-W incandescent white bulbs mounted 1.2 m above the tunnel floor and operated at 30 V to provide 0.2 lx at floor level during bioassays. Females 3 to 6 days old were selected from the mating cages and were acclimated to experimental conditions by holding them in the wind without odors for 0.5 hr prior to testing, which was conducted 2.5-0 hr before lights-out. Odor sources were applied to a 5.5-cm-diam. filter-paper disk held 20 cm above the tunnel floor at the upwind end of the tunnel, and the female moths were released at the downwind end in groups of 10 individuals from 5.5-cm-diam. \times 9.0-cm-long screen release cylinders placed on a 15-cm-tall platform. Four categories of female behaviors were recorded: takeoff, flight up the plume, flight to the odor source (those approaching to within 5 cm of the source), and landing on the source. Treatments were presented individually in a randomized complete-block design. Percent response results were analyzed by two-way ANOVA after $\sin^{-1} (x + .005)^{1/2}$ and means were separated using Duncan's new multiple-range test (SAS, 1985), except for response to different quantities of acidulated almond oil, which was subjected to regression analysis.

Crude almond oil and almond soapstock were obtained from Liberty Vegetable Oil Co. (Sante Fe Springs, California). Soapstock is composed of salts of free fatty acids removed during the refining of vegetable oils by treating the oils with potassium or sodium hydroxide. The free fatty acids were reconstituted by making the soapstock strongly acidic (pH 3) with H_2SO_4 . The resulting oil, termed acidulated almond oil, was separated from the aqueous layer and an

unidentified intermediate layer in a separatory funnel. High-purity authentic samples (>99% by capillary GC) of constituents identified from almond oil were obtained from Aldrich Chemical Co. (Milwaukee, Wisconsin) and were stored at -20°C under nitrogen. Acidulated oils from various other commodities also were tested for their ability to evoke orientation by navel orangeworm females; these acidulated oils included peanut, corn, soybean, and palm kernel.

A preliminary fractionation of 0.5 ml crude almond oil was carried out using a silica-gel SepPak (Millipore Corp., Milford, Massachusetts), eluting with 2 ml hexane, 2 ml ether-hexane (5:95), 2 ml ether, and 2 ml methylene chloride. Fractions were bioassayed for behavioral activity by presenting them individually and in combination to females in the wind tunnel. Characterization of active constituents was carried out on a Hewlett-Packard 5890 capillary gas chromatograph interfaced with a Hewlett-Packard 5970 Mass Selective Detector (GC-MS); electron-impact mass spectra were generated at 70 eV. Splitless injections were made onto either DB-1 (30 m \times 0.25 mm ID, 0.25- μm film thickness) or DB-23 (30 m \times 0.25 mm ID, 0.25- μm film thickness) fused-silica capillary columns (J & W Scientific, Folsom, California). Fatty acids were extracted from 1 ml of crude almond oil by washing the oil three times with 4 ml of an aqueous 10% NaHCO_3 solution. The aqueous fractions were combined and brought to pH 3 with H_2SO_4 . This solution then was extracted three times with 10 ml hexane, and the hexane fractions were combined and concentrated to 1 ml under N_2 . Fatty acids were derivatized to their methyl esters with diazomethane generated from 1-methyl-3-nitro-1-nitrosoguanidine (MNNG) using a micro-diazomethane-generation apparatus (Aldrich Chemical Co.). Presence and position of double bonds were confirmed using the epoxidation method of Bierl-Leonhardt et al. (1980). After derivatization of fatty acids to methyl esters, double bonds were epoxidized and the epoxides were submitted to hydrogenation to reduce remaining double bonds in diunsaturated constituents. The resulting products were analyzed using GC-MS.

RESULTS

Wind-tunnel bioassay of the SepPak fractionation of crude almond oil demonstrated full activity to be contained in the ether fractions. Upwind flights to the source were 15/50 (30%) for crude almond oil, 17/50 (34%) for the ether fractions, and 14/50 (28%) for all fractions combined. No response was elicited by the hexane, hexane-ether, or methylene chloride fractions. GC analysis of the active fractions suggested the primary constituents to be fatty acids. Treatment of the fraction with diazomethane followed by GC-MS supported this initial supposition, as the original peaks, which tailed excessively, were now replaced with earlier-eluting peaks of much greater symmetrical shape (Figure

1). Mass spectrometry indicated methyl esters of myristic acid (1%), palmitic acid (16%), stearic acid (3%), oleic acid (58%), and linoleic (22%). The position of double bonds in each was confirmed by epoxidation, in which oleic acid produced the single compound 9,10-epoxyoctadecanoic acid, palmitoleic acid gave rise to 9,10-epoxyhexadecanoic acid, while linoleic acid produced two peaks, 9,10-epoxyoctadecanoic acid and 12,13-epoxyoctadecanoic acid. Diagnostic MS ions used for confirmation of double-bond position were m/z 155 and m/z 199 for 9,10-epoxyoctadecanoic acid, m/z 113 and m/z 241 for 12,13-epoxyoctadecanoic acid, and m/z 127 and m/z 199 for 9,10-epoxyhexadecanoic acid.

That almond-oil fatty acids played a role in navel orangeworm attraction was verified by treating crude almond oil with diazomethane. Only about a quarter as many females were attracted to the diazomethane-treated oil compared to the untreated oil (Figure 2). This level of response to diazomethane-treated oil was not significantly different from that to blank filter paper, which attracted no females. The reduction in the number of females landing on the treated oil was even greater, with a 24-fold higher response to the untreated oil. Navel orangeworm attraction to free fatty acids removed from crude almond oil was compared with that to crude oil using the amount of free fatty acids found in 100 mg of oil (3 mg for this batch of crude oil). Female navel orangeworm flew to the acidulated almond oil at levels significantly higher than to the crude oil ($45 \pm 3.4\%$ vs. $30 \pm 3.7\%$, respectively; $P < 0.05$, six groups of 10

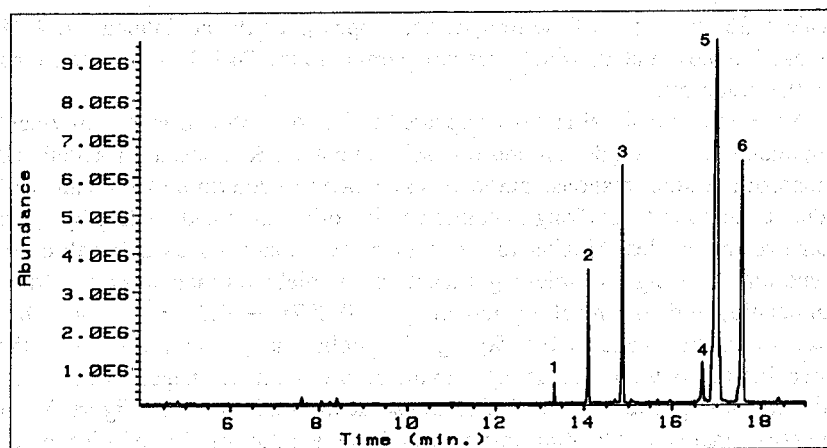


FIG. 1. Capillary gas chromatogram of the behaviorally active silica-gel fraction of crude almond oil after treatment with diazomethane. Column: DB-23 (30 m \times 0.25 mm). 1 = methyl myristate, 2 = 20 ng methyl pentadecanoate (internal standard), 3 = methyl palmitate, 4 = methyl stearate, 5 = methyl oleate, and 6 = methyl linoleate. Temperature program: 30°C increased to 200°C at a rate of 12°C/min.

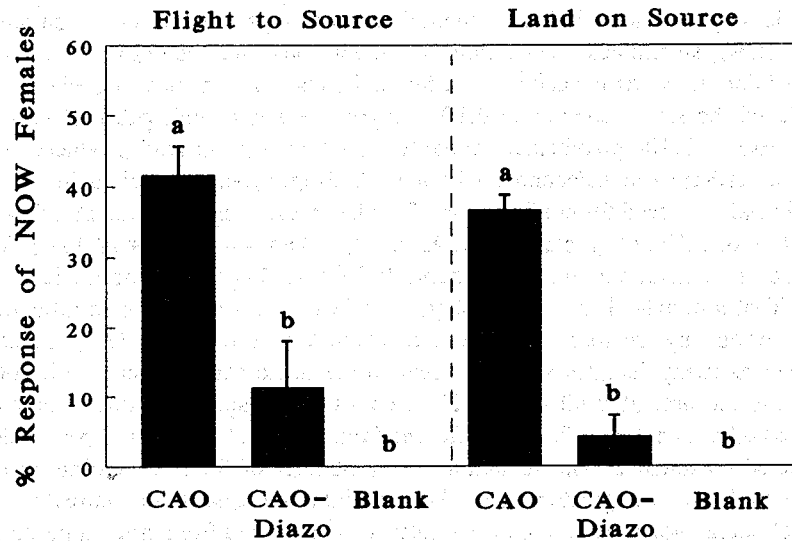


FIG. 2. Response ($\bar{X} \pm \text{SEM}$) of navel orangeworm (NOW) females to 100 mg crude almond oil (CAO), 100 mg CAO treated with diazomethane, or blank filter paper. Bars marked by the same letter are not significantly different ($P < 0.05$, six replicates of 10 females).

females). Furthermore, of the females that approached the acidulated oil, 93% of those females landed, which was comparable to the 94% landing rate found with the crude oil.

Since the behavioral activity appeared to be concentrated in the fatty-acid components of the crude almond oil, subsequent work focused on acidulated almond oil. A dose-response curve was generated to determine the quantity of acidulated almond oil evoking maximal upwind orientation and landing by navel orangeworm females. Flights to the source were analyzed as a fourth-order polynomial. The highest-order significant polynomial we found was a quadratic relationship, with the resulting model: $y = 0.057x - 0.001x^2$, $r^2 = 0.81$. Thus, within the range of 0.5–50 mg, the probability of female flight to the source increased with increasing amount of oil, with the negative quadratic indicating a slight leveling off of response at the highest dose (Figure 3). A regression analysis of landing response and the quantity of almond oil yielded a similar model: $y = 0.054x - 0.001x^2$, $r^2 = 0.81$. Furthermore, there was no evidence of premature arrestment at the higher levels of oil, as landing rates were similar in all quantities for which comparisons could be made. At 5 mg, 10 mg, and 50 mg of acidulated almond oil, landing rates were 92%, 90%, and

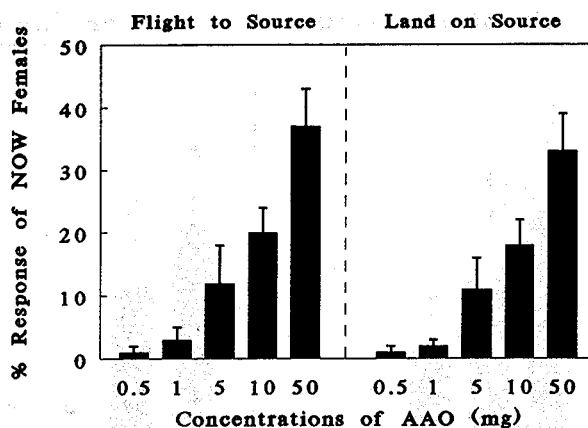


FIG. 3. Response ($\bar{X} \pm \text{SEM}$) of NOW females to different quantities of acidulated almond oil (AAO) (nine replicates of 10 females).

91%, respectively, for those females approaching the source, while percent approaches to the source at the lower concentrations were too low for informative comparisons. Since 50 mg of acidulated oil evoked the greatest long-range response without premature arrestment, this became the positive control in subsequent bioassays to which other treatments were compared.

A wind-tunnel bioassay of acidulated oils from commodities other than almonds indicated that the behaviorally active constituents were not unique to almonds (Figure 4). Acidulated peanut oil evoked the second highest response, with the number of females flying up to and the percentage landing on the source slightly lower than that to acidulated almond oil. The number of flights to acidulated corn oil was lower still, with the number of landings much lower. Responses to acidulated soybean and palm kernel oils were significantly lower than other oils tested, with no females flying to palm kernel oil.

Binary combinations of synthetic samples of either myristic and palmitic acids or palmitic and linoleic acids elicited no flights to the source when presented at the amounts found in 50 mg acidulated oil (Figure 5). Although the combination of oleic and palmitic acids did evoke some flights to source, this activity was not significantly higher than zero. The highest activity elicited among binary combinations was that to oleic plus linoleic acids. This blend attracted 40% of females to the source, not significantly different from that to the five-acid blend. Acidulated almond oil evoked more flights to the source than any combination of synthetic fatty acids tested, 59% of females, although this was not significantly higher than the response to the oleic-linoleic acid blend. The difference in response to natural compared to synthetic odor sources

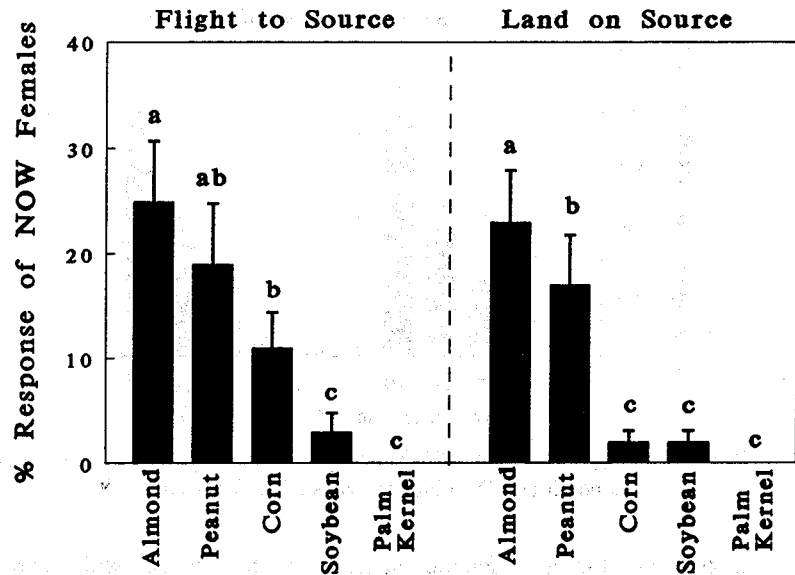


FIG. 4. Response ($\bar{X} \pm \text{SEM}$) of NOW females to 50 mg of various acidulated oils. Bars marked by the same letter are not significantly different ($P < 0.05$, 12 replicates of 10 females).

was much more pronounced when the number of landings were measured. The most active synthetic blend, oleic acid plus linoleic acid, only evoked landing in 14% of females, which represented 35% of those approaching the source, whereas 86% of females approaching acidulated almond oil landed on the source. The proportion of females landing on the oleic-linoleic acid blend was not significantly different from the proportion landing on the total-fatty-acid blend (10% of all females, 32% of source-approaching females). Finally, oleic acid and linoleic acid were tested individually to determine the relative contribution of these two components to navel orangeworm female attraction. When comparing flights to the source, oleic acid elicited a response comparable to that of the synthetic total fatty-acid blend (Figure 6), while linoleic acid elicited no flights to the source. However, the number of females landing on oleic acid was significantly lower than the number landing on the four-acid blend. These overall female landing rates corresponded to 36% of females approaching oleic acid and 65% of females approaching the five-acid mixture. As in the previous experiment, more females approached the acidulated almond oil than approached the synthetic fatty acids, with the difference in response amplified when landing rates were compared; of females approaching the acidulated oil, 81% landed.

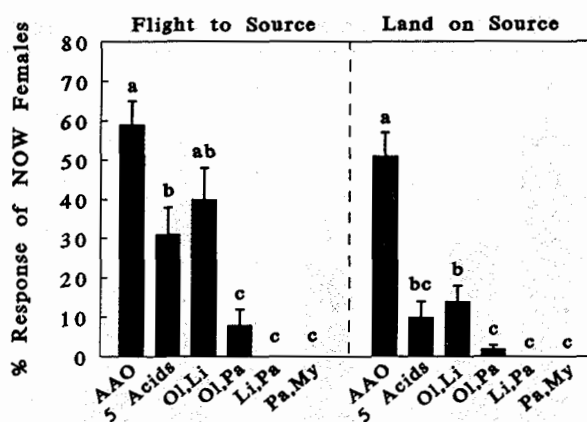


FIG. 5. Response ($\bar{X} \pm \text{SEM}$) of NOW females to 50 mg acidulated almond oil (AAO), a blend of five synthetic fatty acids: 29 mg oleic (Ol), 11 mg linoleic (Li), 8 mg palmitic (Pa), 1.5 mg stearic, and 0.5 mg myristic (My), or various binary combinations of these acids. Bars marked by the same letter are not significantly different ($P < 0.05$, nine replicates of 10 females).

DISCUSSION

The role of volatiles in navel orangeworm ovipositional behavior was first implicated by Ortega (1950), who observed greater navel orangeworm egg-laying in walnuts previously damaged by navel orangeworm larval feeding; Caltagirone et al. (1968) made similar observations in almonds. Curtis and Clark (1979) confirmed this increased egg-laying to be chemically mediated by demonstrating that it also could be elicited by extracts of the larval frass. The results of our bioassay-guided identification of navel orangeworm ovipositional attractants strongly suggest a primary role played by long-chain fatty acids in eliciting this behavior. Our wind-tunnel observations demonstrated that despite the relatively low volatility of these compounds, gravid navel orangeworm females can detect and respond to them from a distance of at least 2 m. Evidence for the behavioral activity of fatty acids derives from our observations: (1) that the behavioral activity of almond oil was concentrated in a single liquid chromatographic fraction whose composition was predominantly long-chain fatty acids; (2) that behavioral activity was lost when either almond oil or the active fraction of that oil was treated with diazomethane, a reagent narrowly reactive with acidic compounds; (3) that full activity could be elicited by a selective extraction of free fatty acids from crude almond oil; and (4) that upwind response by females could be elicited by a blend of synthetic oleic and linoleic acids, albeit at a level less than that elicited by almond oils. Although treatment of the almond

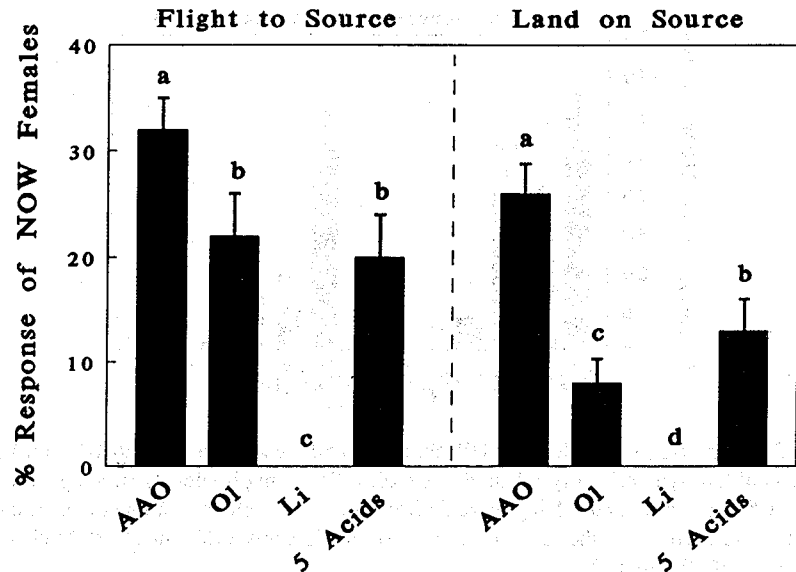


FIG. 6. Response ($\bar{X} \pm \text{SEM}$) of NOW females to acidulated almond oil (AAO), 29 mg oleic acid (Ol), 11 mg linoleic acid (Li), or a blend of five synthetic fatty acids: 29 mg oleic, 11 mg linoleic, 8 mg palmitic, 1.5 mg stearic, and 0.5 mg myristic. Bars marked by the same letter are not significantly different ($P < 0.05$, 22 replicates of 10 females).

oil with diazomethane greatly diminished response, some upwind orientation persisted. This may have been due to the methyl esters acting as fatty-acid analogs, evoking a low level of response in females, or it may indicate that additional non-fatty-acid components of almond odor play a secondary role in navel orangeworm attraction. The fact that acidulated oils from other commodities can elicit a long-range response in navel orangeworm females also is suggestive that ubiquitous long-chain fatty acids are the key components modulating host finding, rather than volatile compounds unique to almonds. Moreover, the level of response to the acidulated oils was correlated with the relative proportion of oleic acid in those oils. Acidulated peanut oil, which we determined to be composed of 57% oleic acid, 18% linoleic acid, and 18% palmitic acid, had the fatty-acid composition most similar to acidulated almond oil and elicited the highest level of response. Acidulated corn oil, which is 26% oleic acid, 59% linoleic acid, and 12% palmitic acid, elicited a lower navel orangeworm response. Acidulated soybean oil is only 22% oleic acid, 55% linoleic acid, 11% palmitic acid, and in addition contains 8% linolenic acid. Acidulated palm kernel oil is predominantly lauric acid (51%) and contains only 15% oleic acid and only 1% linoleic acid. This oil evoked no upwind flights to the source.

In an early attempt to discover chemical attractants for the navel orangeworm, Price et al. (1967) screened over 200 compounds with a variety of chemical functionalities placed in water-bucket field traps. Those compounds consistently eliciting the highest trap catch were all phenyl-containing constituents, with phenyl propionate being the most active compound. The trap catch by all chemicals was strongly female-biased. It is not known what function if any these compounds serve in the chemical ecology of the navel orangeworm; however, they do not appear to be important in ovipositional behavior, as Curtis and Clark (1979) later reported that phenyl propionate actually inhibited navel orangeworm egg-laying. One possibility is that they elicit food-finding behavior in adults foraging for nectar sources. Later, Lieu et al. (1982a,b) identified 42 components from a steam distillation extraction of wheat bran, predominantly aldehydes, and almost 50 components from an ether extract of larval frass, including the same long-chain fatty acids found to be behaviorally active in the present study; however, although both of the original substrates were known to elicit oviposition and presumably attraction in the field (Rice et al., 1976; Curtis and Clark, 1979), none of the identified constituents evoked a significant navel orangeworm response in a laboratory ovipositional bioassay. This was true even when a blend of the four principal long-chain fatty acids was presented. The discrepancy in results between these earlier studies and our own probably are due to the difference in bioassay methods. While Lieu et al. (1982a,b) were measuring an ovipositional response, our use of the wind-tunnel bioassay allowed us to observe the long-range orientation of navel orangeworm females. Since we found a lower landing response to the synthetic fatty acids relative to the almond oils, this probably explains why Lieu et al. (1982a,b) did not measure a significant ovipositional response to these compounds.

Despite the importance of understanding how insects locate their host plants, surprisingly few systems have been characterized for the chemicals responsible in long-range host finding. In fact, this paucity of well-studied examples has led Jermy et al. (1988) to suggest that "distant olfactory attraction to host plants in nature may be much rarer than has been thought." We use the term "long-range response" to chemicals *sensu* Kennedy (1977), who defined it mechanistically as chemically modulated orientation far enough from an odor source to preclude chemotactic response to a longitudinal chemical gradient. In practice, this usually represents a distance greater than a few decimeters. Many studies have suggested a role played by volatiles in host finding and/or selection by phytophagous insects (reviewed by Ramaswamy, 1988). Unfortunately, the evidence typically is circumstantial or at best confounds short-range acceptance behaviors with long-distance orientation to host odors, since conclusions are usually based on "end-result" observations or nondiscriminating bioassays (Kennedy, 1977). Furthermore, tests of synthetic host-plant compounds rarely utilize release rates comparable to a natural odor source. Some of our best doc-

umented cases for the role of volatile chemicals in long-distance host-finding are found in phytophagous flies. In a series of wind-tunnel studies, Hawkes and Coaker (1979, *et ante*) documented host-odor-modulated anemotaxis in the cabbage fly, *Delia brassicae*. In response to volatiles from crucifers, these flies landed in the plume, faced upwind, and walked or made a series of hopping flights to the odor source. The same behaviors also were observed in the field, and it was concluded that response to host odors can occur from greater than 15 m (Hawkes, 1974). This orientation behavior has been characterized more recently in greater detail by measuring flight track angles and insect airspeed in response to discrete plumes and dispersed clouds of allylisothiocyanate, a major volatile constituent of crucifer odors (Nottingham and Coaker, 1985). Similar behavioral responses have been documented for the onion fly (*Delia antiqua*) as reviewed by Miller and Strickler (1984), and the apple maggot fly (*Rhagoletis pomonella*). The latter, whose host-finding behavior also has been examined in the wind tunnel, shows the same chemically modulated response to a blend of synthetic 8- to 10-carbon esters as to an extract of apple volatiles (Fein et al., 1982).

In concurrent and complementary discussions by May and Ahmad (1983) and Lance (1983) on the proximal mechanisms of host finding in oligophages and polyphages, respectively, it is argued that breadth of host utilization by an insect herbivore (among other factors) will be a major determinant in the evolution of long-range response to host odors. The basic premise underlying this argument is that since the host of the specialist is more likely to be rarer and interspersed among nonhosts, there is a more intense selection pressure to be able to recognize and locate the host from a distance. Correspondingly, generalist feeders are less likely to "require accurate, specific, long-distance orientation mechanisms" (Lance, 1983). It is postulated that once the generalist is in contact with a plant, the variation in suitability of plant material is better assessed by gustatory stimuli and/or cues from other modalities. However, although the selection may be less intense for herbivores with broad dietary ranges than for the specialist feeders, nonetheless there is an adaptive advantage in the use of more efficient mechanisms for generalists as well. Thus, while the nature of the chemical cues utilized and the narrowness of the tuning of the herbivore's receptor system would be expected to differ between two species with different breadths of host range, there is no reason to believe that a broad host range would obviate host-plant finding by a long-range response. Furthermore, as pointed out by May and Ahmad (1983), evidence to support the specialist feeder-long-range host-finding model is not only lacking but actually runs counter. For example, the highly polyphagous *Schistocerca gregaria* can use odor-modulated anemotaxis to locate its host from a distance (Kennedy and Moorehouse, 1969), and the Japanese beetle appears to use a diverse group of compounds in finding its hosts, based on observations of beetles flying into

baited traps from a distance (Fleming, 1969; Ladd and McGovern, 1984 and references therein). Long-range chemoorientation to host odors also has been demonstrated recently in another polyphagous feeder, *Trichoplusia ni* (Landolt, 1989), as well as in the broadly feeding nitidulid beetles, *Carpophilus hemipterus* and *C. lugubris* (Blackmer and Phelan, in press; Phelan and Lin, in press), all of which display zigzagging flight up a laboratory wind tunnel to a variety of host odors and/or synthetic blends. The navel orangeworm is extremely broad in its host diet, feeding on the nuts, fruits, and seed pods from plants as diverse as *Acacia*, citrus, almonds, and *Yucca* (Wade, 1961). The detailed behavioral studies on the navel orangeworm (Phelan and Baker, 1987; Haynes and Baker, 1989; and this study) leave little doubt that host finding in this insect also is based primarily on a chemically modulated long-distance response.

In conclusion, we would submit that the proposed relationship between narrower host-plant utilization and increased powers of long-range host location is not supported by the evidence of well-studied examples, including the navel orangeworm. Here we have demonstrated that ovipositional host finding by the broadly feeding navel orangeworm is mediated at some distance from the host by means of a long-range response to a blend of long-chain fatty acids, primarily oleic and linoleic acids. However, although a synthetic blend of these chemicals can elicit upwind flights to the odor source, it does not reproduce the same level of navel orangeworm response as either crude or acidulated almond oils. This difference between response to natural compared to synthetic sources of odor was even greater when close-range behaviors such as landing were considered. Although the behaviorally active acidulated almond oil is composed almost solely of long-chain fatty acids, the relatively low vapor pressure of these components would make their relative abundance in the volatile profile greatly reduced. Thus, minor components of these oils, such as products of fatty-acid breakdown probably represent a significant contribution to almond odors. Work presently is being carried out to characterize the potential behavioral role played by these more volatile constituents in eliciting close-range response to host odors.

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