INFLUENCE OF HOST PLANT ON THE BIOLOGY,

MORPHOLOGY, BIOCHEMICAL, AND GENETIC

CHARACTERISTICS OF *APHIS GOSSYPII* AND

THE EFFECT OF HOST SWITCHING IN
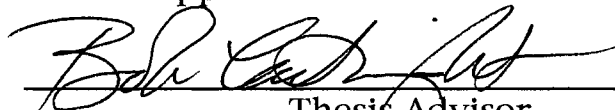
LYSIPHLEBUS TESTACEIPES

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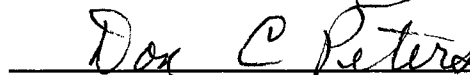Colorado State University
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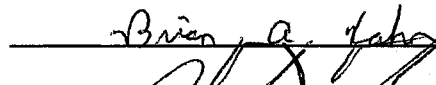INFLUENCE OF HOST PLANT ON THE BIOLOGY,

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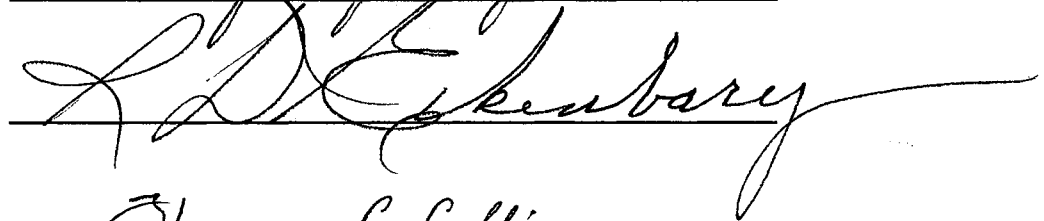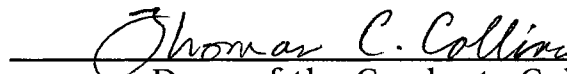
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TABLE OF CONTENTS

APPENDICES

LIST OF FIGURES

Chapter   Page

IV

INTRODUCTION

The Purpose

Aphis gossypii (Glover) is an important pest of agriculture. It has achieved this status by its adaptability to a wide range of different hosts, and its ability to transmit some of the most destructive plant viruses. The most important crops that this aphid damages by feeding are in the Malvaceae (cotton and okra) and Cucurbitaceae (melons, squash, cucumbers). At high densities the aphid can kill its host , but losses occur well before this point (watermelon: Cartwright 1992, cotton: Andrews & Kitten 1989) from aphid feeding. In some crops, damage also occurs from contamination with honeydew which is sticky and promotes the growth of mold.

In the past, this aphid has been controlled with a wide array of different insecticides including dichlorodiphenyltrichloroethane (DDT) and Arsenic. The growing concern over the use of pesticides is a major theme in much of agriculture mainly due to concern over environmental contamination, and the economic impact of pesticide resistance. Part of the response in the USA is to promote reduced dependence on pesticides, and an increased reliance on beneficial organisms to control pests. This requires detailed knowledge of the pest's biology, and its interactions with other organisms and the environment.

Overview and Objectives

Why is the parasitoid *Lysiphlebus testaceipes* (Cresson) effective in controlling *Aphis gossypii* in the greenhouse but is not usually a significant source of mortality for this aphid in the field? Among the many possible answers, it is possible that the wasp has difficulty switching between different host plant - host aphid systems. For example, in controlling *A. gossypii* in

1

watermelon, the wasp must change host plant and host aphid to survive the winter in Oklahoma. As the crop is harvested the plants are destroyed and the wasp must change to some other ecosystem to survive. It must then change back when melon aphid populations reform on watermelon the following summer. This phenominon of host switching resulted in two related questions. What is the biological cost to the wasp of switching aphid species and what is the cost to the wasp of switching to a different host plant? The literature contains several papers which suggest that there should be a cost involved when the wasp changes aphid-plant systems, but the effect has not been examined in any detail. To further complicate the experiment, there is not a great deal known about the influence of host plant on the aphid, and without knowing a great deal about the aphid-plant system it is very difficult to unequivocally evaluate the wasp-aphid-plant system.

As a preliminary step in evaluating the effect of aphid-plant switching in *L. testaceipes*, it was important to determine if there were biological differences in *A. gossypii* colonies on different host plants. To achieve this objective, *A. gossypii* was reared on four host plants. Squash, watermelon, and cotton are all common hosts for this aphid and were selected as host plants for this reason. Wheat was chosen as the fourth host because it is highly unusual to find *A. gossypii* on this host. Phylogenetically, wheat is only distantly related to the other hosts so it provided an extreme observation with which to compare the results from experiments using squash, watermelon, and cotton.

Variation in the aphid on the hosts was measured using morphological characters, epicuticular hydrocarbons, internal fatty acids, and RAPD-PCR which identifies differences in the genome. The birth rate of the aphid was also examined as one measure of the significant biological differences that could separate the aphids on different hosts.

After an examination of the aphid-plant interaction the thesis returns to the original question about the effect of the aphid and aphid host on the parasite. The host plants chosen for this were watermelon and wheat. Wheat was used as the other host not only because of its function as an unusual host, but also because a common pest aphid of wheat, the greenbug (*Schizaphis graminum* (Rodani)), is an alternate host for *L. testaceipes* and could help tmaintain parasite populations during periods when melon aphid is scarse.

3

REVIEW OF THE LITERATURE: *Aphis gossypii*

Aphis gossypii (Glover) is an important pest of agriculture. It has achieved this status by its adaptability to a wide range of different hosts, and its ability to transmit some of the most destructive plant viruses. The most important crops that this aphid damages by feeding are in the Malvaceae (cotton and okra) and Cucurbitaceae (melons, squash, cucumbers). At high densities, aphids can kill their host plant, but losses occur well before this point (watermelon: Cartwright 1992, cotton: Andrews & Kitten 1989) from aphid feeding. In some crops, such as cotton and cantaloupe, damage also occurs from contamination with honeydew which is sticky and promotes the growth of mold.

In the past, this aphid has been controlled with a wide array of different insecticides including DDT and arsenic. The growing concern over the use of pesticides is a major theme in much of agriculture mainly due to concern over environmental contamination, and the economic impact of pesticide resistance. Part of the response in the USA is to promote a reduced dependence on pesticides and an increased reliance on beneficial organisms to control pests. This requires a detailed knowledge of the biology of the pest, and its interactions with other organisms and the environment.

This review is designed to summarize the literature on *A. gossypii* in an effort to point out areas that require further research. One possible flaw in the review is the taxonomic uncertainty surrounding this aphid. This review assumes that all research projects dealing with the biology of the aphid are all using *A. gossypii*. This review is most comprehensive between 1970 and 1992. Articles in languages other than English were examined, but critical evaluation of procedures and analysis was frequently not possible. In cases

4

with an apparent conflict between text and data presented in tables and figures, it was assumed that the table or figure was correct. Articles dealing with pesticide efficacy have been omitted except in cases where they provide insight or corroborative detail on the biology of the aphid.

Because the host plant is an important aspect of the biology of this aphid, an effort has been made to convert old taxonomic names into their more modern equivalents. Where possible the work by Huxley et al. (1992) has been used along with the conventions used therin. When the plant was not found there Tanaka (1976) was used. If the plant was not found in either work, it was left as used in the original paper. If the name required changing, the name used in the original usage is listed in parentheses following an equals sign.

TAXONOMY

SYNONYMS: Ilharco and van Harten (1987) stated that there are 41 synonymous scientific names for this aphid. Some of the more recent common names given to this aphid include: melon aphid, cotton aphid, betelvine aphid, green aphis, and brinjal aphid. Of these, the first two are the accepted common names by the Entomological Society of America. Brinjal aphid is frequently used in literature from India.

MORPHOLOGY: The classical method of distinguishing species is through the morphology of individuals. Morphology is also useful for distinguishing between different stages in insects and other organisms. Singh and Srivastava (1989) used cornicle length as a means to distinguish between instars of *A. gossypii* reared under fluctuating temperatures. There was considerable overlap between instars, but there was no overlap between nymphs and adults. Inaizumi and Takahashi (1989) reported on methods to distinguish between

5

instars of aphids reared at constant temperature using a number of different characters. Inaizumi and Takahashi reported that first instar nymphs may be distinguished by having only 4 antennal segments, whereas second instars have 5 segments. Differences between second and third instars are fairly small but at constant temperatures they can be separated using a combination of characters. Third instars have no setae on the margin of the genital plate, while fourth instars have such setae. Second instar nymphs with developing wings appear to have shoulders, third instar nymphs have small wing pads, and the developing wings are prominent on fourth instar nymphs.

The following stages have been illustrated by Inaizumi (1980) for this aphid in Japan: fundatrix, fundatrigeniae, alienicola, gynoparae, oviparous female, alate and apterous male, and hibernating viviparae. Ghovanlou (1974) provided illustrations of the alate and apterous viviparae from aphids in Iran. Morphological differences based on the setae of the 8th abdominal tergite were reported by Inaizumi (1983) for the virginandroparae, androparae, heteroparae, and androgynoparae in addition to those forms listed previously. There are also occasional individuals with partly developed wings from nearly apterous to nearly functionally winged (Inaizumi 1968). Miyazaki (1987) and Moran (1992) provided definitions for the different stages of the life cycle of aphids.

The internal morphology of *A. gossypii* has not been given much attention, but there is a paper that describes the morphology of the brain of *A. gossypii* reared on *Brassica* sp. (Satija and Dhindsa 1968).

LIFE HISTORY

HOST RANGE: The world wide distribution of *A. gossypii* is due in part to its broad host range (Table 1). The table is organized using the phylogenetic

6

relationship of the hosts according to the Cronquist system of classification (in Jones & Luchsinger 1986). The families listed are ones where at least one plant species has been recorded as a host, but the quality of the host is uncertain. The species listed, are plants useful to man where there is some indication that *A. gossypii* has adapted to the host, usually as documented by papers on the chemical control of the aphid. This organization emphasizes both the diversity of the host range and the impact this aphid has on human activities. Two observations suggest that this list could apply to a single species rather than a hodgepodge of closely related species. ONE) Inaizumi (1980) examined population growth over a fifteen day period for *A. gossypii* transferred from plants in the Scrophulariaceae, Brassicaceae, Asteraceae, Lamiaceae, Rosaceae, and Malvaceae to plants in the Asteraceae, Solanaceae, Cucurbitaceae, Liliaceae, Portulaceae, Commelinaceae, and Araceae. TWO) Batchelder (1927) transferred aphids from plants in the Cucurbitaceae to plants in the Begoniaceae, and Onagraceae with the colonies surviving for at least 3 months. In addition, we were able to transfer *A. gossypii* from plants in the Cucurbitaceae to plants in the Poaceae, and have the colony survive for over two years.

REPRODUCTIVE BIOLOGY: Reproduction in *A. gossypii* is mostly asexual with either alate or apterous females. In warmer environments, this aphid exhibits an anholocyclic life cycle, while in cooler areas the aphid also has a sexual phase, exhibiting either a heteroecious or autoecious holocyclic life cycle (Zhang & Zhong 1990, Slosser et al. 1989). The heteroecious cycle involves a migration from a primary host to a secondary host in the spring and a return to a primary host in the fall. It is usually assumed that the primary host was the original host of the aphid. A primary host may be defined as a host where

the aphid lays eggs to survive cold temperatures. In Japan this aphid lays eggs on *Citrus* (Rutaceae), *Hibiscus syriacus* L. (Malvaceae), *Rhamnus dahuricus* Pall. (=*Rhamnus nipponica*) (Rhamnaceae), *Celastrus orbiculatus* Thunb. (Celastraceae), and *Rubia cordifolia* L. (Rubiaceae) (Inaizumi 1980, Komazaki et al. 1979). In the USA this aphid lays eggs on *H. syriacus* and *Catalpa bignonioides* Walter (Bignoniaceae) (Kring 1959). In the Peoples Republic of China this aphid lays eggs on *Zanthoxylum simulans* Hance (Rutaceae), *Rhamnus* sp. (Rhamnaceae), and *Punica granatum* L. (Lythraceae) (Zhang & Zhong 1990). Zhang and Zhong (1990) suggest that *Z. simulans* was the original host of this aphid, arguing that it is the most primitive host where the aphid overwinters and produces sexuals. Furthermore, the life cycle of the aphid is better synchronized with *Z. simulans* relative to the other two hosts they examined, *P. granatum*, and *Rhamnus sp.* However, these arguments are flawed. According to the Cronquist system of classification (in Jones & Luchsinger 1986), *P. granatum* is more primitive than *Z. simulans*. Arguments using the degree of synchronization between life cycle of host and aphid are subject to controversy until the "true" point of origin of the aphid is identified. Until this is known, it would be expected that different authors will find different plants best synchronized with the aphid based on local hosts availability and climate. Zhang and Zhong (1990) argue against *H. syriacus* as the primary host because *A. gossypii* is almost completely autoecious on this host, and this host is more advanced than either of the two previously listed. Their plant phylogeny is correct in this case, but Inaizumi (1980) reported that *A. gossypii* on *H. syriacus* in Japan will move onto secondary hosts, and of the primary hosts, the aphids did best in the transfer from *H. syriacus* relative to the other primary hosts examined (*Z. simulans* was not examined by Inaizumi). The original host for this aphid may remain unknown because this

aphid has demonstrated the ability to acquire new primary hosts. Considering its polyphagous nature, it may secondarily adopt a new primary host that is more primitive than the "true" original host.

Reproductive rates in *A. gossypii* have been reported in two forms; birth rate as measured in nymphs produced per day per aphid; and net reproductive rate (R_0) which is an interaction between birth rate and survival rate (Wilson & Bossert 1971). R_0 is frequently reported along with other life table parameters and is useful in projecting future population trends. The additional information required to estimate R_0 is more difficult to obtain than just the birth rate. As a result, authors have either chosen to intensively study the aphid on a single host plant to estimate R_0 and other life table parameters, or they have used multiple host plants but only report the birth rate.

The following authors reported R_0 for this aphid on selected host plants: Aldyhim & Khalil (1993) on squash (*Cucurbita pepo* L.), Komazaki (1982) on Citrus (*Citrus unshiu* Marc.), Liu & Perng (1987) on pumpkin (may be squash, no scientific name provided), Nozato (1987a) on *Veronica persica* Poir, Setokuchi (1981) on taro (*Colocasia esculenta* (L.) Schott. (= *C. antiquorum*), and Wyatt & Brown (1977) on cucumber (*Cucumis sativus* L.). In comparing results from different studies, host plant, temperature, light, and an interaction between temperature and host plant all influence reproductive rates in this aphid. The interaction is apparent when examining R_0: Aldyhim & Khalil (1993) give the highest R_0 (79.7) at 25°C with a 15% decrease at 30°C with squash, examining temperatures between 10 and 30° C with 5 degree increments; Komazaki (1982) gives the highest R_0 (58.68) at 19.8°C with a 6% decrease at 29.7° C with citrus, examining 5 temperatures between 15.2 and 29.7° C; Liu & Perng (1987) give the highest R_0 (109.14) at 21°C with a 44%

9

decline at 30°C in pumpkin, examining temperatures of 16, 21, 25, 27, 28.5, and 30° C.

One could argue that these differences are due to innate variability in the aphid, and this certainly could explain some or all of the differences. However, Akey and Butler (1993) in Arizona and Isely (1946) in Arkansas both looked at the effect of temperature on the reproductive rate of *A. gossypii* feeding on cotton (populations separated in space and time). The development time was minimized at 27.5° C and 28° C as reported by each author(s) respectively. At these temperatures the aphids took 5.0 and 5.18 days to reach maturity. The optimal temperature for fecundity as measured by these author(s) (in nymphs/adult/day) was significantly different (25° C versus 20° C), which resulted in 2.85 versus 2.69 nymphs per adult per day at the respective temperatures. The similarity of the results between these authors supports the validity of comparing R_0 as was done in the previous paragraph.

The following authors used birth rates to look at differences between colonies of this aphid feeding on different host plants. Kishaba and Coudriet (1985) reported birth rates of this aphid reared on several hosts in the Cucurbitaceae, and found decreased reproduction on a resistant muskmelon line relative to a susceptible line. Kandoria and Jamwal (1988) reported birth rates for this aphid reared on okra (*Abelmoschus esculentus* (L.) Moench.), eggplant (*Solanum melongena* L.), and chili (*Capsicum annuum* var. annuum L.), and found no significant differences. Ekukole (1990) found significant differences in birth rates of this aphid reared on cotton (*Gossypium hirsutum* L.), watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai), and groundnut (*Arachis hypogaea* L.). Moursi et al. (1985) found significant differences in the reproductive potential of this aphid on cotton, watermelon, sesame (*Sesamum indicum* L.), and eggplant. Ghovanlou (1976) reported that

10

development time was shortest on cotton, longest on melon, with watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai (=Cucurbita citrillus)) splitting the difference.

Based on these studies, differences in reproductive potential among different host plants appears to be common, and many authors have found reproductive rate highly correlated with host plant. However, after examining 90 aphid species on 120 hosts, Llewellyn and Brown (1985) reported that there is a significant host plant effect, but if the goal is to estimate the birth rate, models using only aphid size are as good as models that include host plant. Furthermore, the coefficient for host plant is not significantly different from zero in models using size that also include host plant. Llewellyn and Brown's observation was confirmed in *A. gossypii* by the author.

ALATE PRODUCTION: Reinhard (1927) reported on factors inducing wing formation in *A. gossypii* reared on cotton. In general, starvation and crowding induced alate production, and apterous adults had a greater tendency to produce alates than did alate adults under similar conditions. In looking at stress effects, the author starved aphids for 6 to 8 hours during a 24 hour period. Increased alate progeny resulted if adults were starved during development or during the reproductive period. Increased alate progeny also resulted when adults were well fed, but nymphs were starved. In looking at crowding effects, Reinhard left the aphids on the plant to reproduce - as opposed to the uncrowded condition where nymphs were removed. Uncrowded aphids never produced alates while under crowded conditions alates would be produced. Reinhard did further experiments which strongly indicate that nutritional deficiencies are not the cause of alate production under crowded conditions. Reinhard reported that temperature alone was insufficient to

induce alate production within the mean temperature range of 21.6° C to 31.5° C with extremes of 15.6° C to 38.9° C. Reinhard (1927) also suggests that relative humidity does not influence alate production, though this factor was not directly examined. The effect of starvation for 6 to 8 hours on alates can be assessed by determining the length of time it takes to starve to death. Nozato (1989a) starved alates (probably from *Veronica persica*) at different temperatures. Alates lived an average of 12 days at 12° C, 5 days at 18° C, and about 2 days at 27° C. Unfortunately, Reinhard (1927) did not provide the temperature nor humidity at which his experiments were done.

COLOR VARIATION: Wall (1933) examined color variation in *A. gossypii*. Extreme individuals were easily categorized as yellow or green, but intermediate forms created an almost continuous series from a light yellow-green to almost black. The yellow form was most frequently associated with hot summer conditions and was usually smaller. The green form was most often associated with cooler temperatures, and uncrowded conditions. Setokughi (1981) provided further evidence that temperature was one of the driving forces in determining color, with yellow more prevalent at higher temperatures. Regupathy and Jayaraj (1973) reported that the relative proportions of the yellow and green morphs were also influenced by host plant. Wall (1933) and Setokughi (1981) demonstrated that color morphs were able to produce progeny of the other morph. Wall (1933) reported green morphs produced more alate offspring than do yellow morphs. However, his observation could be the result of crowding, as the green form also produced more total offspring.

GENETIC CHARACTERS: There are few papers looking at the DNA of this aphid. Khuda-Bukhsh and Datta (1978) reported that in *A. gossypii* 2n=8 (found on *Ageratum conyzoides* L. (Asteraceae) in India). The chromosomes in cells during metaphase measured 2.3, 3.4, 3.8, and 5.0 μm in length. Using aphids from a different location Khuda-Bukhsh and Pal (1985) reexamined the karyomorphology of this aphid and reported that chromosome lengths were 3.65 ± 0.54, 5.42 ± 0.44, 6.24 ± 0.48, and 7.64 ± 0.85 μm (collected from *Erobtorys japonica* (Rosaceae) in India). Khuda-Bukhsh and Pal (1985) provided further discussion of the processes occurring during cell division. Khuda-Bukhsh and Kar (1989) reported differences in length between members of each pair of chromosomes. They report chromosome lengths of 2.00, 2.25, 3.55, 3.80, 4.00, 4.50, 6.45, and 6.80 μm. The chromosomes are believed to be holokinetic which could simplify structural rearrangement of the chromosomes, and permit the aphid to better adapt to adverse conditions, including new host plants. Chromosomal rearrangement has been implicated in pesticide resistance in the aphid *Myzus persicae* (Blackman et al. 1978). The effect appeared to be due to a translocation which was correlated with an increase in carboxylesterate (est-4) activity.

Another method of looking at DNA, random amplified polymorphic DNA polymerase chain reaction (RAPD-PCR), has been used by the authors to detect differences in *A. gossypii* colonies. Cenis et al. (1993) also used this technique to examine differences between *A. gossypii* and other aphids (Cenis et al. 1993). In both cases differences were found, but the functional significance of the detected differences is not known. Khuda-Bukhsh and Kar (1989) and the author both showed differences in the DNA of *A. gossypii* correlated with host plant, but neither reported conclusive evidence that the differences were due

to host-plant-induced mutation rather than selection of adaptable strains within a parent population.

ABIOTIC ENVIRONMENT: One of the most important abiotic factors affecting the life cycle of this aphid is temperature. Liu & Perng (1987) reported that the lower developmental threshold for the aphid was 7.34° C, using squash in Taiwan. At the other temperature extreme, Aldyhim and Khalil (1993) reported an upper limit to survival of 35° C on squash in Saudi Arabia, but pointed out that on okra the aphid survives under field conditions in locations where the daytime temperature exceeds 45° C. Temperature is also thought to be responsible for some strains of *A. gossypii* remaining holocyclic while others are anholocyclic. Inaizumi (1980) suggested that eggs will be produced in locations where the average temperature during November does not exceed 13°C.

Light intensity and day length are also important abiotic factors in the reproductive capacity of this aphid. Aldyhim and Khalil (1993) found that longer days increase the reproductive capacity of this aphid on squash. Increasing daylength from 6 to 12 to 18 hours significantly increased the intrinsic rate of increase (r_m). Other population parameters measured by Aldyhim and Khalil (1993) would indicate that a 12 hour day was best for this aphid. Wyatt & Brown (1977) reported *Aphis gossypii* subjected to longer days (8 versus 16 hours) increasing light intensities (800, versus 4000, versus 8000 lux) had increased reproduction on cucumber at 18°C with r_m increasing from 0.22 to 0.44. At 24°C, the maximum r_m (0.45) occured at 4000 lux and 16 hour days. Ghovanlou (1976) demonstrated the effect of day length on development time for this aphid on gourd. At all three temperature ranges examined Ghovanlou found that development time was shortest for aphids subjected to a

12 hour photoperiod. Development time increased at 16:8 (L:D) and increased further at 8:16 (L:D) photoperiod. Auclair's (1967b) results regarding light intensity conflict with the results of Wyatt & Brown (1977). Auclair reports that high intensity light (550 lux or brighter) inhibits feeding and colonization, and aphids feeding on diets exposed to 550 lux would move to diets exposed to 54 lux. There is no obvious reconciliation between these two studies other than to suggest that 1) different clones will respond differently to light intensity; or 2) the difference is due to experimental conditions. Wyatt and Brown used leaf discs illuminated only with incandescent bulbs, and it is not clear if the lighting was direct, or "filtered" through the leaf disc. Auclair used artificial diet back lighted with incandescent and fluorescent lights and adjusted for light intensity by filtering through paper discs.

BIOCHEMISTRY

HOST ADAPTATION: When *A. gossypii* is moved to a new host it requires some time to adapt. Knowing the length of this adaptation period is critical in biological and nutritional studies because during this period the response of the aphid is a combination of the effect of the new host and a stress response. Kishaba and Coudriet (1985) reported that field collected aphids from various cucurbits could adapt to a susceptible muskmelon line in 6 months, as measured by an increase in the total number of aphids over five days. They could also demonstrate the aphid adapting to pumpkin, but in 6 months it did not achieve comparable reproductive potential relative to similar aphids transferred to watermelon or muskmelon. Saito (1991) reported that the aphid would not adapt to a new host plant in 3 months in transferring clones between plants in the Cucurbitaceae and Solanaceae.

INSECTICIDE RESPONSE: Aphids reared on different plants show different levels of susceptibility to some insecticides. However, such studies to date have not eliminated aphid strain as a confounding factor. Juneja and Sharma (1973) reported differential susceptibility for DDT, lindane, endrin, endosulfan, malathion, ethyl parathion, methyl parathion, dimethoate, phosphamidon, and carbaryl for aphids reared on six cucurbitaceous hosts. Aphids on cucumber were consistently less susceptible to all insecticides relative to aphids from the original culture on bottle gourd (*Lagenaria siceraria* (Molina) Standl.), but other than this, there was no consistency in the level of resistance and host plant. Organizing the data based on relative toxicity, Juneja and Sharma (1973) reported that relative toxicity between different insecticides changed on the different hosts. In all cases phosphamidon was most toxic followed by methyl parathion, and p,p' DDT was the least toxic. However, there were differences in relative toxicity of the other insecticides based on host plant. Selander et al. (1972) reported a increased susceptibility in *A. gossypii* reared on a resistant chrysanthemum cultivar treated with parathion or nicotine. Saito (1991) reported elevated aliesterase levels in aphids reared on cucurbitaceous crops (melon and cucumber), relative to aphids from the solanaceous crops (eggplant and potato). Aphids with high aliesterase activity maintained original levels of aliesterase activity even when moved to solanaceous crops, and aphids with low aliesterase activity maintained low levels when moved to cucurbitaceous crops. This represents a difference between two strains of this aphid which appears to be correlated with a difference in host plant. Other authors have also reported significant differences in esterase patterns as detected by various electrophoresis procedures. They have shown that such differences are correlated with insecticide resistance (Takada and Murakami

16

1988, Hama and Hosoda 1988, Furk et al. 1980) and with host plant preference (Furk et al. 1980).

In addition to differences in aliesterase level, other biochemical differences can influence the pesticide-insect-plant interaction. Moores et al. (1988) reported insensitivity of acetylcholinesterase in *A. gossypii* populations that were resistant to organophosphate and carbamate insecticides. Sun et al. (1987) reported the same effect, but added that differences in the cuticle also play a role in insecticide resistance in parathion and paraoxon. Sun et al. (1987) also reported that while mixed function oxidases (MFOs) may play a role in detoxification reactions, the esterases and carboxylesterases showed more conspicuous differences between the susceptible and resistant aphid strains. As some insecticides are systemic, and the aphid must deal with some phytotoxins, it is not too surprising that aphid salivary organs would contain enzymes to detoxify certain chemicals. Miles and Peng (1989) reported on peroxidase levels in salivary glands, "sheath material", and excretions of *A. gossypii* and two other aphids. It is not clear exactly what compounds were being detoxified by the aphid, but the peroxidases were effective in detoxifying hordenine and gossypol (secondary plant compounds in cotton).

Grafton-Cardwell (1991) reported alate adults on cotton were more resistant than apterous adults to oxydemeton-methyl, chlorpyrifos, dicrotophos, biphenate, and endosulfan.

Another factor in the pesticide - insect - plant interaction is pest resurgence. Depending on the pesticide chosen, pest resurgence can be due to the action of the pesticide on the insect, the action of the pesticide on the plant, the action of the pesticide on natural enemies, or some combination of the three. Classical thought attributes most or all of pesticide resurgence to a reduction in natural enemies. However, under field conditions it is difficult to

control for the other two factors, and they are often ignored. Kerns and Gaylor (1993) report sulprofos treated cotton fields had elevated numbers of *A. gossypii*, but the cotton plants in these fields had significantly elevated levels of threonine and "essential" amino acids. Sithanantham et al. (1973) reported an increase in size and weight in aphids feeding on cotton plants treated with the systemic insecticides disulfoton, phorate, dimethoate, and lindane. Treated plants had lower sugar content, lower nitrogen content, lower carbohydrate to nitrogen ratio, and higher amino acid content. Regupathy and Jayaraj (1974b) reported an increase in aphid size and increased numbers of aphids in okra treated with phorate. They also reported a change in plant physiology due to the pesticide resulting in elevated levels of ammoniacal nitrogen, potassium, and a decrease in carbohydrates, magnesium, and calcium (amino acid levels were not reported). Although altered plant physiology may account for aphid resurgence in some cases, it is not the only cause. Gajendran et al. (1986) showed that direct applications to the aphid of deltamethrin, methyl parathion and carbaryl stimulated the reproductive rate of *A. gossypii*. They also showed that LC_{10} doses of deltamethrin and methyl parathion stimulated feeding. Other authors also showed elevated aphid populations following pesticide applications, but did not examine causes (Patel et al. 1986, Surulivelu and Sundaramurthy 1986, Thimmaiah and Kadapa 1986).

APHID NUTRITION: The effect of starvation was discussed earlier, but the aphid can be stressed in more subtle ways by depriving the host plant of essential nutrients. Isely (1946) stressed plants by growing them in sand and fertilizing them with solutions containing 10% of the nitrogen or 5% of the potassium of the full fertilizer. *Aphis gossypii* took longer to mature, and had a lower birth rate on nutrient stressed plants, but only nitrogen stressed plants had a

18

significant reduction in total offspring and total duration of reproductive period. The importance of fertilizers especially nitrogen was also recorded by Banerjee and Raychaudhuri (1987) on eggplant in West Bengal, El-Saadany et al. (1976) on potato in Egypt, Beckham (1970) on cotton in USA, and Rasmy and Hassib (1974) on cotton in Egypt.

Weismann et al. (1970) reported on the effect of drought on the development and fecundity of alate *A. gossypii* on cotton in Egypt. Weismann et al. reported that the aphid did better on leaves with sap densities under 11%, and that such leaves occur on the lower part of the plant during flowering. Hassib and Rasmy (1974) reported that aphid population density increased on potted cotton plants as the frequency of watering decreased from once every 3 days to once every 6 days to once every 9 days (the quantity of water used in each irrigation episode was not reported). However, Hassib and Rasmy also reported that decreased irrigation increased plant nitrogen levels and decreased carbohydrate levels in the foliage. Banerjee and Raychaudhuri (1987) reported that of carbohydrate, nitrogen, fat, sterol, and inorganic salts, only nitrogen levels had a significant influence on aphid populations on eggplant. Thus, some of the effect of drought on the aphid may be due to an altered nutritional status in stressed plants, but other factors like sap density and microclimate changes associated with changes in canopy structure (Weismann et al. 1971) are confounding factors.

Auclair (1965) reported an artificial diet for the pea aphid which also worked for *A. gossypii*. Aphids transferred to the artificial diet survived, and produced progeny, but the progeny produced by these aphids did not survive very long (Auclair 1967a). Auclair examined the effect of changing pH and sugar concentration on the growth and birth rate of *A. gossypii*. Auclair (1967a) reported an optimum pH of 7.4 to 7.8. The optimal sucrose

concentration for settling was 40%, but the optimal sucrose concentration for growth and reproduction was 20 to 30 percent (Auclair 1967b). Auclair (1967b) also reported the effects of replacing some or all of the sucrose with one of the following: raffinose, sorbose, melezitose, glactose, lactose, ribose, or cellobiose. Invariably such diets were less suitable that those with only sucrose.

Hendrix et al. (1992) reported the concentrations of sugars in the honeydew of *A. gossypii* on cotton. The data were reported as % of total sugar excreted by each species. *Aphis gossypii* excreted 24.6% monosaccharides, 11.6% sucrose, 1.1% trehalose (spelled trehalulose in original paper), 38.3% melezitose, 0.0% turanose, and a small quantity of other sugars.

The nutritional requirements of *A. gossypii* have been examined by Turner (1971, 1977), but the interpretation of the results is confounded with a deficiency present in the diet developed by Auclair (1965). The diet is insufficient for long term (weeks or longer) growth and reproduction of *A . gossypii*, and until the problem is solved experiments examining essential nutrients will be questionable. With this in mind, several papers examine the effect of modifying the diet on a growth index: defined using both total aphids produced in 6 days and the weight of those aphids. Both cysteine and methionine are required for maximum growth. Concentrations of either amino acid above 30 mg/ml are toxic. Inorganic sulfur, as sodium sulfate or ammonium sulfate, is not suitable as a substitute for these amino acids when present in equivalent molar concentrations to the amino acids. While the concentration of methionine is sufficient in Auclair's diet, Turner recommends 700 mg more cysteine be added. Turner also examined the effect of altered concentrations of tyrosine, phenylalanine, and tryptophan in Auclair's diet. He shows that the aphid will continue to reproduce on diets lacking all three amino acids, but that the aphid does better with them present.

Phenylalanine concentrations from 0 to 8 mg/ml were examined, and the aphids did best at 2 mg/ml (+100 mg to Auclair's diet). Tryptophan concentrations from 0 to 8 mg/ml were examined, and the aphids did best at 4 mg/ml (+300 mg to Auclair's diet). Tyrosine concentrations from 0 to 0.40 mg/ml were examined and the aphids did best at 0.4 mg/ml (+20 mg to Auclair's diet).

BEHAVIOR

Several authors have examined the behavior and developmental timing associated with flight in *A. gossypii*. Once airborne, the aphid must cue in on suitable places to land and it does so using visual and olfactory cues. Movement of the alates and nymphs on their host determines their position on the host and will influence the aphids survival, reproductive rate, and the success of resulting progeny. In colder climates this aphid is holocyclic and egg laying behavior is an important element of the aphid's life cycle.

Nozato (1987b) reported on the take-off behavior of *A. gossypii* from colonies reared on *Veronica persica*. Nozato reported that the preflight period (from molt to flight) lasted from 1 to 31 hours with most activity between 10 and 24 hours after molt. The time of molting appeared to be independent of time of day. Adults flew from about sunrise to early afternoon, but a few individuals continued to fly after dark. With first light at 6:00 AM, and last light at 7:30 PM, no aphid flight was detected from 11:00 PM to 7:00 AM. Nozato (1989b) further manipulated the day length and came to the conclusion that this aphid does not fly in the dark. Nozato (1990) (assumed host = *Veronica persica*) reported that the flight period lasted from 1 to 4 days in a laboratory colony. Older colonies (using middle versus late developmental stage) produced fewer alates that flew for one day and more that flew for two days. Aphids flew from

21

one to several (about 5) times each day. The first flight of each day was invariably the longest. Alates that flew longer had a shorter reproductive period and produced fewer total progeny. Alates larviposited after flight, and flew again when the number of embryos with pigmented eyes per ovariole decreased. Nozato (1990) examined fore wing length, teneral period, and first flight duration as possible factors influencing the flight period, and found no correlation. Nozato (1989a) reported that the duration of the preflight period decreased with increasing temperatures from 12° to 28° C. Nozato (1989a) also estimated a developmental threshold of 10.47° C during the teneral preflight period. Nozato (1989b) and Reinhard (1927) both reported that alates will not produce offspring on leaves that have already been colonized.

Auclair (1967b) examined the effect of different wavelengths of light on aphids feeding on a holidic diet, and reported that diets illuminated at 570-595 nm were attractive to the aphid and diets illuminated at 420-485 nm were repellent. This apparently contradicts the findings of Pospisil (1971) who reported on the effect of different wavelengths on aphids collected from the field and held for a few days on cucumber or Comelina erecta L (=Comelina elegans). Preference was measured by placing aphids in a glass Y tube with each arm of the Y supplied with a light source of different wavelength. The prefered wavelength was determined by the arm chosen by the aphid as it moved along the glass tube. Newly molted alate adult individuals had a strong preference for short wavelengths down to 357 nm. Adults of mixed age also preferred this short wavelength light, and their preference declined with increasing wavelength. However, there was a significant increase in preference beginning at 547 nm, peaking at 562 nm, and rapidly declining after the peak (data points at 583, 638, and 800 nm). This peak is approximately where Auclair did his studies, and could explain the different results. Auclair

22

(1967b) also reported that the adults were more sensitive to different wavelengths than were nymphs.

Pospisil (1972) investigated the olfactory behavior of *A. gossypii*, and reported that the alates had a positive orientation to increased humidity. Orientation to host plants was significant at 6 hours after wing development, but was highly significant after 24 hours. Alates were also able to distinguish between different plants; *Cucurbita pepo* and *Thunbergia laurifolia* were attractive, and were common hosts for this aphid in Cuba. The occasional host *Hibiscus rosa-sinensis* L. was neither attractive nor repellent, and the non-host plant *Lantana camara* L. was repellent. (Note: *Lantana macrophylla* Schau. is a reported host from the Los Angeles State and County Arboretum USA (Leonard and Walker 1971)).

On a larger scale, the distribution of the aphid within fields, between seasons, and on host plants is another aspect of behavior. On cotton grown in the former Soviet Socialist Republic, Tshernyshev et al. (1981) reported that *A. gossypii* migrated from the stem apex to the upper leaves and then to the lower leaves in the morning. During the day the aphids were mostly on the underside of leaves, and they migrated back to the stem apex at night. The table in Tshernyshev et al. (1981) indicated that many individuals did not conform to this pattern. In cotton fields from the USA, O'Brien et al. (1991) found that the distribution of *A. gossypii* differed significantly within the canopy, but the pattern was not consistent between fields or time of year. O'Brien et al. did not report a consistent time of day when samples were collected. The results of Tshernyshev et al. (1981) could account for some of the inconsistencies in the spacial pattern reported by O'Brien et al. (1991). In eggplant from India, Banerjee and Raychaudhuri (1985) reported that the aphid settles on older mature eggplant leaves. It moves to the younger tissues

only when population pressure forces it to; thus aphid populations are always greatest on the older leaves. In cantaloupe (*Cucumis melo* L.) Edelson (1986) reported the aphid to be most abundant on the basal portion of vines. In cotton O'Brien et al. (1993) reported the aphid was most abundant in the middle canopy, followed by the upper canopy. This pattern was in part a result of high aphid mortality from a fungal pathogen in the lower canopy. Senapati and Mohanty (1980) also reported that the aphid was most abundant at mid canopy in cotton, followed by upper canopy, and lowest at the basal part of the plant. Senapati and Mohanty (1989) did not report on the occurrence of fungal pathogens.

In cotton fields from the Ivory Coast, Duviard et al. (1976) examined the dispersal of *A. gossypii* from savanna to cotton using pan traps. Their data showed that most aphids settled at field margins, although there was also settlement in the field. They also reported that pan traps at ground level caught more *A. gossypii* than traps further from the ground. From their graphs, it appears that most of the aphids were caught no more than 1 meter from the soil surface, and that the closer to the surface, the more aphids were caught.

Egg laying on *H. syriacus* occurred mostly between the leaf scar and the twig near where the buds would emerge in spring (Inaizumi and Takahashi 1989). Some eggs were also laid at the branching point of twigs. However, from the wandering behavior of the oviparous females, Inaizumi and Takahashi (1989) conclude that the females were searching for protected places to lay eggs rather than for specific parts of the plant.

SPECIES INTERACTIONS

This section begins with ways host plants defend themselves from attack by this aphid. Since almost nothing is known about the interaction at the biochemical level, the discussion is mostly limited to physical characteristics. The presence of biochemical interactions is suggested by the number of reports on resistant cultivars of a wide range of crops, but in only two cases are specific mechanisms explored. In addition to the aphid, plants must deal with the viruses transmitted by this aphid. The section ends with a discussion of the suitability of this aphid as a source of food for other organisms.

One of the easiest defenses to measure is changes in morphology which alter aphid abundance. Dunnam and Clark (1938) reported that glabrate cotton supported fewer aphids than more pubescent cotton (0.52 to 4.48 hairs/mm^2). However at 6.09 hairs/mm^2 the number of aphids began to decline. Wang (1983) suggested that resistance in some cotton lines was due to heavy pubescence. Kennedy et al. (1978) reported that pubescent muskmelon was probed less frequently relative to a glabrous strain of 'Top Mark'.

Many crops have some level of resistance to this aphid. There are three general categories for types of resistance in host plants. A plant can be tolerance, repellent (antixenosis), or toxic (antibiosis). The causes for resistance have been explored in some detail in muskmelon and cucumber. Resistance has also been documented in the following crops: okra [Gunathilagaraj et al, (1977) and Uthamasamy et al. (1976)]; *Gossypium hirsutum* and *Gossypium arboreum* [Chakravathy and Sidhu (1986)]; *Antigastra catalunalis* [Muralidharan et al. (1977)]; *Citrullus lanatus* [MacCarter and Habeck (1973)]; *Solanum melongena* [Sambandam and Chelliah (1970)]; *Colocasia esculenta.* [Palaniswami et al. (1980)].

Muskmelon: Kennedy and Kishaba (1977) examined resistant lines of *Cucumis melo* and found that resistance was due to antixenosis. The effect remained in excised leaves for at least 4 days. It was not translocatable across a graft union. Kishaba et al. (1976) using a different set of resistant plants (than Kennedy and Kishaba 1977) found that antixenosis was due to a single dominant gene, but that other genes also had some effect. Bohn et al. (1973) reported that several genes were involved in tolerance. There appeared to be a single gene which controled the curling response of the plant to aphid attack. The leaves of tolerant plants did not curl. Some muskmelon strains also showed differences in size after infestation. Kennedy et al. (1978) reported that aphid probing in the resistant line 91213 resulted in more branched stylet sheaths relative to the susceptible line 'Top Mark'. The total number of contacts with phloem cells was greater in resistant plants. However in the resistant line, a smaller proportion of the contacts resulted in ingestion, and the periods of ingestion were 2 to 3 times shorter. These observations were based on electronic recordings. Their histological data contradicted these findings, but Kennedy et al. pointed out that the electronic recordings may better reflect what the aphid is actually doing while the histological observations are from a brief snapshot in time and are subject to other sources of error. They concluded that the source of resistance is due to some factors in the plant which inhibit ingestion.

Cucumber: Haynes and Jones (1975) reported that aphids on non-bitter *Cucumis sativus* had a higher average daily reproductive rate, and achieved much higher densities than aphids on bitter plants. However, aphids on bitter plants had a shorter development time. The *Bi* gene permits cucurbitacin production in cucumbers.

VIRUS - APHID - PLANT INTERACTIONS

The most important impact *A. gossypii* has on world agriculture is through its ability to transmit plant viruses. Table 2 is a list of plant viruses transmitted by this aphid. The list does not contain many older references because of problems in proper identification of the aphid and the viruses; see Kennedy et al. (1962) for older references.

The type of transmission is classified as persistent, semipersistent, and nonpersistent using the system first proposed by Watson and Roberts (1939) and later modified by Sylvester (1956). Pirone & Harris (1977) recommend the use of stylet-borne and circulative to categorize aphid transmission of viruses. However, I have retained the old system because most of the literature uses the old systems, and in many cases it is not known if the virus is stylet-borne or not. As a general rule, stylet-borne viruses are nonpersistent, and circulative viruses are persistent.

This review proposes that the plant-aphid-virus system be modeled as an equation of interactions which combine to give the level of disease: (Plant x Aphid) + (Plant x Virus) + (Aphid x Virus) = % disease. Breeding plants resistant to virus modifies the Plant x Virus interaction. Modifying other parts of the equation will also reduce the incidence of disease. However in programs designed to breed plants for resistance it is important to properly document the cause of resistance. This will also reduce possible confusion in the literature where plants are selected for antixenosis and are then reported as being resistant to a virus.

The following three sections are short literature reviews of citrus tristeza virus, cucumber mosaic virus, and the viruses in the potyviridae. They describe the virus and its interaction with the melon aphid.

Citrus Tristeza

Citrus Tristeza is a phloem-limited virus that is mostly confined to plants in the Rutaceae. It is a filamentous particle 11x2000 nm belonging to the closterovirus group. Its genome is a single strand of RNA. *A. gossypii* transmits this virus semi-persistently, remaining infectious for over 24 hours (Bar-Joseph et al. 1989). The aphid is able to acquire the virus more easily from some citrus cultivars, than from others. The acquisition period can be as short as 5 minutes, but was more efficient at periods of 30 minutes to 24 hours. Infectivity was lost within 48 hours of acquisition, but feeding on alternate host plants does not reduce infectivity. The inoculation period should be 4 to 6 hours (Bar-Joseph & Loebenstein 1973). *Aphis gossypii* was able to transmit the virus to certain cultivars more efficiently than to others (Roistacher & Bar-Joseph 1984).

The system is not sensitive to the culture host of the aphid but is sensitive to temperature. *Aphis gossypii* reared on cucumber were able to acquire the virus when fed on infected citrus as easily as aphids reared on citrus (Bar-Joseph & Loebenstein 1973). This was also true of aphids reared on muskmelon (*Cucumis melo* L.), and kenaf (*Hibiscus cannabinus* L.) (Roistacher et al. 1984, Norman & Sutton 1969). Bar-Joseph & Loebenstein (1973) also showed significantly lower transmission rates when plants were held at 31°C relative to those at 22°C. When the plants were cooled (31°C to 22°C) it took about 6 days for an increase in transmission rate. When the plants were warmed (22°C to 31°C) it took 12 to 20 days for transmission rates to decline. The apparent reason for this effect was different virus titers in trees at the two temperatures, and these differences caused the observed change in transmission rate.

Different strains of *A. gossypii* do not differ in their ability to transmit Tristeza virus, but different strains of the virus do differ in their transmission rates by this aphid (Raccah et al. 1980). There is a clear relationship between the number of infectious aphids and the success rate of transmission of virus (Roistacher et al. 1984).

Cucumber Mosaic Virus

Cucumber Mosaic Virus (CMV) is the type member of the cucumovirus group. It is transmitted non-persistently on the styletts of the aphid vector. It has the widest host range of any virus, attacking plants from 85 plant families (Palukaitis et al. 1992). The virus is a set of three isometric particles 29 nm in diameter each consisting of a protein coat built from 180 identical subunits, and encapsulating four main single stranded RNA molecules, several minor strands, and a variable number of satellite RNA molecules (molecules requiring the virus for replication and encapsidation, but unnecessary for virus function). In order of decreasing size, the major RNA strands are designated RNA 1, 2, 3, and 4. The minor strands are designated RNA 4a, 5 and 6. The active virus is a set of three distinct particles all of which must be transmitted for infection: one particle has RNA 1, one particle has RNA 2, and the third has RNAs 3 and 4. The remaining RNA molecules may or may not be present (Palukaitis et al. 1992).

The RNA codes for proteins that have several functions. These functions may be coded for on one strand or may require proteins from several strands. RNA 1 is necessary for infection. It plays some role in symptom severity and rapidity of expression of the symptoms. RNA 1 also plays a role in aphid transmission (Zitter & Gonsalves 1991, Francki et al. 1985). RNA 1 is necessary for replication. RNA 2 is required for infection and replication. RNA 3 has the

code for coat protein, but requires RNA 4 to express the trait. RNA 3 is also necessary for aphid transmission. In some cases RNA 3 determines the host plant reaction while in others it is RNA 2, or both (Francki et al. 1985). RNA 4 is generated from RNA 3. RNA 4 is necessary for coat protein synthesis, but not for infectivity.

Acquisition time can be very short (under 1 minute), but transmission rate increases with longer feeding times at least up to 15 minutes (Camino-Lavin 1970). Aphids will lose their ability to transmit following probing or after fasting for about four hours. Different aphid clones differ in their ability to transmit CMV (Simons & Eastop 1970). Aphid transmission of CMV is an interaction between the virus coat protein and aphid mouth parts. Palukaitis et al. (1992) indicated that amino acids 129 and 168 of the coat protein are key locations in mediating aphid - virus interactions. Changes in the coat protein can change the effectiveness of aphids in transmitting the virus (Gera et al. 1979). However, another common factor that affects transmission rate is virus concentration in the host plant. Banik & Zitter (1990) showed that a virulent isolate reproduced faster than a less virulent isolate in muskmelon with a corresponding decrease in transmission of the less virulent isolate.

Unlike tristeza, different host plants change the ability of the aphid to acquire the virus (Jacquemond 1982).

An enzyme linked imunosorbant assay (ELISA) has been used to detect CMV from individual aphids (Gera et al. 1978). The aphid transmissible strain carried 0.01 to 0.1 ng of virus per aphid. The non-transmissible strain was not detectable on the aphid.

Potyviridae

Other viruses are also economically important but less intensively studied in relation to the melon aphid. Many members of the potyviridae are transmitted by the melon aphid, including potato virus Y (PVY), Watermelon mosaic virus I and II (WMVI, WMV2), Zucchini Yellow Mosaic Virus (ZYMV), and papaya ringspot virus (PRV). These viruses consist of a flexuous rod 680-900 nm long and ±12 nm in diameter. The genome is a single molecule of single stranded RNA (Francki et al. 1985). Singh et al. (1983) reported that different life stages had different vectoring potential of PVY with the adult alate stage having the lowest transmission efficiency. Differences in virus composition in ZYMV changed the ability of the aphid to transmit the virus (Lecoq et al. 1991). Different clones of the aphid differ in their ability to transmit PRV (Lupoli et al. 1992). Acquisition and transmission times for both ZYMV and WMV2 can be as short as 15 seconds (Perring et al. 1992). The host plant for the aphid and virus is probably also important (Simons 1959, Gooding & Kennedy 1985), but it is difficult to distinguish between a Plant x Virus effect and a Plant x Aphid effect.

Several conclusions can be drawn about the nature of non-persistent viruses. From the short acquisition time it is likely that the source of the virus is in the epidermis of the host plant (Pirone & Harris 1977). Thus, the aphid could acquire the virus with only a brief probe. This hypothesis would be consistent with aphid feeding patterns where many short probes occur prior to a much longer sustained feeding probe. If aphids are to acquire the virus in only a few seconds of probing, the virus needs to be available in the tissues invaded by short probes. This is also consistent with the observation that starvation increases virus acquisition because short probes become more frequent following starvation (Powell 1993). It is also likely that the virus is

31

not a physical contaminant on the aphid stylet, but rather a chemical reaction takes place on some part of the stylet. If the interaction was physical, one should not observe differences in transmission rates from different aphid clones, and one would not expect there to be specific sites in the virus genome to alter transmission rates.

One of the major procedures employed to control virus diseases is through plant breeding. The Plant x Aphid interaction is exemplified by plants which are repellent to insects, or lack cues which the insect uses to distinguish host plants from non-host plants: e.g. Pitrat & Lecoq (1980) report that some melons are resistant to virus transmission, but the cause appears to be due to antixenosis. The Plant x Virus interaction could occur by a modification of leaf cuticle hydrocarbons. This would have the same effect as spraying the crop with oil which has been shown to decrease transmission of non-persistent and semi-persistent viruses (Singh 1981, Vanderveken 1977). The Aphid x Virus interaction can occur if the virus coat protein changes (Gera et al. 1979). One would also expect that this could occur if the binding sights on the aphid were to change, but this has not yet been demonstrated.

OTHER BIOLOGICAL INTERACTIONS

Articles on biological control provide a list of organisms that the aphid needs to deal with if it is to survive and reproduce; that is, those organisms that help regulate aphid populations.

ANTS: Nozato and Nagano (1988) reported a beneficial effect to the aphid of the presence of ants *Camponotus japonicus* Mayr in Japan. Aphid populations tended by ants increased in spite of the presence of the coccinellid predator *Coccinella septempunctata bruckii* L. However, the level of protection afforded

by the ant was highly variable. Verghese and Tandon (1987) reported a positive association between *A. gossypii*, its coccinellid predator *Menochilus sexmaculatus* (Fabrecius), and the ant *Camponotus compressus* Fabrecius in a guava (*Psidium* sp.) orchard in India. They reported a negative relationship between ant abundance and presence of the coccinellid. The cause for this effect was not investigated, and it was unclear what effect this had on aphid densities. In a laboratory test, Vinson and Scarborough (1989) reported on the effect of *Solenopsis invicta* Buren on the predators *Hippodamnia convergens* Guerin-Meneville, *Chrysopa carnea* Stephens, *Scymnus louisianae* Chapin, and *Syrphus* sp. feeding on *A. gossypii* on cotton in the USA. With ants present, all predators except *Syrphus* were unable to control aphid densities. Without ants all predators were able to control aphid densities.

PREDATORS: A large number of predators have been examined for their effectiveness in controlling this aphid. The effectiveness of these predators is highly variable depending on environmental factors, the host plant of the aphid, and availability of alternative prey. The effect of alternate prey was reported by Nordlund and Morrison (1990) for *Chrysoperla rufilabris* (Burmeister) which preferred *Helicoverpa* (=*Heliothis*) *virescens* (Fabricius) larvae to aphids, but preferred aphids to *H. virescens* eggs. Presence of *A. gossypii* was shown to decrease predation on *H. virescens* eggs by the following predators: *Hippodamnia convergens*, *Chrysopa carnea*, and *Orius insidiosus* (Say) (Ables et al. 1978).

Syrphid flies have shown potential in controlling aphid populations under greenhouse conditions (Chambers 1986, Adashkevich and Karelin 1988, Babayan and Hovhannisian 1984). However, Adashkevich and Karelin (1988) reported that on older plants colonization by the syrphid was decreased, and

older larvae would not transfer to more mature plants. The suggested cause for the latter effect was leaf pubescence. Sanborn (1912) examined the feeding rate of various coccinellid species, two neuropterans, and a syrphid on *A. gossypii*. The high feeding rates suggest that all these species could control aphid populations, but there are no articles that demonstrate this effect under field conditions. Nyffeler et al. (1989) reported on prey capture of orb weaving spiders in a cotton field in Texas. There was no direct identification of prey as *A. gossypii*, but the aphid is a dominant pest in cotton fields, and alate and apterous aphids were the dominant prey.

PARASITES: The parasites of this aphid are of two dominant classes: parasitic hymenoptera, and entomopathic fungi. Two articles were found which dealt with parasitic Hymenoptera. Luo and Gan (1986) reported changes in parasitism based on the age structure of *A. gossypii* populations feeding on cotton. The parasites *Trioxys* spp. and *Aphelinus* sp. would rarely parasitise first and second instar aphids. As the proportion of older aphids increased, so did the percent parasitization. These authors also reported altered parasitization rates based on aphid density, but not with leaf location on the plant.

Singh and Srivastava (1990) looked at hyperparasitization of primary parasites by *Alloxysta pleuralis* (Cameron). Among the species examined were *Lipolexis scutellaris* Mackauer, and *Trioxys indicus* Subba Rao & Sharma parasitizing *A. gossypii*. There was a significant decline in the rates of hyperparasitization of *T. indicus* parasitizing *A. gossypii* feeding on solanaceous crops (*Capsicum frutescens* L., and *Solanum melongena*) versus crops in the Fabaceae (*Cajanus* sp., *Dolichos* sp.), and Cucurbitaceae (*Lagenaria* sp., and *Luffa* sp.). There was also a significant host aphid effect in *T. indicus*

where wasps parasitizing *A. gossypii* had a higher parasitism rate compared to *Aphis craccivora* Koch and *Myzus persicae* (Sulzer).

Entomopathic fungi are a common source of mortality in aphid populations. The two dominant pathogens are *Neozygites fresenii* (Nowakowski), and *Cephalosporium (=Verticillium) lecanii* (Zimm.). Several other fungal pathogens have also been reported: *Arthrobotrys* sp., *Entomophthora aphidis* Hoffm., and *Entomophthora delphacis* Hori (Sanchez-Peña 1993, Shimazu 1977).

Steinkraus et al. (1993) reported that *Neozygites fresenii* takes 3, 4, 5-6, and 6-8 days to develop at temperatures of 30, 25, 20, and 15° C respectively. They also reported that at 35° C the fungus did not kill aphids. However, it is unclear whether the fungus failed to infect the aphids, failed to continue growth, or was killed at this temperature. *Neozygites fresenii* is able to produce up to 9,835 conidia from a single aphid. Steinkraus et al. (1993) reported the number of conidia per aphid was correlated with aphid size as measured by the prothoracic tibia, but suggested that handling or storage properties of larger aphids could also explain their observation. This fungus can be a major cause of aphid mortality in cotton grown in the Texas/ Arkansas area of the USA (Steinkraus et al. 1993, Steinkraus et al. 1991), and has been recorded from Australia (Milner and Holdom 1986). This fungus has not been reared on artificial media, but Steinkraus et al. (1993) reported on propagation in an aphid colony and longevity of the fungus in cold storage.

Cephalosporium lecanii is an important source of mortality for aphids under greenhouse conditions, but there are no reports of its impact on *A. gossypii* under field conditions. The effectiveness of the fungus is emphasized by its use as an "aphicide" in commercial greenhouses in the UK (Sopp et al. 1990, Hall 1985). Its success in this capacity is partly due to the ability of the

fungus to grow in artificial media. As one might expect, different strains of the fungus show different growth rates and different levels of pathogenicity (Kitazawa et al. 1984, Yokomi and Gottwald 1988, Hall 1982).

OTHER INTERACTIONS: Potts and Gunadi (1991) reported a decrease in *A. gossypii* populations in potato that is intercropped with *Allium cepa* L. or *Allium sativum* L. To get the reduction, the onions had to be planted within 0.75 meters of potato plants. However, intercropping poses a problem when the minor crop harbors a disease of the primary crop. Such a system has been documented in Taiwan where banana was interplanted with cucumber which can harbor banana mosaic virus (Tsai et al. 1986). Tsai et al. also reported on a similar effect when plants harboring the disease are in neighboring fields.

Competition is another form of species interaction. Regupathy and Jayaraj (1974a) report a negative relationship between *A. gossypii* and *Amrasca devastans* (a leafhopper) on okra with an r^2 of 0.6 . The relationship was significant only for aphid and leafhopper nymphs, not leafhopper adults. Presumably this effect is a result of crowding and host quality reduction at high aphid densities. The effect of host quality decline due to feeding by *A. gossypii* is a problem during the commercial production of Lac insects (*Kerria lacca* (Kerr)) on *Flemingia macrophylla* O. KZE. ex Prain (=*Moghania macrophylla*) (Sen et al. 1987). Aphid feeding causes premature leaf drop, wilting, and desiccation of the plant. Sen et al. did not examine the role, if any, crowding may have played in reducing Lac insect densities.

FUTURE RESEARCH

There are a number of important questions that remain unanswered. Near the top of the list is a useful definition of biotype for this aphid. Several

authors have identified strains of this aphid as the "French biotype", or the "Western biotype", or some other designation for distinguishing between local differences. It would be very useful to have a world wide system for classifying the variability in different strains of this aphid. Until this is done, the application of research by Japanese scientists will have to be redone by Chinese scientists, and redone by American scientists, etc.

Another important question is what makes this aphid able to feed on such a diverse array of different hosts? Is it because it is able to deal with a large array of different plant secondary compounds? Is it because it has lost the ability to distinguish between it original host and other hosts? Is it because it is able to survive under a wide array of diets with different nutrient compositions?

It would be highly desirable to have a holidic diet available. Such a tool could be used to determine the essential nutrients for the aphid. It could also be used to evaluate critical nutrient concentrations which in turn could be used to assess the validity of the hypothesis that the aphid is polyphagous because it can adapt to hosts with disparate nutrient compositions.

As a final note, there are two things that I would change about many of the articles used in this paper. First: although, research is easier using leaf cages or excised leaves, these procedures modify the biology of the aphid by modifying the environment in which the aphid lives. For valid comparisons to other research such influences should be avoided. This means that aphids are kept on whole undamaged plants, and are permitted free access to all parts of the plant. Even small variations in the size, shape, or composition of a cage will invalidate direct comparison of current results with results from the literature. Second: auxiliary information such as light source, light intensity, temperature, relative humidity, and aphid size as measured by body length and

tibia length should be included as routine measurements. For the aphid measurements, one probably needs a sample of no more than 15 aphids from each treatment. It is also important to document the conditions under which the aphid is being reared, because different instars are differentially susceptible to different toxicants, and the stage distribution of the colony is linked to the level of crowding.

Acknowledgments

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Table 1: This is a list of the plant families that have members that serve as hosts for Aphis gossypii. Under each plant family is a list of individual members that are a source of food, fiber, or other commodity to humans. The table is organized according to the Cronquist system of classification as found in Jones & Luchsinger (1986).

Family	Species	Common Name	Damage*	Citation
Division: Pinophyta (Gymnosperms) Class: Coniferopsida				
Order: Coniferales				
Cupressaceae				2
Division: Magnoliophyta Class Magnoliopsida (Dicots)				
Subclass: Magnoliidae				
Order: Magnoliales				
Annonaceae				1
Order: Laurales				
Lauraceae	*Persea americana* Mill. †	Avocado	F	61
Order: Piperales				
Piperaceae	*Piper betle* L.	Betelvine	F	53
Order: Ranunculales				
Ranunculaceae				58
Subclass: Hamamelidae				
Order: Hamamelidales				
Hamamelidaceae				2
Order: Urticales				
Ulmaceae				1
Cannabinaceae				1
Moraceae				1,2
Urticaceae				1
Order: Casuarinales				
Casuarinaceae				2
Subclass: Caryophyllidae				
Order: Caryophyllales				
Nyctaginaceae				1
Chenopodiaceae				1
Amaranthaceae				1
Portulacaceae				2
Caryophyllaceae	*Dianthus caryophyllus* L.	Carnation	V	50

57

Order: Polygonales
Polygonaceae

Order: Polygonales					
Polygonaceae				1	
Subclass: Dilleniidae					
Order: Plumbaginales					
Plumbaginaceae				2	
Order: Theales					
Dipterocarpaceae				1	
Theaceae				2	
Clusiaceae				2	
Order: Malvales					
Tiliaceae				1	
Malvaceae				1,2	
	Hibiscus cannabinus	Kenaf	N	4,5	
	Hibiscus esculentus	Okra	F,V	6,7,	31
	Gossypium hirsutum	Cotton	F	9,10	
	Gossypium hirsutum	Cotton	V?	11	
Order: Violales					
Violaceae				1	
Cucurbitaceae				1	
	Cucumis sativus L.	Cucumber	F,V	13,	38
	Cucurbita pepo	cv. 'Michlo Lavan'	V	32	
		Zucchini	V	36	
	Cucumis melo L.	Muskmelon, cv. 'Saticoy'	V	36	
Begoniaceae				60	
Order: Capparales					
Capparidaceae				1	
Brassicaceae				1	
	Brassica campestris L.	Turnip, cv. Yorii	V	45	
Order: Ericales					
Ericaceae				2	
Order: Ebenales					
Ebenaceae	*Diospyros virginiana* L.	Persimmon	F	61	
Subclass: Rosidae					
Order: Rosales					
Pittosporaceae				2	
Crassulaceae				2	

Saxifragaceae			2
Rosaceae			1,2
	Pyracantha sp.	Pyracantha cv. 'Santa Cruz' F	1 8
	Malus pumila Mill.	Apple F	19, 20
	Fragaria sp.	Strawberry cv. 'Tufts' N	5 5
	Pyrus communus L.	pear N	5 7
Order: Fabales			
Mimosaceae			2
Caesalpiniaceae			1
Fabaceae			1
	Vigna unguiculata (L.) Walp.	Cowpea, line TVu54 V	3 4
	Phaseolus vulgaris L.	Bean cv. 'The Prince' V	3 4
	Glycine max (L.) Merrill	Soybean V	3 4
	Trifolium alexandrinum	Egyptian Clover V	3 5
	Vigna radiata (L.) R. Wilcz. †	Greengram V	3 9
	Vigna mungo (L.) †	Blackgram V	4 7
	Maughania macrophylla	C	4 9
Order: Proteales			
Proteaceae	*Macadamia* sp.	Macadamia Nut F	2, 61
Order: Myrtales			
Lythraceae			1
Myrtaceae			1,2
	Psidium guava	Guava N	5 7
Punicaceae			1
Onagraceae			2
Combretaceae			2
Order: Celastrales			
Celastraceae			2
Order: Euphorbiales			
Euphorbiaceae			1
Order: Rhamnales			
Vitaceae			1
Order: Sapindales			
Burseraceae			1
Anacardiaceae			2

Rutaceae				1,2
	Citrus sinensis (L.) Osbeck	"Marrs" Sweet Orange	V	3
	Citrus aurantifolia (Christm.)Swingle	Mexican Lime	V	3
Order: Geraniales				
Oxalidaceae				1
Balsaminaceae				1
Order: Apiales				
Araliaceae				1,2
Apiaceae				1
Subclass: Asteridae				
Order: Gentianales				
Apocynaceae				1,2
Asclepiadaceae				1
	Calotropis procera		V	51
Order: Solanales				
Solanaceae				1,2
	Solanum melongena	Eggplant	F, V	8, 26, 27
	Capsicum annuum L.	Chilli	V	22, 23, 30
	Solanum tuberosum L.	Potato	F, V	24, 29
	Nicotiana tabacum L.	Tobacco	V	30, 37, 41
Convolvulaceae				1
	Ipomoea batatas (L.) Poir.	Sweet potato	V	33
Order: Lamiales				
Boraginaceae				1,2
Verbenaceae				1,2
Lamiaceae				1,2
Order: Plantaginales				
Plantaginaceae	*Plantago ovata* Forsk.	Isabgol	F	12
Order: Scrophulariales				
Scrophulariaceae				58
Myoproaceae				2
Acanthaceae				1
Pedaliaceae	*Sesamum indicum*	Sesame (=gingelly)	F	59
Bignoniaceae				1,2
Order: Rubiales				

Rubiaceae   1,2
    Gardenia augusta (L.) Merrill †   Gardenia   F   52
Order: Dipsacales
Caprifoliaceae   2
Order: Asterales
Asteraceae   1,2
    Dendrathema grandiflorum Kitam. †   Chrysanthemum   F   14, 15, 16, 17
    Helianthus annuus L.   Sunflower   V   42
    Zinnia elegans Jacq.   Zinnia   V   46
    Lactuca sativa L.   Lettuce cv. 'Iceberg' N   56

Division: Magnoliophyta   Class: Liliopsida (Monocots)

Subclass: Arecidae
Order: Arales
Araceae   1
    Colocasia esculenta (L.) Schott   Taro

Subclass: Commelinidae
Order: Commelinales
Commelinaceae   1
Order: Cyperales
Poaceae
    Saccharum officinarum L.   Sugarcane   V   40
    Zea mays L.   Corn   V   44
    Triticum aestivum L.   Wheat   N   54

Subclass: Zingiberidae
Order: Zingiberales
Musaceae   *Musa acuminata* Colla.   Banana   V   28
    Musa textilis Née   Abaca   V   43
Zingiberaceae   1
Cannaceae   1

Subclass: Liliidae
Order: Liliales
Liliaceae   2
    Lilium longiflorum Thunb.   Easter lily   F   21
    Allium sativum   Garlic   V   48
Iridiaceae   1

*V= virus vector. **F**= feeding Damage. **C**= competition. **N**= present, but nature of problem not directly stated (a case is where the authors use phrases like "injurious", or "subject to attack").

1) Roy 1983 2) Leonard & Walker 1971 3) Smith & Farrald 1988 4) Norman & Sutton 1969 5) Norman et al. 1972 6) Kisha 1978 7) Kishore & Rai 1982 8) Dhandpani & Kumaraswami 1982 9) Hassanein et al. 1971 10) Abdel-Wahab & Rizk 1970 11) Cauquil 1981 12) Sagar & Jindla 1984 13) Binnis 1971 14) Adams & Hall 1990 15) Adams et al. 1990 16) Webb & Argauer 1974 17) Furk & Vedjhi 1990 18) Pinnock et al. 1974 19) Hameed & Dinabandhoo 1978 20) Hameed et al. 1975 21) Doucette 1962 22) Nandanwar et al. 1976 23) Wadnerkar & Deshpande 1977 24) Nderitu & Mueke 1986 25) Fukumoto & Tochihara 1978 26) Seth & Raychaudhuri 1977 27) Vyanjane & Mali 1981 28) Summanwar & Marathe 1982 29) Singh et al. 1984 30) Gahukar & Nariani 1982 31) Regupathy & Jayaraj 1972 32) Antignus et al. 1989 33) Kennedy & Moyer 1982 34) Atiri et al. 1986 35) Mishra et al. 1980 36) Banik & Zitter 1990 37) Gooding & Kennedy 1985 38) Brouwer & Dorst 1975 39) Ramakrishnan et al. 1973 40) Khurana & Singh 1972 41) Suzuki & Akazawa 1978 42) Theuri et al. 1987 43) Retuerma 1982 44) Shaunak & Pitre 1973 45) Fujisawa 1985 46) Sastry et al. 1973 47) Benigno 1979 48) Ahlawat 1974 49) Bhattacharya & Srivastava 1987 50) Singh & Singh 1989 51) Mohan & Sharma 1987 52) Miller & Williams 1989 53) Raut & Bhattacharya 1987 54) Fagundes & Arnt 1978 55) Trumble et al. 1983 56) Hinsch et al. 1991 57) El-Nagar et al. 1985 58) O'Brien et al. 1993 59) Muralidharan et al. 1977 60) Batchelder 1927 61) Swirski et al.1991

† name changed from that in citation

Table 2: Virus and host where Aphis gossypii is a possible vector. Virus type is based on Francki et al 1985. The question mark after the virus type indicates a tentative placement in that group. Viruses of unknown afinity may be new viruses that have not been placed, or may be variants of a virus already listed.

Type	Virus	Host Plant	Country	Source
unknown Afinity	Calotropis Mosaic Virus	Calotropis procera	India	43
	Carnation Mottle Virus	Dianthus caryophyllus	India	42
	Citrus Woody Gall Virus	Citrus	Peru	7
	Greengram Mosaic Virus	Vigna mungo & other hosts	India	23
	Infectious Chlorosis	Banana	India	36
	Leaf Crinkle of Sunflower	Sunflower	Kenya	15
	Mosaic of Bean	Vigna mungo	Philippines	4
	Mosaic of Garlic	Allium sativum L.	India	3
	Muskmelon Yellow Stunt Virus	Cucumis melo & Cucurbita pepo	France?	39
	Solanum torvum Mosaic Virus	Solanum torvum	India	6,35
	Yellow Blotch of Sunflower	Helianthus annuus	Kenya	15
	Yellow Vein Mosaic Virus	Abelmoschus esculentus	India	32
Alfalfa Mosaic Virus	Alfalfa Mosaic Virus	Trifolium alexandrinum	India	28
		Eggplant	India	37
Carlavirus?	Chinese Yam Necrotic Mosaic Virus	Dioscorea batatas	Japan	41
Carlavirus	Lily Symptomless Virus			2
Caulimo-virus	Cauliflower Mosaic Virus			2
Clostero-virus 1	Citrus Tristeza Virus	Citrus	USA	5,16
Cucumo-virus	Cucumber Mosaic Virus	Zinnia elegans	India	8
		Turnip	Japan	9
		Banana	India	11
		Cucumber	Japan	12
			Netherlands	24
		Capsicum spp.	India	17,33
		Cucumis melo & Cucurbita pepo	USA	27
		Nicotiana tabacum & other hosts	India	40
Luteovirus	Potato Leafroll Virus	Potato	India	34
Potyvirus	Bean Common Mosaic Virus			2
	Cowpea Aphid-Borne Mosaic Virus	Vigna unguiculata	Nigeria	29

63

	Virus	Host	Country	Ref.
	Onion Yellow Dwarf Virus			2
	Papaya Ringspot Virus			2
	Pepper Veinal Mottle Virus	Pepper (Capsicum sp.)	Nigeria	25
	Potato Virus Y	Nicotiana tabacum	Japan,USA	18,26
		Capsicum annuum & other hosts	India	21
		Potato	India	34
	Sri Lankan Passion Fruit Mottle Virus	Passiflora edulis f. flavacarpa	Sri Lanka	44
	Sugarcane Mosaic	Sugarcane	India	19
		Corn	USA	10
		Musa textilis	Philippines	13
	Turnip Mosaic Virus	Turnip	Japan	1,9
		radish	Japan	1
	Watermelon Mosaic Virus 1	Cucumber	Japan	12
		Cucurbita maxima & other hosts	Japan	20
		Cucumis sativus, & other hosts	Mexico	22
	Watermelon Mosaic Virus 2	Cucurbita spp.	Israel	31
	Yam Mosaic Virus			2
Potyvirus ?	Commelina Mosaic Virus	Commelina diffusa	USA	38
	Sweet Potato Feathery Mottle Virus	Ipomoea nil	USA	30
	Zucchini Yellow Mosaic Virus	Pumpkin	Japan	14
		Cucurbits	Israel	31

1) Fujisawa & Iizuka 1985 2) Smith 1972 3) Ahlawat 1974 4) Benigno 1979 5) Roistacher et al. 1984 6) Singh, et al. 1975a 7) Wallace & Drake 1969 8) Sastry et al. 1973 9) Fujisawa 1985 10) Shaunak & Pitre 1973 11) Mali & Rajegore 1979 12) Yamamoto & Ishii 1983 13) Retuerma 1982 14) Ohtsu et al. 1985 15) Theuri et al. 1987 16) Yokomi & Damsteegt 1991 17) Singh & Singh 1977 18) Suzuki & Akazawa 1978 19) Khurana & Singh 1972 20) Yonaha et al. 1977 21) Khatri & Sekhon 1974 22) Camino-Lavin, et al. 1974. 23) Ramakrishnan, et al. 1973 24) Brouwer & Dorst 1975 25) Atiri & Dele, 1985 26) Gooding & Kennedy, 1985 27) Banik & Zitter, 1990 28) Mishra et al. 1980 29) Atiri et al. 1986 30) Kennedy & Moyer 1982 31) Antignus et al. 1989 32) Regupathy & Jayaraj 1972 33) Gahukar & Nariani 1982 34) Singh et al. 1984 35) Singh et al. 1975b 36) Summanwar & Marathe 1982 37) Vyanjane & Mali 1981 38) Morales & Zettler 1977 39) Risser et al. 1981 40) Seth & Raychaudhuri 1977 41) Fukumoto & Tochihara 1978 42) Singh & Singh 1989 43) Mohan & Sharma 1987 44) Dassanayake & Hicks 1992

LITERATURE REVIEW: *Lysiphlebus testaceipes* (Cresson)

TAXONOMY AND IDENTIFICATION: *Lysiphlebus testaceipes* (Cresson) has 18 synonyms. It has been placed in the genera *Trioxys, Aphidius, Adialytus, Aphidaria,* and *Lysiphlebus.* Eleven of the 18 synonyms are members of the genus *Lysiphlebus.* In addition to the usual taxonomic characters, the larval meconia, color of mummy, and characters associated with the exit hole have been used to distinguish this wasp from other aphid parasites of greenbug (Schizaphis graminum) in the United States (Johnson et al. 1979)

LIFE HISTORY: *L. testaceipes* is distributed over much of the world, but is native to North America. This wasp is an internal parasite of many different aphid species (Table 1).

Female wasps attempt to parasitize many species of aphid. Larvae take 6 to 14 days to form mummies. A single female can produce from 12 to 75 mummies in aphid-plant systems that support this species (Ramaseshiah et al. 1968). About 70% of the mummies formed will yield an adult wasp. Kring and Kring (1988) reported a sex ratio slightly less than 2:1 females : males when the parasite is reared on greenbug, but this ratio changes depending on the age of the aphid. Wasps parasitizing aphids less than 1 day old usually produce males, but if older aphids were used, the progeny of the wasp will be mostly females (Ruth et al. 1974, Hight et al. 1972). The wasp was able to parasitize a 15 minute old aphid and the resulting larva will be able to complete its development within the aphid (Ruth et al. 1974).

There is no difference in the developmental rate between females and males when reared at temperatures ranging from 12 to 32°C (Kring & Kring 1988). The maximum temperature for survival is approximately 32°C (Ramaseshiah et al. 1968, Kring & Kring 1988). Below 12°C it takes 11 to 25 days

for the parasite to emerge. *Lysiphlebus testaceipes* has poor survival when subjected to freezing or near freezing temperatures (1.7 to 7°C). Mummies have a greater cold tolerance than do adults (3 emerged from 54 mummies after storage for 30 days at -4.4°C and 2 emerged after 60 days at -1.1°C) Archer et al. (1973). The lowest temperature examined for the adults was 1.7°C. Adults subjected to temperatures below 10C produced fewer offspring. Archer et al. (1973) reported that the optimal storage temperature is between 1.7 and 4.4°C. Even at the optimal temperature, mummies do not store well beyond 30 days, although a few will last over 90 days. It was also apparent that adults do not store as well as mummies.

HOST PLANT RESISTANCE: In developing an IPM program it is beneficial to know how the different control measures will interact. In this particular system it is important to know the effect of an aphid resistant plant on the biology of the parasite. No studies of this nature have been done with watermelon, but there have been some using greenbug on resistant sorghum cultivars. Starks et al. (1972) found that the parasite enhanced control when the greenbug was fed on resistant sorghum. This relationship also occurred when greenbug resistant vs. susceptible barley was used. Starks et al. also found that resistant cultivars decreased the adult weight of the parasite. In a later study Starks et al. (1974) found no significant parasite effect when the aphids were reared on resistant sorghum. Schuster and Starks (1975) found that *L. testaceipes* preferred resistant cultivars of rye, barley, sorghum, wheat, and oats to non-resistant cultivars in olfactometry experiments. This suggests that *L. testaceipes* could complement greenbug control via resistant plant varieties.

Salto et al. (1983) performed a similar set of experiments using a susceptible and resistant oat cultivar to feed biotype C and E greenbugs. There

66

were no differences between the four possible treatments with respect to the following variables: Days to mummy formation, number of mummies, % males, and % emergence.

COMPATIBILITY WITH PESTICIDES: Survival after pesticide application depends on the method of application (direct contact, contact with residues) and the age of the parasite at the time of exposure. Lingappa et al. (1972) found that parasite larvae less than 4 days old did not survive applications of parathion or disulfoton. However over 70% emerged if the parasite had developed for 8 days prior to exposure. Some pesticides are more damaging than others (Tyler et al. 1974, Hardee et al. 1990). Tyler et al. working in sorghum (*Sorghum bicolor* (L.)) found that acephate (sprayed or as a seed treatment), and disulfoton had no effect relative to the control while carbofuran (applied either with the seed or sprayed on foliage) and aldicarb both significantly reduced the number of parasite mummies. Hardee et al. reported on the effects of the pesticides profenofos, chlorpyrifos, acephate, phosphamidon, and endosulfan in cotton. These pesticides were applied directly and indirectly to aphid mummies. Chlorpyrifos was the most toxic with an 11% adult survival rate. Profenofos was the least toxic after direct application while endosulfan was the least toxic following indirect exposure.

HYPERPARASITES: One of the problems with using this parasite in control programs is the effectiveness of the hyperparasites in the system. The hyperparasites have been used in control measures for *L. testaceipes* in experimental aphid colonies (Burton and Starks 1977). The following have been recorded as hyperparasites of *L. testaceipes*:

Asaphes americana (Spencer 1926)

Pachyneuron apidivorum (Spencer 1926)

Pachyneuron siphonophorae (Jackson et al. 1970)

Charips sp. (Burton & Starks 1977)

Xystus brassicae (Spencer 1926)

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Table 1: Host plants and host aphids of *Lysiphlebus testaceipes*

Aphid Host	Common Name	Plant Host	Source
Aphis citricola		*Citrus* sp. **	11
Aphis craccivora		*Glyricida maculata* *	7
Aphis craccivora		Dolichos lab-lab	7
Aphis gossypii	cotton aphid	Chinese hibiscus	10
Aphis gossypii		*Abelmoschus esculentus*	7
Aphis gossypii		Eggplant	7
Aphis gossypii		*Capsicum annum*	7
Aphis gossypii		Palay rubber plant	6
Aphis gossypii		*Citrus* sp.	11
Aphis helianthi		*Pittosporum tobira*	10
Aphis helianthi		Sunflower	9
Aphis lutescens		*Nerium oleander*	10
Aphis medicaginis		Alfalfa	10
Aphis medicaginis		*Salsola kali*	10
Aphis pomi	apple aphid	Apple **	3
Aphis pseudohederae		*Fatshedera lizei*	10
Aphis pseudohederae		*Hedera helix*	10
Aphis rumicis		Curled dock	10
Aphis spiraecola		*Citrus* sp. **	11
Duraphis noxia	Russian Wheat Aphid	Sorghum	2
Duraphis noxia		Wheat	2
Duraphis noxia		Barley	2
Macrosiphum ambrosiae		*Encelia actoni*	10
Myzus persicae	green peach aphid	*Vinca minor*	10
Myzus persicae		*Achillea filipendulina*	10
Rhopalosiphum madis	corn leaf aphid	Sorghum	1,5
Rhopalosiphum madis		Barley	10
Rhopalosiphum madis		Corn	10
Rhopalosiphum padi	oat-bird cherry aphid	Sorghum	5
Schizaphis graminum	greenbug	Sorghum	1,2,4,5,8, 12
Schizaphis graminum		Kansas winter wheat	8
Schizaphis graminum		Wheat	2,12
Schizaphis graminum		Johnsongrass	12
Schizaphis graminum		Barley	2,12
Schizaphis graminum		Oats	12
Schizaphis graminum		Rye	12
Toxoptera aurantii		*Citrus* sp.	11

* *L. testaceipes* did not form a viable population, though some individuals survived.

** *L. testaceipes* dies when reared with this combination, though the interaction occurs naturally in the field.

Key to Sources: 1)Archer et al. 1974; 2)Campbell et al. 1990; 3)Carroll & Hoyt 1986; 4)Hight et al. 1972; 5)Jackson et al. 1970; 6)Knight 1944; 7)Ramaseshiah et

al. 1968; 8)Rice & Wilde 1988; 9)Rogers et al. 1972; 10)Schlinger & Hall 1960; 11)Tremblay et al. 1978; 12)Walker et al. 1973.

RANDOMIZATION TESTS FOR ANALYSIS OF MORPHOLOGICAL DIFFERENCES

BETWEEN COLOR MORPHS OF *Aphis gossypii*

ABSTRACT

A new set of procedures in data analysis are being developed which make use of the increased power of computers to overcome some of the limitations imposed by classical statistics. Randomization tests are one of the computer intensive procedures which are becoming popular among ecologists. However, computer intensive procedures in general and randomization tests in particular have not been utilized by researchers in agriculture and other applied disciplines. Assuming that this is simply due to a lack of information in the literature, we briefly review randomization tests, and present a SAS program that will perform two-tailed tests for significant differences between means of two groups. A discussion is also provided to increase the program's flexibility to include other test statistics and multiple groups. Modifications to the program are also described which enable a researcher to determine if the average of several observations is different from a constant. For example, this could be used to determine if the average length of aphids is significantly different from 4mm. An extension of this procedure is also suggested which could be used when the null-hypothesis is that there are differences, and one wants to be able to reject this and conclude that there are no differences. This could be useful in areas of research like habitat restoration where one would assume that the restored habitat is different from the original, but would like to conclude that it is not different from the original.

The second part of the paper looks at the effect of the number of randomizations on the accuracy of the results. This is examined both as the difference between means at a fixed alpha level of significance, and as the p-

value given a fixed degree of difference between means. The conclusion is that a minimum of 10,000 randomizations are required to conduct a test at the 0.01 level.

The data set used to demonstrate an approximate randomization procedure consists of measurements of four morphological characters between two color morphs (yellow and green) of the melon aphid <u>Aphis gossypii</u> (Glover). The four measurements were aphid length, length of metathoracic tibia, cornicle length, and the maximum distance between the outer margines of the eyes.

INTRODUCTION

Computer intensive procedures are becoming more popular as a method for analyzing data. Crowley (1992) provides a list of areas within ecology where computer intensive approaches have been implemented. However, he did not find any articles using randomization tests in the category of "agriculture/fisheries." In the areas of competition, community structure, density dependence, demography, behavior, and evolutionary ecology there were a total of 103 articles. From the importance of these areas in agriculture one might assume that researchers in agriculture/fisheries are generally unaware of this type of analysis, or that this type of analysis is inaccessable. This paper briefly explains one type of computer intensive procedure, a randomization test, and some of the benefits and problems associated with the method. Morphological measurements of green and yellow <u>Aphis gossypii</u> (Glover) (Homoptera: Aphididae) are used as a data set to provide examples. Additional information on computer intensive procedures, as well as programs in FORTRAN and other languages, can be found in Edgington (1987), Noreen (1989), and Manly (1991).

74

The popularity of randomization methods stems from the fact that they are more flexible than standard tests and they do not assume the data conform to a specific distribution. In many cases, standard parametric tests (e.g. the Student's t-test) are sufficient, and deviations from the assumptions of the model are too small to affect the conclusions. However, violations of assumptions in parametric models are important in cases where the exact significance level is an important element in the analysis and conclusions. The effects of violating the assumptions of the model are also important in cases where a significance level is chosen (e.g. 0.05) and the p-value is close to this cut-off point (e.g. 0.049 or 0.051). Randomization tests are also useful in cases where conventional tests are inappropriate due to a small sample size or experimental design (Crowley 1992).

Randomization tests are used to examine differences in some statistic (e.g. mean, standard deviation, slope of a regression line, etc.) between two or more treatments or groups of observations. Randomization tests involve pooling all data from all treatments and then randomly, and without replacement, reassigning them to each treatment level such that all treatments have the same number of observations as they had in the original data set. If the total number of possible redistributions is small then all of them are used and the test is exact. If the number of redistributions is large, then a subset of all possible redistributions is used and the test is called a "sampled randomization test" (Crowley 1992) or an "approximate randomization test" (Noreen 1989). Following redistribution, a test statistic is calculated, and the process is repeated. For example, one could calculate the average length of a group of 40 aphids which were randomly assigned to two groups of 20 each, and take the difference in average length. After doing this several thousand times one would observe that some differences in average length were

observed frequently, while others were unusual. By plotting the number of times each difference occurs one generates a frequency distribution of calculated differences. One can then compare the observed difference in average length to the frequency distribution, and find out how often the observed difference would occur given a random arrangement of the data into two groups of 20 observations. The p-value is the number of observations as large or larger than the observed result divided by the total number of randomizations plus one. Since the randomization procedure guarantees that there is no correlation between the observed values and the treatments, this is a direct test of the null-hypothesis: there are no differences between treatments, or in the data used as an example, there are no differences between green and yellow morphs of the aphid.

In this test, first randomize the order of the data. Using the observed distribution of the data as one of the randomizations could seriously bias the results. Consider, if only two randomizations are used, and one of them is the observed distribution, then the observed distribution would occur half the time. This bias becomes small as the number of randomizations increases, but it will always persist in approximate randomization tests where the calculations begin by using the data in the observed order, or some other non-randomly determined order.

Randomization tests can be performed using any data set, but to generalize the conclusions from the data to the populations, a number of assumptions are required. The observations in randomization tests should be independent (Mantel's (1967) test is an exception). The samples should be a random subset from the population of interest, otherwise the results will apply only to the data used in the test (Manly 1991). It is the researcher's responsibility to determine the validity of generalizing to the total population.

However, this is frequently very similar in both effect and application to the assumption in more conventional analyses that the data are a random sample from the population of interest when in fact the observations were chosen arbitrarily from some subset of the population to which the researcher had easy access (Manly 1991). Second, randomization tests of differences between means are sensitive to differences in the variance, skewness, and other moments. This assumption can be satisfied by assuming that all observations come from the same distribution (Crowley 1992). Third, it is desirable for all sample sizes to be equal (Crowley 1992).

There is one problem that has nothing to do with the randomization test itself, but is critical in the implementation of approximate randomization tests. Because approximate randomization tests depend on a large number of random numbers, the quality of the random number generator (RNG) is critical to the accuracy of the test. Most RNGs have a periodic bias in their random numbers, with better RNGs having longer periods (Ferrenberg et al. 1992, Grassberger 1993). At present no RNG is universally accepted. The problem is complex, and made more complex because there may be significant interactions between the kind of random number generator used and the statistical procedure used for analysis (Ferrenberg et al. 1992). A resonable solution to the problem is to use a well known RNG, and report exactly what type was used. The RNG used in this paper is the Ranuni(0) function in SAS (SAS Institute 1989), which is a linear congruential RNG using modulo $2^{31}-1$ with a multiplier of 397204094, and is described further in Fishman and Moore (1982, 1986).

METHODS

In this paper, an approximate randomization procedure is used to examine differences in morphological characters between two color morphs

(yellow and green) of the melon aphid <u>Aphis gossypii</u> (Glover). All aphids were reared on a single watermelon plant (<u>Citrullus lanatus</u> (Thunb.) Matsum. & Nakai cultivar "Jubilee"). The plant was in a 10cm plastic pot with vermiculite-peat moss potting soil. The seed was germinated in the greenhouse, and the plant was moved to a walk-in growth chamber at the three true-leaf stage. The growth chamber was held at $25\pm0.4°C$: $23\pm0.4°C$ with the higher temperature during the 16 hour photophase. The relative humidity was $58\pm10\%$. Light was provided by both fluorescent and incandescent light bulbs with a light intensity of $4.09\mu mol$ s^{-1} m^{-2} at 660 nm, and $0.853\mu mol$ s^{-1} m^{-2} at 730 nm (chlorophyll is most sensitive to wavelengths at 660nm and 730nm, and melon aphids are sensitive to different wavelengths (Wyatt and Brown 1977)). This light intensity was the average of measurements taken at the level of the pot at the corners and center of the growth chamber. The plant was infested with 5 adult apterous aphids from a parent colony reared on the same cultivar of watermelon. The colony was allowed to develop for two weeks and then adult apterous aphids were removed, sorted by color into yellow or green and frozen. Morphological measurements from 20 adult apterous aphids of each color morph were taken.

Morphological characters were measured using an Olympus Stereoscopic microscope with an ocular micrometer calibrated to 0.0167mm. Aphid length was measured from the tip of the cauda to the extreme frontal part of the head as suggested by Ilharco & van Harten (1987). Length of metathoracic tibia, length of cornicle (= siphunculi) and the maximum distance between the outer margins of the compound eyes (eye) were also measured.

The approximate randomization test was implemented by pooling the measurements from the yellow and green aphids, and randomly, and without

replacement, reassigning each observation to a group. The mean for each group was calculated, and the difference calculated. A frequency distribution for the differences between the two means is generated by repeating this procedure up to 30,000 times. The p-value is calculated as (nge)÷(n+1) where nge is number of differences greater than or equal to the observed difference, and n is the total number of iterations used in the analysis (Manly 1991). The standard deviation for the p-value is calculated as $(p \times (1-p) \div n)^{1/2}$ (Potvin & Roff 1993) where p is the calculated probability from the frequency distribution of differences, and n is the total number of iterations.

The approximate randomization procedure for determining if the mean is different from some constant is similar to that described above. However, in this case the data used in the program consist of measurements from only one group (yellow or green) and a copy of this data set forms the contrasting group. This results in two groups with identical distributions and sample sizes, and with a difference of zero. The resulting frequency distribution is converted to probabilities of finding an observation some distance from the mean by taking the difference between the constant and the mean, and locating this difference on the frequency distribution. This procedure can also be used to obtain confidence intervals about a mean. The 95% confidence interval is the mean ± the difference where 95% of the randomizations are smaller than or equal to that difference. For the output used in this paper, begin by multiplying the total number of iterations by 1-å. For the 95% confidence interval with 30,000 iterations one would use the difference found where the cumulative sum of the number of randomizations is 28,500. The 95% confidence interval is the mean ± this difference.

One of the problems researchers face is determining the degree of similarity (or least difference) between two or more sets of observations.

Usually differences between groups are either significant, or not significant. However, this classification is too restrictive. In research areas such as habitat restoration, it is actually more important to determine the degree to which restored habitat is the same as the original, rather than reporting an inability to find significant differences. In other words, what does one do if the null-hypothesis states "there are differences" in contrast to the alternative hypothesis that "there are no differences"?

The first step is to examine the variability in the data set. The reason for doing so is that there are two causes for non-significant differences in means; the distance between means could be small, or the variability in one or both groups could be large. In deciding that two sets of observations are statistically similar, one needs to minimize the possibility that one is looking at variables that are so variable that they mask the "treatment" effect. If one assumes that all the variables follow identical distributions, one could use the CV of a variable which shows significant differences between the groups to screen other variables. Variables which do not show significant differences between groups and have a CV equal to or less than a variable that does show significant differences are singled out for further examination.

The next step is to construct separate frequency distributions for differences between the original data and its copy for each group. The frequency with which the observed difference in means between both groups occurs in the frequency distribution generated for the separate groups is then calculated. This results in two numbers: the frequency one would expect to find the observed difference in group "A" given that the true difference is zero, and the frequency one would expect to find the observed difference in group "B" given that the true difference is zero. If one decides that "A" will be statistically similar to "B" at some level, this test will result in one of three

conditions: 1) neither "A" nor "B" achieve the specified level ; 2)either "A" or "B" but not both achieve the specified level; 3) both "A" and "B" achieve the specified level. Only in the latter case would one conclude that the two groups are statistically similar. This analysis relies heavily on the assumption that the sample size for each group adequately summarizes the within-group variability of the "true" population.

The following SAS program was designed to analyze data consisting of two groups, each with 20 observations. The program was written in SAS because many people already use SAS for data analysis. SAS also has the advantage of having a well known random number generator and an efficient sort procedure. The program will run on both personal computers and mainframe systems so long as the name of the data file is in the proper format.

The program starts by setting up a macro called "repete" in line 1. This is done because SAS saves files to disc for temporary storage which limits the size of the do loop in line 4. Line 1 permits further increases in the total number of iterations. As written the program will perform a total of 10 iterations as two sets of 5 iterations each. When used for analysis, lines 1 and 4 should be modified to increase the number of iterations to 10,000 or more. Line 2 opens an external data file and reads it. The file name is specified in line 20. Line 3 drops unnecessary variables from the data set to decrease execution time and memory requirements. Line 4 makes multiple copies of the data set, and assigns each record a random number. If too many copies of the data are made, a "disc full" error may occur at this point or during one of the sort procedures. Line 5 sorts by copy and within each copy it sorts by the random number. The mod function in lines 7 and 8 compares the record number to the total number of records and assigns the first 19 and last record to the first group and the other records to the second group. The net effect is to randomly

assign each record to one of two groups such that each group has 20 records. Line 9 sorts the data set so that proc means in line 10 can calculate the mean for each group within each copy of the data set. Line 11 tells proc means to only output the mean, and names the variable where proc means will store the mean. Line 12 deletes unused information from the data set. Line 13 breaks the data set into two data sets, the first with the means for group one, and the second with the means for group two. These two data sets are merged in lines 14 and 15 to create a single data set with two variables, the first with means for the first group and the second with means for the second group. Line 17 takes the absolute value of the difference in the means. In line 18 the results are appended to the file "result" which is carried over from one execution of the macro to the next. The macro and the do loop end with line 19. Line 20 starts execution of the macro, names the initial data set a, and names the file that has the data. Lines 21 and 22 generate a frequency distribution for differences in means between the two groups. Because SAS will only keep track of a few thousand categories in forming the frequency distribution, the differences between groups were rounded to three decimal places using the format command. Line 23 deletes all the old data files so that they do not interfere with the next execution of the program.

```
1    %macro repete (new, in=inone); %do i=1 %to 2;
2    data &new; infile &in; input length tibia corn eye color;
3    data &new; set &new; drop tibia corn eye color;
4    data &new; set &new; do rep=1 to 5; r=ranuni(0); output;
     end;
5    proc sort data=&new; by rep r;
6    data &new; set &new;
7    if 0 le mod(_n_,40) le 19 then trt=1;
8    if 20 le mod(_n_,40) le 39 then trt=2;
9    proc sort data=&new; by rep trt;
10   proc means noprint data=&new; var length; by rep; class trt;
11   output out=outstat mean=length;
12   data f; set outstat; if _TYPE_=1;
13   data g1 g2; set f; if trt=1 then output g1; if trt=2 then output g2;
14   data f;
```

```
15    merge   g1(rename=(length=length1))   g2(rename=(length=length2));
16    by rep;
17    data f; set f; diff=abs(length1-length2);
18    proc append base=Result data=f;
19    %end;  %mend repete;
20    %repete(a,  in='a:colormor.txt');
21    proc freq data=result;
22    format diff 6.3; table diff/norow nocol nopercent;
23    proc datasets; delete a f result outstat;
24    run;
```

In entering the program make sure that no space exists between the % and the function name ("%macro" not "% macro). The same rule applies to the use of the & sign. Also, be aware that in line 10 "means" is the name of a procedure while in line 11 "mean" is a command word within that procedure. It is recommended that a carriage return be entered after each semicolon. This will make error messages in the data log easier to correct. By changing the numbers in lines 7 and 8 the program can deal with groups of unequal size. The number within the parentheses needs to be the total number of observations. The upper limit in line 7 needs to be one less than the number of observations in the first group. The entire program can be modified to deal with multiple groups by extensions of lines 7-8, 13, 15, 17, and 22.

Modifications to the program are required to deal with groups containing missing data. The missing data for the variable of interest need to be removed by inserting a new line of code between lines 2 and 3: "data &new; set &new; If var ne . then output &new;" where "var" is the name of the variable with missing values and "." is the symbol used to designate a missing value.

The program requires modification to perform the similarity analysis. First, two lines must be inserted between the existing lines 2 and 3: "data &new; set &new; If color=1 then output &new;" and "data &new; set &new; do rep=1 to 2; output; end;". The first line removes one of the groups from the data set, and the second line duplicates each remaining observation. If the variable

contains missing data these lines should follow the code that takes care of that problem. When looking at the expected variation in the CV under the null-hypothesis, replace "mean" with "cv" in line 11.

This program, like all programs performing randomization tests, relies heavily on a random number generator. The quality of the RNG influences the results, and there may be interactions between the RNG and the statistic of interest - in this case the mean. Even if the random number generator was "perfect", there still would be variability in the estimated p-values for differences between means. By definition one would expect that some of the estimates would be greater and smaller than the actual value which could be obtained by using all 40! ÷ 20! x 20! possible permutations of this data set. Some subset of this total is necessary to keep computation time reasonable. The total effect is estimated by repeating the analysis ten times using 10, 100, 1000, and 10000 iterations of the program. The ten "replicates" are then used to calculate a mean and standard deviation for the estimated p-value using a fixed distance between means of 0.0775mm and 0.1392mm for the variable length. The variables length, cornicle, and eye are used in the same way to predict an expected difference between means at a fixed alpha level.

RESULTS & DISCUSSION

As a prelude to presenting the results of the computer intensive procedure, a brief description of the data is provided. Means, standard deviations, and significant differences are presented in table 1, which shows the green color morph of A. gossypii was larger than the yellow morph under the conditions in the growth chamber. This difference was significant for all characters at $p \leq 0.0001$ for univariate models with color as the dependent variable and morphological characters as independent variables. The ratios

also show significant differences between the two color morphs with the exception of the ratio of length/eye. By inspection, it is also clear that larger means have larger variances which is a clear violation of the assumption that the mean and variance are uncorrelated.

With a computer intensive approach using an original group and a copy, it is possible to obtain 95% confidence limits for means. Table 2 compares the 95% confidence limits using the computer intensive approach to the 95% confidence limits obtained using the t distribution. The last column in the table presents the results of the Shapiro-Wilk test for normality. This is provided to show how far each variable deviates from the assumption of normality assumed by the t distribution. There are two tests for normality in each row, but only the least significant result is reported. It is apparent that the computer intensive procedure for this data produces a consistently wider confidence interval.

Four models were chosen for additional analysis: cornicle, length, and the ratios of length/tibia, and length/eye. Cornicle was chosen because the model is highly significant with a high coefficient of determination (r^2). Length is also highly significant, but has a low r^2. The ratio of length/tibia is a significant model, but has a very low r^2. The ratio of length/eye is not a significant model, and also has a very low r^2. Of these models cornicle has the highest coefficient of variation. Thus the decreased power of the other models to discriminate between green and yellow aphids cannot be attributed to a simple increase in variability.

The first column in table 3 presents the results of the two-tailed test for differences between the color morphs using the data from both groups combined into a single data set with observations randomly reassigned without replacement to each group. These values are very close to the P>F values in

85

table 1. The second and third columns in table 3 present results from a similarity analysis. The ratio of length/eye exhibits the least difference between green and yellow aphids, but shows little overlap between the two groups. It shows similarity only at the 5% level - that is 95% of the time differences would be smaller than the observed difference if there were actually no differences between the two groups. From tables 1 and 2, one can see that using this set of characters the different color morphs have many significant differences and no similarities.

Figure 1 is a frequency distribution of differences in means using the absolute value of the difference. This figure shows one important feature that is usually true for frequency distributions. The difference occurring with the greatest frequency is some number slightly larger than zero. This result is intuitively obvious because one would expect that the number of ways to arrange any set of numbers into two groups such that their difference is zero should be less than the number of ways to arrange them such that there is a small difference. This observation could be used as a highly restrictive test for deciding that two samples are the same. So two sets of observations are the same only if the observed difference between them is less than the difference observed most frequently - in Fig. 1 this difference would be about 0.01. In most cases this definition may be far too restrictive. It would be better for each researcher to decide on a case by case basis what constitutes a reasonable definition for similarity based on the cost of drawing an incorrect conclusion.

A problem in computer intensive analysis is determining how many iterations are needed to accept or reject a null hypothesis at a given alpha. Table 4 shows the change in p-value given a fixed difference in means using the variable length. The important features of table 4 are: 1) at a low number of iterations, the predicted standard deviation overestimates the calculated

value; 2) though the difference is small, the predicted value underestimates the standard deviation when the number of iterations is large; and 3) the variability in the estimate decreases as the number of iterations increases. The first and second conclusion could either be due to a flaw in the equation for the predicted variance, or a problem with the random number generator. One important feature that the predicted equation does not take into account is shown in table 5 where a variable with a lower CV will have a smaller deviation about the predicted difference at a fixed alpha level.

In decision making, one often wants to know how large a difference is required to be judged significant at some level of alpha. Table 5 shows this for a fixed alpha of 0.10 and 0.01 for the variables cornicle, length, and eye. The important parts of table 5 are: 1) the coefficient of variation decreases with increasing number of iterations; and 2) a variable with a larger coefficient of variation has a higher coefficient of variation in estimating a significant difference. The few exceptions apparent in table 5 are artifacts of the data caused by using a discontinuous sequence of numbers to estimate a continuous function. For example, the distance between green and yellow aphids for the variable eye at alpha = 0.01 and 10,000 iterations is either 0.01875mm or 0.01792mm. There is no way to arrange the 40 observations into two groups such that the difference is some number between these values. This increases the variability in estimating the "true" distance between the groups above what one would normally expect. A similar effect explains the CV of zero for variable eye at alpha = 0.10 and 10,000 iterations. Here, the distance between 0.12083mm and its nearest neighbors in the frequency distribution is much larger than the difference between this estimated value and the "true" value for the population. As a result, there is no observed variability in the estimate.

Potvin and Roff (1993) suggest that 5000 iterations are sufficient to make the standard error negligible, but Jackson & Somers (1989) recommend using 10,000 to 50,000 iterations. From our results, it appears that a minimum of 100 x (1÷ alpha) iterations are required to accurately estimate the p-value, where alpha is the rejection level for the standard null-hypothesis. The required number of iterations varies to some extent based on the level of variation present in the data. However, if the calculated P - value is close to some designated significance level (e.g. 0.05) one should increase the number of iterations. The number of iterations should also be increased if the data are highly variable. Of course the cost of increasing the number of iterations is that the computer is unavailable for other activities for extended periods of time: A 33 megahertz 486 IBM clone using a 4 megabite ramdrive takes about 90 minutes to do 10,000 iterations with two groups of twenty observations each.

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Table 1: Morphometric characters of different color morphs from adult apterous aphids reared on a single watermelon plant.

| Parameter (mm) | Morph | | | | Model | |
	Green (n=20) mean ± sd	CV	Yellow (n=20) mean ± sd	CV	r^2	P>F
Body	1.335 ± 0.142	10.60	1.149 ± 0.129	11.27	0.33	0.0001
Tibia	0.715 ± 0.056	7.82	0.573 ± 0.082	14.27	0.52	0.0001
Cornicle	0.267 ± 0.037	13.94	0.186 ± 0.030	15.99	0.60	0.0001
Eye	0.334 ± 0.017	5.05	0.301 ± 0.014	4.77	0.54	0.0001
Body/Tibia	1.868 ± 0.148	7.94	2.025 ± 0.210	10.38	0.16	0.0097
Body/Cornicle	5.082 ± 0.761	14.97	6.246 ± 0.695	11.12	0.40	0.0001
Body/eye	3.994 ± 0.363	9.09	3.810 ± 0.340	8.92	0.07	0.1062
Tibia/Cornicle	2.713 ± 0.286	10.56	3.086 ± 0.149	4.83	0.41	0.0001
Tibia/eye	2.139 ± 0.117	5.47	1.893 ± 0.191	10.10	0.39	0.0001
Cornicle/eye	0.798 ± 0.104	13.07	0.616 ± 0.074	12.00	0.52	0.0001

Table 2: Comparison of the 95% confidence intervals using the t distribution and the computer intensive method.

	Morph				
	Green (n=20)		Yellow (n=20)		
	t (0.975, 19)	Computer intensive	t (0.975, 19)	Computer intensive	$P < W^1$
Body	0.0665	0.0867	0.0608	0.0800	0.78
Tibia	0.0262	0.0333	0.0384	0.0500	0.44
Cornicle	0.0173	0.0225	0.0140	0.0175	0.36
Eye	0.0079	0.0100	0.0066	0.0083	0.02

The 95% confidence interval is the mean from table 1 ± the numbers in the body of this table.
1) The Shapiro-Wilk test for normality. The smaller the number the greater the departure from normality.

Table 3: Probabilities of differences greater than or equal to the observed difference between the two groups.

	Joint	Green=Yellow	Yellow=Green
Body	0.00002	0.00007	0.00000
Cornicle	0.00000	0.00000	0.00000
Body/Tibia	0.01007	0.00063	0.01934
Body/Eye	0.11523	0.10670	0.09330

Values are based on 30,000 iterations. Joint probability uses data from both groups. Green=Yellow uses data only from the green morph , while Yellow=Green uses data only from the yellow morph.

Table 4: Error associated with estimating the p-value for the variable length based on the number of iterations.

Distance	Iterations	mean P-value ± sd	predicted sd	CV
0.0775	10	0.18182 ± 0.08571	0.12197	47.14
	100	0.12277 ± 0.02847	0.03282	23.19
	1000	0.13976 ± 0.01398	0.01097	10.00
	10000	0.13748 ± 0.00348	0.00344	2.53
0.1392				
	10	0.00909 ± 0.02875	0.03001	316.23
	100	0.00792 ± 0.00781	0.00886	98.60
	1000	0.00679 ± 0.00204	0.00260	30.06
	10000	0.00634 ± 0.00093	0.00079	14.61

Each iteration was replicated ten times to give mean, standard deviation, and CV. The total average (both color morphs) is 1.24208 mm ± 0.16365 with a cv = 13.18.

Table 5: Error in estimating a significant mean difference for variables cornicle, length and eye given alpha=0.10 and alpha=0.01.

Alpha	Iterations	Cornicle cv = 23.21 difference ± sd.	CV	Length cv = 13.18 difference ± sd.	CV	Eye cv = 7.16 difference ± sd.	CV
0.10	10	0.03842 ± 0.01265	32.92	0.10783 ± 0.01900	17.62	0.01200 ± 0.00154	12.87
	100	0.02725 ± 0.00218	8.00	0.08117 ± 0.00618	7.61	0.01150 ± 0.00097	8.40
	1000	0.02733 ± 0.00088	3.23	0.08517 ± 0.00225	2.64	0.01183 ± 0.00040	3.40
	10000	0.02717 ± 0.00026	0.97	0.08500 ± 0.00088	1.03	0.12083 ± 0.00000	0.00
0.01	100	0.04617 ± 0.00648	14.05	0.13867 ± 0.01451	10.46	0.01883 ± 0.00169	8.96
	1000	0.04242 ± 0.00181	4.26	0.12933 ± 0.00512	3.96	0.01792 ± 0.00056	3.10
	10000	0.04217 ± 0.00061	1.46	0.13083 ± 0.00136	1.04	0.01842 ± 0.00043	2.34

There are ten replicates per level of iteration. The CV listed across the top are for the data set (both colormorphs). The CVs listed in columns are for the differences.

Figure 1: Frequency distribution for the ratio length/tibia for 30,000 iterations.
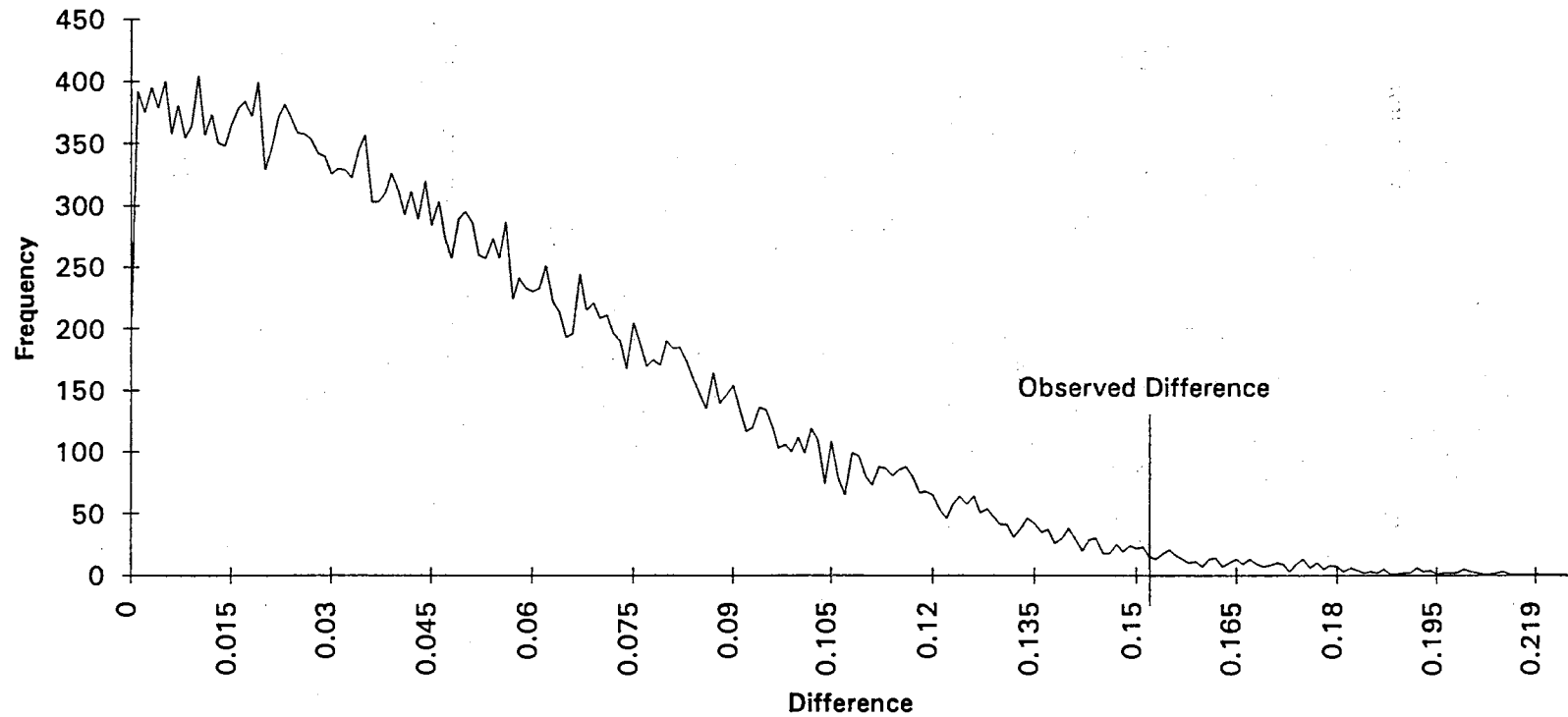
The probability of observing a difference greater than or equal to the observed difference is the area under the curve past the line titled "observed difference." There were 203 iterations with zero difference between the two groups.

DESCRIPTION OF NON–CLONAL *Aphis gossypii* (Glover) (Homoptera: Aphididae) COLONIES REARED ON SQUASH, WATERMELON, COTTON, AND WHEAT, USING MORPHOLOGICAL, BIOCHEMICAL, AND GENETIC CHARACTERS

ABSTRACT

The goal of this research was to describe four non-clonal colonies of *Aphis gossypii* (Glover). Each colony had been maintained on one of four host plants 18 months prior to data collection. The hosts were squash, watermelon, cotton, or wheat. Aphids were described using morphological characters, epicuticular hydrocarbons, internal fatty acids, and genomic DNA. We conclude that *A. gossypii* is different on different host plants, and that this difference can be detected using morphology. However, epicuticular hydrocarbons of the aphid provide clearer distinction between colonies. RAPD-PCR was also able to detect differences between colonies which were greater than differences within colonies.

INTRODUCTION

Morphology is the classical measure used to separate individuals into groups: species, subspecies, variety, etc. The methodology involves using qualitative and quantitative differences between individuals, and analyzing the data using a clustering procedure to group individuals based on shared characters (Mayr 1969). This is still the primary methodology employed in distinguishing species. However, classification based on morphological characters requires highly skilled personnel, and often fails to distinguish between biotypes, strains, etc.

Analysis of epicuticular hydrocarbons in insects provides additional taxonomic characters for distinguishing individuals. The chemical

composition of the epicuticlar lipid is important because it can play a significant role in intra- and interspecific communication. Epicuticular lipids also act as a barrier to the environment, protecting insects from desiccation, toxins, and pathogens (Blomquist & Dillwith 1985). For these reasons alone, the chemical composition of the epicuticle should be fairly unique within groups of organisms, and therefore, good characters to use for characterizing populations of organisms. Other researchers have used the composition of the epicuticular lipids to identify closely related organisms: e.g. greenbug biotypes (Dillwith et al. 1990), fruit flies (Goh et al. 1993), Russian wheat aphids (Bergman et al. 1990), Anopheles mosquitoes (Milligan et al. 1986), and *Simulium* spp. (Phillips et al. 1985).

The fatty acid profile of an insect is less likely to be taxonomically useful because the profile is variable based on environmental conditions and diet (Stanley-Samuelson et al. 1988). However, because of their importance in metabolism, fatty acids should provide information on insect health. There are several common strategies exhibited by starved insects. Starved individuals may store energy in preparation for emigration; they may increase reproduction to insure that a few individuals survive until better times; or they may increase development rate to reach a resting stage. Given a particular strategy, other features should be correlated with the fatty acid profile. For example, starved insects tend to be smaller, have a lower reproductive output, and shorter life span. If starved insects choose to store energy in preparation for emigration, there should be a correlation between increased storage fat and size. Therefore, even though the fatty acid profile is not taxonomically useful, it represents another biologically important set of differences in the aphids which are associated with differences in host plant.

Random Amplified Polymorphic DNA amplified by the Polymerase Chain Reaction (RAPD-PCR) is a recent technique first described by Williams et al. (1991). Black et al. (1992) used this procedure on aphids to provide characters useful for distinguishing between individuals. The process uses a ten oligonucleotide sequence (decamer) as a primer, permits the primer to bind to a purified DNA sample, and then uses a thermostable DNA polymerase to copy the DNA. The products are separated into bands based on molecular weight using gel-electrophoresis. The researcher then selects bands which appear to be consistent within a group (a genetic fingerprint), and the presence or absence of such bands are used to classify individuals. As expected, this methodology is useful for detecting minute differences between individuals. It has been used on aphids (Black et al. 1992, Cenis et al. 1993), mosquitoes (Kambhampati et al 1992), *Aspergillus* (Megnegneau et al. 1993), *Gelidium* (algae) (Patwary et al. 1993), wheat (He et al. 1992), potato (Baird et al. 1992), grasshoppers (Chapco et al. 1992), conifers (Carlson et al. 1991), and fungal endophytes (McCutcheon and Carroll 1993) to name a few. The methodology is also used in other fields of endeavor: as a tool to examine genetic variation in populations of rare and endangered species (Brauner et al. 1992); and plant breeding (He et al. 1992, Wilde et al. 1992, Baird et al. 1992).

The genetic code has regions that are highly conserved, while others are highly variable. This should provide a wide assortment of characters which could be used to classify organisms at all levels. Furthermore, DNA fingerprints are a direct measure of differences between individuals, while differences in other characters (morphology, hydrocarbon, etc.) arise from interactions between the environment and genome. The advantage of RAPDs is that nothing needs to be known about the DNA. The decamer binds to all appropriate sites and transcription begins. However, because nothing is

known about the function of the amplified regions it may be difficult to find a decamer that distinguishes between individuals or closely related groups. Additionally, failure to identify differences using a single decamere is not an indication that the two organisms are genetically the same, it only means that no difference was detected.

The research presented here is a description of four non-clonal *A. gossypii* colonies. It examines the degree of separation between the colonies using morphological, biochemical, and genetic traits. All colonies have been identified on several occasions as *A. gossypii* by Dr. Manya B. Stoetzel (USDA ARS Beltsville Agricultural Research Center). This represents the first time that all of these methodologies have been used to characterize a group of individuals.

METHODS

Aphid cultures were maintained on four host plants; 1) Squash - *Cucurbita pepo* var. melopepo (L.) Alef. cultivar 'Lemondrop-L'; 2) Watermelon - *Citrullus lanatus* (Thunb.) Matsum. & Nakai cultivar 'Jubilee'; 3) Wheat - *Triticum aestivum* L. cultivar 'Chisholm' (89 OK FSS); 4) Cotton - *Gossypium hirsutum* L. cultivar 'Pioneer 75' (1988 seed). Plants were grown in a greenhouse in 10cm diameter plastic pots. Pots of wheat had 4 or 5 plants, while the other species were potted individually. Plants were potted in a mix of vermiculite and peat moss and fertilized once per week with 4 grams Peters solution (20-20-20) per liter of water, but fertilization was uneven as only sufficient water to dampen the potting mix was applied. Plants were transferred to a walk-in growth chamber at least 3 days prior to aphid infestation. All host plants had 2 or 3 true leaves when transferred to the growth chamber; by this time cotton cotyledons had begun to senesce. The

chamber maintained 60±15% relative humidity and 16:8 (L:D) hour photoperiod with a fluctuating temperature of 23°±0.4C: 21°±0.4C corresponding to the photoperiod. The chamber used fluorescent and incandescent light sources which provided a light intensity of 4.09μmol s^{-1} m^{-2} at 660 nm, and 0.853μmol s^{-1} m^{-2} at 730 nm (note: chlorophyll is most sensitive to wavelengths at 660nm and 730nm, and melon aphids are sensitive to different wavelengths (Wyatt and Brown 1977)). Light intensity was measured 10cm further from the lights than the leaf surface.

Aphid colonies on squash and watermelon originated from aphids collected at the Wes Watkins Agricultural Research and Extension Center (WWAREC) in Atoka County Oklahoma. Aphids on wheat came from the squash and watermelon colonies. The aphids on cotton came from Harmon County Oklahoma, which is at least 330 km (as the crow flies) west of WWAREC. Colonies had been maintained under similar conditions on their respective host plants for at least 18 months prior to the start of the experiment.

Aphid colonies were started by infesting each pot with approximately 15 adult apterous aphids. Adult aphids were removed two days later. Samples consisting entirely of adult apterous aphids were collected the day after the first new nymphs appeared. Samples for biochemical analysis were placed into hexane washed glass vials and covered with a foil lined lid. Each vial contained 50 to 150 aphids taken from as many as 6 different pots. No cages of any type were used to confine aphids. Aphids were prevented from changing host plant by the short duration of the colony and by keeping pots sufficiently separated from one another to prevent crossover. Low aphid density assured that no alates were produced (Reinhard 1927). Adult apterous aphids were collected for morphological examination, after samples for biochemical analyses were collected. Samples for hydrocarbon and fatty acid anaylsis were frozen in a

standard refrigerator-freezer until processed. All samples contained only the green color morph, but aphids from cotton were much darker than aphids from other hosts. Samples for analysis using RAPD-PCR were frozen at -70°C until the DNA could be extracted.

Morphological characters were measured using an Olympus Stereoscopic microscope with an ocular micrometer calibrated to 1/60th millimeter. Aphid body length was measured from the cauda to the extreme frontal part of the head as suggested by Ilharco & van Harten (1987). Length of metathoracic tibia (tibia), length of cornicle (= siphunculi) and maximum distance between outer margins of compound eyes (eye) were also measured.

Aphids collected for analysis of epicuticular hydrocarbons were washed with 10 ml hexane and refrozen for later extraction of fatty acids. An internal standard of 0.67 μg nC_{24} was added to each sample. The hydrocarbon fraction was isolated from the crude lipid extract by elution through a pasteur pipette packed with Bio-Sil A 100-200 mesh silica gel (Bio-Rad Laboratories, Richmond, California). The samples were dried and reconstituted in 50 μl hexane. They were analyzed using a Hewlett-Packard Series II 5890 gas chromatograph with a 15 meter fused silica DB-1 capillary column (J&W Scientific) with a film thickness of 0.15 μm. One μl of sample was injected using an autosampler and cool on column injection. The carrier was helium flowing at 1 ml/min. The column temperature started at 50° C and ramped at 40° C/min to 175° C. After maintaining that temperature for 1 minute the temperature was increased to 320° C at 8° C/min and maintained there for 1 minute. Epicuticular hydrocarbon data were converted to equivalent chain lengths using a standard curve generated using straight, even chain length, hydrocarbons from C_{20} to C_{40}. Variables are reported to the nearest tenth of 1 carbon unit.

To check for possible contamination of aphid samples with plant hydrocarbons, samples from uninfested plants were also collected. Individual leaves were washed in hexane, and the crude extract purified using the same procedure used in processing the aphid samples.

Analysis of the epicuticular hydrocarbons was done using percent composition and as hydrocarbon proportional to surface area (Hydrocarbon :: Area). The total hydrocarbon for percent composition was the sum of all detected peaks, less the quantity of standard present. To use surface area it was assumed that aphids are of constant density. If this is true, then weight is proportional to volume. With a spheroid to approximate an aphid, surface area is proportional to volume to the 2/3 power. The surface area was calculated by first dividing the sample weight by the number of aphids present, raising this to the 2/3 power, and multiplying by the number of aphids in the sample. It is necessary to examine the data both ways because the relative proportion of different compounds can change and the total amount present can change. Percent composition measures changes in the proportion of each compound present. Hydrocarbon :: area measures the total present over a surface. The two measures do not necessarily have to yield the same answer.

Fatty acids from aphids were extracted using the methodology reported by Bligh & Dyer (1959). Aphids were homogenized in a 2:1:0.8 (v/v/v) chloroform-methanol-water solution. One ml of additional chloroform and 1 ml water were added to the homogenate to induce separation. The sample was mixed and centrifuged for 10 minutes and the bottom layer removed. One ml of chloroform was added, mixed, centrifuged, and the bottom layer was added to the sample already separated. Another 1ml of chloroform was added, mixed, centrifuged, and combined with the previous fraction. The chloroform fraction was then dried in a sand bath at 60°C under nitrogen. For GLC

analysis, the lipids were hydrolysed by heating in a 5.0% (w/v) solution of KOH in methanol at 60°C for 1 hour. Fatty acid methyl esters were generated by adding 1 ml of 14% w/v boron trifloride in methanol and heating the sample for an additional 30 minutes. After cooling 2ml of water was added to stop the reaction. The fatty acid methyl esters (FAMEs) were extracted with 6ml of chloroform, and filtered through a Pasteur pipette plugged with glass wool and a small amount of magnesium sulfate to remove the remaining water. The sample was dried and reconstituted in hexane. This was then eluted through a Pasteur pipette packed with Bio-Sil A 100-200 mesh silica gel (Bio-Rad Laboratories, Richmond, CA.), using 5% diethyl ether in hexane. After drying, the sample was reconstituted in 50 µl hexane. The sample was analyzed with a Hewlett-Packard 5840A gas chromatograph with a DB-225 capillary column, 30m x 0.25mm, 0.15µm film thickness (J&W Scientific). The temperature program started at 60°C for 5 minutes, +10°C per minute to 200°C, and finished with +5°C per minute to 220°C. The temperature remained at 220°C for 4 minutes. The analysis was done using percent composition and micrograms fatty acid per milligram aphid weight.

Aphid DNA for RAPD-PCR was extracted by homogenizing individual aphids in 100 µl of extraction buffer. The buffer consisted of 100mM ultrapure tris (tris(hydroxymethyl)-aminomethane) adjusted to pH 8.0 with HCl, 250mM NaCl, and 25mM EDTA (ethylenedinitrilo tetraacetic acid), and 1% SDS (sodium dodecyl sulfate) disolved in "type 1" water (distilled, filtered, autoclaved water with a resistance of at least 18MΩ). The homogenate was heated for 10 minutes at 37°C, and 80µl phenol (equilabrated with 0.1M tris buffer at pH 8) was added, and the mixture agitated for 2 minutes. Next, 40 µl of chloroform was added, agitated, and then centrifuged at 13,000 RPM for 5 minutes. The chloroform extraction was repeated once. The aqueous phase was removed, and 30µl

isopropanol was added to precipitate the DNA. The sample was centrifuged and rinsed in 50 µl of 70% ethanol. The tubes were drained, and the DNA resuspended in TE (10mM Tris-HCl, pH 7.5, 1mM EDTA, disolved in type 1 water). The extracted DNA was stored at -20°C.

Samples were analyzed for DNA content using a Hoefer Scientific Instruments DNA fluorometer model TKO 100. The dye was Hoechst 33258 dissolved at 1mg/ml and stored. The working dye solution consisted of 1µl dye stock dissolved in 1ml of a modified TE buffer: 0.2M NaCl, 10mM Tris-HCl, and 1mM EDTA with the pH adjusted to 7.4. The buffer was filtered through a 0.22µm membrane to remove particulates. Fresh dye solution was made daily. With each fresh batch of dye the fluorometer was calibrated using a 10ng/µl solution of *E. coli* DNA. Each reading consisted of 2ml of dye solution and 2µl of extracted aphid DNA. The results were an average of three measurments from each sample. All samples were then diluted using TE to a final concentration of 3.3 ng /µl.

Samples were analyzed using primers C01 (TTCGAGCCAG), C04 (CCGCATCTAC), A09 (GGGTAACGCC), C09 (CTCACCGTCC), and C10 (TGTCTGGGTG) from Operon Technologies Inc ((Alameda CA). Also used was BAM (ATGGATCCGC), prepared by Genosys (The Woodlands, TX). The reaction mixture consisted of 50 µl reaction buffer (50 µl 10x buffer provided by Promega, 50 µl 15mM MgCl, a total dNTP concentration of 200mM (1:1:1:1 dATP, dGTP, dCTP, dTTP), and 396 µl water), 30ng primer, and 10 ng aphid DNA. This was covered with 40 µl of oil in a reaction tube, and placed in a PTC-100 programmable thermal controler (MJ Research Inc. Watertown MA). The temperature program and addition of 0.20µl 5units/µl Taq (a thermostable DNA polymerase from *Thermus aquaticus* strain YT1 (Chien et al. 1976)) (Promega Corporation, Madison WI) followed the procedure outlined in Black et al. (1992).

Amplification products were analzed using agrose gel electrophoresis. The gels consisted of 5 g SYNERGEL (Midwest Scientific), 7.5 g MetaPhor fine analytical grade agrose, and 7.5 g DNA grade Agrose (Bio-Rad Laboratories) disolved in 1 l of buffer (22.5mM Tris-borate, and 0.5M EDTA). Each gel consisted of 75 ml of the gel plus 10 μl of ethidium bromide at 10 mg/ml. Gels were run in the same buffer solution used to make the gels. The power supply was set for constant voltage to run at 4.8 volts per centimeter. Products were detected using a 302 nm ultraviolet light source. When sufficient resolution was achieved, gels were stained for 15 minutes in an ethidium bromide bath (0.5ug/ml water) and rinsed in a water bath for 1 hour. Gels were photographed under UV light with a Polaroid MP-4 camera and Polaroid 55 positive/negative film. Bands were scored by visual examination of the photographs. If a band was present it was scored as 1, else it was scored as 0. Bands ranging in weight from 3000 to 200 base pairs (bp) were scored. Specific bands were identified using a pdi model DNA 35 scanner connected to a SPARC workstation (pdi Inc., Huntington Station NY). The software used to determine the size of specific bands given the pGem standard was Quantity One version 2.4 (copyright pdi Inc.). In a few cases, difficulties arose in identification of bands between photographs. Such problems were resolved using the estimated size of the fragments.

The analysis was performed using three procedures. First, each variable is examined individually in its ability to discriminate between different colonies. Multivariate models were then developed to examine the overall difference between the aphid colonies. Since the colonies were significantly different, but all had been identified as *Aphis gossypii*, a computer intensive approach was used to look for relationships between colonies which showed little or no difference.

The morphological, epicuticular hydrocarbon, and fatty acid data were analyzed using SAS version 6.03 (SAS Institute 1989) running on a IBM 486 clone. The presentation of the analysis is organized by the method of analysis: univariate analysis, multivariate analysis, and computer intensive procedures. The RAPD-PCR results are described in a separate section.

Multiple comparisons of means were performed using the GLM procedure in SAS using the Ryan-Einot-Gabriel-Welsch multiple range procedure (REGWQ) to control the experiment wise error rate (SAS Institute Inc. 1989). All tests were done at the 0.01 level.

The multivariate analysis section involves two separate analyses which provide two statistics for evaluating differences between groups. Discriminant analysis is used as a measure of model quality by providing an estimate of the probability of classifying an observation into the wrong group. Canonical discriminant analysis is used to determine how far apart the different groups are using a statistic called the Mahalanobis distance. Mahalanobis distance was used in preference to Euclidean distance because the Mahalanobis distance takes into account correlations between variables (Manly 1991).

Mantel's test (Mantel 1967) as modified by Smouse et al. (1986) is a computer intensive procedure designed to determine the degree of correlation between to matrices. In a previous analysis, matrices of Mahalanobis distances were created using morphology, hydrocarbon, and fatty acid profiles, showing the separation between the different groups. For any two matrices a Z value is calculated by multiplying each element of one matrix by the corresponding element of the other matrix and summing all the products. The frequency distribution is generated by randomly reassigning the numbers from only one of the matrices to a new location within that matrix and recomputing Z. If the observed Z value is unusually large with respect to the other possible Z values

(P>Z is small) the two matrices are positively correlated. If the observed Z is unusually small (P>Z is large), the two matrices are negatively correlated (Manly 1991).

Having observed that aphids from different colonies are distinct, identification of characters useful in classifying the colonies as a single species are needed. Following the procedure proposed in chapter 4, an approximate randomization procedure was used to test for similarities in means between the aphid colonies. The general procedure involves randomly redistributing observations among the different groups 10,000 times. The difference in means between the different groups is calculated after each randomization. The number of times a difference is found is then plotted to form a frequency distribution of differences between groups. This was done using data from one group and comparing it to its copy. This is used to analyze the data with a null hypothesis that there are differences between all aphids, versus the hypothesis that there are no differences. The procedure is repeated for aphids from each host plant. For any pair of observations, the procedure is performed separately on each group giving the degree of similarity between group A and B, and between Group B and A. The two observations are similar at the lowest level between these two tests. The probability level used in this paper for deciding that two groups are similar is 0.10, which is the greatest degree of similarity between green and yellow morphs of this aphid growing on a single host plant (chapter 4).

The probabilities for the computer intensive procedures are reported as approximate p values. The actual value may be slightly larger or slightly smaller than the reported value. Ten thousand iterations were used for all computer intensive tests. This should accurately detect effects at the 0.01 level (chapter 4, Jackson & Somers 1989).

107

Analysis of the RAPD-PCR results was done with a special program written in SAS (SAS Institute Inc. 1989). The program converted the raw data into a distance matrix, and analysed the distance matrix using method=average in proc cluster. The clustering method was an unweighted pair group method using arithmetic averages (UPGMA) which is similar to the procedure used by Black et al. (1992). The distance matrix was formed under the assumption that 0-0 matches between individuals was important. Thus, the distance between two individuals is one minus the number of bands coded as either 1 or 0 for both individuals divided by the total number of scored bands. This is described as simple matching by Anderberg (1973).

RESULTS

Univariate Statistics

Aphids feeding on cotton were larger than aphids from other colonies for all measurements (Table 1). Aphids from wheat were the smallest. The Pearson correlation coefficients between pairwise arrangements of the morphological variables were greater than 0.78 for all comparisons with the pooled data. This strong relationship broke down within host plant for the variable length. In melon and wheat length was uncorrelated with the other measures, while for cotton length was only correlated with eye. Length was correlated with tibia, cornicle, and eye only for squash. Within each host plant the variables tibia, cornicle, and eye had correlation coefficients between 0.48 and 0.83. Within each morphological character, larger means had larger standard deviations.

The chromatograms in Figures 1 through 4 illustrate differences between leaves of different ages, and between plants and aphids. The numbers identifying each peak are equivalent chain lengths (ECL). The ECL identifies

compounds using the retention time of a standard curve generated by analyzing a known mixture of straight chain hydrocarbons. In this paper, the ECL is usually listed as a subscript to a capitol C, as in $C_{25.0}$ refers to a compount with an ECL of 25.0. The first peak in Figures 1 through 4 is the standard, $nC_{24.0}$. All chromatograms are plotted on roughly the same time scale, so compounds with the same molecular weight will have peaks near the same position in each chromatogram. Chromatograms are arranged such that each column of figures starts with plant samples and ends with a sample from aphids reared on that host plant. Chromatographs from the epicuticular hydrocarbon data showed no contamination from plant samples, and showed that aphid epicuticular hydrocarbons do not come from the plant. If aphids were getting hydrocarbon from the plant or if aphid samples were contaminated with plant hydrocarbons, then the chromatograms for aphids should have corresponding changes with those observed in the plants. Squash and melon had more $C_{31.0}$ and $C_{33.0}$ than any other component. Cotton had less $C_{33.0}$ and more $C_{29.0}$ relative to squash or watermelon. Wheat had more $C_{25.0}$, $C_{27.0}$, and $C_{33.0}$ relative to the other plants. However, the dominant epicuticular hydrocarbon components in aphids were $C_{27.0}$ and $C_{29.0}$, regardless of which host plant they were feeding on (Figs 1,2,3,4). The simplest explanation for this pattern is that the aphids synthesized their own epicuticular hydrocarbons.

The percent hydrocarbon composition of all aphids was dominated by $C_{27.0}$ and $C_{29.0}$. The next most abundant was $C_{25.0}$ which was especially abundant in the colony from watermelon. Aphids reared on wheat had the least $C_{27.0}$, but the most in 7 out of the remaining ten hydrocarbon variables (table 2). Aphids from cotton had the next greatest levels of hydrocarbon for all variables. Aphids from squash tended to be intermediate between aphids on

109

cotton and those on wheat. Aphids from watermelon showed no distinctive pattern relative to aphids from the other colonies.

For the pooled data, some variables were highly correlated with Pearson correlation coefficients as high as 0.99 while others were uncorrelated. Within each group of host plants, there were four comparisons that had correlation coefficients above 0.70 for all within host comparisons: $C_{31.0}$ vs. $C_{33.0}$, $C_{27.5}$ vs. $C_{29.9}$, $C_{29.0}$ vs. $C_{31.0}$, and $C_{29.0}$ vs. $C_{33.0}$.

The fatty acid composition of all the colonies was dominated by 16:0 (table 3). Aphids on cotton and wheat had abundant 14:0, and aphids on cotton had large quantities of 18:2. For the pooled data, eight comparisons were significantly correlated with Pearson correlation coefficients between 0.70 and 0.97. Of these, 12:0 vs. 14:0, 18:0 vs. 18:1, and 18:2 vs. 18:3 also had correlation coefficients above 0.70 for all of the within host comparisons.

Since epicuticular hydrocarbon data and fatty acid data came from the same aphids it is possible to look for correlations between the two sets of data. Analysis revealed 57 significant correlations at the 0.05 level. Of these models, the 6 highly significant models were the pairwise comparisons between the hydrocarbons $C_{29.0}$, $C_{31.0}$, $C_{33.0}$ and the fatty acids 12:0 and 14:0. The model with the highest correlation coefficient is shown in figure 5. However, aphids from each host plant form distinct groups, and a regression line for data from squash, watermelon, and cotton would not follow the overall pattern. The regression equation with standard errors is $C_{29.0} = 0.0850$ (± 0.0095) $+ 0.7403$ (± 0.0917) x 14:0. The coefficients are significantly different from zero at the 0.0001 level, and the regression has an r^2 of 0.64.

Two additional features of the correlation between epicuticular hydrocarbons and fatty acids are worth mentioning. First, aphids reared on squash, watermelon, and cotton all had about 25 comparisons (of a total 110)

110

which showed significant correlations, while aphids from wheat had only 3. Second, all three significant comparisons in wheat were shared by aphids on squash, but the sign was opposite.

Multivariate Analysis

The morphometric data were analyzed using discriminant analysis and canonical discriminant analysis. The test for homogeneity of within covariance matrices was significant with a probability of a greater chi-square $(P>\approx^2)$ = 0.054, so the classification used within-group matrices. Using this method the model misclassified observations 12.5% of the time. The greatest source of error was misclassifying aphids from squash as aphids from either wheat or melon. No aphids were misclassified as aphids from cotton, however two aphids from cotton were misclassified as aphids from squash. Table 4 (Fig 6) gives the Mahalanobis distances between all groups. All three canonical correlations are significant $(P>F \leq 0.0001)$. All distances are significant at the 0.0001 level by the F test.

Epicuticular hydrocarbon data were analyzed using discriminant analysis and canonical discriminant analysis. The test for homogeneity of the within covariance matrices was significant $(P>\approx^2 \leq 0.0001)$ for both models (% composition and hydrocarbon :: area). Using within group covariance matrices the model using % composition correctly classified all observations. The model using hydrocarbon :: area had a 3% error rate, misclassifying one observation from cotton as coming from squash. Table 5 (Fig. 7) gives the Mahalanobis distances between all groups for both models. Mantel's test indicated that these matrices were correlated $(P>Z \approx 0.02)$, but were not correlated with Mahalanobis distances from morphology (% composition $P>Z \approx$ 0.50, and hydrocarbon :: area $P>Z \approx 0.32$). All canonical correlations were

111

significant with a P>F ≤0.0003 with the exception of the third correlation of the model using hydrocarbon :: area which was significant at P>F = 0.01. All distances were significant at the 0.03 level.

Since cuticular hydrocarbons are used as taxonomic characters, and several of these characters were present in both aphids and plants, it is useful to analyze the shared characters as a separate data set. Both aphids and plants had the following set of hydrocarbons in common: $C_{27.0}$, $C_{29.0}$, $C_{31.0}$, $C_{33.0}$. As expected, aphids were all relatively close together, and plants formed a relatively diffuse grouping within which the distances were generally smaller than the distances between aphids and plants (table 6, and Fig. 8). All differences are significant at the 0.0001 level except for comparison of aphids from squash and cotton which was not significant (P>F 0.77).

Fatty acid composition was analyzed using discriminate analysis and canonical discriminant analysis. The test for homogeneity of within covariance matrices was significant (P>$\approx^2$) = 0.0001 for both the model using % composition and μg fatty acid/mg aphid. The model using % composition had an error rate of 4.55%. One observation from wheat was misclassified as watermelon, and an observation from cotton was misclassified as wheat. The model using μg/mg had an error rate of 2.27%. One observation from wheat was misclassified as watermelon. Table 7 (Fig. 9) gives the Mahalanobis distances between all groups. Mantel's test indicated that these matrices were correlated (P>Z ≈ 0.004). They were uncorrelated with Mahalanobis distance matrices for epicuticular hydrocarbon, P>Z ranging from 0.35 to 0.79 for the four comparisons. Mantel's test indicated that the distance matrices in table 7 were negatively correlated with the distance matrix based on morphology: P>Z ≈ 0.82 for % composition, and P>Z ≈ 0.88 for μg/mg. The significance level of the relationship was not high, but may be strong enough to warrant further

study. All canonical correlations were significant with a P>F ≤0.0001, and all distances in table 7 are significant with P>F of 0.0001.

Computer Intensive Analysis

The short summary of the above results is that all the colonies were very different. However, it was stated at the beginning that these colonies are all one species. Given that these aphids are the same species, one would expect to find characteristics in common between the aphids on different host plants. Since all variables showed differences (tables 1, 2, and 3) interactions between pairs of variables (expressed as a ratio) were used to look for similarity.

Morphological characters show the least similarity between the four aphid colonies (tables 8-10). Aphids from wheat and melon were similar when compared using the ratio body length to distance between the compound eyes. The ratio metathoracic tibia length to cornicle length shows similarity between aphids from wheat and cotton. This was also shown in table 11 where wheat was separated from all other colonies only if the variable showed differences between all colonies. This pattern suggests that wheat is intermediate between cotton and melon, and aphids from squash are the most different.

Epicuticular hydrocarbons showed the greatest similarity between the four aphid colonies. The greatest degree of similarity between any two groups was that between squash and watermelon for $C_{29.0}/C_{29.9}$. If one aggregates groups based on degree of similarity (table 9) one finds that aphids from squash are most similar to those from watermelon. Aphids from these two plants then cluster with aphids from cotton, and finally at a similarity of 0.233 or lower, the aphids from wheat cluster with the others. This is exactly what one would expect based on the phylogenetic distance between host plants.

However, this pattern is not what one would expect from examining table 11, where melon is frequently separated from the other colonies (24 out of the 36 listed ratios).

Fatty acid ratios showed less distinction between aphid colonies relative to morphological or hydrocarbon characters. By aggregating groups based on degree of similarity (table 9) one finds that aphids from squash and watermelon are most similar to aphids from wheat. Next, cotton clusters with watermelon, and watermelon and squash also cluster. Finally at the 0.10 level cotton merges with squash and wheat. This pattern is close to what one would expect based on colony origins, where the aphids from wheat came from the colonies on cucurbits, and the cotton colony was from a separate field collection. The relationship between wheat and melon or squash in table 10 does not appear in table 11 where wheat is separated from the others most frequently (17 out of 29 ratios shown and 3 of 10 original variables). An unusual pattern in table 11 is that 5 of 6 18:X fatty acids ratios separate aphids on squash from aphids on the other host plants.

RAPD-PCR results are shown in figures 10-14. Each figure shows a pGEM size standard at the far left, followed by amplification products from two aphids from each of the colonies: squash, watermelon, cotton, and wheat. Two individuals from each colony which were chosen to represent the within colony variability from the 10 individuals examined for that primer. All the primers examined showed differences between individuals, but primers C10 (Fig. 12), and BAM (not shown) did not show differences between colonies. The remaining four primers were useful in distinguishing between colonies.

UPGMA cluster analysis successfully identified aphids from both wheat and cotton (Fig. 15), but the level of within colony variability was too high to permit separation of aphids on squash from aphids on watermelon. The

dendogram comes from the analysis of data collected from ten aphids per colony. The dark bars joining two groups are places where individuals from two or more colonies join to form a cluster. The first such joining is with melon 8 and squash 7, where melon 8 is the 8th individual taken from the aphid colony on watermelon and squash 7 is the 7th individual taken from the aphid colony on squash.

One can see in figures 10-14 at least part of the pattern observed in the dendogram (Fig. 15). For example, Primer C01 (Fig. 10) shows a similarity between wheat and cotton in the second lightest band which is present in aphids on wheat and cotton but not in aphids on squash or watermelon. Primer C09 (Fig. 11) shows similarities between aphids squash and watermelon where both colonies have one each of two distinct patterns - three simple bands versus a heavy band, a pair of mid range bands, and a triplet of lighter weight bands. Primer A09 (Fig. 13) separates wheat from cotton with the heaviest band present in aphids from wheat. This primer also shows some overlap between aphids on squash and watermelon, and some of the diversity present in the watermelon colony. In primer C04 (Fig. 14) wheat has a very distinctive pattern of four evenly spaced heavy bands. The pattern in cotton is also distinctive both in the heavy bands and in the lightest bands. Once again there is little difference between the aphids on squash and watermelon.

DISCUSSION

It is obvious that these aphids show significant differences, and the relationship between them is dependent on the characters selected for study. Further interpretation on the taxonomic status of these aphids is not warranted due to insufficient information. Any attempt to designate these well characterized colonies as different biotypes would be a serious mistake. These

colonies have gone through several periods where the colony has been reduced to only a few dozen aphids. Thus these colonies may consist of only a few different strains. By giving the colonies a biotype designation there is the risk of having to designate each clonal population in the field as a "new" biotype. As a result, this paper only documents some of the variability one can find in *A. gossypii.*

Given this data set, there are two expected patterns. first, aphids from squash, watermelon, and wheat may be more similar than aphids from cotton because the aphids from cotton did not come from the same geographic location. Observations consistent with this pattern should show that cotton has the greatest separation, but the remaining comparisons can be in any order. Second, differences between the colonies could be related to the phylogenetic relationship between the host plants. The predominant theory is that the original host of this aphid is a close relative of cotton. Since squash and watermelon are much closer to cotton than wheat is to any of these, it would be expected that aphids on squash and watermelon would be most similar. These would then be more similar to cotton, and wheat would be most different.

Morphometric characters show significant differences between aphids on cotton and all other hosts. Squash appears to be equidistant from watermelon and wheat (tables 1, 5). This pattern is consistent with the first pattern described above. One would also like to conclude that the wheat colony came from aphids on squash, because the distance from watermelon to wheat is much greater than the distance from squash to wheat. However, the analysis presented in table 9 would contradict this observation.

Epicuticular hydrocarbons show significant differences between aphids on wheat and all other hosts , while squash and cotton are the least different (table 3, 6). Table 10 supports the unique composition of the aphids on wheat,

116

and suggests that aphids on squash are closest to aphids from watermelon. The clear separation of aphids from wheat is consistent with the phylogenetic relationship between the plants. The similarity between squash and watermelon is also consistent with this pattern, but the results from table 6 are not in complete agreement with the pattern.

Fatty acid profiles show clear differences between cotton and all other hosts (table 4, 8). This is consistent with the first pattern, but the pattern from table 11 is not so clear. Furthermore, table 12 would indicate that wheat is the most different rather than being midway between the watermelon and squash colonies.

The dendogram from RAPD-PCR results (Fig. 15) does not follow either of the expected patterns. It does show that aphids from squash are most similar to aphids on watermelon, but if this was to follow plant phylogeny cotton should join the squash-watermelon cluster. The alternate pattern is also violated as the wheat cluster joins the cotton cluster before it joins either squash or watermelon. The difference in wheat could be explained as a clone in the parent colony which died out between the time the colony was founded and the time the samples were taken.

In summary it appears that morphological characters distinguish between the aphid colonies in a pattern consistent with the origins of the colonies. Epicuticular hydrocarbons distinguish between the aphid colonies in a pattern that is most consistent with the phylogenetic relationship between the host plants. Fatty acid profiles and RAPD-PCR results do not appear to follow either pattern.

There are several other conclusions one could arrive at which would be inappropriate. It is clear that the epicuticular hydrocarbon composition is different for aphids on the different host plants. However, there is no clear

117

cause and effect relationship between host and hydrocarbon composition because the differences could be due to differences in genotype. The differences in genotype might be caused by differences in host plant, but could be caused by selection of pre-adapted individuals within the overall population of *A. gossypii*. It will require additional work using clonal colonies to answer these questions.

Note 1: The authors have also examined the reproductive rate of this aphid using the same system of four host plants. Mantel's test using the morphometric data from both experiments indicates that these aphids are most similar to those for 'early spring' of chapter 5 ('late summer': $p>Z \approx 0.4965$, and 'early spring': $p>Z \approx 0.0990$).

Note 2: The data used in this manuscript were published in the senior author's doctoral dissertation at Oklahoma State University, Stillwater Ok. 74078.

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Table 1. Average length in millimeters of several morphological characters of aphids reared on different host plants.

Morphological Character	Squash n=20		Watermelon n=20		Cotton n=20		Wheat n=20	
Body	1.427 ± 0.111	B	1.441 ± 0.114	B	1.883 ± 0.127	A	1.304 ± 0.107	C
Tibia	0.690 ± 0.037	C	0.810 ± 0.045	B	0.910 ± 0.046	A	0.608 ± 0.033	D
Cornicle	0.238 ± 0.022	C	0.295 ± 0.026	B	0.350 ± 0.026	A	0.228 ± 0.017	C
Eye	0.335 ± 0.010	C	0.362 ± 0.010	B	0.383 ± 0.014	A	0.319 ± 0.008	D

Different letters within rows indicate significant differences at the 0.01 level of significance using the Ryan-Einot-Gabriel-Welsch multiple comparison procedure.

Table 2. Mean and standard deviation for cuticular hydrocarbons from melon aphids feeding on different host plants.

ECL	Squash n=11**		% Composition* (all numbers multiplied by 10^2) Melon n=8**		Cotton n=9**		Wheat n=10**	
$C_{25.0}$	6.167 ± 2.213	BC	14.460 ± 3.651	A	9.403 ± 2.560	B	4.743 ± 1.519	C
$C_{27.0}$	26.758 ± 2.580	B	32.967 ± 2.098	A	27.985 ± 3.207	B	21.212 ± 3.342	C
$C_{27.5}$	5.557 ± 0.909	A	2.687 ± 1.111	B	3.597 ± 0.662	B	5.135 ± 1.059	A
$C_{29.0}$	22.091 ± 3.331	B	14.115 ± 3.855	C	22.216 ± 2.556	B	32.144 ± 3.358	A
$C_{29.2}$	3.552 ± 0.871	A	3.513 ± 0.464	A	3.123 ± 0.232	AB	2.496 ± 0.303	B
$C_{29.6}$	2.927 ± 1.057	B	1.658 ± 0.661	B	2.036 ± 0.978	B	5.222 ± 1.339	A
$C_{29.9}$	2.937 ± 0.272	A	1.692 ± 0.261	C	2.328 ± 0.168	B	2.706 ± 0.199	A
$C_{31.0}$	3.442 ± 0.732	B	1.533 ± 0.467	C	2.992 ± 0.720	B	6.423 ± 0.928	A
$C_{31.4}$	5.224 ± 0.836	A	4.269 ± 0.547	B	4.306 ± 0.428	B	3.979 ± 0.507	B
$C_{33.0}$	2.945 ± 0.450	B	1.381 ± 0.609	C	2.618 ± 0.975	B	6.023 ± 1.007	A
$C_{35.0}$	2.133 ± 0.306	A	1.975 ± 0.406	AB	1.550 ± 0.205	B	2.171 ± 0.252	A

123

ECL	μg Hydrocarbon :: Aphid Surface Area***				(all numbers multiplied by 10^3)			
	Squash		Melon		Cotton		Wheat	
$C_{25.0}$	1.444 ± 0.483	B	6.528 ± 2.838	A	3.129 ± 0.708	B	2.296 ± 0.452	B
$C_{27.0}$	6.339 ± 0.805	B	14.688 ± 4.002	A	9.428 ± 1.477	B	10.452 ± 1.031	B
$C_{27.5}$	1.323 ± 0.267	B	1.119 ± 0.514	B	1.214 ± 0.266	B	2.568 ± 0.591	A
$C_{29.0}$	5.283 ± 1.132	B	6.227 ± 2.203	B	7.522 ± 1.533	B	16.037 ± 2.405	A
$C_{29.2}$	0.831 ± 0.167	B	1.582 ± 0.569	A	1.052 ± 0.139	B	1.265 ± 0.108	A
$C_{29.6}$	0.719 ± 0.248	B	0.706 ± 0.315	B	0.686 ± 0.277	B	2.644 ± 0.804	A
$C_{29.9}$	0.694 ± 0.064	B	0.720 ± 0.188	B	0.795 ± 0.097	B	1.390 ± 0.163	A
$C_{31.0}$	0.823 ± 0.210	B	0.676 ± 0.253	B	1.018 ± 0.322	B	3.218 ± 0.626	A
$C_{31.4}$	1.223 ± 0.169	C	1.909 ± 0.618	AB	1.440 ± 0.112	BC	1.982 ± 0.320	A
$C_{33.0}$	0.706 ± 0.154	B	0.610 ± 0.309	B	0.892 ± 0.373	B	3.032 ± 0.699	A
$C_{35.0}$	0.504 ± 0.075	C	0.880 ± 0.310	B	0.531 ± 0.101	C	1.140 ± 0.066	A

* calculated as peak area÷total area where total area is the total from C_{25} to C_{36}

** Listed n is the maximum. Some cells have missing values, but no cell has a n lower than 7.

*** calculated as peak area÷standard÷(aphids in sample*(weight per aphid)$^{2/3}$)

Different letters within a row indicate significant differences at the 0.01 level using REGWQ multiple comparison proceedure. ANOVA indicates that all models are significant with P>F ≤0.0001.

Table 3. Mean and standard deviation for fatty acids from melon aphids feeding on different host plants.

% Composition*   (all numbers multiplied by 10^2)

	Squash n=12		Melon n=11		Cotton n=11		Wheat n=11	
12:0	0.079 ± 0.020	C	0.081 ± 0.021	C	0.174 ± 0.079	B	0.315 ± 0.113	A
14:0	4.287 ± 1.326	C	4.915 ± 0.604	C	10.152 ± 3.255	B	16.250 ± 3.043	A
14:1	0.056 ± 0.015	B	0.084 ± 0.020	AB	0.139 ± 0.052	A	0.114 ± 0.065	A
16:0	76.458 ± 1.970	A	75.661 ± 2.835	A	65.760 ± 6.677	B	68.556 ± 2.974	B
16:1	2.395 ± 0.337	AB	2.554 ± 0.420	A	2.561 ± 0.512	A	1.963 ± 0.229	B
18:0	5.430 ± 0.426	A	4.579 ± 0.716	AB	5.333 ± 1.027	A	3.736 ± 0.572	B
18:1	5.730 ± 0.525	A	4.625 ± 0.753	A	5.672 ± 1.729	A	3.184 ± 0.474	B
18:2	3.932 ± 0.595	B	5.320 ± 0.992	B	7.342 ± 2.412	A	3.744 ± 0.614	B
18:3	0.619 ± 0.141	C	1.033 ± 0.265	AB	1.373 ± .5223	A	0.677 ± 0.131	BC
20:0	0.065 ± 0.123	B	0.693 ± 0.209	B	1.004 ± 0.334	A	0.613 ± 0.152	B

μg Fatty Acid/mg aphid**

	Squash		Melon		Cotton		Wheat	
12:0	0.004 ± 0.001	B	0.005 ± 0.002	B	0.006 ± 0.003	B	0.023 ± 0.010	A
14:0	0.214 ± 0.068	B	0.271 ± 0.052	B	0.363 ± 0.136	B	1.156 ± 0.331	A
14:1	0.003 ± 0.001	B	0.005 ± 0.001	B	0.005 ± 0.002	B	0.008 ± 0.004	A
16:0	3.880 ± 0.729	A	4.209 ± 0.852	A	2.430 ± 0.791	B	4.833 ± 0.801	A
16:1	0.122 ± 0.032	AB	0.141 ± 0.035	A	0.092 ± 0.026	B	0.140 ± 0.360	A
18:0	0.274 ± 0.487	A	0.248 ± 0.023	A	0.190 ± 0.046	B	0.260 ± 0.033	A
18:1	0.288 ± 0.047	A	0.251 ± 0.032	AB	0.198 ± 0.056	B	0.221 ± 0.028	B
18:2	0.195 ± 0.019	B	0.288 ± 0.037	A	0.256 ± 0.076	A	0.260 ± 0.037	A
18:3	0.030 ± 0.004	B	0.055 ± 0.008	A	0.047 ± 0.015	A	0.047 ± 0.008	A
20:0	0.032 ± 0.006	A	0.037 ± 0.006	A	0.035 ± 0.011	A	0.042 ± 0.008	A

* calculated as peak area ÷ total area where total area is the total from 12:0 to 20:0
** calculated as peak area ÷ peak area of standard ÷ aphid weight

Different letters within a row indicate significant mean differences at the 0.01 significance level using REGWQ multiple comparison proceedure. ANOVA finds all models significant with a probability of a larger F no larger than 0.0025.

125

Table 4. Mahalanobis distance between aphids on squash, melon, cotton, and wheat with respect to morphological characters.

	Squash	Melon	Cotton
Melon	10.207		
Cotton	36.920	17.763	
Wheat	7.502	27.713	65.924

Table 5. Mahalanobis distance between aphids on squash, melon, cotton, and wheat with respect to % Hydrocarbon composition, and with respect to hydrocarbon composition :: area.

% Composition	Squash	Melon	Cotton
Melon	158.241		
Cotton	25.995	126.545	
Wheat	147.055	367.534	134.302
:: Area			
Melon	125.400		
Cotton	13.304	101.390	
Wheat	453.340	896.088	504.499

Table 6. Mahalanobis distances between aphids and plants using cuticular hydrocarbons shared by all species.

| | | Plant | | | | Aphids | | |
		Squash	Melon	Cotton	Wheat	Squash	Melon	Cotton
Plant	Melon	11.37						
	Cotton	164.21	202.61					
	Wheat	67.00	62.20	164.40				
Aphid	Squash	160.81	190.31	147.95	52.36			
	Melon	191.92	209.80	259.95	62.10	18.68		
	Cotton	162.31	188.59	158.71	49.58	0.40	14.25	
	Wheat	147.36	181.34	64.52	64.58	19.92	75.61	24.54

Table 7. Mahalanobis distance between aphids on squash, melon, cotton, and wheat with respect to % fatty acid composition, and with respect to µg/mg fatty acid composition.

% Composition	Squash	Melon	Cotton
Melon	93.813		
Cotton	161.294	34.939	
Wheat	165.522	53.429	24.020
µg/mg			
Melon	59.710		
Cotton	63.756	32.675	
Wheat	109.677	58.370	38.882

Table 8. Similarities between ratios of different morphological variables.

	Mean		CV	Squash	Watermelon	Cotton	Wheat
body/eye							
Squash	4.2513	B	6.398	--1--	0.001	0.000	0.057
Watermelon	3.9826	B	8.575	0.010	--1--	0.000	0.310
Cotton	4.9234	A	5.680	0.000	0.000	--1--	0.000
Wheat	4.0906	B	7.676	0.100	0.274	0.000	--1--
tibia/cornicle							
Squash	2.9127	A	6.762	--1--	0.009	0.000	0.000
Watermelon	2.7536	B	5.253	0.000	--1--	0.000	0.068
Cotton	2.6083	B	6.289	0.000	0.000	--1--	0.279
Wheat	2.6708	B	4.195	0.000	0.015	0.071	--1--

Different letters next to means indicate significant differences at alpha = 0.01 using the Ryan-Einot-Gabriel-Welsch multiple comparison procedure. In addition to tibia and eye, the ratio of these two measures distinguishes between aphids on all four host plants. The CVs for the ratio are intermediate between those of eye and tibia which range from 2.6 to 5.5.

Table 9. Similarities between ratios of different hydrocarbon components.

	Mean		CV	Squash	Watermelon	Cotton	Wheat
$C_{29.0}/C_{29.9}$							
Squash	7.8204	C	18.426	--1--	0.990	0.003	0.000
Watermelon	7.8220	C	13.162	0.944	--1--	0.000	0.000
Cotton	9.5871	B	9.616	0.000	0.000	--1--	0.000
Wheat	11.6583	A	6.951	0.000	0.000	0.000	--1--
$C_{26.9}/C_{29.9}$							
Squash	8.9969	C	14.927	--1--	0.000	0.000	0.000
Watermelon	19.7567	A	14.833	0.000	--1--	0.000	0.000
Cotton	11.7869	B	14.311	0.000	0.000	--1--	0.000
Wheat	7.4677	C	13.738	0.000	0.000	0.000	--1--
$C_{31.0}/C_{33.0}$							
Squash	1.2214	A	7.755	--1--	0.233	0.414	0.000
Watermelon	1.1723	A	14.381	0.549	--1--	0.860	0.228
Cotton	1.1868	A	11.680	0.606	0.824	--1--	0.072
Wheat	1.0725	A	6.512	0.000	0.000	0.000	--1--

Different letters next to means indicate significant differences at alpha = 0.01 using the Ryan-Einot-Gabriel-Welsch multiple comparison procedure.
The hydrocarbon ratio C29.0/C31.0 is the only hydrocarbon ratio that distinguishes between all four hosts. The CVs for this ratio were 10.6, 7.1, 12.4, and 7.9 following the order in the table. A smaller difference between the CVs in the table and the CV for cotton and the largest CV for the other variables would be observed 55%, 25%, and 20% of the time.

Table 10. Similarities between ratios of fatty acids.

	Mean	CV	Squash	Watermelon	Cotton	Wheat
14:0/16:0						
Squash	0.0564 C	32.966	--1--	0.263	0.000	0.000
Watermelon	0.0651 C	13.765	0.020	--1--	0.007	0.000
Cotton	0.1572 B	34.902	0.000	0.000	--1--	0.000
Wheat	0.2389 A	22.144	0.000	0.000	0.000	--1--
16:0/16:1						
Squash	32.5569 A	15.575	--1--	0.306	0.006	0.166
Watermelon	30.4491 A	18.904	0.399	--1--	0.194	0.037
Cotton	27.2206 A	32.677	0.149	0.395	--1--	0.022
Wheat	35.3906 A	13.195	0.144	0.007	0.000	--1--
16:1/18:0						
Squash	0.4463 A	19.882	--1--	0.000	0.254	0.004
Watermelon	0.5721 A	24.477	0.029	--1--	0.155	0.640
Cotton	0.4877 A	21.496	0.378	0.058	--1--	0.207
Wheat	0.5444 A	27.244	0.122	0.675	0.384	--1--
18:2/20:0						
Squash	6.1826 A	17.908	--1--	0.000	0.004	0.754
Watermelon	7.9612 A	19.453	0.001	--1--	0.402	0.004
Cotton	7.4017 A	20.051	0.036	0.373	--1--	0.078
Wheat	6.3250 A	17.966	0.794	0.000	0.046	--1--
16:0/18:0						
Squash	14.1720 BC	9.325	--1--	0.000	0.010	0.000
Watermelon	16.9183 AB	16.692	0.016	--1--	0.000	0.126
Cotton	12.9067 C	26.431	0.381	0.004	--1--	0.000
Wheat	18.7155 A	15.190	0.000	0.139	0.000	--1--
18:1/18:3						
Squash	9.5515 A	16.617	--1--	0.000	0.000	0.000
Watermelon	4.1570 B	30.671	0.000	--1--	0.079	0.675
Cotton	4.2500 B	9.360	0.000	0.049	--1--	0.001
Wheat	4.7528 B	8.237	0.000	0.275	0.000	--1--

Different letters next to means indicate significant differences at alpha = 0.01 using the Ryan-Einot-Gabriel-Welsch multiple comparison procedure. The comparison 14:0 to 16:0 showed the maximum separation of any variable.

132

Table 11. Differences shown by different ratios.

Ratios of the original variables	Original Measures
Morphology. 1 Difference:	
7*≠(2*,3*,5*): lenleye	
2≠(5,3,7): tiblcor	
5≠(7,3,2): lenltib	2 Differences:
2 Differences:	7≠(5,2)≠3: length
7≠5≠(2,3): corleye	7≠5≠(2,3): cornicle
3 Differences: tibleye	3 Differences: tibia, eye
Hydrocarbon. Same: 24.8l27.5, 26.9l27.5, 26.9l29.2, 27.5l29.9, 29.0l29.6, 31.0l33.0	Other: 35.2, 29.2, 24.8
1 Difference:	1 Difference:
5≠(7,3,2): 24.8l29.0, 24.8l29.6, 24.8l29.9, 24.8l31.0, 24.8l33.0, 27.5l35.2, 29.2l29.9,	
29.2l31.0, 29.2l33.0, 29.6l33.0	
3≠(2,7,5): 29.2l35.2, 29.6l29.9, 29.6l35.2	3≠(2,7,5): 29.6
2≠(5,7,3): 27.5l29.0	2≠(3,5,7): 31.4
(5,7)≠(2,3): 24.8l35.2	
2 Differences:	2 Differences:
7≠5≠(3, 2): 24.8l26.9, 24.8l29.2, 24.8l31.4, 26.9l29.9	(2,3)≠7≠5: 29.9
5≠(7, 2)≠3: 26.9l29.0, 29.9l31.0, 29.9l31.4, 29.9l33.0, 31.0l31.4, 31.0l35.2, 31.4l33.0,	3≠5≠(7,2): 33.0, 31.0, 26.9,
33.0l35.2	29.0
3≠7≠(5, 2): 29.0l29.9	
5≠2≠(7,3): 29.0l35.2	(2,3)≠(7,5): 27.5
3 Differences: 29.0l31.0	
Fatty Acid. Same: 12:0l14:0, 16:0l16:1, 16:1l18:0, 16:1l20:0, 18:2l20:0	Other: 14:1, 16.1, 18:0, 18:3
1 Difference:	1 Difference:
7≠(2, 3, 5): 16:0l20:0	7≠(2,3,5): 18:2, 20:0
3≠(2, 7, 5): 12:0l14:1, 12:0l16:1, 12:0:18:0, 12:0l18:1, 12:0l18:2, 12:0l18:3, 12:0l20:0,	3≠(2,5,7): 18:1
14:0l14:1, 14:0l18:1, 14:0l18:2, 14:0l18:3, 14:0l20:0, 16:0l18:1, 18:0l18:1	
2≠(5, 7, 3): 18:0l18:3, 18:0l20:0, 18:1l18:2, 18:1l18:3, 18:1l20:0, 18:2l18:3	(2,5)≠(3,7): 16:0
2 Differences:	
3≠7≠(5, 2): 12:0l16:0, 14:0l16:0, 14:0l16:1	2 Differences:
	3≠7≠(2,5): 12:0, 14:0

As numbers within parentheses are not significantly different, their order is not taken into consideration when placing them into categories. Differences were determined using REGWQ with alpha = 0.01.

Differences that did not provide clear distinctions between groups are not listed for the ratios, but are listed as 'other' for original observations. There were a total of 6 morphometric ratios, 55 hydrocarbon ratios, and 45 fatty acid ratios.

*these numbers code for the different host plants by colony; 2=squash, 3=wheat, 5=watermelon, 7=cotton.

Figure 1. Gas chromatograph trace of the cuticular hydrocarbons from squash.
A) cotyledon; B) second true leaf; c) aphids feeding on squash. The x axis is
retention time on column. Peaks are identified by their equivalent chain
length.
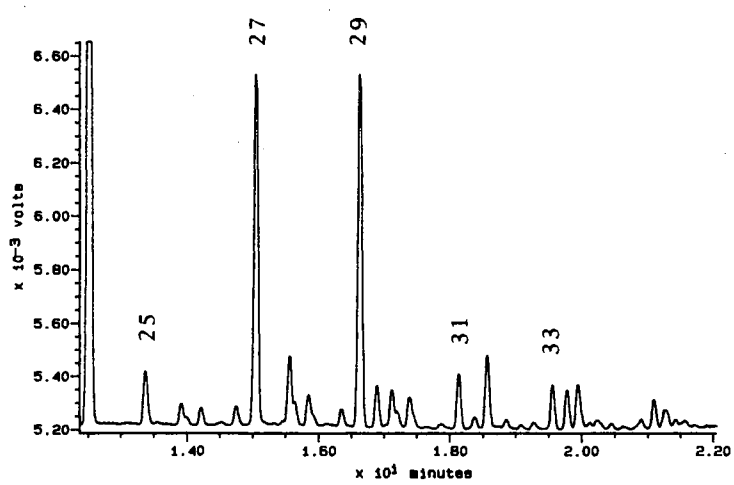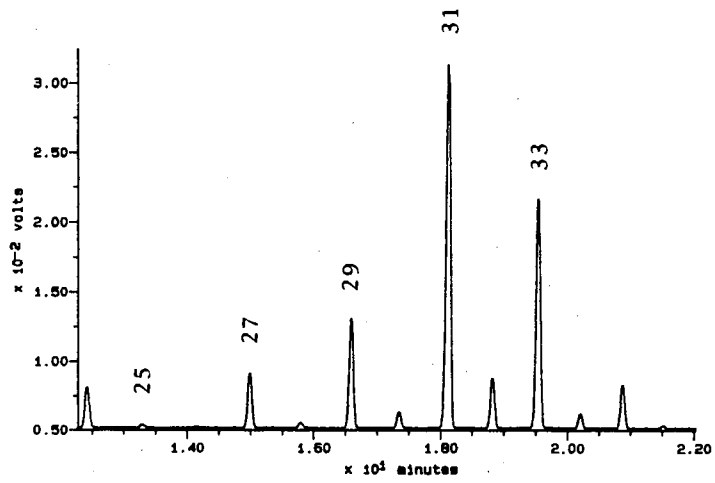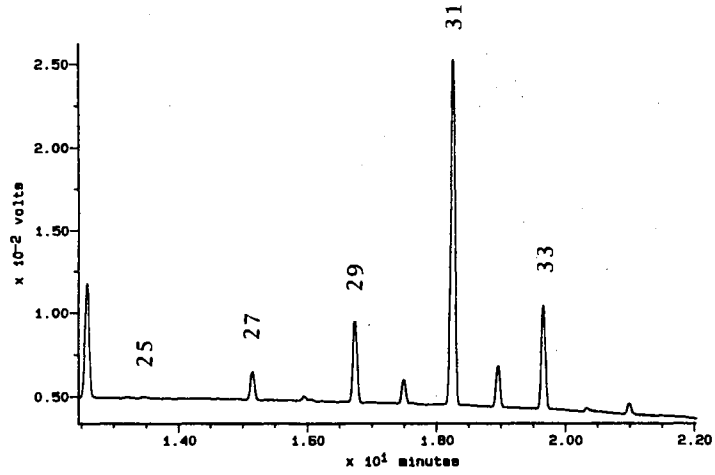
Figure 2. Gas chromatograph trace of the cuticular hydrocarbons from watermelon. A) cotyledon; B) second true leaf; C) aphids feeding on watermelon. The x axis is retention time on column. Peaks are identified by their equivalent chain length.
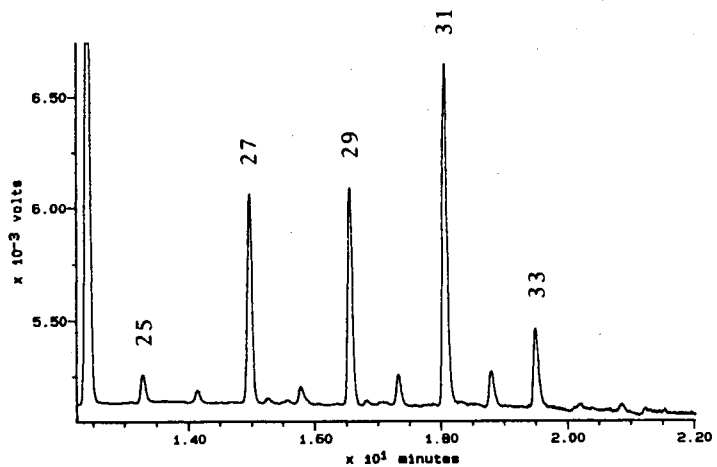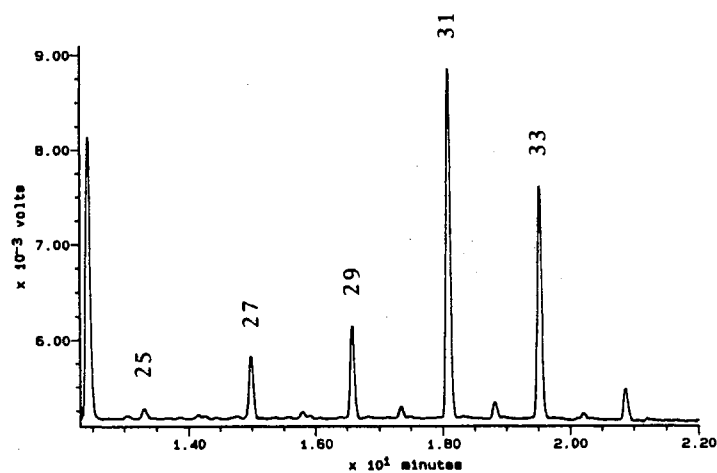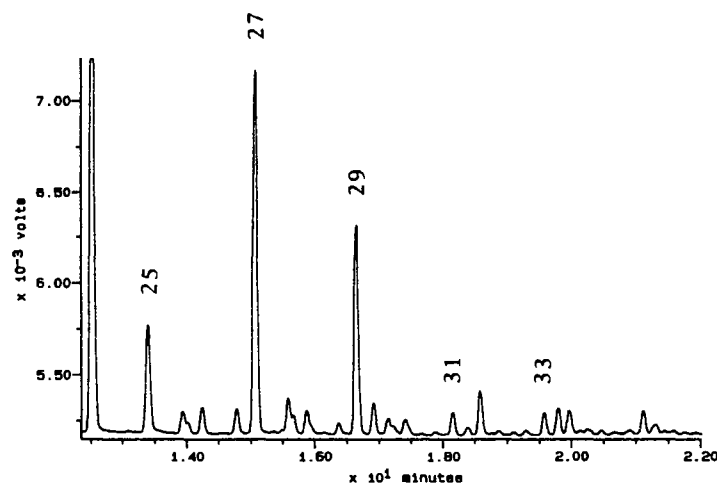
Figure 3. Gas chromatograph trace of the cuticular hydrocarbons from cotton. A) second true leaf; B) meristem plus first few immature leaves; C) aphids feeding on cotton. The x axis is retention time on column. Peaks are identified by their equivalent chain length.
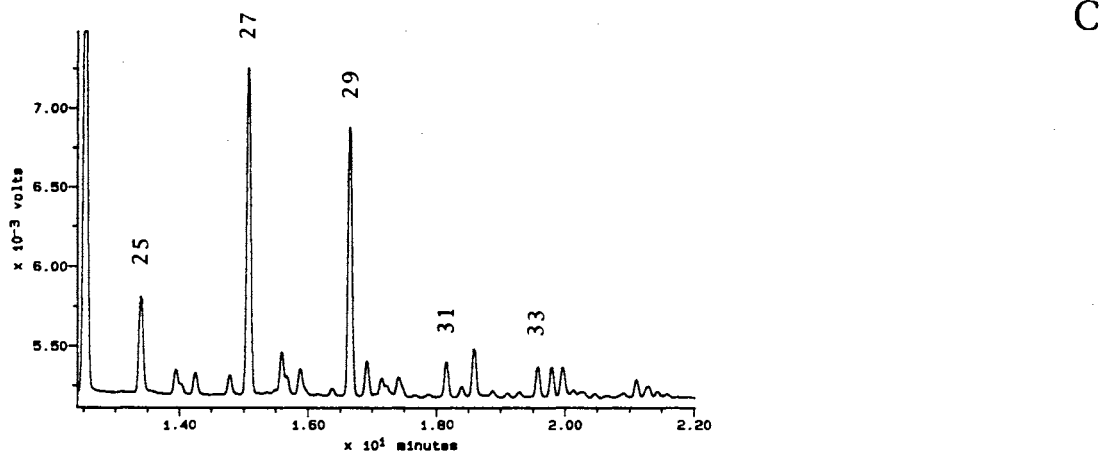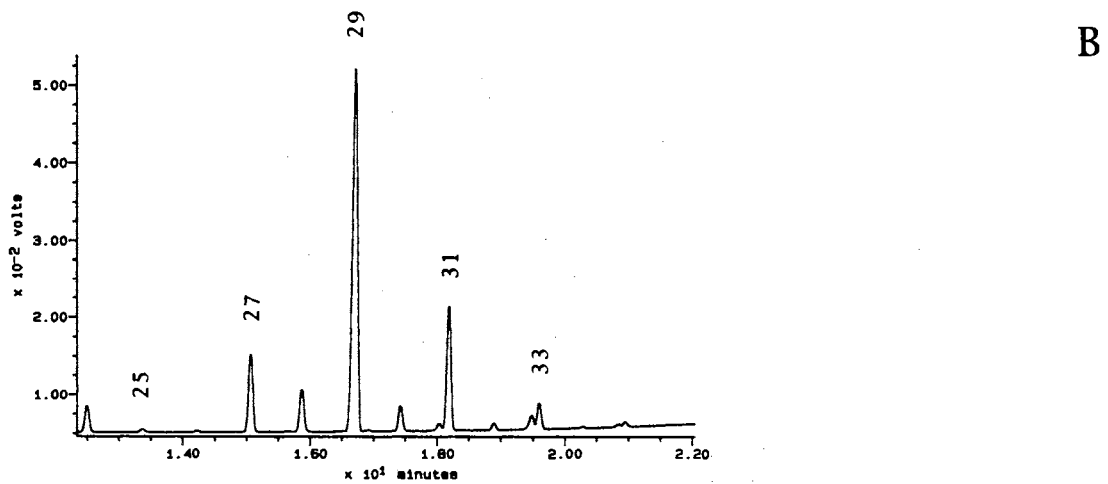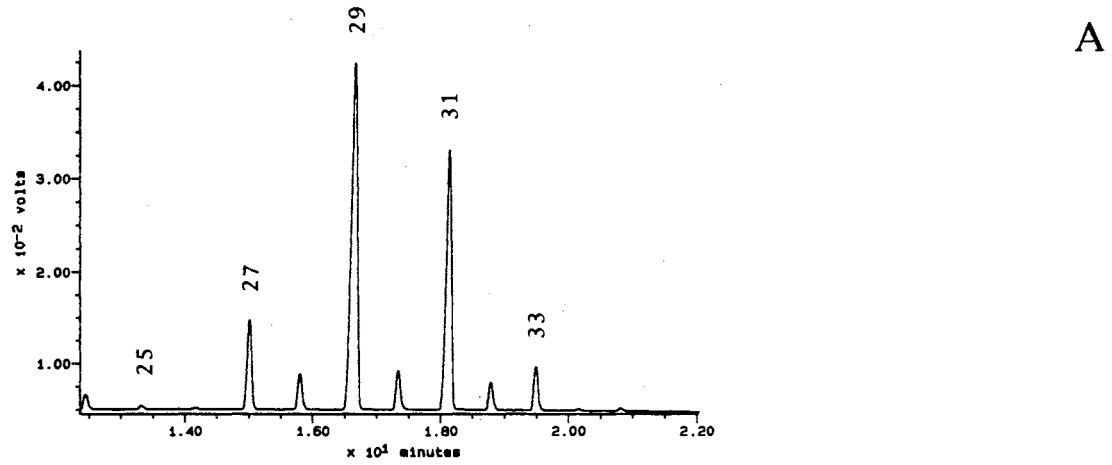
Figure 4. Gas chromatograph trace of the cuticular hydrocarbons from wheat. A) a leaf; B) aphids feeding on wheat. The x axis is retention time on column. Peaks are identified by their equivalent chain length.
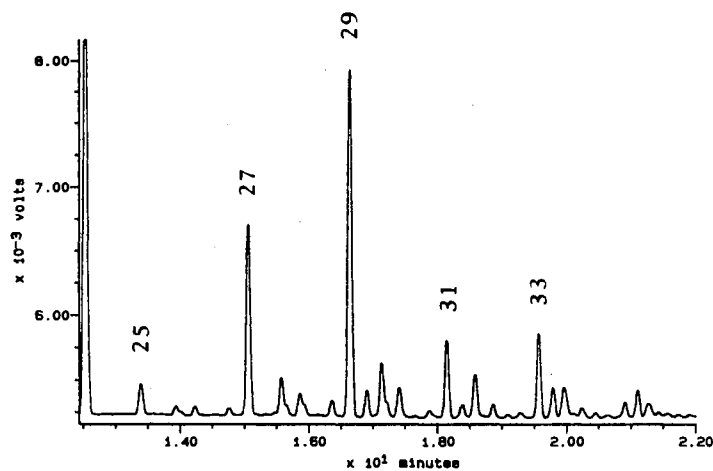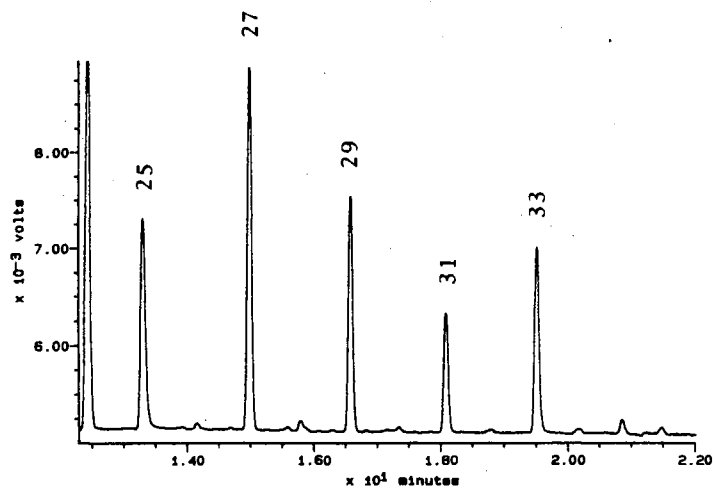
Figure 5. Linear regression and 95% confidence interval for fatty acid 14:0 versus C29.0. The regression equation with standard errors is $C_{29.0}$ = 0.0850 ($\pm$0.0095) + 0.7403 ($\pm$0.0917) $\mathbf{x}$ 14:0.

139
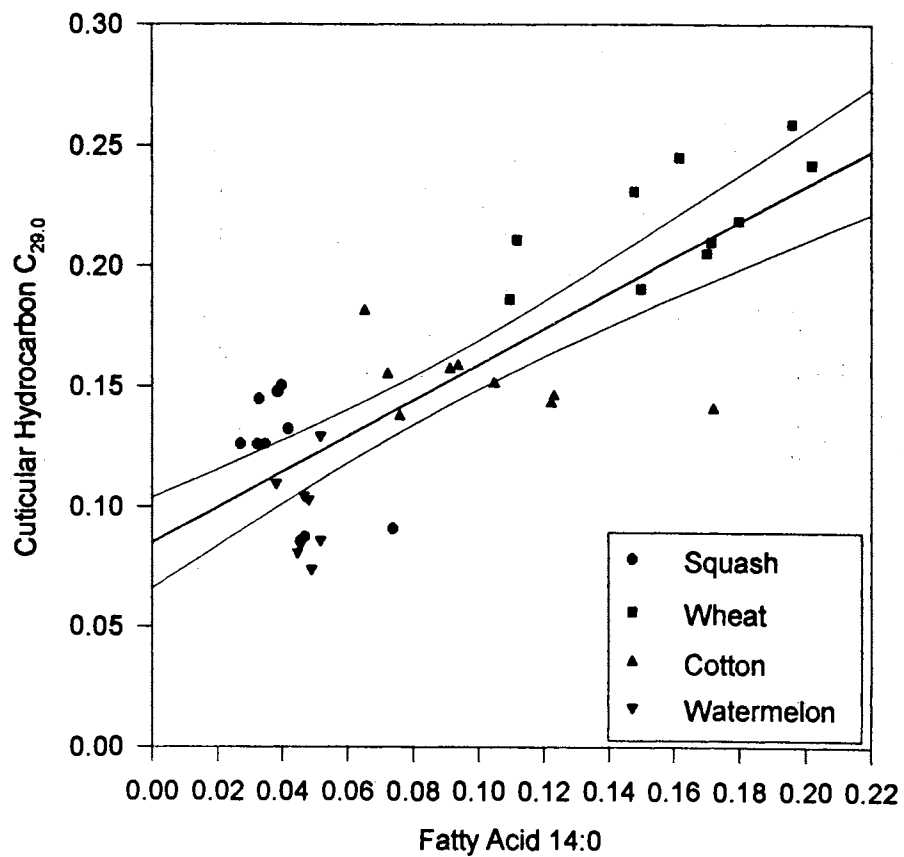
Figure 6. Graph of the first three canonical correlates used to classify aphids by host plant using morphological characters

heart   Squash
spade   Watermelon
diamond Cotton
club   Wheat
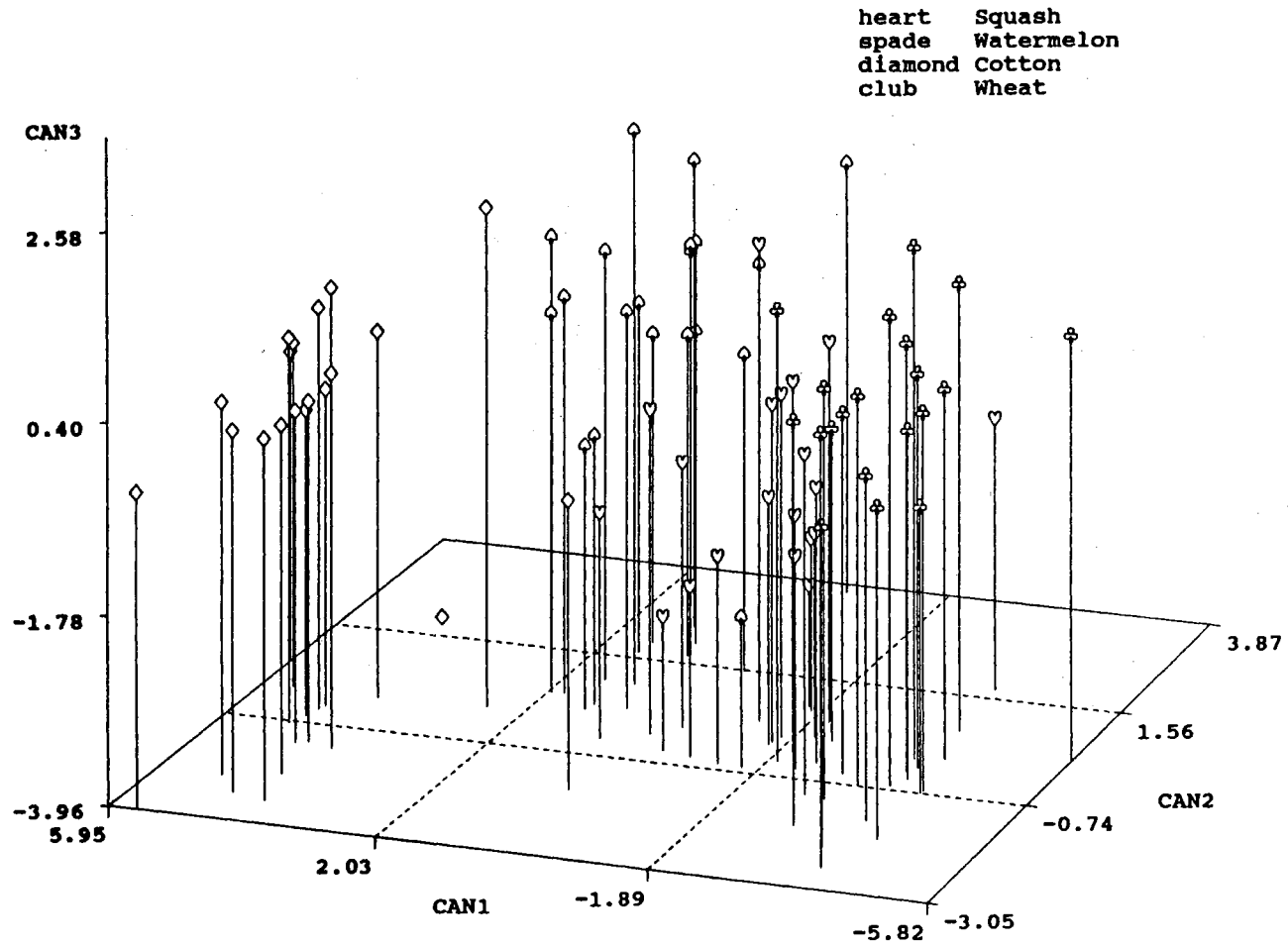
Figure 7. Graph of the first three canonical correlates used to classify aphids by host plant using epicuticular hydrocarbons
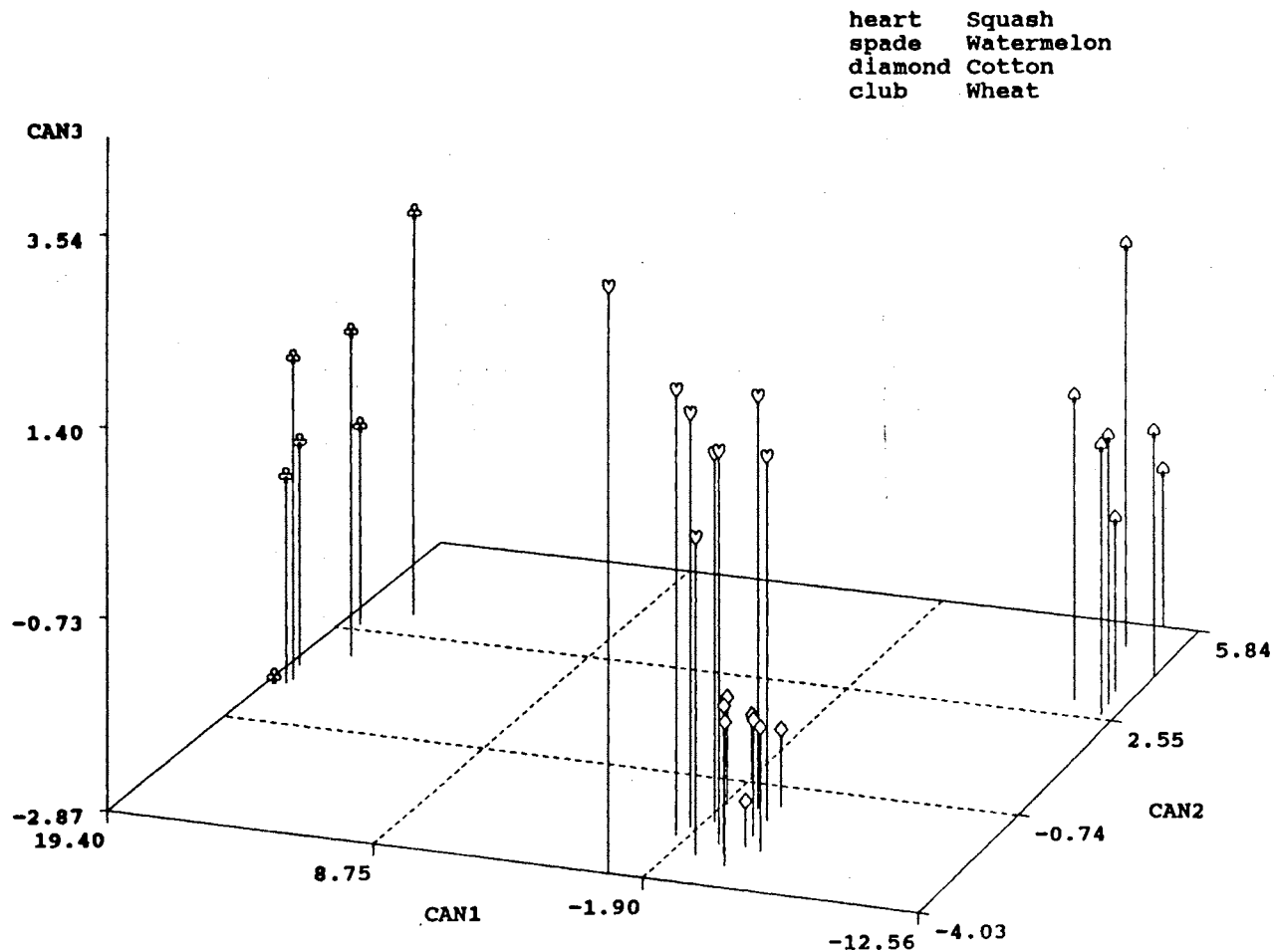
Figure 8. Graph of the first three canonical correlates used to classify aphids and plants by shared cuticular hydrocarbons

heart & balloon   Squash & Aphid on Squash
spade & flag   Watermelon & Aphid on Watermelon
diamond & cross   Cotton & Aphid on Cotton
club & star   Wheat & Aphid on Wheat
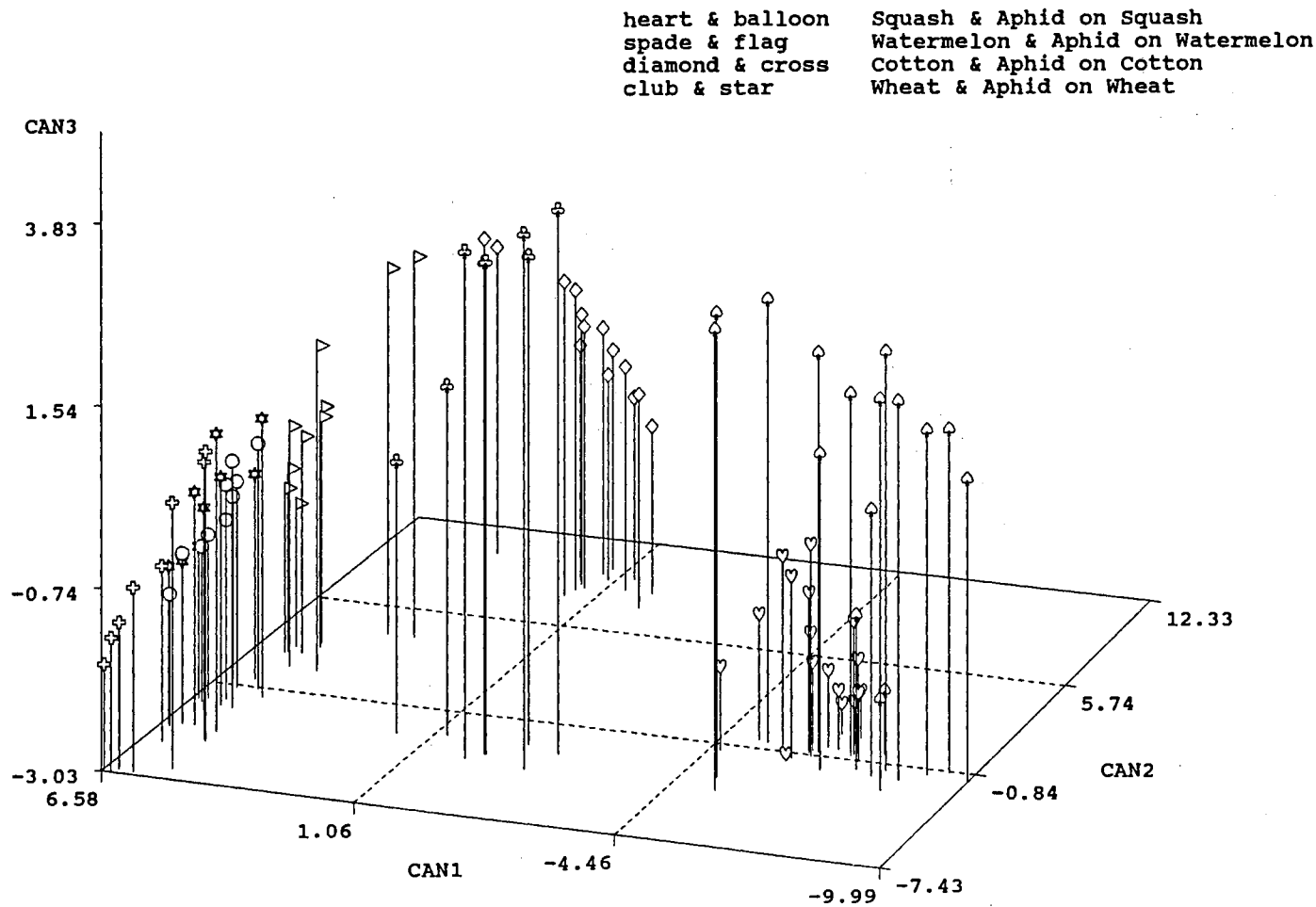
Figure 9. Graph of the first three canonical correlates used to classify aphids by host plant using internal fatty acids

heart   Squash
spade   Watermelon
diamond   Cotton
club   Wheat

CAN3

2.28

-0.46

-3.19

-5.93
4.79

1.91

CAN2

-0.97

-3.84 5.19

-10.39

-5.20

-0.00   CAN1
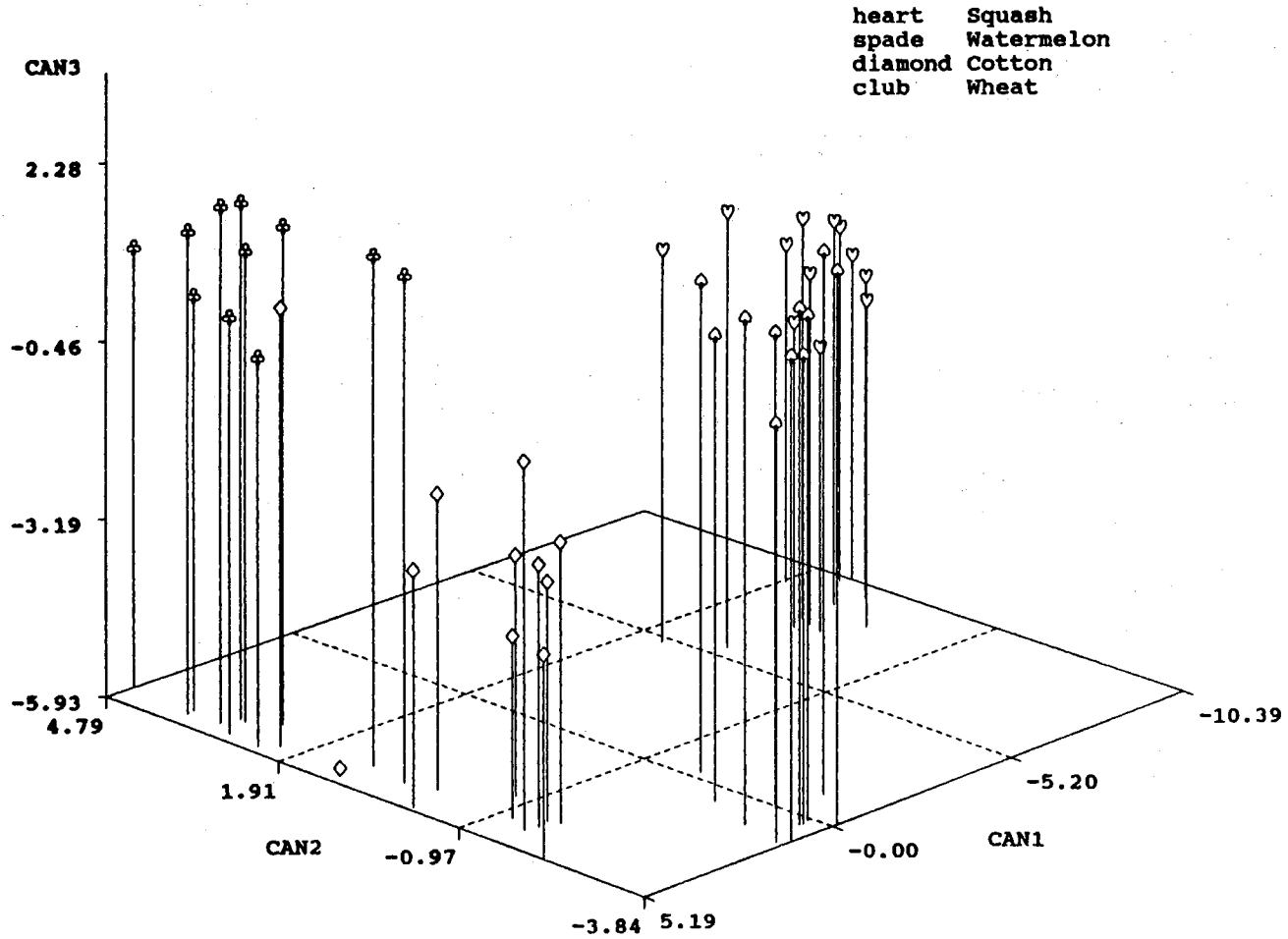
Figure 10. RAPD-PCR results for all colonies with primer C01.
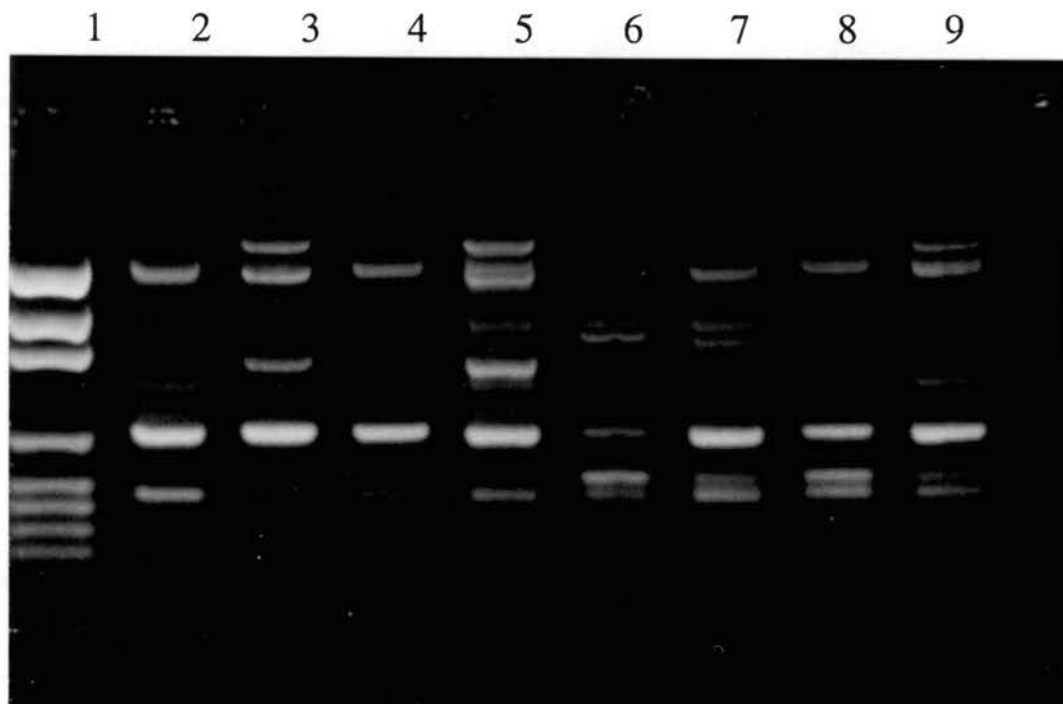
Number in parentheses corresponds to the lane number
PGem Size Marker (1)   Cotton (6,7)
Squash (2,3)   Wheat (8,9)
Watermelon (4,5)
The fragment sizes of pGem marker in base pairs from top to bottom are: 2645, 1605, 1198, 676, 517, 460, 396, 350, and 222.

Figure 11. RAPD-PCR results for all colonies with primer C09.
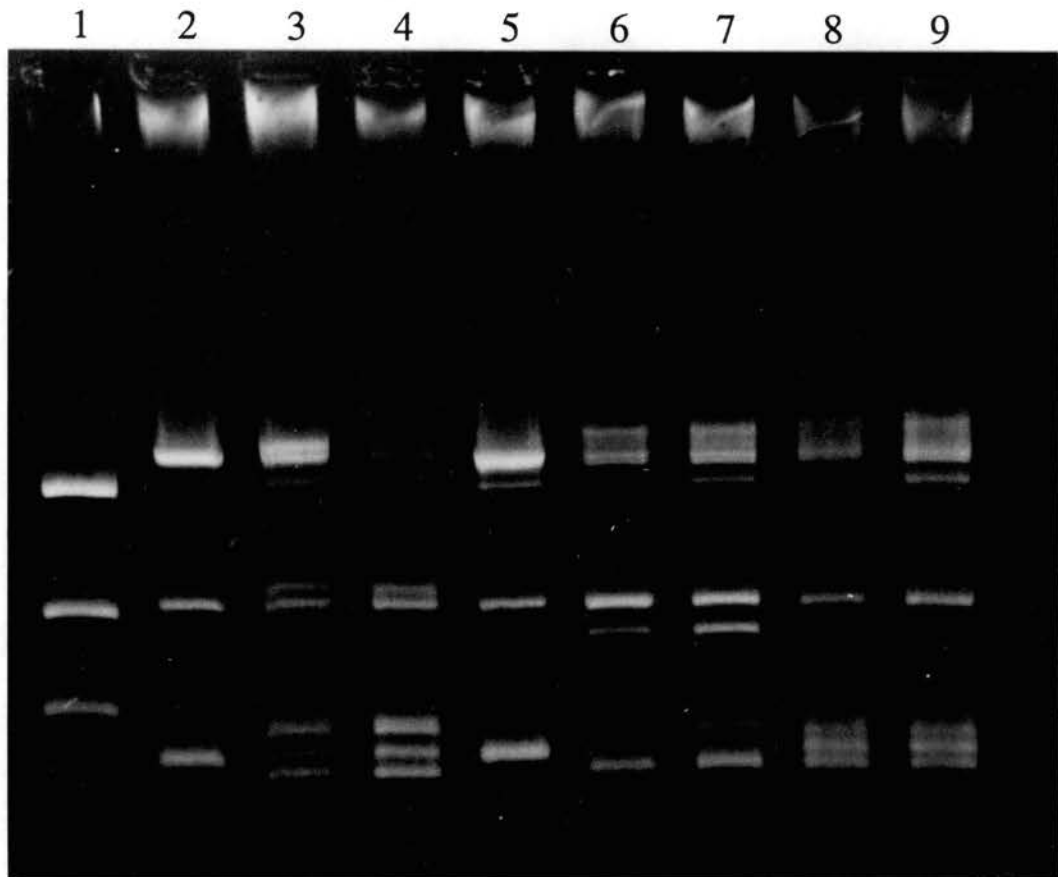
Number in parentheses corresponds to the lane number
PGem Size Marker (1)   Cotton (6,7)
Squash (2,3)   Wheat (8,9)
Watermelon (4,5)
The fragment sizes of pGem marker in base pairs from top to bottom are: 2645,
1605, and 1198.

Figure 12. RAPD-PCR results for all colonies with primer C10
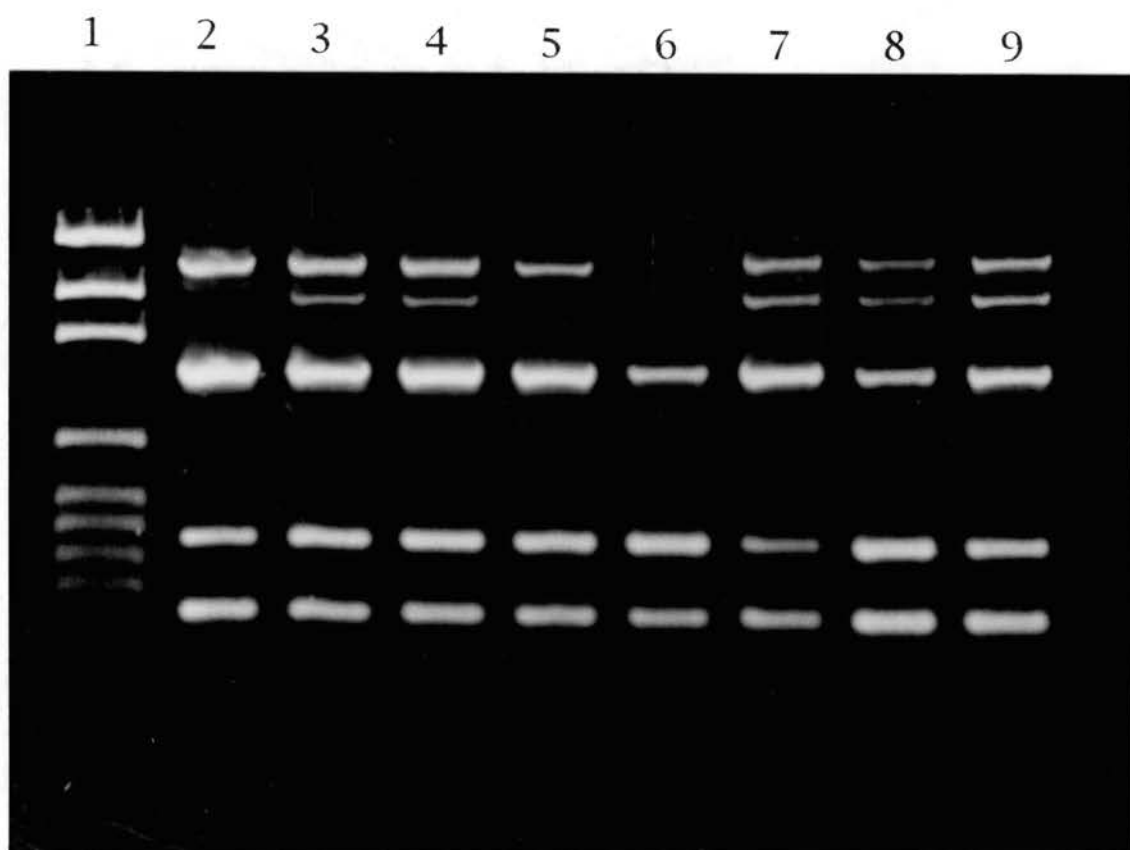
Number in parentheses corresponds to the lane number
PGem Size Marker (1)   Cotton (6,7)
Squash (2,3)   Wheat (8,9)
Watermelon (4,5)
The fragment sizes of pGem marker in base pairs from top to bottom are: 2645, 1605, 1198, 676, 517, 460, 396, 350, and 222.

Figure 13. RAPD-PCR results for all colonies with primer A09
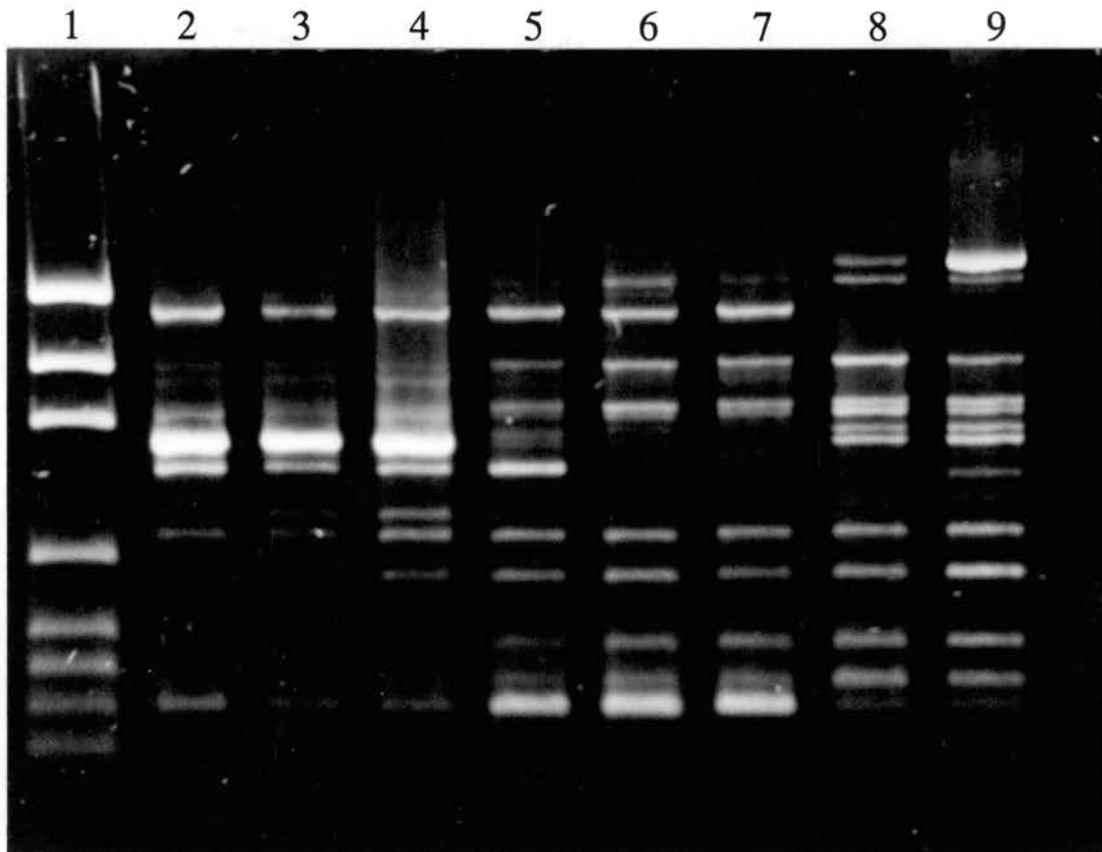
Number in parentheses corresponds to the lane number
PGem Size Marker (1)   Cotton (6,7)
Squash (2,3)   Wheat (8,9)
Watermelon (4,5)
The fragment sizes of pGem marker in base pairs from top to bottom are: 2645, 1605, 1198, 676, 517, 460, 396, and 350.

Figure 14. RAPD-PCR results for all colonies with primer C04
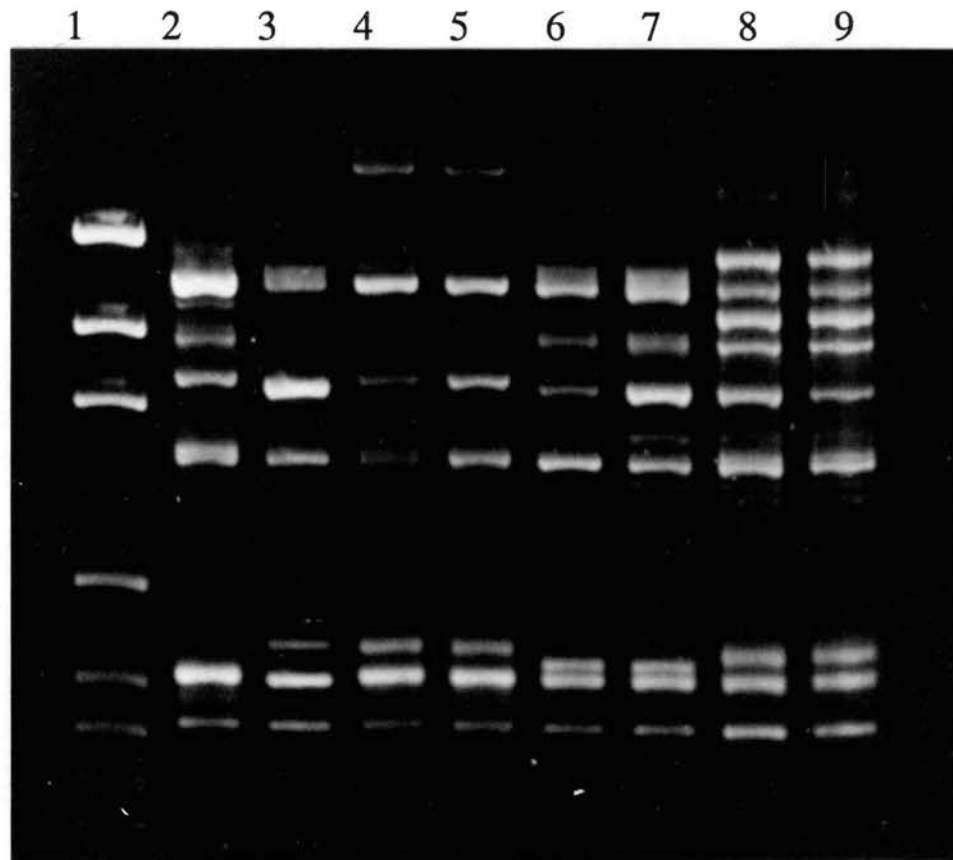
Number in parentheses corresponds to the lane number
PGem Size Marker (1)   Cotton (6,7)
Squash (2,3)   Wheat (8,9)
Watermelon (4,5)
The fragment sizes of pGem marker in base pairs from top to bottom are: 2645, 1605, 1198, 676, 517, and 460.

Figure 15. Dendogram from RAPD-PCR results.
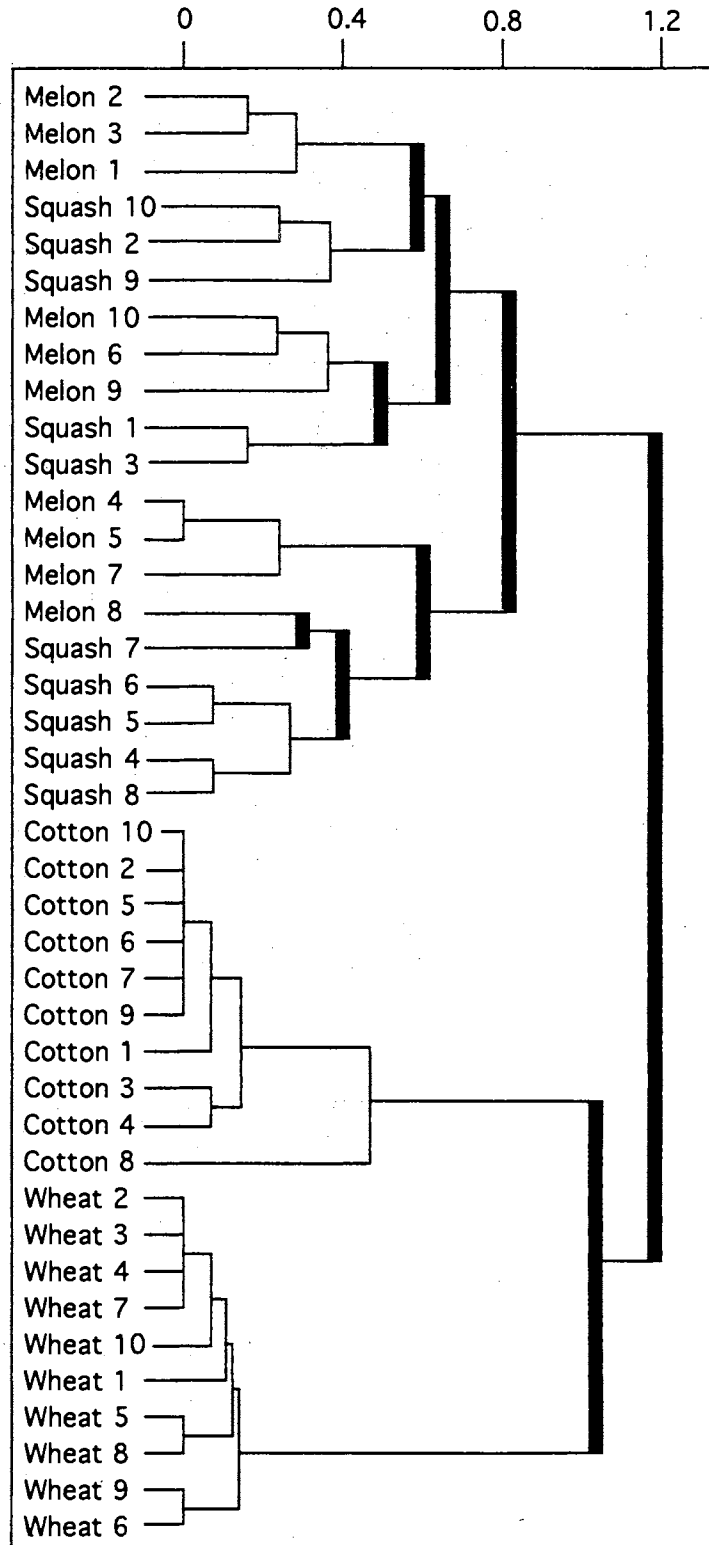
Numbers at the top are a measure of the dissimilarity between individuals or clusters. Lines joining clusters indicate the level at which clusters join. Clusters joining further to the right are more dissimilar.

MODELING BIRTH RATE IN *Aphis gossypii* (Glover) (Homoptera: Aphididae)

WITH HOST PLANT, ABIOTIC FACTORS, AND MORPHOLOGICAL CHARACTERS

ABSTRACT

Reproductive output of *Aphis gossypii* (Glover) was examined on four

host plants including squash (*Cucurbita pepo* L.), watermelon (*Citrullus*

lanatus (Thunb.) Matsum. & Nakai), cotton (*Gossypium hirsutum* L.), and wheat

(*Triticum aestivum* L.). Data were collected during the late summer of 1992 and

early spring of 1993. Host plant and date of sample collection significantly

influenced the birth rate as measured in nymphs per aphid per day. Host plant

and date also significantly influenced the size of the aphid. The two effects

were highly correlated yet if aphid body length was the first variable in

models predicting birth rate from host plant, temperature, and size the other

variables dropped out of the model. Furthermore, multivariate models were not

significantly better than univariate models using only aphid size to predict

the birth rate (based on r^2). Therefore, if one is interested in predicting birth

rate, one could use aphid size, and ignore these other factors with no

significant loss in the accuracy of the model.

INTRODUCTION

Aphis gossypii (Glover) is an important pest of agriculture worldwide. It

has been reported on over 50 crop plants, and is especially damaging to crops

in the Cucurbitaceae and Malvaceae. In addition to direct yield losses, it causes

damage by contaminating harvested products with honeydew, e.g. melons and

cotton, and serves as a vector for more than 30 viruses. Concomitant with its

significance as a crop pest, a number of studies have been reported which

examine the reproductive potential of this aphid. The following authors

constructed life tables for this aphid on selected host plants: Aldyhim & Khalil (1993) on squash (*Cucurbita pepo* L.), Komazaki (1982) on *Citrus* sp., Liu & Perng (1987) on an unspecified *Cucurbita* spp., Nozato (1987) on *Veronica persica* Poir, Setokuchi (1981) on taro (*Colocasia esculenta* (L.) Schott), and Wyatt & Brown (1977) on cucumber (*Cucumis sativus* L.). In these studies, reproductive rate was presented as the intrinsic rate of increase for the aphid population. Comparison of previous research suggests that host plant, temperature, and light influence reproductive rates in this aphid. The interaction between temperature and host plant has been observed in the reproductive rate (R_0) of *A. gossypii*. Aldyhim & Khalil (1993) reported the highest R_0 (79.7) at 25°C with a 15% decrease at 30°C with squash, while Komazaki (1982) reported the highest R_0 (58.68) at 19. 8°C with a 6% decrease at 29.7° C with citrus. Similarly, Liu & Perng (1987) reported the highest R_0 (109.14) at 21°C but there was only a 44% decline at 30°C with their *Cucurbita* species.

Kishaba and Coudriet (1985) examined the birth rate of this aphid reared on several hosts in the Cucurbitaceae, and found decreased reproduction on a resistant muskmelon line relative to a susceptible line. Kandoria and Jamwal (1988) compared birth rates of this aphid reared on okra (*Abelmoschus esculentus* (L.)), eggplant (*Solanum melongena* L.), and chili (*Capsicum annuum* var. annuum L.), and found no significant differences among hosts. Ekukole (1990) found significant differences in birth rates of this aphid when reared on cotton (*Gossypium hirsutum* L.), watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai), and groundnut (*Arachis hypogaea* L.). Moursi et al. (1985) found significant differences in the reproductive potential of this aphid on cotton, watermelon, sesame (*Sesamum indicum* L.), and eggplant.

Based on these previous studies, differences in reproductive potential among different host plants appears to be common. However, Llewellyn & Brown (1985) suggested that a generalized model for predicting birth rate could be constructed using aphid size where the effects of host plant are not significant elements in the regression model. The objectives of our studies were to examine the differences in birth rate and morphology of *A. gossypii* reared on four different host plants.

METHODS

Aphid cultures were maintained in 1 meter square cloth sided cages on four host plants; 1) Squash - *Cucurbita pepo* var. melopepo (L.) Alef. cultivar 'Lemondrop-L' hybrid seed [Violales: Cucurbitaceae]; 2) Watermelon - *Citrullus lanatus* (Thunb.) Matsum. & Nakai cultivar 'Jubilee' [Violales: Cucurbitaceae]; 3) Cotton - *Gossypium hirsutum* L. cultivar 'Pioneer 75' (1988 seed) [Malvales: Malvaceae]; 4) Wheat - *Triticum aestivum* L. cultivar 'Chisholm' (89 OK FSS) [Cyperales: Poaceae]. Plants were grown in a greenhouse in 10 cm diameter plastic pots. Pots of wheat had 4 or 5 plants, while the others were potted individually. Plants were potted in a mix of vermiculite and peat moss and fertilized once per week with 4 grams Peters solution (20-20-20) per liter of water, but fertilization was uneven as only sufficient water to dampen the potting mix was applied. Plants were transferred to a walk-in growth chamber set for 60±15% relative humidity and a photoperiod of 16:8 (L:D) h 3 days before aphid infestation. The data were collected at two times: late summer, and early spring. Temperatures in the growth chamber were maintained at 25±0.4° C: 23±0.4° C during late summer and 23±0.4° C: 21±0.4° C during early spring with the warmer temperature occurring during the hours of illumination. The chamber used fluorescent and incandescent light sources

which provided a light intensity of $4.09\mu mol$ s^{-1} m^{-2} at 660 nm, and $0.853\mu mol$ s^{-1} m^{-2} at 730 nm (note: chlorophyll is most sensitive to wavelengths at 660nm and 730nm, and melon aphids are sensitive to different wavelengths (Wyatt and Brown 1977)). Light intensity was measured 10cm further from the lights than the leaf surface.

Aphid colonies on squash and watermelon were started with field collected aphids from plants grown at the Wes Watkins Agricultural Research and Extension Center (WWAREC) in Atoka County Oklahoma. Aphids from wheat came from one of these two colonies, but it is not known which one. The cotton aphid colony was established from field collected aphids from cotton grown in Harmon County Oklahoma, which is at least 330 kilometers (map distance, not driving distance) west of WWAREC. All colonies had been maintained under similar conditions in a greenhouse on their respective host plants for at least 18 months before the start of the experiment. Colony conditions were cooler in early spring, and warmer in late summer, but overall the temperature ranged from 15°C to 43°C. The rearing facility allowed exposure to sunlight, therefore light intensity and duration were also different. Shortly before the start of the experiment, specimens were submitted to Dr. Manya B. Stoetzel (US Department of Agriculture, Agricultural Research Service, Beltsville Agricultural Research Center, Beltsville, MD) for identification. All aphids were identified as *A. gossypii*. Voucher specimens were retained by Dr. Stoetzel, and additional specimens have been deposited in the K. C. Emerson Entomology Museum (Oklahoma State University, Stillwater, OK).

Individual apterous nymphs were transferred from the greenhouse colony to a corresponding host plant in the growth chamber - one aphid per 10 cm plastic pot. Aphids were not confined by cages, but all plants were separated sufficiently to prevent aphids from moving to other hosts. After the

aphid molted to an apterous adult and commenced reproduction, the nymphs were counted and removed every day. After 7 days, the adult was removed, weighed, and measured. Morphological characters were measured using an Olympus Stereoscopic microscope with an ocular micrometer calibrated to 0.0167 mm. Aphid body length was measured from the cauda to the extreme frontal part of the head as suggested by Ilharco & van Harten (1987). Maximum body width, maximum body height, length of metathoracic tibia (tibia), length of cornicle (= siphunculi) and maximum distance between outer margins of compound eyes (eye) were also measured. Volume was calculated as $(4/3)\pi(Body/2)((Width + Height)/4)^2$, based on the assumption that the volume of an aphid is best approximated by a prolate spheroid. Aphids were weighed to the nearest 0. 01 mg using a Denver Instruments A-200DS electronic balance.

The analysis assumes that each aphid is a replicate - it was arbitrarily pulled from the parent colony, and placed on a separate plant in a separate pot. The total number of aphids used in the analysis was 62, of which 7, 12, 13, and 9 came from squash, melon, cotton, and wheat, respectively, for late summer. For early spring 5, 2, 6, and 8 came from squash, melon, cotton, and wheat, respectively. The sample size in some cases is small, but previous work (unpublished) indicated that 10 aphids would be sufficient to construct a 95% confidence interval for the colonies during the late summer, and 4 aphids during the early spring (for all variables). This is based on the formula $n=(s\div(0.05 \times \bar{x}))^2$ where n is the expected sample size, s is the standard deviation, $\bar{x}$ is the mean, and 0.05 is the predetermined standard error (Southwood 1987). These results are based on 40 adult apterous aphids from each host in late summer, and 20 adult apterous aphids per host in early spring.

The analysis started with a description of the data set using mean and standard deviation. Differences between means were detected using the Ryan-Einot-Gabriel-Welsch multiple range procedure (REGWQ) to control the experimentwise error rate (SAS Institute Inc. 1989). All tests were done at the 0. 01 level. By inspection, this showed the relative value of each variable for detecting differences between the aphid colonies. A multivariate approach was used to determine the overall difference between the colonies. The Mahalanobis distance is used to measure the separation between aphid colonies. Mahalanobis distances were calculated using the CANDISC procedure in SAS. The Mahalanobis distance was used rather than Euclidean distance because the Mahalanobis distance takes into account correlations between variables (Manly 1991). Distances were calculated separately for each sampling time to clearly show differences between colonies within each sampling time, and clearly test for differences between the two sampling times. This procedure was necessary because unmeasured abiotic differences confounded the aphid–plant relationship between sampling times.

To test for differences between the two sampling times, the Mahalanobis distances were arranged as a matrix. The relationship between these two matrices was examined using Mantel's test (Mantel 1967) as modified by Smouse et al. (1986). The modified Mantel's test uses a Z value which is the sum of the element wise products of two matrices, in this case a distance matrix for each sampling date. One of the matrices then has all elements randomly reassigned to a new location in the matrix, and the Z value is recalculated. Since the matrices are symetric, only the elements below the main diagonal were used. The randomization was done 10,000 times to generate a frequency distribution of Z values. If the observed Z value is unusually large the two matrices are positively correlated. If the value is small the matrices are negatively

correlated. If the value is close to the average Z value the matrices are uncorrelated (Manly 1991).

Having described the data set, a regression analysis was performed to model birth rate. The analysis was done using the REG procedure in SAS (SAS Institute Inc. 1989). Multivariate models were constructed with birth rate as the dependent variable and sampling date, host plant, and morphological features as the independent variables. The type III sums of squares was used to test for significance of the variables. Models where only one variable was significant were reanalyzed using a univariate model.

All regression models used natural log transformed variables. This linearized the regression analysis from the general form of $y = ax^b$, where y is the dependent variable, x is the independent variable, and a and b are regression coefficients. The exponent was tested for differences from its nearest integer using the formula $t^* = \dfrac{b - I}{s(b)}$ where b is the estimated value of the exponent, I is an integer, and s(b) is the standard error. This was compared to the value of the t distribution at the 0.05 significance level with 59 degrees of freedom.

RESULTS AND DISCUSSION

All measurements detected significant differences among host plants (Table 1), and there was a distinct difference between aphids from late summer and early spring. During the late summer aphids from squash were the largest, and aphids from cotton were the smallest. In early spring the aphids from cotton were much larger than any others and the aphids from wheat were the smallest. For all colonies, aphids from late summer were smaller than ones from early spring, but the difference in the aphids from cotton were the most striking. To measure the difference among colonies, the variables body,

156

tibia, cornicle, and eye were used to construct matrices of Mahalanobis distances between aphids from different hosts (Table 2). The matrices were negatively correlated ($P>Z = 0. 9622$). The overall conclusion is that aphids on different hosts are morphologically different and that differences change from late summer to early spring.

Regression analysis indicated that most of the variability in the number of nymphs produced per day was explained by aphid weight (Fig. 1, table 3). The effects of host plant, time, and interaction terms with other independent variables to predict reproductive rates were not significant ($P>|t| >0.10$). This effect is seen in the change in R^2 for models presented in table 5. Models (Table 5) with body length all have an R^2 of about 0.75. All other models have considerably smaller R^2 values. These results are consistent with the findings of Llewellyn and Brown (1985) who suggest that host plant is not a significant variable in regression models using size as a predictor of reproductive rate measured in nymphs for aphids. The values for slope and intercept of the regression model for weight are given in table 3. They are very similar to those of Llewellyn and Brown (1985) who examined 90 aphid species on 120 different host plants. Table 3 also presents equations for each host plant. Aphids from cotton have the greatest influence on the model because they were the largest and the smallest of the aphids examined. This was also reflected in the r^2 values where aphids with the largest difference in means from late summer to early spring had the largest r^2. The overall improvement in the model from using all the data was shown by a decrease in the error associated with the estimated regression coefficients.

Llewellyn and Brown (1985) described a negative exponential relationship between embryo number per unit body weight and body weight, suggesting that as adult size increases the reproductive potential plateaus. This

relationship was also found in these data (table 3, fig. 2) for predicting nymphs/day/weight with body weight.

In some ecological studies it is desirable to gain some estimate of the biomass of an organism. The equations for predicting weight based on linear measures are fairly general but models from other species may have small but significant errors relative to the "true" relationship for the insect under investigation (Sample et al. 1993). Table 4 provides regression coefficients for several models predicting aphid weight. The exponent (b) for all regression equations are different from their nearest integer at the 0.05 level, with the exception of the model using body length where the exponent is not significantly different from 3 (P>t > 0.20). Figure 3 shows the variability in the data around the regression line predicting weight from volume. It is apparent that there are no outlying values, so the few outliers in the previous figures are due to variability in the number of nymphs produced per day.

Since all variables were highly correlated, predicting nymphs per day based on simple morphometric characters would be a useful tool for studying aphid populations. Using a simple measure of length to predict reproductive rate would make field measurements easier, and would permit analysis of dead specimens. Table 4 presents regression models for predicting nymphs per day based on morphological characters. The exponent for the equation using body length is not significantly different from 2. The exponent for the equation using body x width is significantly different from 1 at the 0.10 level but not at the 0.05 level. The model using volume is not significantly different from 1 at the 0.15 level. The exponent for the remaining model is significantly different from its nearest integer at the 0.005 level. It is interesting to note that the regressions using morphological characters to predict nymphs per day had higher r^2 values relative to the equation using weight (Tables 3, 4).

The finding that host plant had a significant effect on the reproductive rate of the aphid, but that the reproductive rate could be modeled using only aphid size, is a potential leap forward for the study of aphids in agriculture. It suggests that population level processes could be predicted for many aphids using one life table based on aphid size. If true, it would simplify aphid research by freeing researchers from creating a specific life table for every aphid under every environmental condition.

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Table 1. Mean and standard deviation for measurements on A. gossypii reared on 4 different host plants

Late Summer	Squash n=7		Watermelon n=12		Cotton n=13		Wheat n=9	
Volume (mm^3)	0.2050 ± 0.07776	AB	0.2611 ± 0.13937	A	0.0945 ± 0.11071	B	0.1107 ± 0.04058	B
Weight (mg)	0.2152 ± 0.07412	AB	0.2378 ± 0.09252	A	0.1202 ± 0.08013	B	0.1463 ± 0.03354	AB
Nymphs/day	4.3673 ± 0.90310	A	5.4387 ± 1.61804	A	2.9631 ± 2.26833	A	2.9999 ± 0.63074	A
Body (mm)	1.2976 ± 0.13521	A	1.3208 ± 0.17439	A	0.9821 ± 0.16308	B	1.1389 ± 0.09501	AB
Tibia (mm)	0.6524 ± 0.08412	A	0.5882 ± 0.10532	AB	0.3910 ± 0.06033	C	0.4907 ± 0.02778	BC
Cornicle (mm)	0.2333 ± 0.04488	A	0.2090 ± 0.05464	AB	0.1109 ± 0.02532	C	0.1667 ± 0.01614	B
Eye (mm)	0.3155 ± 0.02001	A	0.3021 ± 0.02413	AB	0.2481 ± 0.02480	C	0.2741 ± 0.01410	BC
Early Spring	Squash n=5		Watermelon n=2		Cotton n=6		Wheat n=8	
Volume (mm^3)	0.4354 ± 0.06829	B	0.4791 ± 0.13184	B	0.8432 ± 0.16783	A	0.1558 ± 0.07029	C
Weight (mg)	0.3418 ± 0.03931	B	0.3863 ± 0.06317	B	0.5564 ± 0.07448	A	0.1798 ± 0.03735	C
Nymphs/day	5.0854 ± 1.71925	B	8.1430 ± 0.00000	A	8.6822 ± 0.85180	A	3.7500 ± 0.52751	B
Body (mm)	1.4067 ± 0.04386	B	1.4583 ± 0.05893	AB	1.6625 ± 0.06785	A	1.1750 ± 0.12599	C
Tibia (mm)	0.6217 ± 0.03206	B	0.7583 ± 0.01179	A	0.7778 ± 0.06576	A	0.4542 ± 0.05909	C
Cornicle (mm)	0.1767 ± 0.00697	B	0.2708 ± 0.00589	A	0.2833 ± 0.03944	A	0.1479 ± 0.03235	B
Eye (mm)	0.3127 ± 0.01278	BC	0.3375 ± 0.00589	AB	0.3639 ± 0.00861	A	0.2771 ± 0.02980	C

161

Length, Cornicle, and eye had significant models (P>F <0.0004), while the rest were not significant (P>F >0.05) for late summer. All models were significant for early spring (P>F <0.0001). Different letters within rows are significant using Ryan-Einot-Gabriel-Welsch multiple comparison procedure with alpha=0.01.

Table 2. Mahalanobis distances between aphids on different host plants for the aphids in late summer and early spring.

Late Summer		Squash	Watermelon	Cotton
	Watermelon	2.828		
	Cotton	13.601	6.976	
	Wheat	6.061	1.850	2.160
Early Spring				
	Watermelon	18.120		
	Cotton	13.246	9.922	
	Wheat	21.135	36.617	44.652

The matrices are negatively correlated by modified Mantel's test (p > Z = 0.9622).

Table 3. Regression models predicting nymphs (y) and the decline in reproductive rate per unit body weight [N/D/W] (y) from weight (x).

y	n	ln(a) ± se	b ± se	r^2	P>F
			Regression Parameters		
Nymphs/day	62	2.469 ± 0.098	0.648 ± 0.056	0.69	0.000
Squash	12	2.089 ± 0.272	0.425 ± 0.189	0.34	0.048
Watermelon	14	2.336 ± 0.227	0.431 ± 0.146	0.42	0.012
Cotton	19	2.552 ± 0.142	0.704 ± 0.072	0.85	0.017
Wheat	17	2.087 ± 0.337	0.486 ± 0.181	0.32	0.000
N/D/W	62	2.469 ± 0.098	-0.352 ± 0.056	0.40	0.000
Squash	12	2.089 ± 0.272	-0.575 ± 0.189	0.48	0.012
Watermelon	14	2.336 ± 0.227	-0.569 ± 0.146	0.55	0.021
Cotton	19	2.552 ± 0.142	-0.296 ± 0.072	0.49	0.001
Wheat	17	2.087 ± 0.337	-0.514 ± 0.181	0.35	0.012

Table 4. Regression models predicting weight and nymphs produced per day based on linear measures.

Model	Regression Parameters		
	ln(a) ± se	b ± se	r^2
ln(wt) = ln(Body)	-2.275 ± 0.033	3.146 ± 0.116	0.92
ln(wt) = ln(Body x width)	-1.392 ± 0.019	1.619 ± 0.046	0.95
ln(wt) = ln(Body x width x height)	-0.785 ± 0.025	1.064 ± 0.025	0.97
ln(wt) = ln(vol)	-0.113 ± 0.039	1.069 ± 0.025	0.97
ln(nymphs) = ln(Body)	0.963 ± 0.046	2.198 ± 0.166	0.74
ln(nymphs) = ln(Body x width)	1.580 ± 0.033	1.133 ± 0.079	0.77
ln(nymphs) = ln(Body x width x height)	1.983 ± 0.056	0.717 ± 0.057	0.72
ln(nymphs) = ln(vol)	2.442 ± 0.087	0.725 ± 0.056	0.73

All models are significant by F test at the 0.0001 level

Table 5. Regression models predicting birth rate based on host plant, color form, sample time, and body length.

Model	R^2
s q	0.0087
m e	0.1088
c o	0.0133
w h	0.0743
Host	0.0002
Color	0.2420
Time	0.1695
Color Time	0.4540
sq wh me Color Time	0.4877
Host Color Time	0.4641
Body Length	0.7416
Body sq	0.7568
Body me	0.7636
Body co	0.7510
Body wh	0.7571
Body Host	0.7667
Body Time	0.7468
Body Color	0.7443
Body Color Time	0.7466
Body Host Color Time	0.7669

sq, wh, me, co are binary variables coded 1 if the aphid was on that host, and 0 otherwise.
Host is coded 2=squash, 3=wheat, 5=melon, 7=cotton.
Time is coded 0 if the sample was from the first set of experiments and 1 if from the second set.
Color is coded 0 if yellow, 1 if green.

Figure 1. Relationship between nymphs per day and aphid weight including the 95% confidence interval for the regression: ln(nymphs) = ln(2.47) + ln(weight$^{0.648}$).

Figure 2. Relationship between nymphs per day per weight and aphid weight including the 95% confidence interval for the regression: $\ln(\text{nymphs}) = \ln(2.47) + \ln(\text{weight}^{-0.352})$.
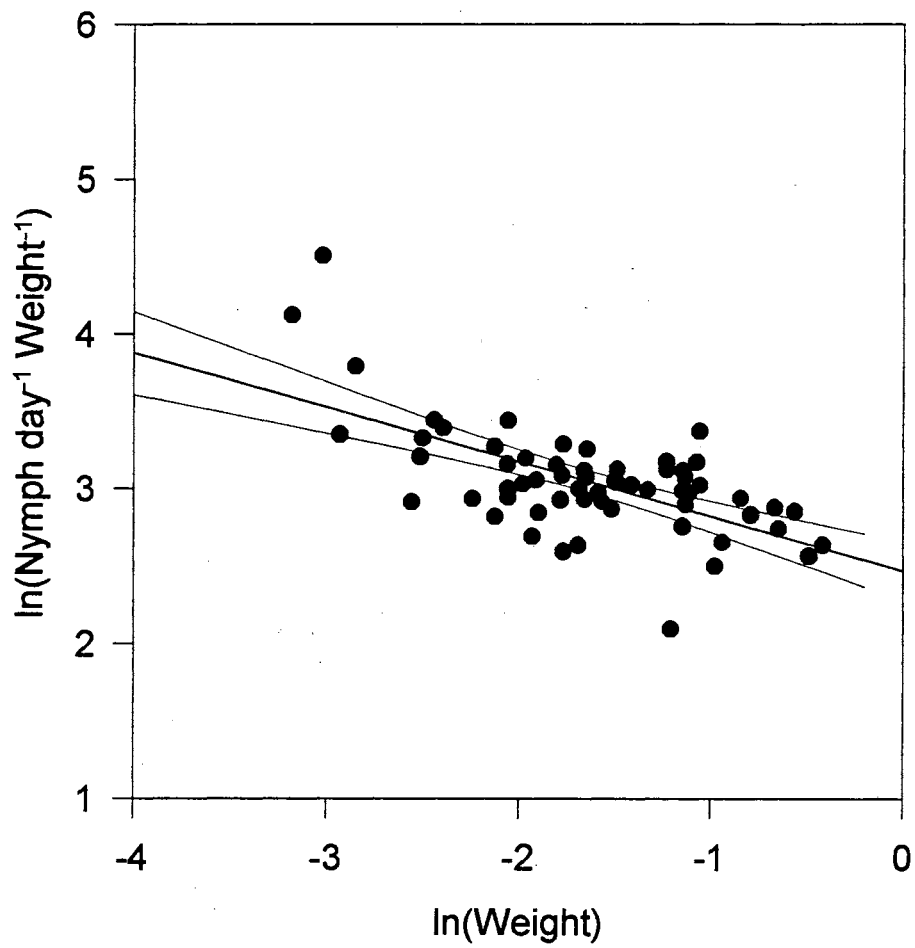
Figure 3. Relationship between weight and volume, including the 95% confidence interval for the regression: $\ln(\text{weight}) = \ln(-0.113) + \ln(\text{volume}^{1.07})$.
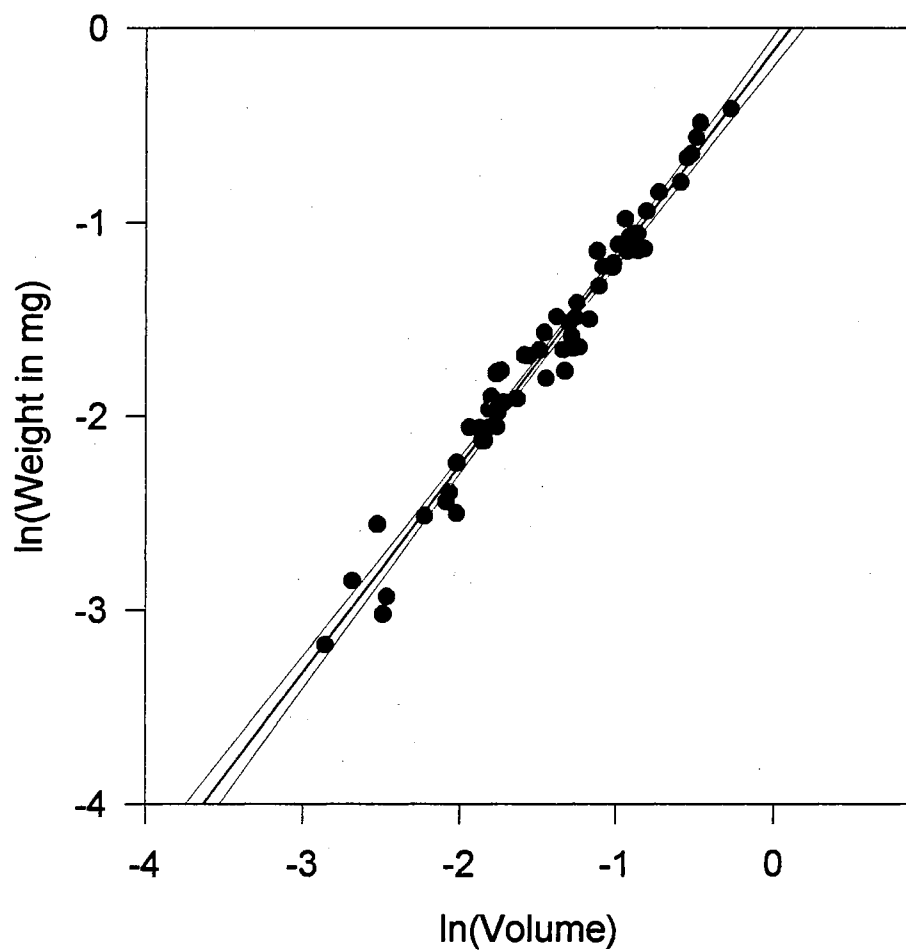
TRITROPHIC INTERACTIONS BETWEEN *Lysiphlebus testaceipes*, MELON APHID, GREENBUG, WHEAT AND WATERMELON MEASURED USING MORPHOLOGICAL CHARACTERS

ABSTRACT

Biological control of aphids is one way to reduce our reliance on chemical controls. In order for this approach to work a great deal needs to be known about the biology of all species involved, and how they interact. This paper deals with the interaction of *Lysiphlebus testaceipes* Cresson, a hymenopterous parasitoid, *Aphis gossypii* (Glover), an aphid pest of cotton and watermelon, *Schizaphis graminum* biotype E, a pest of small grains, *Citrullus lanatus* commonly known as watermelon, and *Triticum aestivum* commonly known as wheat. All pairwise aphid - plant colonies were established except *S. graminum* on watermelon. The conclusion is that in this system aphid species played the greatest role in determining the size of the progeny wasps. The effect of the plant was relatively minor. From results published in the literature, we would predict that generalizing to other wasp-aphid-plant systems would not be appropriate.

INTRODUCTION

Aphis gossypii is a serious pest of watermelon causing economic losses both from feeding injury and from virus transmission. In the past, this aphid has been controlled with a wide array of different pesticides including organophosphates and carbamates. The growing concern over the use of pesticides is a major theme in much of agriculture mainly due to concern over environmental contamination, and the economic impact of pesticide resistance. Part of the response in the USA is to promote a reduced dependence

on pesticides, and an increased reliance on beneficial organisms to control pests.

A possible biological control agent for this aphid is the braconid wasp *Lysiphlebus testaceipes*. As aphid populations build during middle and late summer, this wasp can easily be found parasitizing melon aphid in commercial watermelon fields, but is seldom sufficiently abundant to control aphid populations. However the parasitoid can be successful at controlling aphid populations in greenhouses. There are a number of possible explanations for this difference between greenhouse and field. One explanation is that there is a biological cost involved in switching to a new aphid-plant system as would be required for a wasp to survive and reproduce during periods when an annual crop was not present in the field. The difference could be due to differences in searching behavior required to efficiently search plants with different phenology, and locate aphids with different biochemical cues. However, the cost could also involve an altered physiology required to deal with secondary plant compounds which may be present in the aphid host, or an altered physiology required to deal with a different nutritional balance present in different aphid species. Also, changes associated with aphid size could influence wasp size because a large aphid would provide the wasp larva a much greater nutritional resource pool than would a smaller aphid.

Lysiphlebus testaceipes must deal with these problems on a regular basis in order to survive in Oklahoma in the melon aphid - watermelon agroecosystem. During warm summer months watermelon is one of the major vegetable crops in Oklahoma (Allred & Lucier 1990), but cold weather during the winter kills the plants. Additionally, it is not until late summer that there are sufficient melon aphids to support a large and growing wasp population.

Therefore, the wasp must find alternate aphid-plant systems to survive and reinvade the melon aphid - watermelon agroecosystem each summer.

One of the possible alternate ecosystems that this wasp could use, the greenbug-wheat agroecosystem, is common in Oklahoma. While it does not provide a complete bridge between watermelon cropping cycles, it does provide a major bridge between cycles, and the wasp could remain on greenbug but switch to the sorghum and then corn agroecosystems. Another reason for using wheat is that there is a well established melon aphid colony on wheat that has been well characterized by several previous studies (see Chapter 5 & Chapter 6).

METHODS

Aphid cultures were maintained on one of two host plants; 1) Watermelon - *Citrullus lanatus* (Thunb.) Matsum. & Nakai cultivar 'Jubilee'; or 2) Wheat - *Triticum aestivum* L. cultivar 'Chisholm' (89 OK FSS). Colonies were maintained in a greenhouse. Plants were grown in plastic flower pots 15cm wide and 18cm deep. Plants with two well developed leaves were used in the experiment. Plants were infested with forty aphids each and covered with a polycarbonate plastic (Lexan® from General Electric Company) cage 14 cm in diameter and 31 cm high. Cages had two 10 cm ventilation holes in the side. Both the top and the ventilation holes were covered with fine mesh cloth to prevent escape of aphids and wasps. The aphids and plants were permitted three days to adjust to the conditions in the growth chamber prior to introducing the wasps. Conditions in the growth chamber were maintained at 60±15% relative humidity and a photoperiod of 16:8 (L:D) h, and 25±0.4° C: 23±0.4° C with the warmer temperature occurring during the day. The light intensity was about 4.09 μmol s^{-1} m^{-2} at 660 nm, and 0.853 μmol s^{-1} m^{-2} at 730

nm (chlorophyll is most sensitive to wavelengths at 660nm and 730nm, and melon aphids are sensitive to different wavelengths (Wyatt and Brown 1977)). However, due to the screening effect produced by the cages, aphids and wasps probably experienced a higher relative humidity and a lower light intensity than the reported levels. Light intensity was measured 10cm further from the lights than the leaf surface.

The *A. gossypii* colonies came from a stock colony started on watermelon from aphids on watermelon found near Lane Oklahoma. A colony on squash was also started about the same time from other aphids near Lane. The colony on wheat was formed by forcing aphids from both the watermelon and squash colonies to feed on wheat or die. Following establishment on wheat, the aphids were allowed to adapt to their new host for about 18 months before this experiment was started. The *S. graminum* was started from a biotype E colony maintained by Dr. Don C. Peters at Oklahoma State University.

The experiment used two wasp colonies. The first wasp colony came from adult wasps collected by the senior author from a commercial watermelon field in Rush Springs (Grady County), Oklahoma (ca. 60 km south west of Oklahoma City). This colony was confined to melon aphid on watermelon. From the time the wasps were collected in the field until they were used in the experiment at least 40 days had elapsed (this represents 3 to 4 generations). The second wasp colony originated from wasps supplied by Dr. Timothy J. Kring at the University of Arkansas at Fayetteville. Originally these wasps were on an unknown greenbug biotype on corn leaves, but upon arrival at Lane they were forced to use biotype E greenbugs feeding on wheat. They were maintained in this system for at least 30 days prior to use in the experiment (30 days represents about 2 to 3 generations).

Three days prior to the beginning of the experiment, plants were taken from the greenhouse, infested with 40 aphids, caged, and moved into the growth chamber. During this time, 300 to 400 mummies were individually confined in gelatin capsules. Each day the gelatin capsules were checked for emergence. Wasps under 48 hours old were sexed, paired, and allowed to mate in small 10 ml glass vials sealed with a cotton plug. Adults were given a dilute honey solution by wetting the cotton plug until the solution soaked through. Adults were allowed to mate for 3 to 4 hours, and then they were released into the cages. Adults were removed 24 hours later. Plants were watered twice during the 12 days between removal of the wasps and mummy formation with 4 grams Peters solution (20-20-20) per liter of water. However, fertilization was uneven as only sufficient water to dampen the potting mix was applied. Watering was done by placing the pot in a small dish and letting water soak through the drainage holes in the bottom of the pot. After mummy formation the mummies were removed from the cages by cutting the plant tissue surrounding the mummy, and then they were placed individually into gelatin capsules and held for emergence.

Wasps which emerged were left to desiccate in the gelatin capsule. After they were dry each mummy was measured using an Olympus Stereoscopic microscope with an ocular micrometer calibrated to 0.0167 mm. Aphid length was measured from the cauda to the extreme frontal part of the head as suggested by Ilharco & van Harten (1987). Length of metathoracic tibia (tibia), length of cornicle (= siphunculi) and maximum distance between outer margins of compound eyes (eye) were also measured. The wasp was measured using a Zeiss Axioplan trinocular compound microscope with an ocular micrometer set to 0.005 mm per division. The maximum distance between the outer margins of the eyes, and the length of the metathoracic femur were

174

measured. To accomplish this the head of the wasp was severed, and the wasp was placed on a microscope slide along with a thick solution of methylcellulose. A coverslip was used to press all of the parts flat. This worked well for the head, but at times the femur could not be positioned parallel to the slide. Thus, the head was measured with somewhat greater precision than the femur.

The extrapolation from morphological measures to population differences in the field rests on the assumption that measurements of size are good indicators of life table characteristics. That is, it is assumed that larger individuals will be more fecund, and will live longer than smaller individuals. This has not been proven for any of the organisms used in this paper, but size is a good predictor of birth rate in *A. gossypii*. Furthermore, Reiss (1989) discusses the strong relationship between the metabolic energy devoted to reproduction and the weight of individuals for a wide array of different species from aphids to mammals. Given the strong relationship between weight and size it is reasonable to expect a similar relationship between size and reproductive potential.

Probably the biggest flaw in the analysis is the treating of each progeny wasp as a separate replicate. One should treat the average from each cage as a replicate. However, the power of the estimated value for a cage is not the same for each cage - some cages yielded 60 wasps while others yielded only one progeny wasp. Also, the behavior of the wasp assures one that selection of host aphids is not random, i.e. certain ages, stages, or locations on the plant will be preferred over others. We decided that the best solution was to treat each wasp as a replicate, and acknowledge the problem.

The experimental design was essentially two randomized block designs with two treatments each at two levels with one missing cell. The two

randomized block designs were a result of using wasp colonies from two sources. The missing cell was a result of not having a greenbug colony on watermelon. This inevitably weakens the power with which one can test for the simple effects of plant and aphid and prevents evaluation of interaction effects. In gathering the data it became apparent that there were two other treatments that were "applied" and required appropriate modifications in the analysis. These treatments consisted of the gender of the wasp, and the stage of the aphid when it was mummified. To avoid additional problems with missing cells in the analysis, mummies from alate aphids were not used, so mummy stage was either adult apterous or nymph.

The analysis consists of ANOVA output as implemented in SAS (SAS Institute inc.1989). Since all of the "treatment" variables were binary, all comparisons used the significance test for the model to test for significant effects. The overall design consisted of the five "treatments": host plant (melon, wheat), aphid (*S. graminum*, *A. gossypii*), and source of the wasp colony (Rush Springs, Fayetteville), gender of the wasp (male, female), and mummy stage (adult, nymph). The analysis consisted of comparing results from two cells while keeping the others constant.

RESULTS AND DISCUSSION

The main question focused on the relative contribution of the aphid and the aphid host plant to changes in the morphology of the wasp. The data are summarized in tables 1 and 2 which list mean, standard deviation, and sample size. These tables also list the number of cages from which wasps were taken to achieve the sample size. In preparation for answering the main question it would be valuable to know the role of the following treatments: wasp gender, mummy stage, and source of the parent wasps.

176

There were significant differences between male and female wasps (table 3). These differences were more pronounced in wasps from nymphal mummies. However, for both adult and nymphal mummies there was a significant difference between male and female wasps from parent wasps from the greenbug colony that parasitized geenbug.

The difference between male and female wasps was not associated with aphid stage or size (tables 3 & 4). In table 3 aphid measurements were not a significant predictor of wasp gender, and neither male nor female wasps showed a preference for a particular stage (table 4). This is consistent with the findings of Hight et al. (1972) who reported that greenbugs which were parasitized as nymphs could mature to produce offspring. Hight et al. also reported that *L. testaceipes* will parasitize greenbugs only 24 hours old. Ruth et al. (1974) took this further and found that *L. testaceipes* would attack and could develop from a greenbug only 15 minutes old. Both Hight et al. (1972) and Ruth et al. (1974) reported no difference in the sex ratio for wasps from the different age classes.

As expected, there were significant differences between the different stages for the mummies (table 3). However, a very unusual feature of table 4 is that the variable eye was not a good predictor of differences between aphid stage for the melon aphid, but was for greenbug. Other data suggest that the variable eye should be a good predictor of stage for both aphid species.

Significant differences due to the source of the parent colony were sporadic, but most pronounced in progeny from greenbugs on wheat (table 5). It appears that there are more significant differences between the aphids selected by the parents than there are differences in the progeny wasp. Body length is expected to be a poor predictor of aphid stage given this observation since the wasp changes the shape of the aphid as it forms the mummy: aphids

177

tend to become more spherical as the wasp mummifies the aphid. Thus, if all the wasps are of roughly the same size, one would expect that the size of the mummy should not be different. The lack of difference in the variable eye may be due to either a weak development of the tentorial structures in the head thereby permitting considerable deformation, or the wasp may break such structures either in feeding or mummy formation.

Given that there are differences in source of the wasp, stage of the aphid, and gender of the wasp, it is not reasonable to ignore these effects when examining the effect of host plant and host aphid on this wasp.

The first four rows in table 6 show the effect of host plant on the wasp. The only significant differences due to the transfer of wasps from melon aphid on melon to melon aphid on wheat were observed in female wasps emerging from nymphal mummies. Under the conditions in the cages, there were no significant differences in the mummies at the .05 level for the variables tibia, cornicle, and eye. There were significant differences in length at the .05 level, but only for female wasps from adult mummies, and male wasps from nymphal mummies. This suggests that conditions differed significantly between observations from the growth chamber proper, and conditions in the cages. Previous studies have demonstrated that under the conditions in the growth chamber melon aphid on watermelon should be larger than the melon aphids on wheat (chapter 5).

The second set of four rows in table 6 examine the effect of switching aphid. Clearly, a change in aphid had a much greater effect than a change in host plant. The reason for this is not certain, but this could be due exclusively to the difference in size between melon aphid and greenbug, and there may or may not be other factors involved.

178

The last eight rows in table 6 examine the total effect of changing plant and aphid and the interaction effect between the two.

In summary, it is clear that the aphid host has a strong influence on the wasp. A dramatic example of the importance of host aphid was reported by Carroll and Hoyt (1986). They reported that *Praon unicum* was a natural parasite of *Aphis pomi* De Geer on apple, but larvae died before emerging as an adult. However, this parasite was able to complete its life cycle on other aphids feeding on apple. Campbell et al. (1990) also reported a host plant effect for this wasp reared on greenbug feeding on resistant and susceptible barley and sorghum cultivars. However Campbell et al. (1990) did not report on possible changes in the aphids feeding on these hosts, so it is not possible to unequivocally conclude that host plant was the direct cause of the differences they report.

As a speculative conclusion from the results presented in table 3, one might observe that there were no size differences in the aphid mummies between male and female wasps, but that there were significant differences in the size of the wasps. This might indicate that male wasps are less efficient in their use of available aphid biomass than are the females. The male wasps were significantly smaller, even though they used aphids that were not significantly different from those used by the larger female wasps.

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Table 1: Mean and Standard deviation for morphological characters of wasps and mummies from adult apterous aphids.

Adult Apterous	Female Wasps			Male Wasps		
	A.g. on Melon	A.g. on Wheat	S.g. on Wheat	A.g. on Melon	A.g. Wheat	S.g. on Wheat
A.g. on Melon*	2	2	5	3	1	4
Sample Size	9	9	13	14	11	13
Wasp Femur	0.262 ± 0.0376	0.263 ± 0.0125	0.323 ± 0.0261	0.264 ± 0.0395	0.259 ± 0.0205	0.314 ± 0.0299
Wasp Eye	0.363 ± 0.0449	0.374 ± 0.0158	0.437 ± 0.0272	0.358 ± 0.0398	0.354 ± 0.0184	0.420 ± 0.0243
Aphid Length	1.222 ± 0.0777	1.328 ± 0.0682	1.713 ± 0.1474	1.252 ± 0.1008	1.288 ± 0.0857	1.667 ± 0.1497
Aphid Tibia	0.532 ± 0.1092	0.489 ± 0.0534	0.696 ± 0.0613	0.518 ± 0.0951	0.506 ± 0.0639	0.660 ± 0.0293
Aphid Cornicle	0.186 ± 0.0503	0.168 ± 0.0207	0.253 ± 0.0258	0.185 ± 0.0366	0.171 ± 0.0237	0.249 ± 0.0219
Aphid Eye	0.281 ± 0.0300	0.279 ± 0.0172	0.347 ± 0.0214	0.288 ± 0.0195	0.277 ± 0.0182	0.335 ± 0.0186
S.g. on Wheat*	10	2	9	5	1	6
Sample Size	37	7	37	9	3	31
Wasp Femur	0.277 ± 0.0422	0.284 ± 0.0224	0.332 ± 0.0324	0.259 ± 0.0427	0.253 ± 0.0275	0.299 ± 0.0291
Wasp Eye	0.392 ± 0.0423	0.410 ± 0.0187	0.451 ± 0.0330	0.371 ± 0.0350	0.363 ± 0.0301	0.412 ± 0.0301
Aphid Length	1.261 ± 0.1371	1.336 ± 0.0836	1.686 ± 0.1548	1.213 ± 0.1950	1.189 ± 0.1084	1.614 ± 0.1389
Aphid Tibia	0.473 ± 0.0566	0.563 ± 0.0836	0.713 ± 0.0733	0.451 ± 0.0641	0.483 ± 0.0726	0.719 ± 0.0687
Aphid Cornicle	0.170 ± 0.0330	0.187 ± 0.0267	0.266 ± 0.0217	0.153 ± 0.0276	0.161 ± 0.0096	0.268 ± 0.0270
Aphid Eye	0.288 ± 0.0262	0.301 ± 0.0270	0.361 ± 0.0160	0.285 ± 0.0306	0.261 ± 0.0192	0.357 ± 0.0180

Table is in two parts. Top part, wasps originally from *A. gossypii* on watermelon, bottom part wasps originally from *S. graminum* on wheat.
*Numbers in these rows indicate the number of cages from which progeny wasps were recovered

Table 2: Mean and standard deviation for morphological characters of wasps and aphid mummies from aphid nymphs.

Adult Apterous		Female Wasps			Male Wasps	
	A.g. on Melon	A.g. on Wheat	S.g. on Wheat	A.g. on Melon	A.g. Wheat	S.g. on Wheat
A.g. on Melon*	1	3	5	2	3	5
Sample Size	9	12	34	7	10	35
Wasp Femur	0.293 ± 0.0215	0.258 ± 0.0292	0.311 ± 0.0242	0.266 ± 0.0276	0.271 ± 0.0196	0.294 ± 0.0211
Wasp Eye	0.402 ± 0.0168	0.370 ± 0.0274	0.419 ± 0.0256	0.366 ± 0.0282	0.378 ± 0.0209	0.397 ± 0.0203
Aphid Length	1.204 ± 0.0904	1.179 ± 0.0725	1.434 ± 0.1214	1.110 ± 0.0907	1.240 ± 0.1364	1.438 ± 0.0936
Aphid Tibia	0.359 ± 0.0600	0.381 ± 0.0427	0.545 ± 0.0864	0.352 ± 0.0485	0.408 ± 0.0967	0.559 ± 0.0634
Aphid Cornicle	0.122 ± 0.0195	0.130 ± 0.0176	0.194 ± 0.0285	0.119 ± 0.0178	0.131 ± 0.0333	0.199 ± 0.0263
Aphid Eye	0.290 ± 0.0207	0.272 ± 0.0196	0.312 ± 0.0239	0.277 ± 0.0172	0.290 ± 0.0319	0.321 ± 0.0201
S.g. on Wheat*	8	1	7	4	1	7
Sample Size	23	5	39	6	3	26
Wasp Femur	0.284 ± 0.0391	0.270 ± 0.0197	0.322 ± 0.0231	0.262 ± 0.0463	0.258 ± 0.0126	0.296 ± 0.0246
Wasp Eye	0.402 ± 0.0387	0.388 ± 0.0208	0.439 ± 0.0247	0.372 ± 0.0497	0.375 ± 0.0100	0.407 ± 0.0224
Aphid Length	1.176 ± 0.1076	1.177 ± 0.0813	1.448 ± 0.1002	1.122 ± 0.1576	1.161 ± 0.1005	1.394 ± 0.0696
Aphid Tibia	0.374 ± 0.0674	0.397 ± 0.0492	0.582 ± 0.0544	0.340 ± 0.0539	0.417 ± 0.0289	0.571 ± 0.0503
Aphid Cornicle	0.128 ± 0.0245	0.135 ± 0.0208	0.201 ± 0.0197	0.111 ± 0.0297	0.142 ± 0.0220	0.196 ± 0.0244
Aphid Eye	0.288 ± 0.0236	0.278 ± 0.0217	0.329 ± 0.0259	0.281 ± 0.0340	0.292 ± 0.0083	0.329 ± 0.0236

The table has two parts, the top for the parent colony on *A. gossypii* feeding on watermelon, and the bottom for the parent colony from *S. graminum* feeding on wheat.
*Numbers in these rows indicate the number of cages from which progeny wasps were recovered

Table 3. P>F vlaues for differences in gender of wasp.

Stage	Source*	Weye	Wfem	Body	Tibia	Cornicle	Eye
Adult	1-1	0.762	0.902	0.455	0.739	0.957	0.527
	1-2	0.020	0.603	0.272	0.529	0.792	0.787
	1-3	0.108	0.410	0.436	0.069	0.686	0.134
	3-1	0.158	0.269	0.393	0.303	0.166	0.759
	3-2	0.016	0.094	0.047	0.191	0.153	0.051
	3-3	0.000	0.000	0.051	0.720	0.762	0.335
Nymph	1-1	0.008	0.044	0.058	0.807	0.743	0.222
	1-2	0.463	0.227	0.196	0.391	0.931	0.124
	1-3	0.000	0.002	0.885	0.454	0.437	0.097
	3-1	0.121	0.242	0.333	0.265	0.154	0.552
	3-2	0.359	0.400	0.817	0.552	0.682	0.359
	3-3	0.000	0.000	0.021	0.423	0.364	0.899

Weye is the eye of the progeny wasps, while wfem is the metathoracic femur of the progeny wasps.
* Source codes follow a standardized format. The first number is 1 if the parent wasp came from *A. gossypii* on melon, and 3 if it came from *S. graminum* on wheat. The second number is for the progeny wasp and follows the same pattern as for the parent, but if it is 2 then the progeny wasp came from *A. gossypii* on wheat.

Table 4. P>F values for differences in stage.

Gender	Source*	Weye	Wfem	Body	Tibia	Cornicle	Eye
Male	1-1	0.618	0.933	0.005	0.000	0.000	0.234
	1-2	0.014	0.175	0.343	0.013	0.005	0.243
	1-3	0.002	0.011	0.000	0.000	0.000	0.000
	3-1	0.960	0.925	0.360	0.004	0.016	0.788
	3-2	0.559	0.789	0.761	0.214	0.234	0.065
	3-3	0.514	0.702	0.000	0.000	0.000	0.000
Female	1-1	0.029	0.050	0.648	0.001	0.003	0.503
	1-2	0.679	0.619	0.000	0.000	0.000	0.440
	1-3	0.044	0.139	0.000	0.000	0.000	0.004
	3-1	0.395	0.530	0.014	0.000	0.000	0.928
	3-2	0.084	0.280	0.008	0.003	0.005	0.150
	3-3	0.088	0.111	0.000	0.000	0.000	0.000

Weye is the eye measurement for the wasp. Wfem is the femur measurement for the wasp. The remaining variables are from mummies.
* Source codes follow a standardized format. The first number is 1 if the parent wasp came from *A. gossypii* on melon, and 3 if it came from *S. graminum* on wheat. The second number is for the progeny wasp and follows the same pattern as for the parent, but if it is 2 then the progeny wasp came from *A. gossypii* on wheat.

Table 5. P>F values for differences between different sources (Oklahoma vs. Arkansas).

Stage	Progeny	SEX	Weye	Wfem	Body	Tibia	Cornicle	Eye
Adult	1	0	0.443	0.784	0.529	0.078	0.034	0.782
	1	1	0.074	0.341	0.423	0.027	0.233	0.500
	2	0	0.493	0.716	0.117	0.604	0.494	0.222
	2	1	0.001	0.029	0.837	0.048	0.143	0.061
	3	0	0.379	0.113	0.040	0.303	0.100	0.103
	3	1	0.171	0.373	0.704	0.016	0.020	0.000
Nymph	1	0	0.816	0.849	0.859	0.678	0.563	0.832
	1	1	0.996	0.527	0.496	0.563	0.514	0.814
	2	0	0.848	0.320	0.378	0.889	0.613	0.932
	2	1	0.200	0.398	0.951	0.525	0.609	0.578
	3	0	0.084	0.727	0.049	0.413	0.672	0.179
	3	1	0.001	0.057	0.603	0.030	0.198	0.004

Weye is the eye measurement for the wasp. Wfem is the femur measurement for the wasp. The remaining variables are from aphids.
Progeny codes are: 1 = *A. gossypii* on melon, 2 = *A. gossypii* on wheat, 3 = *S. graminum* on wheat.
Sex codes are: 0 = male, 1 = female.

Table 6. P>F values for models assessing effect of host aphid and host plant.

Control	Test	Effect	Stage	SEX	N	Wasp eye	Wasp femur
1-1	1-2	Plant	adult	0	24	0.751	0.672
			adult	1	18	0.516	0.967
			nymph	0	17	0.366	0.649
			nymph	1	21	0.006	0.007
3-3	3-2	Aphid	adult	0	34	0.012	0.015
			adult	1	44	0.003	0.0005
			nymph	0	29	0.023	0.016
			nymph	1	43	0.0001	0.0001
1-1	1-3	all	adult	0	27	0.0001	0.001
			adult	1	22	0.0001	0.0002
			nymph	0	42	0.0014	0.004
			nymph	1	42	0.060	0.043
3-3	3-1	all	adult	0	40	0.0013	0.0029
			adult	1	74	0.0001	0.0001
			nymph	0	32	0.011	0.0156
			nymph	1	61	0.0001	0.0001

See table 3 for the codes used for Control and Test. Effect is the "treatment" effect, of which there is one estimate for each of plant and aphid, and two estimates of the combined effect of plant + aphid + plant*aphid.
Sex codes are: 0 = male, 1= female

SUPPLEMENT TO CHAPTER VI

Data were collected as described in the previous chapter using the same equipment. The colonies all came from the same location as described previously. The aphids used to gather the data presented in this section were reared in a trailer house. Artificial light was provided by fluorescent bulbs. The conditions in the trailer were highly variable. Temperature ranged from 65F to 100F. The relative humidity was never measured. The day-night cycle was variable. Windows provided natural light, but the timers for the different lighting circuits were not synchronized.

In the analysis alate aphids and aphids which had well developed wing pads were removed from the data set prior to analysis.

Table 1 is equivalent to table 4 in the previous chapter. It shows that non-parasitized aphids show a much greater separation between nymph and adult apterous stages.

Table 2 is in further support of the differences observed between melon aphid on melon and melon aphid on wheat.

Both tables also clearly show the usefulness of the eye measurement in distinguishing different stages and differences between aphids on different hosts.

Table 1. P>F for differences between adult apterous and nymphs of aphids from three colonies: greenbug on wheat, melon aphid on wheat, and melon aphid on melon.

Aphid	Plant	Length	Tibia	Cornicle	Eye
S. graminum	Wheat	0.0001	0.0001	0.0001	0.0001
A. gossypii	Wheat	0.0001	0.0001	0.0001	0.0002
A. gossypii	Melon	0.0001	0.0001	0.0001	0.0009

Table 2. P>F differences in aphids from watermelon and wheat by stage of aphid, adult apterous and nymph.

Stage	Length	Tibia	Cornicle	Eye
Adult	0.0001	0.0001	0.0001	0.0001
Nymph	0.0255	0.0056	0.0240	0.0001

The following table contains the raw data used in chapter 4. Length is the total length of the aphid from the rostrum to the cauda. Tibia is the metathoracic tibia. Eye is the maximum distance between the outer margins of the eyes. Color is Divide length, tibia, cornicle, and eye by 60 to get length in millimeters.

length	tibia	cornicle	eye	color
98	45	16	21	1
80	42	17	20	1
74	32	11	18	2
82	38	12	19	2
70	32	11	18	2
84	41	15	19	1
81	41	12	21.5	1
74	43	15	19.5	1
68	39	15.5	18.5	1
80	39	15	20	1
65	37	13	18	2
65	30	10	17	2
54	30	9	17	2
69	34	11	18	2
72	41	13	19	2
78	35	12	18	2
71	33	11	17.5	2
69	38	13	19.5	1
77	44	17	21	1
90	46	16	20.5	1
83	48	18.5	20.5	1
79	49	21	22	1
91	47	18	20.5	1
87	45	17	20	1
66	39	19	18.5	1
74	42	14	19.5	1
82	42	14	19	1
89	44	17	20	1
81	46	17	21.5	1
69	38	13	19	1
60	27	8	17	2
66	33	10	18	2
79	35	11	18	2
74	41	13	18.5	2
63	37	12	18.5	2
81	46	15.5	20.5	2
66	36	12	19	2
71	33	11	18	2
62	32	10	17.5	2
57	25	8	17	2

The following tables contain the raw data used in chapter 5. In all of these tables a "." within a cell indicates missing data. the code under the column "sample" refers to a single vial of aphids. Every place where the sample code appears the data following was collected from the same vial of aphids. The tables are arranged in the following order:

Morphology: The first table contains the raw data for morphological features, and uses the same conventions described previously.

Hydrocarbon profiles: the total for each observation includes the value for the standard. The first part contains observations for the aphids. The second part contains the observations for the plants. The "num" column contains the number of aphids that were placed in the vial. Weight contains the weight of the aphids in the sample in mg. In this part, vials te138 and te139 were mixed during processing, thus the aphids and weight reflect the combined total. All hydrocarbon variables are listed by their equivalent chain lengths.

Fatty Acids: the total for each observation includes the value for the standard. Since the sample numbers in this table refer to the same samples used for epicuticular hydrocarbons, please refer to the previous section to obtain the host plant, number of aphids per vial, and weight of aphids in the vial. 17:0 was the standard. In this section te138 and te139 were kept separate. te138 had 100 aphids weighing 35.50mg, while te139 had 135 aphids weighing 52.31mg.

Morphology

host	length	tibia	cornicle	eye
melon	96	48	17	21.5
melon	83	50	17	22
melon	95	48	17	21.5
melon	69	47	17	21.5
melon	92	40	13	20
melon	94	50	19	22
melon	82	50	18	22
melon	89	48.5	20	22.5
melon	85	48	17	21.5
melon	76	50	17	22
melon	92	51	19	21.5
melon	88	54	20	22
melon	81	49	18	21.5
melon	88	48	18	21
melon	91	49	18	22.5
melon	93	49	19	22.5
melon	85	50	17.5	21.5
melon	80	50	19	22
melon	85	45	16	21.5
melon	85	48	18	22
squash	78	41	15	20
squash	95	44.5	16.5	21.5
squash	69	37	12	19.5
squash	85	41	15	20.5
squash	92	44	15.5	21
squash	85	38	14	19.5
squash	83	41	13	20
squash	83	39	13.5	19.5
squash	79	43	13.5	19.5
squash	85	39.5	13	20
squash	84	41	12.5	20
squash	86	39	13	19.5
squash	88	42	14	19.5
squash	97	46	16	21
squash	83	43	17	21
squash	80	41	15	19.5
squash	96	43	14	20.5
squash	92	42.5	14	20
squash	86	41	14	20
squash	86	41	15	20.5
cotton	124	53	21	24.5
cotton	111	56	21	23
cotton	112	58	22	23.5
cotton	113	56	21	23
cotton	128	56	22	23
cotton	107	55	21	23
cotton	122	54	21.5	23
cotton	111	54	21	22.5
cotton	112	55	21	22.5
cotton	112	56	22	23.5
cotton	108	55	22	22.5
cotton	123	55	22	23.5

cotton	98	52	21	22.5
cotton	99	45	16.5	20.5
cotton	108	55	22	22.5
cotton	119	53	21	22.5
cotton	109	55	17	23.5
cotton	115	56	22	23.5
cotton	116	54	21	22.5
cotton	113	59	22	24
wheat	87	37	14.5	19.5
wheat	77	36	13	19
wheat	77	35	13	19
wheat	70	38	15	19
wheat	81	37	14	19.5
wheat	85	35.5	13	18.5
wheat	74	37	14	19
wheat	77	36	13.5	19.5
wheat	82	41	16	20
wheat	75	37	14.5	19
wheat	79	40	14	19.5
wheat	83	35	13	19
wheat	81	38	14	19.5
wheat	62	33	12	18
wheat	77	35	12	18.5
wheat	85	33.5	12.5	19
wheat	83	37.5	14.5	19.5
wheat	70	37	14	19.5
wheat	87	34.5	14	19
wheat	73	36	13	19

Aphid Epicuticular Hydrocarbons

sample	Host	num	weight	gcsum	standard	24.8	26.9
te135	melon	102	40.34	362422	126921	24079	71192
te136	melon	100	37.74	135050	45112	9793	31014
te137	melon	44	17.75	103003	44404	5490	19796
te138+9	melon	235	87.81	624439	107733	92955	165970
te140	melon	107	40.04	262198	75906	33094	63084
te141	melon	113	42.85	244570	71489	27463	63152
te142	melon	106	42.42	306959	104229	33012	65338
te143	melon	110	41.76	456009	87912	63649	112404
te144	melon	103	42.51	305571	.	.	.
te125	cotton	115	38.80	169540	50409	8200	34196
te126	cotton	61	30.44	167592	80128	5623	20613
te127	cotton	103	61.20	90654	28628	8608	21113
te128	cotton	100	54.78	282480	88886	24647	60065
te129	cotton	149	94.56	390933	87642	32508	84659
te131	cotton	101	54.82	161631	51327	9727	31255
te132	cotton	108	48.43	700392	199334	38136	123386
te133	cotton	107	56.88	243439	71156	15450	48040
te134	cotton	123	71.11	430287	112672	27284	81851
te104	squash	106	35.20	159282	78520	5758	21351
te105	squash	100	34.16	146955	63769	4424	20679
te106	squash	114	38.75	151592	63238	6460	22003
te107	squash	103	38.22	130998	57942	4025	19684
te108	squash	100	37.85	154860	71242	4079	20484
te109	squash	138	44.88	108082	39907	3637	19786
te110	squash	111	35.20	156738	69982	4037	23188
te111	squash	118	42.94	130211	52700	3174	19643
te112	squash	113	39.75	319256	130401	7503	46190
te113	squash	110	33.02	136559	70580	5415	18512
te114	squash	110	31.80	111869	52543	6779	19634
te115	wheat	126	29.59	190560	53278	3774	21825
te116	wheat	100	27.43	104538	37028	4188	15708
te117	wheat	113	30.74	81727	22940	2265	11784
te118	wheat	105	27.17	128705	38683	3872	16422
te119	wheat	113	27.37	39071	12415	1350	6306
te120	wheat	102	22.47	75426	30594	3647	12286
te121	wheat	107	29.60	90913	28898	2750	12770
te122	wheat	110	29.44	153113	41872	4552	21217
te123	wheat	101	26.94	67650	24814	2165	10237
te124	wheat	116	31.01	161073	41228	4244	24019

sample	27.5	29.0	29.2	29.6	29.9	31.0	31.4
te135	9220	37889	8338	5200	4455	4551	11701
te136	2727	17520	2715	2462	1954	1827	3681
te137	2314	11318	2204	.	.	1251	3021
te138+9	12495	53755	19244	4453	7277	5369	20684
te140	4586	22046	6159	2662	2922	2341	7326
te141	3901	25197	4762	1697	2780	2943	6102
te142	6108	22754	8458	3555	3428	2220	8906
te143	1658	36873	14090	6031	5545	3944	15023
te144	.	.	.	.	.	.	.
te125	4214	30722	3448	2300	2696	4794	4679
te126	3930	23043	2361	3776	2289	3719	4309

194

te127	1870	13231	1966	.	.	1494	2779
te128	5161	39706	6211	2351	4094	4496	7643
te129	8272	55849	10396	3782	6524	6803	14055
te131	4686	25630	3411	2028	2682	3401	4834
te132	18965	110093	14928	10849	11206	15410	17955
te133	6603	37694	5668	2972	4191	4910	7235
te134	12916	64993	10619	5885	7557	8473	14828
te104	3957	13908	3552	.	2475	2187	5595
te105	4542	18546	3260	1679	2434	2829	4963
te106	5218	19135	3275	3094	2650	3006	4746
te107	4610	17343	2282	1764	2133	2484	3675
te108	5557	19525	2961	3169	2782	3606	4206
te109	3027	15949	1684	752	1591	2402	2669
te110	5592	22694	2191	2463	2428	3882	3772
te111	5229	19583	2397	3402	2356	3054	4138
te112	10121	47173	4985	6346	5219	7358	8667
te113	2851	12387	3199	.	2109	1866	3913
te114	2723	9595	2853	.	.	1173	2978
te115	5671	40144	3103	8239	3920	8972	5336
te116	1781	19913	2024	1325	1710	3599	2795
te117	3362	18864	1434	2914	1620	3834	2638
te118	4856	26403	2303	5509	2424	5501	3829
te119	1506	10118	.	1691	.	2273	1300
te120	2748	14038	1197	1845	.	2489	1752
te121	3685	19083	1665	3697	1654	3798	2469
te122	6005	33468	2610	5838	2746	6540	3718
te123	2422	16371	.	2664	1325	3147	1608
te124	5627	39475	2406	6342	3093	7555	3781

sample	33.0	35.2
te135	4234	5617
te136	1906	1913
te137	1319	1564
te138+9	3738	8026
te140	1822	2854
te141	2490	3061
te142	1770	4125
te143	3183	6371
te144	.	.
te125	4521	1985
te126	3963	1659
te127	1162	.
te128	3222	2262
te129	5274	4433
te131	2946	1698
te132	14000	8002
te133	4034	2563
te134	6838	5022
te104	1961	2115
te105	2514	2147
te106	2443	1996
te107	2203	1581
te108	2675	1797
te109	1944	1259

te110	3064	1527
te111	2503	1624
te112	6373	3245
te113	1342	1549
te114	.	1141
te115	9653	3128
te116	3332	1634
te117	3633	1272
te118	5088	1891
te119	2112	.
te120	2053	.
te121	3429	1537
te122	6120	2234
te123	2897	.
te124	7350	2091

Plant Hydrocarbon

Sample	Plant	Leaf	Standard	25.0	27.0	28.0
te59	squash	third	49500	.	64800	6370
te60	squash	second	141000	11400	83800	14000
te61	squash	cotyledon	106000	2120	26200	5130
te62	squash	third	157000	5080	117000	16900
te63	squash	second	130000	6050	50300	20900
te64	squash	cotyledon	105000	.	12100	5040
te65	squash	third	145000	19100	232000	37900
te66	squash	second	138000	9030	87400	17900
te67	squash	cotyledon	133000	.	19200	4970
te95	squash	second	49000	40400	276000	45700
te96	squash	cotyledon	49500	.	36800	8120
te97	squash	third	49600	7870	80100	19400
te98	squash	second	37100	5340	55800	15500
te99	squash	cotyledon	41300	.	28300	6840
te100	squash	third	38000	.	12500	.
te101	squash	second	52900	.	13500	.
te102	squash	cotyledon	41200	.	4750	.
te12	wheat		38800	19200	32200	0
te13	wheat		75800	42900	66100	0
te14	wheat		68900	39200	60000	0
te15	wheat		71000	22200	33300	0
te17	wheat		283000	11900	23800	0
te18	wheat		541000	65100	61100	0
te19	wheat		465000	75700	53000	0
te20	wheat		613000	38700	70700	0
te68	cotton	first	93400	7490	190000	60700
te69	cotton	second	157000	20829	454000	126000
te70	cotton	third	115000	27124	622000	154000
te71	cotton	fourth	135000	31739	695000	231000
te75	cotton	first	22800	.	29800	9230
te76	cotton	second	101000	6628	150000	67900
te77	cotton	third	32800	.	95300	43700
te78	cotton	fourth	25700	5803	97300	59900
te79	cotton	crown	55900	.	189000	77000
te80	cotton	first	26400	.	43900	22700
te81	cotton	second	21700	.	69800	24600
te82	cotton	third	27000	6441	162000	64300
te83	cotton	fourth	13100	7347	126000	35400
te84	cotton	crown	55900	7177	163000	90800
te51	melon	second	63800	.	15000	.
te52	melon	cotyledon	45200	.	16700	.
te53	melon	third	75900	.	15100	.
te54	melon	second	48800	.	6810	.
te55	melon	cotyledon	97700	.	18200	.
te56	melon	third	50300	.	11800	.
te57	melon	second	154000	12988	81400	.
te58	melon	cotyledon	51500	.	8360	.
te85	melon	third	51600	.	14700	.
te86	melon	second	48900	.	13500	.
te87	melon	cotyledon	28600	.	6610	.
te88	melon	third	47700	.	37700	.
te89	melon	second	37900	.	12800	.

te90	melon	cotyledon	36300	.	8120	.
te91	melon	third	43800	.	36500	.
te92	melon	second	25700	.	5100	.
te93	melon	cotyledon	39100	.	5500	.

Sample	29.2	30.1	31.4	32.2	33.2	34.1
te59	123000	18000	440000	56800	266000	16000
te60	242000	39700	949000	107000	518000	27600
te61	76500	25000	329000	39500	93700	4530
te62	262000	41200	849000	125000	521000	34000
te63	220000	44000	743000	103000	430000	35200
te64	87100	39400	494000	71400	128000	22100
te65	463000	80500	1820000	239000	1130000	68100
te66	281000	48500	1190000	164000	691000	88900
te67	76400	22700	354000	42100	102000	.
te95	823000	198000	2860000	356000	683000	18600
te96	234000	69300	969000	96800	158000	4920
te97	494000	186000	2910000	463000	951000	36400
te98	324000	115000	1540000	232000	415000	12400
te99	200000	58600	802000	75700	118000	.
te100	52500	12700	238000	30900	103000	6370
te101	66200	25900	289000	47400	86900	.
te102	41700	17700	194000	27300	43300	.
te12	19300	0	9660	0	13400	0
te13	41900	0	22100	0	34900	0
te14	38000	0	19900	0	31700	0
te15	24400	0	13800	0	23400	0
te17	16100	0	9570	0	16400	0
te18	47400	0	31200	0	31900	0
te19	40800	0	26600	0	27700	0
te20	39800	0	24700	0	41800	0
te68	966000	93700	744000	57700	68100	.
te69	1790000	173000	1140000	98200	127000	6883
te70	1860000	128000	1040000	101000	148000	6583
te71	2940000	247000	1730000	177000	330000	17900
te75	137000	19200	88000	7850	7370	.
te76	902000	106000	653000	49700	57400	.
te77	648000	62200	437000	37000	44500	.
te78	854000	93700	673000	61200	75900	.
te79	751000	42900	249000	13200	55800	.
te80	350000	43600	318000	27200	28000	.
te81	320000	35300	281000	25800	31000	.
te82	872000	70000	553000	47900	74100	.
te83	423000	31600	245000	20800	32500	.
te84	902000	53100	250000	13800	54100	2371
te51	14800	.	40000	.	20200	.
te52	16700	.	28200	.	6860	.
te53	22300	.	115000	.	68500	.
te54	8700	.	32000	.	15100	.
te55	18900	.	40400	.	11000	.
te56	15200	.	59000	.	39600	.
te57	46200	.	101000	8066	43500	.
te58	9200	.	22900	.	6090	.
te85	11000	.	40500	.	23100	.

te86	15000	.	63000	.	27800	.
te87	6370	.	19400	.	7610	.
te88	67100	.	347000	.	134000	.
te89	59300	.	404000	.	126000	.
te90	42400	.	216000	.	48000	.
te91	24000	.	45400	.	23900	.
te92	4590	.	15200	.	5970	.
te93	6930	.	14300	.	.	.

Sample	35.1	37.1
te59	49200	11400
te60	90200	22300
te61	10700	10000
te62	97000	28200
te63	88700	41100
te64	29600	22400
te65	214000	59300
te66	186000	107000
te67	11300	.
te95	35100	7480
te96	.	.
te97	65800	13500
te98	28300	6360
te99	2180	24300
te100	15800	.
te101	9590	.
te102	.	.
te12	0	0
te13	0	0
te14	0	0
te15	0	0
te17	0	0
te18	0	0
te19	0	0
te20	0	0
te68	4794	0
te69	10214	0
te70	11676	0
te71	35264	0
te75	.	0
te76	4220	0
te77	.	0
te78	5314	0
te79	10454	0
te80	.	0
te81	.	0
te82	4872	0
te83	.	0
te84	5673	0
te51	.	.
te52	0	.
te53	8326	.
te54	.	.
te55	0	.

te56	5560	.
te57	.	.
te58	0	.
te85	2730	.
te86	2550	.
te87	0	.
te88	11200	.
te89	8030	.
te90	0	.
te91	2850	.
te92	.	.
te93	.	.

Fatty Acids

sample	total	12:0	14:0	14:1	16:0	16:1	17:0
te103	36116	38	2205	20	27850	974	174
te104	67949	60	3173	48	51130	1563	464
te105	44902	42	1552	23	35150	911	269
te106	117998	53	3184	36	92900	2246	592
te107	373052	255	15570	249	276800	8460	2178
te108	87184	74	2800	40	66660	2143	432
te109	196783	103	7586	99	150900	5738	692
te110	62171	46	2031	28	48270	1659	297
te111	107870	61	4280	44	83080	2072	484
te112	212564	165	8120	123	161400	4988	854
te113	310174	316	22900	264	225000	7096	2134
te114	92656	82	4212	64	67260	2582	866
te115	89384	139	9968	61	64780	1612	460
te116	78567	238	11760	79	53840	1635	438
te117	55078	171	8136	34	38050	1068	241
te118	131724	513	23720	135	88500	2505	632
te118	86491	300	14700	89	60860	2090	336
te119	98050	400	19200	119	61030	1929	400
te120	71426	46	7808	36	51180	1287	494
te121	82016	265	14050	68	55920	1289	443
te122	565710	2061	101600	1491	366500	12380	3448
te123	103066	473	20790	210	68760	2096	588
te124	71219	227	11510	62	49140	1263	347
te125	35171	45	2380	19	26720	587	203
te125	50274	69	3270	29	37570	967	302
te126	62063	78	4703	64	43110	1495	412
te127	69297	124	8526	145	39780	1926	324
te128	155054	574	26670	227	104700	2938	777
te129	141125	237	17250	283	81320	3784	487
te130	66291	137	8190	115	44660	1977	249
te131	66123	122	6180	93	43040	2101	354
te132	55171	96	5025	69	36580	1522	304
te133	53546	25	3867	75	30590	1647	301
te134	26791	49	2802	46	16270	715	247
te135	266633	242	12380	232	209900	6814	1079
te136	169670	186	8734	164	129800	4677	668
te137	70948	57	2704	26	56290	1472	654
te138	62193	43	2894	52	46690	2052	288
te139	85616	81	4722	93	62630	2359	299
te140	72252	29	3276	68	50550	1745	468
te141	78716	61	3769	52	60480	1413	269
te142	128129	86	6247	116	96320	3740	561
te143	56162	63	2501	38	42600	1363	243
te144	63842	46	3381	62	45740	1413	382
te144	25102	19	1528	24	19050	688	115

sample	18:0	18:1	18:2	18:3	20:0
te103	1590	1647	1168	179	154
te104	3795	3897	2718	445	503
te105	2236	2442	1745	244	223
te106	6912	6184	3872	531	875
te107	21450	23470	16420	2799	3057

te108	4666	4985	3519	559	494
te109	10620	11590	6996	1019	1234
te110	3303	3516	2191	318	318
te111	6366	6179	3829	597	738
te112	12100	12890	7876	1189	1439
te113	16970	16930	13760	2484	2320
te114	4719	6110	4910	841	672
te115	3689	3018	3648	664	630
te116	3105	2730	3400	596	510
te117	2152	1991	2405	445	361
te118	4797	3718	4272	834	838
te118	2349	2041	2380	390	246
te119	3069	2766	3294	608	473
te120	3390	2768	3175	573	608
te121	3316	2625	2906	505	558
te122	19360	20060	24500	4882	3656
te123	3293	2669	3089	540	477
te124	2845	2251	2510	420	491
te125	1580	1330	1735	297	261
te125	2498	2093	2582	437	422
te126	3198	3242	4188	756	586
te127	4426	5190	6472	1150	961
te128	5795	4587	5265	948	1024
te129	8504	10020	13070	2554	1949
te130	2760	2990	3884	692	395
te131	3277	3896	5211	988	533
te132	2995	3098	3998	730	545
te133	3886	4569	6228	1270	873
te134	1546	1815	2379	476	269
te135	10760	10160	10850	2045	1556
te136	6396	6794	7558	1314	874
te137	2839	2614	2984	521	415
te138	2514	2815	3550	684	300
te139	4129	4323	5013	1020	676
te140	4303	4444	5323	1143	821
te141	3521	3677	3985	725	532
te142	5657	6096	6588	1299	828
te143	2512	2444	2944	545	376
te144	3686	3519	4067	861	633
te144	1094	1031	1194	227	128

The following is the raw data used in analysis of the RAPD-PCR results. There were a total of 50 scored bands: 13 from A09, 5 from C10, 9 from C01, 11 from C04, 9 from C09, and 3 from B1. The bands are listed in the order they appear in the data set. Bands are listed from large fragments to small fragments. First I will provide a listing of the program to generate the distance matrix. The program is a modified version of a program to compute jaccard distances which is provided in SAS/STAT documentation 4th edition version 6.0 in the chapter on proc cluster.

```
data dissimp (type=distance);
obs=40;
var=50;
array dj(*)dj1-dj40;
retain dj1-dj40 .;
do row=1 to obs;
set gossypii point=row;
array grounds(*) a1-a50;
array save(*) save1-save50;
do g=1 to var;
save(g)=grounds(g);
end;
do col=1 to row;
set gossypii (drop=t) point=col;
num=0; den=0; tty=0;
do g=1 to var;
num=num+(grounds(g) & save(g));
if (grounds(g)=0 & save(g)=0) then tty=tty+1;
den=den+(grounds(g)|save(g));
end;
dj(col)=1-(num+tty)/40;

end;
output;
end;
stop;
keep t dj1-dj40;
run;
proc print data=dissimp (obs=8);
id t; var dj1-dj40;
run;
proc cluster data=dissimp method=average pseudo;
id t; var dj1-dj40;
run;
```

```
s 0  0011111110111101111010011010010011001111111111011101
s 1  0011011110111101110110001010010011001111111111011101
s 2  0011011110111111111010011010010011101111111111011101
s 3  0011011110101101110110001010010111001111111111011101
s 4  0111111111111111110010011010010011101111010000010111
s 5  0011111111101111111010011010010011101111010000010111
s 6  0011111111101111111010011010010011101111010000010101
s 7  0011111111111100111101001101001001101111101000010101
s 8  0111111111111111111010011010010011101111010000010111
s 9  0111111111111111111010011010010011101111111111011111
m 0  0010011010101101110111011010010011101111111111011101
m 1  0011011111101111111111111010010011101111111111011101
m 2  0110111110101111111111111010010011101111111111011111
m 3  0111111111101111111111111010010011101111111111011111
m 4  0011011110101101110111011011010011101111010000010101
m 5  0011011110101101110111011011010011101111010000010101
m 6  0011011110111101110111011010010011101111111111011101
m 7  0011011110111111110111011010010011101111010000010101
m 8  0011111111111101111111111010010011101111010000010101
m 9  0010011111111011101110110110100111011111111110111111
c 0  0111011000111111110111001110010111111111101111011101
c 1  0011011000111111110111001110010111111111101111011101
c 2  0111011000111111110111001110010111111111101111011101
c 3  0111011000111111110111000111001011111111110111101101
c 4  0111011000111111110100001110010111111111101111011101
c 5  0111011000111111110111001110010111111111101111011101
c 6  0111011000111111110111001110010111111111101111011101
c 7  0111011000111111110111001110010111111111101111011101
c 8  0011011000111001110000001110010111111111101111011101
c 9  0111011000111111110111001110010111111111101111011101
w 0  1001011101011111111111011101011111101111010101011101
w 1  1001011100111111111111001111011111110111101010101011101
w 2  1001011100111111111111101111011111110111101010101011101
w 3  1001011100111111111111101111011111110111101010101011101
w 4  1001011100111111111111101111011111110111101010101011101
w 5  1001011100111111111111101111011111110111001010101011101
w 6  0001011100111111111111101111011111110111101010101011101
w 7  1001011100111111111111101111011111110111101010101011101
w 8  1001011100111111111111101111011111110111001010101011101
w 9  0001011100111111111111101111011111110111101010101011101
```

The following table contains the raw data for chapter 6.

Time: The time period during which the sample was collected. 1 is for late summer, and 2 is for early spring.

Color: 1 is yellow, 2 is green, 0 is unrecorded.

Weight is aphid weight in mg

Nymph is average number of nymphs produced per day over a seven day period.

ln is the length of the aphid. divide by 60 to convert to mm

wd is the width of the aphid. divide by 60 to convert to mm

ht is the height of the aphid. divide by 60 to convert to mm

tibia is the length of the metathoracic tibia. divide by 60 to convert to m m

corn is the length of the cornicle. divide by 60 to convert to mm

eye is the maximum distance between outer margins of the compound eye. divide by 60 to convert to mm

host	weight	larvae	ln	wd	ht	tibia	corn	eye	color	time
melon	31.800	7.167	90	48	40	41	16	18.5	0	1
melon	29.250	7.000	82	49	36	34	12.5	18	0	1
melon	34.800	7.143	88	50	39	40	15	19.5	0	1
melon	14.786	3.143	70	40	28	30	8	17	0	1
melon	31.714	6.286	90	47	38	39	14.5	19	0	1
melon	22.571	5.143	74	43	32	31	11	16.5	0	1
melon	29.286	6.667	85	46	35	34	12	18	0	1
melon	4.8750	4.429	56	29.5	20	25	7	16	2	1
melon	19.286	5.000	83	44	32	38	16	19.5	1	1
melon	17.063	4.571	78	43	32	45	16	20	1	1
cotton	14.938	2.571	61	40	27	23	7	15	2	1
cotton	10.625	2.000	61	35	25	25	6	15	2	1
cotton	5.7920	2.571	49	29	19	21	5.5	14	2	1
cotton	12.830	2.571	65	38	28	28	8	15.5	2	1
cotton	11.950	2.000	62	38	27	24	6	15	2	1
cotton	8.2083	2.286	57	37	25	22	6	14	2	1
cotton	4.1667	2.571	47	29	16	23	6.5	14.5	2	1
cotton	19.000	4.286	68	44	30	27	7.5	16	2	1
wheat	14.500	2.143	66	37	30	29	10	17	2	1
wheat	12.808	2.429	66	35	29	28	9	16	2	1
wheat	19.050	3.571	79	40	34	31	11.5	17	1	1
wheat	9.1250	2.714	59	35	24.5	28	9	15	2	1
wheat	12.750	3.000	64	36	27	27	9	16	2	1
wheat	18.400	2.571	71	39	31	29	9.5	16.5	2	1
wheat	12.792	4.000	67	38	27	30	10	16.5	2	1
squash	16.423	3.857	73	43	30	35	13	18	1	1
squash	8.7000	2.714	62	33	24.5	31	9.5	17	1	1
squash	20.438	4.000	78	42.5	34	40	14	19	1	1
squash	26.500	5.286	85	45	35	45	17.5	20	1	1
squash	31.750	5.000	84	46	34	43	17	20.5	1	1
squash	24.300	5.000	83	43	32.5	37	13	18.5	1	1
squash	22.500	4.714	80	44.5	32	43	14	19.5	1	1
cotton	12.778	2.571	58	37	27	21	6	14	2	1
cotton	8.0909	2.000	56	32.5	24	23	5.5	15	2	1
cotton	7.7500	1.429	49	28	24	18	5.5	13	2	1
cotton	34.750	10.14	83	55	36	31	11	19	2	1
cotton	5.3333	1.521	50	30	23	19	6	13.5	2	1

205

melon	32.857	6.429	87	47.5	36.5	40.5	14	19.5	1	1
melon	17.063	2.286	68	36	29.5	26	8.5	16	1	1
wheat	18.500	3.714	71	39	30	31	11	16	2	1
wheat	13.786	2.857	72	35	28	32	11	18	1	1
wheat	21.875	3.857	78	41	35	32	12	19	2	2
wheat	22.250	4.714	78	48	33	31	11	18.5	2	2
wheat	19.200	4.143	80	42	34	30	10	18.5	1	2
wheat	16.938	3.714	67	37	28	24.5	7	15.5	2	2
squash	32.188	7.000	85.5	51	41	35	11	18	2	2
squash	29.875	2.428	80.5	50	36	39.5	11	19	1	2
wheat	14.000	3.429	62	37	29	21.5	7	15	2	2
wheat	11.944	3.143	61	37	28	26	7.5	14.5	2	2
wheat	20.813	3.857	72	40	33	27	9	16.5	2	2
squash	39.125	5.571	87	52	40	39	10.5	19.8	2	2
wheat	16.813	3.143	66	38	27.5	26	7.5	15.5	2	2
squash	32.222	5.857	83	51	38	36	10	18	2	2
squash	37.500	4.571	86	48	38.5	37	10.5	19	1	2
cotton	52.500	8.143	95	57.5	44	44	13	21	1	2
cotton	61.500	8.000	99.5	60	42	41.5	16	21.5	1	2
cotton	57.000	9.875	101	57	43	48.5	17	22	1	2
cotton	51.438	9.143	98	58	40.5	47	18	22	1	2
cotton	45.375	7.710	98	55.5	41	46	18	22	1	2
cotton	66.045	9.222	107	64.5	44	53	20	22.5	1	2
melon	34.167	8.143	85	54	34	45	16.5	20	1	2
melon	43.100	8.143	90	53	41	46	16	20.5	1	2

The following table contains the raw data for chapter 7. The table is divided into three parts. The first part contains the data for the progeny wasps. The second part contains the available data for the male parent, and the third table contains the available data for the female parent. All entries are associated by the code in the first column where the first number identifies the source colony, the second number identifies the current host system, and the last number identifies the cage. 1=*A. gossypii* on watermelon. 2=*A. gossypii* on wheat. 3=*S. graminum* on wheat. A few odd numbers appear for cage. This is because a few *A. gossypii* were found to contaminate the *S. graminum* colony. As a result, the actual data are given as the first two numbers, but the intended first two numbers have been inserted in front of the cage number. Thus, 3-2-334 would represent a wasp from the greenbug colony that remained in the greenbug colony, but which parasitized a melon aphid.
Note: the code used to link sections is the identifying code for the female parent.
Note: in general, periods indicate missing values.

The following codes are used to identify the contents of each column:
from-to-cage: is the code for source, "treatment" and replicate for female wasps
G: is the gender of the progeny wasp
Weye is the maximum width between outer margins of the compound eye of the wasp. Divide the number by 200 to get length in mm.
Wfem is the length of the wasp's metathoracic femur. Divide the number by 200 to get length in mm.
Eye is the maximum width between outer margines of the compound eye of the mummy. Divide by 60 to get length in mm.
Tibia is the length of the metathoracic tibia of the mummy. Divide by 60 to get length in mm.
Cornicle is the length of the cornicle of the mummy. Divide by 60 to get length in mm.
Length is the length of the aphid mummy. Divide by 60 to get length in mm.
Exit is the position of the exit hole. 1=hole is above the left cornicle, 2=hole is above right cornicle, 3=hole encompases left cornicle, 4=hole encompases right cornicle, 5=hole is centered between cornicles and may encompas both cornicles.
Stage is the aphid stage of the mummy. 1=adult alate, 2=adult apterous, 3=nymph.
mfrom-mto-mcage has a similar set of codes as "from-to-cage" but is for male wasps. Periods in this section indicate that there is no difference between male and female wasps.
mey is the maximum distance between the outer margins of the eye of the male parent. Divide by 200 to get length in mm.
mfe is the length of the metathoracic femur of the male parent. Divide by 200 to get length in mm.
mti is the metathoracic tibia of the male parent. Divide by 200 to get length in mm.
mae is the maximum distance between the outer margins of the eye of the mummy of the male wasp. Divide by 60 to get distance in mm.
mat is the metathoracic tibia of the mummy of the male wasp. Divide by 60 to get distance in mm.
mac is the cornicle of the mummy of the male wasp. Divide by 60 to get distance in mm.

mal is the length of the mummy of the male wasp. Divide by 60 to get distance in mm.

max is the exit hole code for the male wasp.

mas is the stage of the aphid mummy for the male wasp.

feye is the distance between the outer margins of the compound eye of the female parent wasp. Divide by 200 to get distance in mm.

ffemur is the length of the metathoracic femur of the female parent wasp. Divide by 200 to get distance in mm.

ftibia is the length of the metathoracic tibia of the female parent wasp. Divide by 200 to get distance in mm.

faeye is the maximum distance between the outer margins of the compound eye of the mummy for the female parent wasp. Divide by 60 to get distance in mm.

fatib is the length of the metathoracic tibia of the mummy for the female parent wasp. Divide by 60 to get distance in mm.

facorn is the length of the cornicle of the mummy for the female parent wasp. Divide by 60 to get distance in mm.

falen is the length of the body length of the mummy for the female parent wasp. Divide by 60 to get distance in mm.

fax is the code for the exit hole of the female parent wasp.

fas is the code for the stage of aphid mummy from which the female parent emerged.

ffrom-fto-cage	G	weye	wfem	eye	tibia	cornicle	length	exit	stage
1-1-8	f	85	64	18	25	8.5	79	5	3
1-1-8	f	82	57	18	23	8	72	4	3
1-1-8	f	84	65	20	28	9	80	2	3
1-1-8	f	82	63	17.5	24	8	75	3	3
1-1-8	f	81	59	17	24	9	75	5	2
1-1-8	f	74	53	16	19	7	65	5	3
1-1-8	f	79	57	17	19	7.5	74	4	3
1-1-8	f	85	63	15	27	10	83	5	2
1-1-8	f	80	57	17.5	19	6.5	72	2	3
1-1-8	f	79	55	16	18	5.5	67	5	3
3-1-13	f	67	42	15.5	30	6	73	2	1
3-1-13	f	65	41	16	28	8.5	61	5	2
3-1-13	f	71	49	19	32	12	74	5	2
3-1-13	f	68	47	17	26	9	68	3	2
3-1-13	f	77	55	19	30	10	78	5	2
3-1-13	f	64	41	18	31	11	65	5	3
3-1-13	f	73	51	16.5	28	9.5	71	5	2
3-1-13	f	78	53	16.5	28	9	78	5	2
3-1-13	f	67	44	18.5	32	11	73	5	2
3-1-13	f	83	60	18	22	9	77	3	3
3-3-9	f	94	69	22	47	16	108	3	2
3-3-9	f	93	67	22	38	13	95	5	3
3-3-9	f	98	74	22	49	17.5	112	5	2
3-3-9	f	80	50	20	45	12	100	6	1
3-3-9	f	93	67	19	38	11.5	90	5	3
3-3-9	f	92	69	20	33	12.5	88	5	3
3-3-9	f	93	65	21.5	43	14	116	3	2
3-3-9	f	97	72	21	47	17	107	5	2
3-3-9	f	87	65	19	35	11	89	5	3
3-3-9	f	92	69	21	39	15	100	5	2
1-3-5	m	80	56	20	35	12.5	90	4	3
1-3-5	m	75	55	19.5	38	13	90	5	3
1-3-5	f	78	53	16.5	25	9	75	5	3
1-3-5	f	86	62	20	41	16	98	3	2
1-3-5	m	83	62	19	32	11	85	3	3
1-3-5	m	81	61	21	39	12	87	4	3
1-3-5	f	81	59	19.5	36	12	86	4	3
1-3-5	m	81	55	20.5	38	14	94	4	3
1-3-5	f	84	63	20	39	14	87	4	3
1-3-1	m	76	55	21	33	13	89	5	3
1-3-1	f	77	58	21	47	13	105	3	1
1-3-1	f	78	60	20	34	12	86	4	3
1-3-1	f	83	58	20.5	37	15	95	3	2
1-3-1	f	81	64	18	29	10.5	84	4	3
1-3-1	m	71	52	18	29	11.5	72	4	3
1-3-1	f	75	55	17	21	7.5	77	4	3
1-3-1	f	92	69	20.5	41	15	110	4	2
1-3-1	f	84	64	19	35	13	90	5	3
1-3-1	f	78	59	19	30	12	77	3	3
1-3-1	f	77	56	20.5	37	13	96	5	2
1-3-1	f	83	65	20.5	32	13	86	1	3

1-3-1	f	72	50	17	21	8	67	5	3
1-3-1	m	90	69	20	41	14	100	4	2
1-3-1	f	81	59	18	30	11	84	4	3
1-3-1	m	75	54	17	25	9	74	3	3
1-3-1	f	76	58	18	26	10.5	80	3	3
1-3-1	f	83	62	21	39	12.5	103	5	2
1-3-1	f	81	61	19	38	15	99	4	2
1-3-1	m	78	57	21	38	15	95	6	2
3-3-5	m	74	55	20	35	12	86	5	3
3-3-5	m	79	57	19.5	29	9	81	4	3
3-3-5	m	82	61	21	33	10	82	3	3
3-3-5	m	82	63	20	33	12	90	5	3
3-3-5	f	86	62	21	34	12	85	5	3
3-3-5	f	92	69	21	41	16	108	5	2
3-3-5	m	79	62	19.5	36	11	80	5	3
3-3-5	m	77	58	20	32	11.5	84	5	3
3-3-5	m	76	51	19	27	8	80	4	3
3-3-5	f	95	72	21.5	41	16.5	109	3	2
1-3-4	f	95	72	21	42	16.5	118	3	2
1-3-4	f	81	59	17	35	13	80	5	3
1-3-4	f	84	61	19.5	33	12	86	5	3
1-3-4	f	91	70	20.5	40	13	96	5	3
1-3-4	f	87	65	20	41	12	94	5	3
1-3-4	f	91	68	19	37	13	95	5	3
1-3-4	f	82	59	20	37	14	88	3	3
1-3-4	f	83	61	19.5	37	13	86	5	3
1-3-4	f	84	61	17	36	13	87	3	3
1-3-4	f	96	74	19.5	37	13	96	5	3
1-2-5	f	79	55	15	21	7	73	5	3
1-2-5	f	75	53	15	27	10	77	3	2
1-2-5	f	72	50	17	22	8	71	4	3
1-2-5	f	75	54	17	24	8	76	3.5	3
1-2-5	f	76	53	18	31	13	84	5	2
1-2-5	f	80	55	17.5	28	10	82	3.5	2
1-2-5	f	76	54	16	21	6.5	71	3	3
1-2-5	f	75	51	18	31	11	81	3	2
1-2-5	f	74	52	16	25	10	80	4	2
1-2-5	f	69	49	15	22	7	68	3	3
3-1-4	f	67	41	17.5	27	8	66	5	2
3-1-4	f	77	56	18	29	9.5	74	2	2
3-1-4	f	82	58	17	27	9.5	78	1	2
3-1-4	f	79	56	19.5	32	12	83	4	2
3-1-4	m	63	36	17	27	8	61	5	2
3-1-4	m	74	54	18	34	12	90	5	2
3-1-9	f	79	55	17	28	9.5	70	4	2
3-1-9	f	71	49	15	20	7.5	60	3	3
3-1-9	f	84	58	17.5	20	8	73	4	3
3-1-9	m	72	50	19	29	9	74	3	2
3-1-9	f	75	47	16	33	6.5	70	6	1
3-1-9	f	76	50	15	16	6	64	4	3
3-1-9	m	73	52	17	19	5	64	3	3
3-1-9	f	67	45	16	19	6	59	3	3
3-1-9	f	84	58	18	20	8	72	5	3
3-1-9	f	82	58	17	29	11.5	80	3	2

3-1-9	m	75	54	17	19	7	70	4	3
3-1-8	f	76	51	.	.	.	.	.	.
3-1-8	f	78	51	15	20	7	72	4	3
3-1-8	f	80	57	17	20	7.5	70	5	3
3-1-8	f	81	54	16	25	7.5	73	4	2
3-1-8	f	85	60	18	24	8	76	5	2
3-1-8	f	69	46	17	23	8	65	3	2
3-1-8	f	87	62	17	25	10	82	2	2
3-1-8	m	75	49	17.5	36	8	84	6	1
3-1-8	m	70	46	16	20	8	63	5	2
3-1-8	f	70	45	17	35	8	78	6	1
3-1-11	f	80	55	17.5	25	10	78	3	2
3-2-9	m	75	54	17	24	7.5	69	5	3
3-2-9	f	80	57	15.5	28	9.5	78	3	2
3-2-9	m	77	52	17.5	27	10	76	3	3
3-2-9	m	72	47	15	27	9	71	2	2
3-2-9	m	67	48	15	26	10	65	4	2
3-3-7	f	86	61	20.5	41	16	89	4	2
1-1-2	m	70	52	15	27	9	68	5	3
1-1-2	m	80	60	17	27	9.5	81	4	2
1-1-2	m	62	42	16	18	5.5	55	6	3
3-2-7	f	74	50	15	20	8	65	4	3
3-2-7	f	74	51	17	25	8.5	70	4	3
3-2-7	f	79	55	16	23	7	72	4	3
3-1-5	f	88	69	20	30	10	80	1	3
3-1-5	f	87	65	18	35	14	81	1	2
3-1-5	f	66	43	15	25	14.5	66	4	2
3-1-5	f	94	70	19	35	14	91	4	2
3-1-5	f	80	62	17.5	20	8	70	5	3
3-3-8	f	90	70	20	37	12	93	3	3
3-3-8	f	92	69	22	48	17	105	4	2
3-3-8	f	82	57	21	44	13	99	6	1
3-3-8	f	96	70	20	39	12	94	3	3
3-3-8	f	91	64	23	44	15	101	5	2
3-3-8	f	96	74	23	47	18	109	4	2
3-3-8	f	94	70	19.5	34	13	92	3	3
3-3-8	m	75	52	18	33	12	73	4	3
3-3-8	f	80	55	21	39	14	82	4	2
3-3-8	f	79	53	18	33	13	79	4	3
3-3-8	f	83	59	20	27	9	78	5	3
3-3-8	f	90	66	21	34	12	89	4	3
3-3-8	m	86	59	19	34	12	87	5	3
3-3-8	m	87	62	22	47	16	109	5	2
3-3-8	m	82	54	19.5	30	11	82	3	3
3-3-8	f	87	65	21.5	41	15	102	3	2
3-3-8	f	91	70	23.5	47	17	107	4	2
3-3-8	f	84	61	18	28	10	82	3	3
3-3-8	f	84	62	22.5	45	18	97	3	2
3-3-8	f	87	64	20	35	12	86	5	3
3-1-10	f	83	59	17	20	7	73	5	3
3-1-10	m	82	62	19	29	10.5	87	3	2
3-1-10	f	77	56	17	25	7.5	71	5	3
3-1-10	m	82	60	19	24	8.5	76	5	3
3-1-10	m	67	45	14	24	7	63	4	2

211

3-1-10	f	58	40	14	23	8	57	5	2
3-1-10	f	88	68	17	30	11	80	5	2
3-1-10	f	81	61	17.5	27.5	9.5	80	5	2
3-1-10	f	78	58	16.5	29	9	88	4	1
3-1-10	m	68	45	15	18	5.5	61	4	3
3-1-10	m	75	54	15	27	8	72	5	2
3-1-10	f	80	59	18.5	26	10	77	5	2
3-1-10	m	80	59	19	28	11	84	4	2
3-1-10	f	91	68	18	25	9	80	4	3
1-2-10	f	72	51	16	24	9	74	5	3
1-2-10	m	77	54	17	25	9	75	5	3
1-2-10	f	67	40	14	17.5	6	67	6	3
1-2-10	m	73	48	16	20	6.5	70	5	3
2-2-10	f	79	50	17	28	11	76	3	2
2-2-10	m	75	50	16	28	8.5	70	4	2
1-1-8	m	79	60	16	28	9	78	3	2
1-1-8	m	73	55	16	25	9	71	5	2
1-1-8	m	79	61	17.5	23	9	80	2	2
1-1-8	m	75	54	16	21	7.5	66	2	3
1-1-8	m	78	58	17.5	21	7	68	2	3
1-1-8	m	84	62	17.5	27	10	80	5	2
1-1-8	m	75	52	17	20	6.5	67	5	3
1-1-8	f	81	60	15.5	29.5	9	73	1	2
1-1-8	m	75	56	18	19	7	71	1	3
1-1-8	f	78	56	16.5	19	6	66	2	3
1-1-8	m	80	62	17	27	11	76	5	2
1-1-8	f	77	55	14	23	7.5	72	4	2
1-1-8	m	78	58	17	22	7.5	71	5	3
3-1-1	f	77	52	18.5	25	9	71	5	3
3-1-1	f	87	60	17	21	6.5	69	5	3
3-1-1	f	84	56	17.5	33.5	9	82	3	1
3-1-1	f	84	56	18	35.5	8	90	1	1
3-1-1	f	87	62	19	22	6	73	5	3
3-1-1	f	86	62	19.5	33	11.5	85	3	2
3-1-1	m	88	64	19	25	9	79	1	3
3-1-1	f	86	60	17.5	21	7	71	5	3
3-1-1	f	89	60	18	30	9	85	4	2
3-1-1	f	91	66	18	25	8.5	80	1	3
3-1-1	f	80	54	15	24.5	8.5	70	4	2
3-1-14	f	67	45	15	26	8	61	5	3
3-1-14	f	87	62	19	34.5	10.5	92	3	1
3-1-14	f	80	58	15	27	9	73	5	2
3-1-14	f	75	50	17.5	20	5	61	4	3
3-1-14	f	72	48	14	24	7	68	5	2
3-3-8	f	87	66	22	46	16	94	5	2
3-3-8	f	89	65	17	30	10	84	4	3
3-3-8	f	93	66	22	45	17	110	4	2
3-3-8	f	83	63	22	44.5	15	90	5	2
3-3-8	f	86	66	23	46	16	99	3	2
3-3-8	f	86	64	22	46	16	101	5	2
3-1-12	f	83	59	16	18	6	71	4	3
3-1-12	f	87	66	16	28	9	78	5	2
3-1-12	f	89	67	16	29	11	82	5	2
3-1-12	f	89	69	19.5	30.5	9.5	79.5	2	3

3-1-12	f	88	66	19	28	13.5	87	5	2
3-1-12	f	90	70	19.5	33	13	96	5	2
3-3-4	f	85	61	21	35	13	87	5	3
3-3-4	f	82	68	21	35	14	85	5	3
3-3-4	f	94	70	21.5	39	16	105	5	2
3-3-4	f	75	50	19	27	10	75	5	3
3-3-4	f	92	70	22.5	47	18	108	4	2
3-3-4	f	79	62	19	32	12	80	5	3
3-3-4	f	88	64	21.5	38	13.5	89	3	3
3-3-4	f	89	65	20.5	38.5	13	88	5	3
3-3-4	f	89	67	22	38	13	89	2	3
3-3-4	f	89	63	18.5	40	13	86	5	3
3-3-1	f	91	62	20.5	40	15.5	107	5	2
3-3-1	f	90	68	19.5	42	15	98	3	3
3-3-1	f	84	60	18	35	12	76	4	3
3-3-1	f	80	58	17	33	11	77	4	3
3-2-1	f	84	61	17.5	35	11	90	5	2
3-3-1	m	73	48	15.5	32.5	12	77	5	3
1-3-2	f	91	69	20	34	13	91	3	3
1-3-2	f	89	67	19.5	40	15	103	4	2
1-3-2	f	87	64	18	34	12	84	5	3
1-3-2	f	90	70	21	39	16	97	4	2
1-3-2	f	90	66	19	36	13	95	5	3
1-2-132	f	78	57	17	35	9.5	82	5	2
1-3-2	f	91	68	20	36	11	100	5	3
1-3-2	f	84	63	19	28	9	83	5	3
1-3-2	f	88	63	20	38	14	95	5	2
1-3-2	f	81	57	21.5	43	13.5	105	3	1
1-2-6	f	67	45	17	27	9.5	65	5	3
1-2-6	f	73	52	17	32	9	81	3	2
1-2-6	f	73	52	16	29	9	80	3	2
1-2-6	f	80	57	17	26	9	72	4	3
1-2-6	f	69	48	16	26	9.5	70	4	2
3-1-13	f	71	46	16.5	29	8	64	4	2
3-1-13	m	84	61	17	25.5	9	61	5	2
3-1-13	f	74	51	20.5	36	12.5	74	5	2
3-1-13	f	77	55	18	30	11	77	3	2
3-1-13	m	60	39	14	17.5	5	54	5	3
3-3-2	f	99	77	22	43	17	106	5	2
3-3-2	f	92	68	16	35	10	85	5	3
3-3-2	f	87	64	22	32	12	84	4	3
3-3-2	f	91	69	21.5	35	11.5	91	3	3
3-3-2	f	95	79	21	39.5	15	107	5	2
3-3-2	f	92	68	20.5	35	12	92	5	3
3-2-332	f	82	53	16.5	27	9.5	75	4	2
3-3-2	f	91	66	20	34	12	95	5	3
3-2-332	f	87	64	19.5	33.5	13	82	5	2
3-3-6	f	94	67	21.5	43	16	106	5	2
3-3-6	f	91	65	22.5	37	13	90	5	3
3-3-6	f	90	64	21	35	12	89	5	3
3-3-6	f	96	67	22.5	48	18	104	4	2
3-3-6	f	97	71	24	48	17	110	5	2
3-3-6	f	82	56	20.5	34	13	82	3	2
3-3-6	f	80	57	17.5	35	12	75	5	3

3-3-6	f	93	65	20.5	39	13	96	5	3
3-3-6	f	86	54	20	45	12	94	3	1
3-3-6	f	90	66	20	32	15.5	101	5	2
1-3-8	m	88	61	21	49	14	100	5	1
1-3-8	f	89	64	17	40	15.5	85	5	2
1-3-8	m	75	51	18.5	37	14.5	90	5	2
1-3-8	m	83	62	18.5	35	12	95	4	3
1-3-8	f	87	64	21	41	17	90	5	2
1-3-8	f	85	62	15	30	11	81	5	3
1-3-8	f	96	73	20	42	14	111	5	2
1-3-8	m	79	58	20.5	32	12	86	5	3
1-2-134	m	81	59	18.5	39.5	8	81	3	1
1-3-4	m	.	.	20.5	48	12	101	1	1
1-3-4	m	79	65	20	34	12	87	5	3
1-2-134	m	.	57	17	32	11	77	5	2
1-3-4	m	76	61	21	50	12	99	5	1
1-3-4	m	83	65	19	36	13	94	3	3
1-2-134	m	67	47	18.5	42	8	86	1	1
1-2-4	m	83	63	22	39	13	94	5	3
1-3-4	m	87	69	22.5	44	17	110	3	2
1-3-4	m	79	57	18.5	36	13	88	1	3
1-3-4	f	.	57	18.5	25	10	78	5	3
1-3-4	m	85	66	19	35	12	90	5	3
1-2-134	f	77	54	16.5	22	7.5	65	2	3
1-2-134	m	76	57	18.5	39	12	84	3	2
1-3-4	m	85	63	18.5	36.5	13	90	5	3
1-3-4	m	80	59	18.5	29	9	81	5	3
1-3-4	m	72	53	18	34.5	12	77	5	3
1-3-4	m	87	67	21	46	17	110	3	2
1-3-4	m	80	62	19	37	13	87	5	3
1-2-134	m	72	52	17	25.5	8	72	5	3
1-3-4	m	79	56	19	36	13	94	4	2
1-3-4	m	87	69	20	43	16	103	4	2
1-3-4	m	85	64	20.5	41	15	107	3	2
1-3-4	m	81	60	21	38	13.5	91	5	3
1-3-4	m	80	62	19	37	14	89	5	3
1-3-4	m	78	58	21	35	13	91	4	3
1-2-134	f	69	47	17.5	23	8	68	5	3
1-3-4	m	77	55	19	34.5	13.5	90	4	3
1-3-4	m	90	66	21.5	46	17	115	5	2
1-3-4	m	79	57	18.5	27	9	83	4	3
1-3-4	m	88	68	18	36.5	13	88	5	3
1-3-4	m	89	68	23	45	16	110	4	2
3-3-9	m	82	60	21	43.5	17	108	3	2
3-3-9	f	96	72	20.5	37	12.5	95	3	3
3-3-9	f	95	71	22	43	17	106	3	2
3-3-9	m	87	64	20.5	39	15	99	4	2
3-3-9	m	90	70	23.5	48	16	104	3	2
3-3-9	m	91	68	20.5	36	13	89	4	3
3-3-9	m	84	65	21.5	38.5	13	87	4	3
3-3-9	m	87	64	18.5	38	13	82	3	3
3-2-332	m	73	49	18	24	8	64	4	3
3-3-2	f	.	68	21	35	12	89	3	3
3-3-2	f	98	70	20.5	42	15	104	5	2

214

3-3-2	f	88	62	19.5	35	13	86	5	3
3-2-332	f	75	51	18.5	34	10	76	5	2
3-2-332	m	79	57	17	34	10	78	3	2
3-3-2	f	92	69	21.5	39	15	98	5	2
3-2-332	f	84	60	18.5	28	10	78	5	3
3-3-2	f	88	65	19	36	12	84	5	3
3-2-332	f	83	55	19.5	41	13	79	5	2
3-3-2	f	95	72	21.5	44	16	102	4	2
3-2-332	f	77	54	17	23	7	68	3	3
3-3-2	m	87	66	21	35	11	85	4	3
3-3-2	f	88	65	18	34	12	83	5	3
3-3-2	m	82	61	20	37	13	96	5	2
3-3-2	m	83	63	22.5	49	13	101	4	1
1-2-5	m	72	51	16.5	31	11	80	4	2
1-2-5	m	72	50	17.5	28	8	78	4	2
1-2-5	m	68	49	17.5	30.5	12	82	5	2
1-2-5	m	72	54	15.5	31	10	80	5	2
1-2-5	f	84	62	18	25	8	79	5	3
1-2-5	m	76	55	17	20	7	73	5	3
1-2-5	m	75	56	15	26	9	78	4	2
1-2-5	m	76	56	17.5	24	8	78	5	3
1-2-5	m	69	48	15.5	30	10	76	2	2
1-2-5	m	63	45	15.5	25	9	65	5	2
1-2-5	m	68	52	15	23	7	68	5	3
1-2-5	m	74	54	16.5	20.5	7	74	1	3
1-3-2	f	85	64	18	28	9	83	5	3
1-3-2	m	79	54	20.5	35	13	91	1	3
1-3-2	f	84	65	17.5	32	12	84	4	3
1-2-132	m	76	52	17	20	6	63	5	3
1-3-2	m	81	61	19	28.5	9	84	3	3
1-3-2	m	76	56	16.5	25	8	78	5	3
1-3-2	f	85	60	20.5	35	13	91	5	3
1-3-2	f	86	64	21.5	39	13	93	4	3
1-3-2	f	85	65	17.5	28.5	9.5	79	5	3
1-3-2	m	90	66	20	32.5	12	92	4	3
1-3-2	f	84	63	17.5	36	12	97	4	3
1-3-2	m	81	57	20.5	40	15	87	4	2
1-2-132	m	70	48	17	28	9	72	5	2
1-2-132	m	80	56	19	28	7	77	5	3
1-3-2	m	75	54	18.5	34	12	84	5	3
1-3-5	m	82	58	20.5	35	12	90	5	3
1-3-5	m	76	55	19.5	36	13	79	4	3
1-3-5	m	77	55	21.5	36.5	13.5	85	3	3
3-3-4	m	79	58	22	36	13	84	5	3
3-3-4	m	93	70	22	45	17	109	5	2
3-3-4	m	86	61	20	39.5	15	94	3	2
3-3-4	m	79	57	20.5	39	14	88	3	2
3-3-4	m	94	71	22	45	17.5	108	4	2
3-3-4	m	86	65	20.5	33	11	86	5	3
3-3-4	m	90	68	21	39	15	96	4	2
3-3-4	m	81	59	20	38	13	86	3	3
3-3-4	m	88	66	20	40	16	97	3	2
3-3-4	m	80	58	20.5	43	17	97	3	2
3-3-0	m	83	62	22	49	18.5	103	3	2

3-3-0	m	78	53	20	42	17	94	5	2
3-3-0	m	83	60	22	43	18	106	5	2
3-3-0	f	77	53	21	33.5	15	84	5	2
3-3-0	m	77	53	22.5	45	17	98	3	2
3-3-0	m	85	60	22.5	46	18	100	4	2
3-3-0	m	77	55	22	43	17	90	4	2
3-3-0	m	80	62	21	45	17	95	4	2
3-3-0	m	78	55	23	46	18	97	5	2
3-3-0	m	75	54	21	43.5	17	89	5	2
3-3-0	m	76	55	22	43	13	93	3	2
3-3-0	f	73	53	22	46	17	88	3	2
3-3-0	m	76	53	23	41.5	15	81	5	2
3-3-0	m	83	61	22	49	17	95	5	2
3-3-0	m	87	61	22.5	49.5	17	101	5	2
3-3-0	m	86	60	22.5	47	18	102	5	2
3-3-0	m	83	61	20.5	45	15	99	5	2
3-3-0	m	74	54	21	42	15	85	5	2
3-3-0	f	75	52	19.5	35	13	78	5	2
3-3-0	m	74	52	21.5	33	14	84	3	2
3-3-6	m	80	57	21	36	13	87	5	3
3-3-6	f	82	55	20	43	11	98	1	1
3-3-6	m	83	61	20	37	14	88	3	3
3-3-6	m	70	47	19	34	12.5	77	4	2
3-3-6	m	83	58	20	36.5	12	87	3	3
3-2-336	f	83	57	19.5	38	12.5	81	3	2
3-3-6	m	89	65	21.5	46	16	108	5	2
3-3-6	f	84	57	21	44	10	101	3	1
3-3-6	m	87	65	21	37.5	14	88	3	3
3-3-6	m	84	61	19	35.5	11.5	86	3	3
3-3-6	m	82	57	.	36	13	79	5	3
3-3-6	m	79	59	20	29	9.5	81	3	3
3-3-6	m	78	55	17	35	12	78	4	3
1-3-1	m	75	57	19.5	26.5	9.5	80	3	3
1-3-1	m	82	63	22	39	16	110	3	2
1-2-131	m	70	54	17	33.5	12	78	5	2
1-3-1	m	79	59	19	31	11.5	82	5	3
1-3-1	m	82	61	21	47	12	105	2	2
1-3-1	m	81	61	17.5	32	12	87	3	3
1-1-0	m	61	39	18.5	37	9	72	4	1
1-1-0	m	62	44	18.5	33	10	66	5	2
1-1-0	m	69	50	18.5	45	17	81	4	2
1-1-0	m	61	41	17.5	34	8.5	73	4	1
1-1-0	f	58	40	18.5	34	12	66	5	2
1-1-0	f	75	54	19	44.5	10.5	84	4	1
1-1-0	m	71	54	18.5	31	10.5	81	3	2
1-1-0	m	60	44	18	42	10	80	2	1
1-1-0	f	70	49	18	35.5	10	75	3	2
1-1-0	m	66	52	17.5	33	12	80	3	2
1-1-0	m	70	53	20	49	13	99	4	1
1-1-0	m	64	43	18.5	32	10.5	71	4	2
1-1-0	f	70	49	18	42	16	73	5	2
1-1-0	m	68	46	19	46	11	80	5	1
1-1-0	m	57	37	18	36	13	70	4	2
1-1-0	f	63	45	19.5	39	16	69	4	2

1-1-0	m	68	47	14.5	31	12	63	3	2
1-1-0	m	70	53	17	37	13	74	3	2
1-1-0	f	69	52	16.5	33.5	11	74	4	2

Male wasps

mfrom-to-cage	mfrom-mto-mcage	mey	mfe	mti	mae	mat	mac	mal	max	mas
1-1-0	.-.-.	.	.	.	.	.	.	.	.	.
1-1-2	.-.-.	21.5	16	22	17	25	8	69	.	3
1-1-8	.-.-.	.	.	.	18.5	25	10	72	5	3
1-2-10	.-.-.	.	.	.	19	27	9.5	72	2	3
1-2-131	.-.-.	.	.	.	.	.	.	.	.	.
1-2-132	.-.-.	.	.	.	19	42	17	89	.	1
1-2-134	.-.-.	73	51	77	18	28	9.5	77	1	3
1-2-5	.-.-.	.	.	.	.	.	.	.	.	3
1-2-6	.-.-.	18	.	.	14	29	9.5	65	.	3
1-3-1	.-.-.	.	.	.	.	.	.	.	.	.
1-3-2	.-.-.	.	.	.	19	42	17	89	.	1
1-3-4	.-.-.	73	51	77	18	28	9.5	77	1	3
1-3-5	.-.-.	19	13.5	20	17.5	22	7.5	64	.	3
1-3-8	.-.-.	.	.	.	12	24	7.5	67	5	3
2-2-10	3-2-10	.	.	.	18	29	12	76	4	3
3-1-1	.-.-.	.	.	.	17	24	9	73	.	3
3-1-10	.-.-.	.	.	.	18	29	10	72	.	3
3-1-11	.-.-.	23.5	15	26	19	33	12	77	.	3
3-1-12	.-.-.	.	.	.	19	28	10	77	5	3
3-1-13	.-.-.	79	55	82	19	33	13	79	3	3
3-1-14	.-.-.	69	48	76	17	27	8	74	.	3
3-1-4	.-.-.	.	.	.	18	27	9.5	71	5	3
3-1-5	.-.-.	.	.	.	20.5	26	10.5	80	5	3
3-1-8	.-.-.	.	.	.	17	35	12.5	77	5	3
3-1-9	.-.-.	.	.	.	18.5	22	9	73	.	3
3-2-1	.-.-.	.	.	.	.	.	.	.	.	.
3-2-332	.-.-.	.	.	.	18	30	11	77	4	3
3-2-336	2-2-6	71	47	70	17	22	8	66	5	3
3-2-7	.-.-.	78	53	82	21	34	12.5	82	5	3
3-2-9	.-.-.	.	.	.	18	26	11	73	5	3
3-3-0	.-.-.	.	.	.	.	.	.	.	.	.
3-3-1	.-.-.	.	.	.	.	.	.	.	.	.
3-3-2	.-.-.	.	.	.	18	30	11	77	4	3
3-3-4	.-.-.	71	53	76	18	24	9	67	.	3
3-3-5	.-.-.	78	55	83	17.5	29	10.5	76	.	3
3-3-6	2-3-6	71	47	70	17	22	8	66	5	3
3-3-7	.-.-.	.	.	.	18	25	9	74	5	3
3-3-8	.-.-.	.	.	.	20.5	33	13	78	5	3
3-3-9	.-.-.	.	.	.	22	36	15	89	3	2

Female Wasps

ffrom-fto-cage	feye	ffemur	ftibia	faeye	fatib	facorn	falen	fax	fas
1-1-0	.	.	.	.	.	.	.	.	.
1-1-2	23.5	18	27	20.5	49	18	91	.	1

1-1-8	.	.	.	17	36	10	71	5	3
1-2-10	.	.	.	18.5	27	9.5	70	5	3
1-2-131	.	.	.	.	.	.	.	.	.
1-2-132	.	.	.	19.5	41.5	15	87	.	1
1-2-134	64	49	55	14.5	30	10	64	5	3
1-2-5	.	.	.	17	.	10	.	.	3
1-2-6	17.5	14	21	17	35	12.5	74	.	1
1-3-1	.	.	.	.	.	.	.	.	.
1-3-2	.	.	.	19.5	41.5	15	87	.	1
1-3-4	64	49	55	14.5	30	10	64	5	3
1-3-5	20	14	21	16	26	9	62	.	3
1-3-8	62	43	66	15	25	8.5	62	4	3
2-2-10	.	.	.	17	23	7.5	65	5	3
3-1-1	.	.	.	21	47	16	106	.	2
3-1-10	.	.	.	20.5	35	13.5	75	.	3
3-1-11	.	.	.	18	32	12	77	.	3
3-1-12	.	.	.	21	39	12	84	5	3
3-1-13	.	.	.	19	35	13	79	4	3
3-1-14	.	.	.	19	29	11	78	.	3
3-1-4	.	.	.	21	33	15	81	5	3
3-1-5	.	.	.	19.5	34	12	76	4	3
3-1-8	.	.	.	17.5	23	9	72	5	3
3-1-9	83	60	87	20.5	38	13.5	84	.	3
3-2-1	.	.	.	.	.	.	.	.	.
3-2-332	.	.	.	18.5	34	12	87.5	3	3
3-2-336	84	55	90	19	34	12	76	5	3
3-2-7	.	.	.	20.5	36	13	86	5	3
3-2-9	.	.	.	17.5	34	14	82	5	3
3-3-0	.	.	.	.	.	.	.	.	.
3-3-1	.	.	.	.	.	.	.	.	.
3-3-2	.	.	.	18.5	34	12	87.5	3	3
3-3-4	.	.	.	.	.	.	.	.	.
3-3-5	.	.	.	18	38	14	74	.	3
3-3-6	84	55	90	19	34	12	76	5	3
3-3-8	86	51	89	19.5	28	11	80	5	3
3-3-9	.	.	.	22	42	16	89	5	2

Raw data table for chapter 8.

obs is the observation number
host is the plant upon which the aphids fed 1=grass (a mixture of wheat, rye
and barley, 2=squash, 3=wheat, 4=okra, 5=watermelon, 6=cotton (Texas A&M
colony), 7=cotton (Harmon County Oklahoma), 8=Cotton (Caddo County
Oklahoma)
species is coded 1=melon aphid, 2=greenbug
stage is coded 1=adult alate, 2=late instar alate nymph, 3=nymph, 4=adult
apterous, 5=nymph with "sholders" which eventually will develop into wings
length is the total body length of the aphid
femur is the length of the metathoracic femur
tibia is the length of the metathoracic tibia
cornicle is the lenght of the cornicle
eye is the maximum distance between the outer margins of the compound eyes
Note: divide all distances by 60 to get lenght in mm.

obs	host	species	stage	length	femur	tibia	cornicle	eye
1	1	1	1	61.84	19.38	36.00	9.23	18.46
2	1	1	1	58.15	15.69	32.30	7.38	16.61
3	1	1	1	61.84	15.69	32.30	7.38	16.61
4	1	1	1	51.69	19.38	35.07	8.30	16.61
5	1	1	1	66.46	15.69	34.15	8.76	16.61
6	1	1	1	64.61	17.53	36.00	9.23	17.53
7	1	1	1	66.46	18.46	34.15	8.30	17.53
8	1	1	1	66.46	15.69	35.07	8.30	16.61
9	1	1	1	61.84	15.69	33.23	8.30	16.61
10	1	1	2	62.76	14.76	24.92	8.30	17.53
11	1	1	2	54.46	14.76	24.92	6.92	16.61
12	1	1	2	71.07	16.61	24.92	7.38	17.07
13	1	1	2	52.61	13.84	23.07	7.38	16.61
14	1	1	2	59.07	15.69	24.92	7.38	16.61
15	1	1	2	60.00	14.76	23.07	6.46	16.61
16	1	1	2	64.61	14.76	23.07	8.30	17.53
17	1	1	2	63.69	15.69	24.00	7.38	16.61
18	1	1	2	79.38	15.69	26.76	7.38	17.53
19	1	1	2	60.92	16.61	24.92	8.30	17.53
20	1	1	2	60.92	13.84	22.15	6.46	15.69
21	1	1	3	44.30	11.07	20.30	6.46	14.76
22	1	1	3	35.07	5.53	11.07	2.76	12.00
23	1	1	3	44.30	10.15	17.53	5.53	13.84
24	1	1	3	51.69	15.69	23.07	6.46	15.69
25	1	1	3	48.92	11.07	17.53	4.61	15.69
26	1	1	3	51.69	12.00	21.23	6.46	15.69
27	1	1	3	46.15	12.92	17.53	5.53	15.69
28	1	1	3	40.61	8.30	13.84	4.15	13.84
29	1	1	3	33.23	6.46	9.23	1.84	12.00
30	1	1	3	49.84	9.23	13.84	3.69	13.84
31	1	1	3	68.30	15.69	26.76	7.38	17.53
32	1	1	3	52.61	17.53	21.23	6.00	14.76
33	1	1	3	40.61	7.38	11.07	2.76	13.84
34	1	1	3	35.07	10.15	15.69	4.61	12.92
35	1	1	3	47.07	12.92	19.84	6.46	14.76
36	1	1	3	38.76	10.15	17.53	4.61	10.15

37	1	1	3	31.38	5.53	10.15	1.38	12.92
38	1	1	3	32.30	7.38	10.15	2.76	12.92
39	1	1	3	46.15	10.15	18.46	5.53	13.84
40	1	1	3	64.61	15.69	25.84	8.30	16.61
41	1	1	3	51.69	9.23	17.53	5.53	13.84
42	1	1	3	29.53	5.53	7.84	1.38	10.15
43	1	1	3	27.69	5.53	8.30	1.84	11.07
44	1	1	3	26.76	5.53	9.69	2.76	12.00
45	1	1	3	61.84	17.53	29.53	10.15	16.61
46	1	1	3	27.69	5.53	9.23	1.38	11.07
47	1	1	3	32.30	8.30	13.84	3.69	14.30
48	1	1	3	49.84	13.84	21.23	7.38	15.69
49	1	1	3	36.92	8.30	13.84	3.69	13.84
50	1	1	3	39.69	9.23	17.53	4.61	14.76
51	1	1	3	40.61	7.38	13.38	3.23	13.84
52	1	1	3	71.07	15.69	28.61	9.23	16.61
53	1	1	3	28.61	4.61	9.23	1.84	11.07
54	1	1	3	60.92	17.53	31.38	10.15	16.61
55	1	1	3	43.38	8.76	14.76	3.69	14.76
56	1	1	3	64.61	17.53	31.38	10.15	16.61
57	1	1	3	34.15	6.46	10.15	1.84	12.92
58	1	1	3	29.53	6.46	11.07	1.84	12.00
59	1	1	3	36.92	8.30	12.92	12.92	13.84
60	1	1	3	53.53	13.84	22.15	7.84	15.69
61	1	1	3	26.76	6.46	9.23	1.84	12.00
62	1	1	3	23.07	5.53	9.23	1.84	12.00
63	1	1	3	23.07	5.53	8.30	1.84	10.15
64	1	1	3	44.30	9.23	14.76	4.15	12.92
65	1	1	3	46.15	10.15	17.53	4.61	14.76
66	1	1	3	37.84	8.30	16.61	3.69	12.46
67	1	1	3	24.00	5.53	9.23	1.84	10.15
68	1	1	3	43.38	8.30	13.84	3.69	12.92
69	1	1	3	41.53	10.15	17.53	4.61	15.69
70	1	1	3	54.46	12.00	18.46	5.53	15.69
71	1	1	3	55.38	12.00	21.23	5.53	15.69
72	1	1	3	41.53	7.38	12.00	2.76	13.84
73	1	1	3	59.07	14.76	26.76	10.15	14.76
74	2	1	1	95.00	25.00	45.00	11.00	19.00
75	2	1	1	77.00	19.00	39.00	10.00	18.00
76	2	1	1	85.00	20.00	41.00	10.00	19.00
77	2	1	2	74.00	19.00	28.00	8.00	18.00
78	2	1	2	78.00	17.00	27.00	9.00	18.00
79	2	1	2	62.00	18.00	28.00	9.00	17.50
80	2	1	2	64.00	18.00	28.00	9.00	18.00
81	2	1	2	76.00	19.00	28.00	8.50	18.00
82	2	1	2	74.00	17.00	31.00	9.00	19.50
83	2	1	2	73.00	18.00	31.00	10.00	20.00
84	2	1	3	75.00	15.00	29.00	11.00	16.00
85	2	1	3	69.00	18.00	32.00	10.00	17.00
86	2	1	3	57	14.0	23	7	16.0
87	2	1	3	38	9.5	14	3	14.0
88	2	1	3	71	17.0	31	10	17.0
89	2	1	3	66	11.0	30	8	16.0
90	2	1	3	75	19.0	33	11	19.0

91	2	1	3	84	19.0	35	12	18.0
92	2	1	3	84	16.0	28	10	17.0
93	2	1	3	75	16.0	26	8	18.0
94	2	1	3	47	12.0	19	5	16.0
95	2	1	3	52	12.0	18	5	16.0
96	2	1	3	45	8.0	13	4	14.0
97	2	1	3	75	15.0	29	10	17.0
98	2	1	3	34	8.0	13	3	13.0
99	2	1	3	40	7.0	13	3	19.0
100	2	1	3	75	19.0	34	10	19.0
101	2	1	3	85	21.0	39	12	19.5
102	2	1	3	85	20.0	38	12	19.0
103	2	1	3	83	16.0	33.0	11.0	18
104	2	1	3	82	18.0	34.0	10.0	18
105	2	1	3	78	16.5	33.0	10.5	18
106	2	1	3	57	12.0	22.0	6.0	18
107	2	1	3	61	14.0	25.0	8.0	18
108	2	1	3	81	11.0	29.0	10.0	18
109	2	1	3	55	11.0	22.0	7.0	17
110	2	1	3	35	8.0	13.0	2.0	14
111	2	1	3	44	10.0	18.0	4.0	15
112	2	1	3	34	7.0	13.0	2.0	14
113	2	1	3	30	7.0	13.0	2.0	13
114	2	1	3	29	7.0	11.0	2.0	13
115	2	1	3	46	8.0	15.0	3.0	15
116	2	1	3	44	10.0	16.0	3.0	15
117	2	1	3	78	17.0	19.0	10.0	17
118	2	1	3	36	8.0	13.0	3.0	13
119	2	1	3	51	10.0	17.5	4.0	16
120	2	1	3	36	9	15	3.5	14.0
121	2	1	3	42	8	14	3.0	13.5
122	2	1	3	58	14	23	7.0	16.5
123	2	1	3	29	6	11	2.0	12.5
124	2	1	3	36	9	15	4.0	14.0
125	2	1	3	52	13	23	7.0	17.0
126	2	1	3	59	14	24	7.0	16.0
127	2	1	3	61	13	24	6.0	16.0
128	2	1	3	50	10	12	4.0	15.0
129	2	1	3	44	10	19	5.0	15.0
130	2	1	3	65	13	22	6.0	15.5
131	2	1	4	75	16	30	10.0	17.0
132	2	1	4	69	16	30	10.0	17.0
133	2	1	4	88	23	44	14.0	19.5
134	2	1	4	90	22	42	14.0	19.0
135	2	1	4	82	22	39	14.0	19.0
136	2	1	4	78	19	35	12.0	18.5
137	2	1	4	68	12.0	23.0	7.0	16.0
138	2	1	4	70	17.0	33.0	10.0	17.0
139	2	1	4	69	17.0	33.0	11.0	17.0
140	2	1	4	82	22.0	41.0	14.0	20.0
141	2	1	4	78	18.0	37.0	12.0	18.5
142	2	1	4	75	18.0	35.0	11.0	18.0
143	2	1	4	78	21.0	40.0	14.0	19.0
144	2	1	4	75	19.0	37.0	12.0	18.0

145	2	1	4	69	19.0	37.0	11.0	18.0
146	2	1	4	70	13.5	28.0	9.0	15.0
147	2	1	4	83	23.0	38.0	13.0	18.5
148	2	1	4	86	21.0	41.0	13.0	18.5
149	2	1	4	72	18.0	35.0	12.0	18.0
150	2	1	4	80	20.0	38.0	13.0	18.0
151	2	1	4	78	23.0	43.0	14.5	19.0
152	2	1	4	86	21.0	39.0	13.0	18.5
153	2	1	4	75	21.0	38.5	13.0	19.0
154	2	1	4	74	17.0	35.0	11.0	18.5
155	2	1	4	76	18.0	36.0	11.5	19.0
156	2	1	4	89	23.0	45.0	15.0	21.5
157	2	1	4	87	23.0	42.0	15.5	20.0
158	2	1	4	73	17.0	33.0	11.0	18.5
159	2	1	4	79	21.0	41.0	13.5	20.0
160	2	1	4	94	23.0	43.0	13.0	20.0
161	2	1	4	87	22.0	42.0	13.5	20.0
162	2	1	4	90	23.0	45.0	14.0	20.5
163	2	1	4	98	21.0	40.0	13.0	20.5
164	2	1	4	85	18.0	36.0	12.0	19.5
165	2	1	4	77	16.0	33.0	10.5	17.0
166	2	1	4	62	14.0	28.5	9.0	16.5
167	2	1	4	64	16.0	32.0	12.0	16.5
168	2	1	4	75	15.5	31.0	10.0	17.5
169	2	1	4	70	18.0	35.0	12.0	18.0
170	2	1	4	66	14.0	29.0	8.5	16.0
171	2	1	5	53	12	21	5	17.0
172	2	1	5	49	12	21	6	15.5
173	2	1	5	53	8	23	6	16.5
174	2	1	5	57	13	21	6	17.0
175	2	1	5	51	12	19	6	16.0
176	2	1	5	57	11	20	5	15.0
177	2	1	5	61	12	21	6	17.0
178	2	1	5	59	12	23	7	17.0
179	3	1	1	66	18	38	9	18.0
180	3	1	1	65	16	34	9	17.0
181	3	1	1	69	15	32	8	16.0
182	3	1	1	69	18	37	9	18.0
183	3	1	1	68	18	37	8	17.0
184	3	1	1	63	16	35	8	17.0
185	3	1	2	68	14	24	8	17.0
186	3	1	2	66	14	25	8	17.0
187	3	1	2	62	14	25	8	17.5
188	3	1	2	63	14.0	25.0	8.0	17.0
189	3	1	2	76	14.0	24.0	7.0	17.0
190	3	1	2	62	14.0	27.0	8.0	18.0
191	3	1	2	66	13.0	23.0	6.0	17.0
192	3	1	2	57	14.5	26.0	8.0	18.0
193	3	1	2	86	16.0	28.0	10.0	18.0
194	3	1	2	65	13.0	23.0	6.0	16.0
195	3	1	2	60	13.0	23.0	6.0	16.5
196	3	1	2	62	15.0	27.0	7.0	17.0
197	3	1	2	72	14.0	24.0	7.0	17.0
198	3	1	2	76	15.0	26.0	7.0	17.5

199	3	1	3	32	6.0	11.5	2.5	12.0
200	3	1	3	39	10.5	19.0	5.0	15.0
201	3	1	3	64	11.5	21.0	7.0	16.0
202	3	1	3	28	6.0	10.0	1.5	11.0
203	3	1	3	51	11.0	19.0	5.5	16.0
204	3	1	3	29	6.0	9.0	1.5	11.0
205	3	1	3	58.0	12	20.0	5.5	16.0
206	3	1	3	40.0	7	13.0	3.0	14.0
207	3	1	3	40.0	8	13.0	3.0	14.0
208	3	1	3	28.0	6	10.0	1.5	12.0
209	3	1	3	39.0	7	14.0	3.0	14.0
210	3	1	3	32.0	7	11.5	2.0	12.0
211	3	1	3	38.0	9	15.0	4.0	14.0
212	3	1	3	50.0	10	19.0	6.0	13.5
213	3	1	3	49.0	11	20.0	6.5	15.0
214	3	1	3	43.0	10	19.0	5.5	15.0
215	3	1	3	24.5	6	9.5	1.5	10.0
216	3	1	3	47.0	9	15.0	4.0	14.0
217	3	1	3	46.0	11	17.0	4.0	14.0
218	3	1	3	30.0	5	9.0	1.5	11.0
219	3	1	3	30.0	6	10.0	2.0	11.5
220	3	1	3	56.0	11	19.0	6.0	15.5
221	3	1	3	30.0	6	10.0	1.5	12.0
222	3	1	3	57	12	21	7.0	16.0
223	3	1	3	31	5	9	1.0	12.0
224	3	1	3	22	4	9	1.0	9.0
225	3	1	3	26	5	10	1.0	11.0
226	3	1	3	56	9	17	4.0	16.0
227	3	1	3	47	7	13	3.0	14.5
228	3	1	3	28	5	8	1.5	10.5
229	3	1	3	47	9	17	4.5	14.0
230	3	1	4	61	14	26	7.5	15.0
231	3	1	4	45	13	24	8.0	14.5
232	3	1	4	56	14	24	8.0	15.0
233	3	1	4	60	10	22	7.0	14.0
234	3	1	4	58	14	28	8.0	14.5
235	3	1	4	55	17	32	11.0	17.0
236	3	1	4	50	11	21	7.0	13.5
237	3	1	4	66	14	26	7.0	15.5
238	3	1	4	52	11	19	6.0	14.5
239	3	1	4	57	12	24.0	7.0	15.0
240	3	1	4	58	13	24.0	8.0	15.0
241	3	1	4	55	14	27.5	9.0	15.5
242	3	1	4	66	16	28.0	10.0	16.5
243	3	1	4	55	14	25.0	9.0	14.0
244	3	1	4	69	15	27.0	10.0	16.0
245	3	1	4	71	14	25.0	9.0	16.0
246	3	1	4	51	12	22.0	7.0	14.5
247	3	1	4	49	11	24.0	7.0	15.0
248	3	1	4	42	12	24.0	7.0	15.0
249	3	1	4	53	14	27.0	9.0	14.0
250	3	1	4	50	13	24.0	7.0	15.0
251	3	1	4	55	14	26.0	8.0	15.0
252	3	1	4	64	14	29.0	9.0	16.0

253	3	1	4	47	11	23.0	8.0	14.0
254	3	1	4	52	12	26.0	8.5	15.0
255	3	1	4	59	15	32.0	9.5	17.0
256	3	1	4	49	13.5	27.0	8.0	15.0
257	3	1	4	46	12.0	23.0	7.0	14.0
258	3	1	4	55	13.0	24.0	8.5	15.0
259	3	1	4	49	14.0	25.0	7.0	15.0
260	3	1	4	52	13.5	25.0	8.0	15.0
261	3	1	4	44	12.0	23.5	6.5	14.5
262	3	1	4	53	13.0	25.0	8.0	14.5
263	3	1	4	45	12.0	23.0	7.0	14.0
264	3	1	4	46	14.0	27.0	9.0	15.5
265	3	1	4	47	11.0	22.0	6.5	13.5
266	3	1	4	56	13.0	26.0	8.0	15.0
267	3	1	4	57	13.0	26.0	7.0	16.0
268	3	1	4	55	13.5	25.0	8.5	15.5
269	3	1	4	49	11.0	21.0	6.5	13.5
270	3	1	5	52	11.0	18.0	5.5	16.0
271	3	1	5	28	6.0	10.0	1.5	11.5
272	3	1	5	46	9.0	17.0	5.0	13.0
273	3	1	5	43	10.0	17.0	4.5	15.0
274	3	1	5	66	13.0	22.0	6.0	16.5
275	3	1	5	48	10.0	17.0	4.0	16.0
276	3	1	5	51	11.0	19.5	6.0	16.0
277	3	2	1	89	26.5	49.0	12.0	21.0
278	3	2	1	80	25.0	44.0	11.5	21.0
279	3	2	1	101	27.0	48.0	12.0	21.5
280	3	2	2	92	22.0	35.0	11.0	20.0
281	3	2	2	81	22.0	34.0	11.0	20.0
282	3	2	2	73	19.0	30.0	10.0	19.0
283	3	2	2	90	23.0	33.0	11.0	19.5
284	3	2	2	72	20.0	31.0	10.0	19.0
285	3	2	2	90	23.0	33.0	11.0	19.5
286	3	2	2	72	20.0	31.0	10.0	19.0
287	3	2	3	38	9.0	13.0	3.0	14.0
288	3	2	3	41	9.0	14.0	3.0	14.0
289	3	2	3	44	9.0	14.0	4.0	15.0
290	3	2	3	42	12.0	17	6.0	15.0
291	3	2	3	53	13.0	19	5.0	17.0
292	3	2	3	35	9.0	12	3.5	13.0
293	3	2	3	53	14.0	22	7.0	17.5
294	3	2	3	41	9.0	13	3.0	15.0
295	3	2	3	55	16.0	24	7.0	18.0
296	3	2	3	40	9.0	14	3.0	15.0
297	3	2	3	66	14.0	24	8.0	17.0
298	3	2	3	60	12.0	19	5.0	16.0
299	3	2	3	49	9.5	14	3.0	15.0
300	3	2	3	47	13.0	19	6.0	17.0
301	3	2	3	55	13.0	19	6.0	16.5
302	3	2	3	38	10.0	16	4.0	15.0
303	3	2	3	40	9.0	13	3.0	15.0
304	3	2	3	53	13.0	19	5.0	17.0
305	3	2	3	35	9.0	12	3.5	13.0
306	3	2	3	53	14.0	22	7.0	17.5

307	3	2	3	41	9.0	13	3	15.0
308	3	2	3	55	16.0	24	7	18.0
309	3	2	3	40	9.0	14	3	15.0
310	3	2	3	66	14.0	24	8	17.0
311	3	2	3	60	12.0	19	5	16.0
312	3	2	3	49	9.5	14	3	15.0
313	3	2	3	47	13.0	19	6	17.0
314	3	2	3	55	13.0	19	6	16.5
315	3	2	3	38	10.0	16	4	15.0
316	3	2	3	40	9.0	13	3	15.0
317	3	2	3	55	12.0	19	6	17.0
318	3	2	3	61	15.0	25	8	18.0
319	3	2	3	38	8.0	12	3	13.0
320	3	2	3	51	13.0	19	5	17.0
321	3	2	3	45	13.0	18	5	16.0
322	3	2	3	67	16.0	25	8	18.0
323	3	2	3	73	17.0	27	9	19.0
324	3	2	3	69	18	27	9.0	19.5
325	3	2	3	70	16	24	8.0	18.0
326	3	2	3	77	20	33	11.0	20.0
327	3	2	3	45	9	14	4.0	14.5
328	3	2	3	67	16	24	8.0	17.5
329	3	2	3	50	14	20	7.0	17.0
330	3	2	3	52	12	18	6.0	16.0
331	3	2	3	44	8	13	3.0	14.0
332	3	2	3	41	9	13	3.5	14.0
333	3	2	3	55	13	19	6.0	17.0
334	3	2	3	66	16	25	8.0	19.0
335	3	2	3	44	9	14	3.0	15.0
336	3	2	3	71	16	24	9.0	18.0
337	3	2	3	62	12	17	5.0	15.0
338	3	2	3	84	19	30	10.0	19.0
339	3	2	3	73	16	22	7.0	18.5
340	3	2	3	63	13	20	6.0	18.0
341	3	2	3	87	20	32	10	20.0
342	3	2	3	93	20	33	12	20.5
343	3	2	3	60	13	19	7	17.0
344	3	2	3	59	13	21	7	17.0
345	3	2	3	74	16	25	9	18.0
346	3	2	3	103	22	34	11	20.0
347	3	2	3	89	18	31	10	19.0
348	3	2	3	88	20	31	10	19.5
349	3	2	3	97	20	33	10	19.5
350	3	2	3	65	13	22	8	16.5
351	3	2	3	85	19	29	10	19.0
352	3	2	3	79	18	29	9	19.0
353	3	2	4	94	24	39	14	20.0
354	3	2	4	82	22	36	12	20.5
355	3	2	4	100	25	40	14	20.5
356	3	2	4	89	22	38	15	19.5
357	3	2	4	100	25	40	14	20.5
358	3	2	4	89	22.0	38	15.0	19.5
359	3	2	4	89	26.0	41	15.0	22.0
360	3	2	4	85	22.5	37	14.0	20.5

361	3	2	4	79	23.0	37	13.0	19.0
362	3	2	4	76	20.0	34	12.5	19.0
363	3	2	4	109	29.0	46	17.0	22.5
364	3	2	4	101	25.0	42	15.0	21.0
365	3	2	4	93	22.0	35	12.5	19.0
366	3	2	4	100	21.0	36	14.0	19.0
367	3	2	4	110	24.0	41	15.0	21.0
368	3	2	5	82	17.0	27	9.5	19.0
369	3	2	5	61	12.0	21	7.0	18.0
370	3	2	5	76	21.0	31	11.0	19.0
371	3	2	5	80	18.0	28	10.0	19.5
372	4	1	2	53	14.0	26	7.0	17.0
373	4	1	2	58	13.0	22	6.0	17.0
374	4	1	2	64	14.0	26	7.0	17.0
375	4	1	2	61	15	28	8.0	17.0
376	4	1	2	56	14	26	7.0	17.0
377	4	1	4	52	11	22	5.5	14.0
378	4	1	4	50	12	24	7.0	15.0
379	4	1	4	52	12	23	6.0	15.0
380	4	1	4	53	11	22	6.0	15.0
381	4	1	4	55	12	24	7.0	15.0
382	4	1	4	49	12	24	6.0	15.0
383	4	1	4	45	11	22	6.0	14.0
384	4	1	4	54	14	27	7.0	15.0
385	4	1	4	51	11	23	6.0	15.0
386	4	1	4	48	12	22	6.0	15.0
387	4	1	4	57	12	27	7.5	16.0
388	4	1	4	48	13	26	7.5	15.0
389	4	1	4	51	13	25	7.0	16.0
390	4	1	4	50	11	24	6.0	14.5
391	4	1	4	48	12	24	7.0	15.0
392	4	1	4	47	11.5	23.0	6.0	15.0
393	4	1	4	54	12.0	25.0	7.0	15.0
394	4	1	4	52	13.0	27.0	7.0	15.0
395	4	1	4	50	12.0	22.0	6.0	14.5
396	5	1	1	76	20.0	41.0	10.0	17.5
397	5	1	1	71	19.0	36.0	9.0	18.0
398	5	1	1	71	20.0	40.5	10.0	17.5
399	5	1	1	70	17.5	37.0	9.0	17.0
400	5	1	1	69	18.0	38.0	10.0	18.0
401	5	1	1	72	18.0	37.0	8.5	17.0
402	5	1	1	65	19.0	39.0	8.5	19.0
403	5	1	1	74	20.0	41.5	8.5	18.0
404	5	1	1	73	18.0	36.0	9.0	17.5
405	5	1	1	66	16.0	34.0	9.0	17.0
406	5	1	1	90	20.0	45.0	11.0	19.0
407	5	1	1	78	19.0	41.0	10.0	18.5
408	5	1	1	68	20.0	43.0	10.5	18.5
409	5	1	1	66	20.0	40	9.5	18.0
410	5	1	1	64	16.0	31	7.0	17.0
411	5	1	1	85	21.0	43	9.5	19.0
412	5	1	1	80	22.0	42	10.5	19.0
413	5	1	1	57	15.0	30	7.0	16.0
414	5	1	1	68	16.0	34	7.5	17.0

415	5	1	1	68	16.5	33	7.5	16.5
416	5	1	1	68	21.0	41	9.0	18.5
417	5	1	1	59	16.0	31	6.0	16.5
418	5	1	1	60	15.0	31	7.0	16.0
419	5	1	2	63	18.0	32	10.0	18.5
420	5	1	2	69	18.0	34	10.5	19.0
421	5	1	2	73	16.0	30	8.0	19.5
422	5	1	2	63	15.0	28	8.0	18.5
423	5	1	2	81	17.0	30	9.0	20.0
424	5	1	2	76	15.0	29	8.0	18.5
425	5	1	2	61	14.0	26	8.0	18.0
426	5	1	2	76	15.0	29.0	8.0	19.5
427	5	1	2	68	17.5	31.0	9.5	19.5
428	5	1	2	85	15.5	28.0	9.0	19.5
429	5	1	2	56	14.0	26.0	8.0	17.5
430	5	1	2	71	13.0	24.0	6.5	16.0
431	5	1	2	61	15.0	27.0	8.0	18.0
432	5	1	2	67	14.0	27.0	7.5	18.0
433	5	1	2	52	11.0	23.0	6.5	16.0
434	5	1	2	73	14.5	25.0	7.0	17.0
435	5	1	2	70	14.5	26.0	8.0	18.0
436	5	1	2	77	16.0	31.0	9.0	19.0
437	5	1	2	70	14.0	26.0	6.5	18.0
438	5	1	2	72	16.0	27.5	8.5	18.0
439	5	1	2	57	17.0	30.0	10.0	19.5
440	5	1	2	63	15.0	27.0	7.5	18.0
441	5	1	3	31	7.0	12.0	2.0	13.0
442	5	1	3	30	7.0	12.0	2.0	13.5
443	5	1	3	81	16.0	28	9.0	17.0
444	5	1	3	64	17.0	32	10.0	19.5
445	5	1	3	79	18.0	31	9.5	19.0
446	5	1	3	73	16.5	29	9.0	19.0
447	5	1	3	79	16.5	29	9.0	18.5
448	5	1	3	30	7.0	13	2.0	14.0
449	5	1	3	77	18.0	33	11.0	20.0
450	5	1	3	70	14.0	25	7.0	17.0
451	5	1	3	48	8.0	14	3.0	13.5
452	5	1	3	48	10.0	19	5.0	16.0
453	5	1	3	35	5.0	11	2.0	14.0
454	5	1	3	39	7.0	13	2.5	14.5
455	5	1	3	50	11.0	23	6.0	16.0
456	5	1	3	27	6.0	9	1.0	10.5
457	5	1	3	26	4.5	9	1.0	10.0
458	5	1	3	69	14.0	25	7.5	19.0
459	5	1	3	40	8.0	13	2.0	15.0
460	5	1	3	42	7.0	12.0	2.0	14.0
461	5	1	3	33	7.0	13.0	2.0	13.5
462	5	1	3	60	14.0	24.0	8.0	18.0
463	5	1	3	59	10.5	20.0	5.0	18.5
464	5	1	3	27	6.0	10.0	1.5	11.5
465	5	1	3	30	5.0	9.0	2.0	12.0
466	5	1	3	39	11.0	19.0	5.0	15.5
467	5	1	3	27	5.0	9.0	1.5	11.0
468	5	1	3	30	5.5	10.0	1.0	12.0

469	5	1	3	28	5.0	10.0	1.5	11.5
470	5	1	3	69	13.5	24.0	7.0	17.5
471	5	1	3	30	6.0	10.0	2.0	12.5
472	5	1	3	38	7.0	12.0	2.5	13.5
473	5	1	3	36	9.0	14.0	3.0	14.5
474	5	1	3	57	11.0	19.5	6.0	15.5
475	5	1	3	26	6.0	10.0	1.5	12.0
476	5	1	3	47	8.0	14.0	3.0	14.0
477	5	1	3	26	6.0	11	2.0	11.5
478	5	1	3	57	11.0	19	5.0	16.5
479	5	1	3	72	15.0	28	10.0	20.0
480	5	1	4	89	23.0	44	15.0	19.5
481	5	1	4	82	21.0	40	14.0	19.0
482	5	1	4	61	17.0	34	11.5	18.5
483	5	1	4	73	22.0	40	14.0	20.0
484	5	1	4	66	17.0	32	10.5	16.5
485	5	1	4	63	15.0	30	11.0	16.5
486	5	1	4	62	16.0	29	9.5	16.0
487	5	1	4	92	23.5	45	16.0	20.5
488	5	1	4	61	18.0	34	11.0	18.0
489	5	1	4	67	17.0	32	10.0	16.5
490	5	1	4	66	16.0	31	10.0	16.5
491	5	1	4	70	16.0	30	10.0	17.0
492	5	1	4	72	17.5	35	12.0	17.5
493	5	1	4	76	17.0	30	12.0	17.5
494	5	1	4	59	16.0	32	9.5	16.5
495	5	1	4	66	15.0	30	9.5	16.5
496	5	1	4	62	18.0	34	11.0	18.0
497	5	1	4	60	15.0	30	10.5	17.0
498	5	1	4	64	16.0	30	9.0	16.0
499	5	1	4	58	15.0	29	9.0	15.5
500	5	1	4	55	15.0	28	8.0	16.0
501	5	1	4	69	19.0	37	12.5	18.0
502	5	1	4	62	20.0	39	14.0	19.0
503	5	1	4	80	16.0	29	15.0	18.0
504	5	1	4	65	16.0	31	10.5	17.0
505	5	1	4	75	15.5	30	11.0	17.0
506	5	1	4	72	16.5	34	12.0	17.5
507	5	1	4	63	16.0	31	11.0	16.5
508	5	1	4	60	15.0	28	9.0	16.0
509	5	1	4	57	13.5	29	10.0	16.0
510	5	1	4	67	13.0	26	9.0	15.0
511	5	1	4	66	15.0	30	11.5	16.5
512	5	1	4	60	13.0	25	8.0	15.5
513	5	1	4	78	17.0	32	12.0	17.0
514	5	1	4	64	15.0	29	10.0	15.5
515	5	1	4	62	18.0	33	11.5	17.0
516	5	1	4	68	16.0	31	10.0	16.5
517	5	1	4	64	16.0	30	10.5	15.5
518	5	1	4	73	15.0	29	10.0	16.0
519	5	1	4	66	14.0	30	9.5	16.0
520	5	1	5	56	12.0	22	6.5	18.0
521	5	1	5	59	12.0	21	7.0	18.0
522	5	1	5	47	8.0	14	3.0	15.0

523	5	1	5	52	11.0	20	5.0	16.5
524	5	1	5	65	11.0	20	6.0	16.0
525	5	1	5	44	9.0	16	4.0	16.0
526	5	1	5	53	11.0	21	6.0	16.5
527	5	1	5	61	10.5	20	5.0	17.0
528	5	1	5	70	12.0	23	7.5	18.0
529	5	1	5	60	12.0	21	6.0	16.5
530	5	1	5	68	11.0	21	6.0	17.5
531	5	1	5	45	10.0	17	5.0	15.0
532	5	1	5	47	8.0	16	4.5	14.0
533	5	1	5	49	10.5	20	6.0	15.5
534	5	1	5	57	12.0	22	6.0	16.5
535	5	1	5	54	11.0	20	6.0	17.0
536	5	1	5	45	11.0	20	5.5	16.0
537	5	1	5	62	12.0	19	6.0	17.0
538	5	1	5	58	11.0	19	5.5	16.5
539	5	1	5	49	11.0	17	4.5	16.0
540	5	1	5	60	12.0	23	6.5	18.0
541	5	1	5	54	11.0	21	6.0	17.5
542	6	1	4	52	12.0	25	6.5	14.0
543	6	1	4	52	13.0	25	8.0	15.0
544	6	1	4	52	12.0	22	7.0	13.5
545	6	1	4	58	12.0	27	7.0	15.0
546	6	1	4	50	11.0	22	6.0	13.0
547	6	1	4	58	12.0	23	7.5	15.0
548	6	1	4	45	12.0	23	6.5	14.5
549	6	1	4	47	12.0	26	7.0	15.0
550	6	1	4	46	12.0	22	6.5	14.0
551	6	1	4	48	10.0	21	6.0	14.0
552	6	1	4	42	10.0	21	6.0	14.0
553	6	1	4	47	9.0	22	6.5	14.0
554	6	1	4	47	13.0	25	7.0	15.0
555	6	1	4	47	11.0	23	7.5	14.5
556	6	1	4	45	13.0	23	7.5	15.0
557	6	1	4	39	9.5	20	6.0	14.0
558	6	1	4	44	12.0	23	6.0	14.5
559	6	1	4	45	11.5	24	6.0	15.0
560	6	1	4	46	11.0	24	7.0	14.0
561	6	1	4	43	11.0	23	7.0	14.0
562	6	1	4	55	13	26.0	8.0	16.0
563	6	1	4	42	11	23.0	6.0	14.0
564	6	1	4	49	13	25.0	7.5	14.0
565	6	1	4	44	11	21.5	6.5	14.0
566	6	1	4	50	13	24.0	8.0	15.0
567	6	1	4	48	13	25.0	7.5	14.5
568	6	1	4	49	13	26.0	7.5	15.0
569	6	1	4	52	11	23.0	7.0	14.0
570	6	1	4	40	11	22.0	5.5	13.5
571	6	1	4	44	11	22.0	6.0	14.5
572	6	1	4	46	12	23.0	7.0	15.0
573	6	1	4	51	13	27.0	7.0	15.5
574	6	1	4	47	11	23.0	6.5	14.0
575	6	1	4	43	12	23.0	6.0	13.0
576	6	1	4	48	10	22.0	6.0	14.5

577	6	1	4	49	12	25.0	7.0	15.0
578	6	1	4	49	13	25.5	7.0	14.5
579	6	1	4	46	12.0	26	7.0	14.5
580	6	1	4	49	11.0	23	6.0	14.5
581	6	1	4	45	11.0	22	6.0	13.5
582	7	1	4	59	12.0	23	6.5	14.5
583	7	1	4	45	13.0	25	7.0	14.5
584	7	1	4	60	14.0	28	9.0	15.0
585	7	1	4	43	11.0	20	6.5	13.0
586	7	1	4	46	11.0	21	6.0	13.5
587	7	1	4	60	13.5	25	8.0	15.5
588	7	1	4	58	13.0	27	8.5	16.0
589	7	1	4	52	14.5	28	8.5	16.0
590	7	1	4	55	12.5	25	6.5	15.0
591	7	1	4	44	11.0	21	5.5	14.0
592	7	1	4	56	12.0	25	6.5	15.0
593	7	1	4	47	12.0	26	7.0	15.0
594	7	1	4	56	12.5	28	7.0	16.0
595	7	1	4	49	12.0	24	6.0	15.0
596	7	1	4	50	13.0	25.0	7.0	15.0
597	7	1	4	48	11.0	20.0	5.5	14.0
598	7	1	4	60	15.0	29.0	8.5	16.0
599	7	1	4	55	14.0	26.0	7.5	15.0
600	7	1	4	54	12.0	23.0	5.5	14.0
601	7	1	4	49	13.0	24.0	7.0	15.0
602	7	1	4	48	10.0	21.0	5.5	13.5
603	7	1	4	52	17.0	30.0	8.0	15.5
604	7	1	4	43	11.0	21.0	6.0	14.0
605	7	1	4	62	11.0	22.0	6.5	15.0
606	7	1	4	60	14.0	25.0	8.0	16.0
607	7	1	4	62	15.5	29.0	9.0	17.0
608	7	1	4	57	12.0	24.0	6.5	17.0
609	7	1	4	50	13.0	25.0	7.5	15.5
610	7	1	4	63	15.0	29.5	9.0	16.5
611	7	1	4	55	13.0	26.0	7.0	15.5
612	7	1	4	49	13.0	25.0	8.0	14.5
613	7	1	4	47	11.0	22.0	6.5	14.0
614	7	1	4	52	12.0	25.0	7.5	15.0
615	7	1	4	55	14.0	28.0	8.0	16.5
616	7	1	4	57	14.0	30.0	8.0	16.5
617	7	1	4	54	12.5	26.0	8.0	15.0
618	7	1	4	52	12.0	26.0	7.0	15.0
619	7	1	4	64	15.0	31.0	10.0	16.5
620	7	1	4	52	13.5	26.0	7.5	16.0
621	7	1	4	57	12.0	25.0	7.0	15.0
622	8	1	4	53	15.0	27.0	8.0	16.0
623	8	1	4	50	13.0	25.0	8.0	15.0
624	8	1	4	55	11.5	22.0	7.0	14.5
625	8	1	4	55	11.0	20.5	6.0	15.0
626	8	1	4	50	11.0	22.0	7.0	14.0
627	8	1	4	50	11.5	23.0	6.5	14.0
628	8	1	4	60	12.0	24.0	7.0	15.5
629	8	1	4	54	14.0	28.0	8.0	15.5
630	8	1	4	47	11	25	7.5	14.0

631	8	1	4	63	15	32	10.0	16.5
632	8	1	4	56	17	32	10.0	17.0
633	8	1	4	58	14	27	7.5	15.5
634	8	1	4	68	17	33	9.5	17.0
635	8	1	4	50	12	24	7.0	15.0
636	8	1	4	68	17	32	11.0	18.0
637	8	1	4	60	14	28	8.5	15.5
638	8	1	4	44	13	24	7.5	14.0
639	8	1	4	57	12	24	7.0	15.0
640	8	1	4	51	14	27	9.0	15.5
641	8	1	4	54	13	26	8.0	15.5
642	8	1	4	50	11	23	7.0	14.5
643	8	1	4	60	15	27	8.0	16.0
644	8	1	4	43	15	29	8.0	16.0
645	8	1	4	55	14	30	7.5	15.0
646	8	1	4	53	13	25	8.0	15.5
647	8	1	4	74	19.0	35	13.5	18.0
648	8	1	4	47	13.0	24	7.0	14.5
649	8	1	4	50	11.0	22	6.5	14.5
650	8	1	4	42	11.0	21	6.0	13.5
651	8	1	4	49	12.0	26	7.5	15.5
652	8	1	4	39	10.0	19	5.5	13.5
653	8	1	4	56	11.0	25	7.0	15.5
654	8	1	4	52	12.0	25	7.0	14.5
655	8	1	4	53	14.0	28	9.0	15.0
656	8	1	4	56	11.5	23	6.0	14.5
657	8	1	4	52	12.0	25	8.0	15.0
658	8	1	4	52	14.0	27	8.5	15.5
659	8	1	4	58	14.0	27	9.0	16.0
660	8	1	4	49	13.0	27	8.5	14.0
661	8	1	4	49	12.0	22	6.5	15.0

VITA 2

Timothy A. Ebert

Candidate for the Degree of

Doctor of Philosophy

Thesis: INFLUENCE OF HOST PLANT ON THE BIOLOGY, MORPHOLOGY, BIOCHEMICAL, AND GENETIC CHARACTERISTICS OF *Aphis gossypii* AND THE EFFECT OF HOST SWITCHING IN *Lysiphlebus testaceipes*

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Biographical:

Education: Received Bachelor of Science degree in Entomology from University of California at Davis in 1985. Received Master of Science degree in Entomology from Colorado State University in Spring 1990. Thesis Title: Interactions between pesticide applications and food resources in a *Pasimachus elongatus* population. Completed the requirements for the Doctor of Philosophy degree with a major in Entomology at Oklahoma State University in March 1994.

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Professional Societies: Entomological Society of America, Ecological Society of America