Bionomics of *Empoasca solana* DeLong on Cotton in Southern California

H. R. Moffitt and H. T. Reynolds
This study was initiated (1963) to obtain bionomical knowledge of *Empoasca solana* DeLong, the southern garden leafhopper, which could help improve integrated control measures on cotton. The following subjects were investigated in the field: relationship of populations on cotton to those on other crops in the area; seasonal occurrence and abundance; damage to cotton; association of parasites and predators with *E. solana*; seasonal occurrence and abundance of the parasites; effects of various control measures upon *E. solana* and the parasites. Laboratory investigations supplemented the field studies, with particular emphasis being placed upon the development of *E. solana* under controlled environmental conditions, the differentiation of all species of *Empoasca* found in California cotton fields, and the establishment of the types of injury inflicted upon cotton by the three species most commonly found on this crop in California.

It was found that populations of *E. solana* overwinter in sugar beet fields in California's southern desert valleys. High population levels are reached in late spring on sugar beets, and the populations move into adjacent cotton fields as sugar beets become unattractive to the leafhoppers. Population levels in cotton fields generally peak in early and mid-summer.

(Continued inside back cover)

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**INTRODUCTION**

Cotton in California is seriously affected by a relatively large number of insect pests (Smith, 1942, 1953). However, prior to 1952 no leafhoppers were regarded as serious pests of this crop in the state (Reynolds and Deal, 1956). In 1952 the southern garden leafhopper, *Empoasca solana* DeLong, was found to be seriously damaging plants in a number of cotton fields in the Imperial Valley of southern California, although relatively few fields were sufficiently damaged to require control measures. During subsequent seasons, this insect became increasingly abundant and caused damage of such importance that by 1963 it was considered among the most serious pests of cotton in the Imperial and Coachella Valleys.

The present study was initiated in 1963 to obtain a knowledge of the bionomics of *E. solana* in order to further the implementation of integrated control measures on cotton. During the 3-year study, the following subjects were investigated in the field: seasonal occurrence and abundance of *E. solana*; relationship of populations of *E. solana* on other crops in the area to those on cotton; symptoms produced by feeding of *E. solana*; association of parasites and predators with *E. solana*; and, seasonal occurrence and abundance of parasites of the eggs of *E. solana*. Laboratory investigations included studies on the development of *E. solana* on cotton and sugar beets under controlled environmental conditions, and studies on the type of damage caused by the feeding of *E. solana*.

**DISTRIBUTION AND HOSTS**

A review of the literature shows *E. solana* to be widely distributed throughout the southern United States, Mexico and Central America. Ross *et al.* (1965) show that this species ranges through tropical, subtropical and temperate regions with its northernmost winter record falling somewhere around 31° N. latitude. These authors conclude that the populations of *E. solana* occurring in the central and northern regions are due to seasonal movements each spring from the southern regions. Recent studies (Decker and Cunningham, 1967) support the conclusion that the populations of *E. solana* occurring in the central and northern regions of the U. S. are due to seasonal movements each spring from the southern regions.

This species has been reported from the following states: Alabama, Arizona, Arkansas, California, Colorado, Florida, Georgia, Hawaii, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana,
Mississippi, Missouri, Nebraska, New Mexico, Oklahoma, South Carolina, Tennessee, Texas, and Wisconsin (fig. 1). In California, it has been found primarily in the southern half of the state.

A large number of hosts have been recorded for *E. solana*. DeLong (1931), in the original description of this species, recorded it from potato in Louisiana. The earliest report of *E. solana* as a pest of economic importance was made by Carter (1936) who reported it as causing severe “hopperburn” on watermelon and castor bean in Hawaii; damage was reported to be less severe on potato. Additional hosts in Hawaii were found to be snap bean, lima bean, papaya, *Amaranthus*, “weeds,” lettuce, peanut, bush bean, blackeye cowpea, beet, Swiss chard, celtuce, Irish potato, summer squash, celery, egg plant, castor bean (Swezey, 1933; Carter, 1936; Holdaway, 1940, 1941, 1943; Holdaway and Look, 1941; Martin and Pemberton, 1942; Kraus, 1945; Sherman et al., 1954; Sherman and Tamashiro, 1957). *E. solana* has been reported damaging sweet potato in Barbados (Anon., 1945) and Louisiana (Kantack and Martin, 1956), castor bean in Texas (Wene, 1955), sugar beet in Arizona (Hills et al., 1944) and California (Reynolds et al., 1967), and cotton in California (Reynolds and Deal, 1956).

Poos and Wheeler (1943) report the following additional host plants for *E. solana*: alfalfa, *Aster* sp., black nightshade (*Solanum nigrum* L.), chickweed, dahlia, *Sestrum* sp., chayote (*Sechium edule* (Jacq.) Swartz), lemon, Mexican tea (*Chenopodium ambrosioides* L.), pokeweed (*Phytolacca* sp.), and willow. They also reported it as abundant on cotton in Louisiana in 1937.

In California, *E. solana* has been reported as occurring on alfalfa, *Atriplex Palmeri*, *Chenopodium murale*, *Cucurbita foetidissima*, and *Salsola kali*, and as especially damaging to bean, cotton, and sugar beet (Reynolds and Deal, 1956; Flock et al., 1962; USDA 1966; Reynolds et al., 1967; Goeden and Ricker, 1968).
HISTORICAL REVIEW

A review of the literature pertaining to *E. solana* reveals numerous publications, many of which consist solely of brief notations as to its occurrence upon certain plants, principally those of economic importance. The following chronological summary includes references which, in the authors' opinion, provide information for a better understanding of this species.

DeLong (1931) described *E. solana* on potato from Louisiana.

Poos (1932) made the first observations on the biology of *E. solana* on potato in an outdoor insectary.

Swezey (1933) made the first notation of the verified occurrence of *E. solana* in Hawaii.

Herford (1935) demonstrated that *E. solana* injects diastase into the plant while feeding and also secretes invertase.

Carter (1936) noted differential effects of feeding by *E. solana* upon watermelon, castor bean and potato.

Carter (1939) discussed hopperburn as caused by *E. solana* and *E. fabae*.

Holdaway and Look (1941) listed the economic hosts of *E. solana* in Hawaii and noted its damage to blackeye cowpea.

Martin and Pemberton (1942) discussed damage by *E. solana* to lettuce and celery in Hawaii. This was the first relatively detailed account of damage caused by this species.

Poos and Wheeler (1943) listed the known hosts of *E. solana* and discussed its injury. They placed *E. solana* in the phloem-feeding group.

Hills et al. (1944) conducted the first major studies on *E. solana* in the continental U.S. when they studied its effect on sugar beets grown for seed in Arizona.

Muesebeck et al. (1951) listed the known hymenopterous parasites and predators of *Empoasca* of America north of Mexico.

Wene (1955) noted *E. solana* as damaging castor bean in Texas.

Reynolds and Deal (1956) reported *E. solana* as a new pest of cotton in southern California and discussed its damage and control.

Ross and Cunningham (1960) gave a key to the *E. solana* complex and discussed its evolution.

Plock et al. (1962) reported *E. solana* from sugar beets and several weeds in the Imperial Valley, California. Several egg parasites of *E. solana* were also reported.

Peck (1963) listed the known chalcidoid parasites of nearctic *Empoasca*, including *E. solana*.

Ross et al. (1965) gave the known distribution of *E. solana* and discussed its evolution.

Reynolds et al. (1967) discussed the effects of high populations of *E. solana* upon yields of sugar beets in the Imperial Valley of California.

Decker and Cunningham (1967) reported on the effects of low temperatures upon *E. solana* and other species of *Empoasca*.

SPECIES OF *EMPOASCA* ASSOCIATED WITH COTTON IN CALIFORNIA

A number of species of *Empoasca* have been associated with cotton in California: *E. abrupta* DeLong, 1931; *E. arida* DeLong, 1931; *E. fabae* (Harris) 1841; *E. filamenta* DeLong, 1931; *E. mexara* Ross and Moore, 1957; and *E. solana* DeLong, 1931 (Smith, 1942, 1953; Reynolds and Deal, 1956; Cunningham, 1966). Because several of these species may concurrently occur in
the same field, it is imperative that one
be able to differentiate between them
and to have some knowledge of them as
biological entities. Therefore, morpho-
logical characteristics which may be
used to separate these species and notes
on the distribution and host of each
species are presented.

The species of Empoasca which have
been associated with cotton in Califor-
nia represent only a very small segment
of the genus, which consists of some 600
to 700 described species of which ap-
proximately 300 occur in the Western
Hemisphere (Ross et al., 1965). The six
species considered herein are included
in at least three species groups (Ross et al., 1965; Cunningham, 1962) with
various characters of taxonomic im-
portance. Thus, in considering only
these six species, morphological differ-
ences can be utilized which would not
necessarily be of taxonomic importance
if the entire genus were to be consid-
ered.

Of the many characters used to sep-
arate the species of Empoasca (DeLong,
1931; Young, 1953; Ross and Moore,
1957; Ross, 1959; Cunningham, 1962),
the following have been found sufficient
to separate the species considered in
this study:

1. Development and form of the apo-
demes of the first and second ab-
dominal sternite (apodemes 1s and
2s; see fig. 2).

2. Form of the brachones (fig. 3).

3. Form of the anal hooks (fig. 4).

The form of the brachone is distinc-
tive for most of these species. However,
the use of a combination of the above
characters will yield a more positive
identification.

All of these characters are internal
and most are associated with the genital
capsule of the male. External charac-
ters have been found to be unreliable
for the genus as a whole, but for such
a small and diverse segment of the
genus such as dealt with here it is quite
logical to assume that reliable external
characters could be found. As no reli-
able characters for the separation of the
females of the genus have been estab-
lished except in a few cases (Cunning-
ham and Ross, 1965), the only sure
means of establishing identity of the
female is through association with the
male.

Empoasca abrupta DeLong, 1931. The
brachone in this species is quite distinc-
tive. In ventral view, it is quite broad
and somewhat parallel-margined to
near the apex where it abruptly nar-
rows into finger-like processes on the
outer margins. The anal hook is long
and tapering, directed downward and
forward at the apex. Apodemes 2s are
quite well developed, extending posteri-
orly some two segments.

E. abrupta is very similar in form
and development of apodemes 2s to E.
filamenta and E. solana. However, the
form of the brachone serves to differ-

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Fig. 2. Apodemes of the first abdominal
sternite are shown f-g; apodemes of the second
abdominal sternite are shown a-e.
E. ABRUPTA

E. ARIDA (AFTER DELONG 1931)

E. FABAE

E. FILAMENTA

e

E. MEXARA

E. SOLANA

Fig. 3. Brachones (lateral processes of the pygofer).

The brachone of *E. arida* is quite distinctive in form. From the ventral aspect, the sides are somewhat tapered inwardly for some three-quarters of its length where it narrows quite rapidly and forms a half-circle with the bow pointed towards the sides of the body. The anal hook is long and tapering with the apex directed somewhat forward and strongly downward. Apodemes 2s have not been characterized in the literature. It would appear that the form of the brachone alone would serve to separate *E. arida* from the other species considered in this study.

*E. arida* is recorded from a relatively large number of plants from Arizona, California, Utah, and Washington (DeLong, 1931; Poos and Wheeler, 1943; Lange, 1944; Smith, 1953; Wolfe, 1955; USDA, 1965). It may be that this species does not reproduce on cotton and thus is a vagrant in California cotton entiate *E. abrupta* from the latter two species.

*E. abrupta* has been reported from a large number of host plants from many areas of the United States (Poos and Wheeler 1943; USDA 1965; Goeden and Ricker, 1968). During the course of our study, it was collected from alfalfa, cotton, squash, and sugar beets in the Imperial, Coachella and San Joaquin Valleys. *E. abrupta* is considered to be of economic importance on cotton only on rare occasions (Smith, 1953).

*Empoasca arida* DeLong, 1931. No specimens of *E. arida* were collected during the course of this study nor were any identified specimens available. As a consequence, all drawings of this species and subsequent comparisons are based upon the literature.

Fig. 4. Anal hooks.
fields. It appears to be rarely, if ever, of economic importance to cotton (Smith, 1953).

_Empoasca fabae_ (Harris), 1841. The brachone of _E. fabae_ is so similar to that of _E. mexara_ that separation of these species on this character alone is impossible. The same appears to be also true for the anal hook and apodemes 2s.

The most reliable morphological character for separation of these two species appears to be apodeme 1s which in _E. mexara_ is deeply cleft and in _E. fabae_ is at most somewhat sinuate. The brachone and development of apodemes 2s serve to separate _E. fabae_ and _E. mexara_ from the other species considered.

_E. fabae_ has received by far the greatest amount of attention of any of the North American species of _Empoasca_. According to Ross et al. (1965), _E. fabae_ is restricted to the temperate regions of North America where it is reported from a multitude of plant hosts (DeLong, 1938; Poos and Wheeler, 1943, 1949). In California, it is of greatest economic importance on alfalfa, citrus, cotton, and potato.

_Empoasca filamenta_ DeLong, 1931. In _E. filamenta_ the brachone is somewhat sinuate with attenuated tips. This character alone is usually sufficient to separate this species from the rest of the group. The anal hook is long and tapered with the point directed strongly forward.

Apodemes 2s are very similar to those of _E. abrupta_, differing only slightly in width and length. _E. filamenta_ is the most easily identifiable species of the genus associated with California cotton.

_E. filamenta_ has been reported from numerous plants in many areas of the United States and Canada (DeLong, 1938; Manis and Turner, 1942; Medler, 1942; Poos and Wheeler, 1943; Wolfe, 1955; Bierne, 1956; USDA, 1964). Smith (1953) reported this species from cotton in California but did not consider it to be a pest. During the course of our study this species was collected from sugar beets in the San Joaquin Valley but not from cotton.

_Empoasca mexara_ Ross and Moore, 1957. This species is easily confused with _E. fabae_. The brachone and anal hook and apodemes 2s are similar in both species. These species can be separated on the basis of differences in the shape of apodemes 1s.

_E. mexara_ is reported only from Arizona, California and northern Mexico where it has been associated with alfalfa and sugar beets (Ross and Moore, 1957; USDA, 1964, 1965). This species of _Empoasca_ was collected on cotton in the Imperial Valley during our study.

Some confusion over the occurrence and distribution of _E. mexara_ and _E. fabae_ in the southwestern United States appears to exist. In the San Joaquin Valley, _E. fabae_ is found on alfalfa, citrus and cotton (Lewis, 1942; Smith, 1953; Frazier, 1966) while in the desert areas of southern California it is only unofficially associated with alfalfa and not at all with citrus or cotton. _E. mexara_ is abundant on alfalfa in both Arizona and southern California, and it may well be that _E. mexara_ or some other species of _Empoasca_ may replace _E. fabae_ in the low-elevation desert valleys of Arizona and southern California.

_Empoasca solana_ DeLong, 1931. On the basis of the internal genitalia of the male, _E. solana_ is easily separable from the rest of the species associated with cotton in California. The brachone is even-sided for some three-quarters of its length, with the tip somewhat finger-like and twisted. The anal hook is broad and platelike while apodemes 2s are well-developed, extending some 2 to 3 segments into the abdomen. The apices of the apodemes are obliquely truncate,
with the longer edge on the lateral side.
The distribution, hosts and biology
of \( E. \ solana \) are presented in the appropriate sections of the present report.

METHODS AND MATERIALS: LABORATORY STUDIES

Collection and Maintenance of Colonies

Adults of \( E. \ solana \) were collected in the field with a D-Vac vacuum sampler (Dietrick \textit{et al.}, 1959). Fresh leaves were placed in the sample bag and the bag was placed in an ice box for transportation to the laboratory. Here, the entire sample was placed in a small sleeve cage in a room at 50° F. At this temperature most of the insects in the sample were immobilized, which facilitated the collection of individual leafhoppers.

Individuals were collected by means of small aspirators. Several hundred adults were sucked into the reservoir and then gently shaken into a large cage containing cotton plants. These adults formed the stock laboratory colony. New cotton plants were added, and old ones removed as necessary, to maintain a fresh food source for the leafhoppers. The colonies were maintained in a greenhouse where temperatures fluctuated between 75° and 85° F. A bank of four 40-watt cool white fluorescent lamps was suspended over the cages, and a 14-hour illumination period was maintained.

Life History Studies

Egg deposition was obtained by exposing clean cotton plants to the stock colony in the greenhouse for a 24-hour period. Adults were removed and the plants placed in a rearing room at the desired temperature. Duration of the incubation period was calculated as time from the end of the exposure period to the hatching of the egg. Observations were made at 12-hour intervals.

Egg deposition site preferences were determined by clearing leaves in which eggs had been deposited in a lacto-phenol-glycerine solution (Carlson and Hibbs, 1962). The cleared leaves were then examined through a dissecting microscope using transmitted light. \textit{Empoasca} eggs are easily seen using this method.

Newly hatched nymphs are very delicate and must be handled with extreme care. It was found that considerable mortality resulted when nymphs were picked up on a camel's hair brush so a different method was devised. Each nymph was forced onto a strip of filter paper by placing the paper flat on the leaf and guiding the nymph onto it with a camel's hair brush. The paper with the nymph on it was then placed on a small leaf in a Petri dish and the chasing process reversed. In this manner, little mortality resulted during the transfer. The leaf to which the nymph was to be transferred was placed with the lower surface up on two layers of moist filter paper in a 100 x 15 mm plastic Petri dish (fig. 5). Sufficient distilled water was added to maintain leaf turgidity and to act as a barrier to confine the nymph to the leaf. The leaf was replaced and additional water added as necessary.

It was found that the high humidity present in the closed dish adversely affected the newly emerged adult in that the wings were often stuck together or not completely unfolded, or both. This condition was rectified by cutting a hole in the cover of the dish and covering it with nylon organdy cloth. This ventilated cover was substituted during the
last nymphal instar for the solid cover used during the development of the first four instars. The duration of each nymphal instar was determined by noting when the molt occurred. Observations were made every 12 hours during the period of study.

The adults were studied by isolating them in small cages constructed of clear plastic food containers. A 1.0 pint and a 2.0 pint container were joined together to form a cage (fig. 6). The lids of the two containers were joined top to top by heat-sealing with a soldering iron. A hole was cut through the tops so that a portion of the stem with a leaf could be inserted. A cork with a hole in it the size of the stem was used to ensure a snug fit. The 1.0 pint container was filled with water into which the cut stem was inserted. The 2.0 pint container was fitted with three holes, two of which were covered with nylon organdy cloth to serve for ventilation and one of which was plugged with a cork and served as access to the cage.

In the oviposition study, two males were placed with each female to increase the probability of successful mating. The adults were transferred to a
Fig. 6. Cage used in studying adult development and oviposition of E. solana.

Sampling of Insect Populations

All population studies of adult and nymphal Empoasca solana and its parasites were based upon samples taken by means of the D-Vac vacuum sampler (Dietrick et al., 1959). A sample consisted of 100 individual suctions taken at random within the field. A suction sample was taken by placing the cone (0.5 ft² opening) over the plant or portion of the plant to be sampled. The cone was agitated slightly for several seconds and then removed and placed on the next plant for the next suction.

The bag containing the sample was sealed securely and placed in a portable ice box for transportation to the laboratory. In the laboratory, samples were

Symptoms of Feeding

Small cotton plants were caged and infested with small numbers of adult leafhoppers and held in a greenhouse at the same light and temperature conditions as used for the maintenance of colonies. Infested plants were also held in a lathhouse under normal outdoor conditions. Plants were infested with adults of E. abrupta or E. solana and the symptoms of feeding by each species were observed and characterized. Observations of damage due to feeding by both species were made at irregular intervals as symptoms developed upon infested plants.

METHODS AND MATERIALS: FIELD STUDIES
anesthetized with CO₂ gas and placed in modified Berlese funnels (Dietrick et al., 1959). The insects were collected in jars containing 80 per cent ethyl alcohol and stored until they were identified and counted.

Parasites of eggs of *E. solana* were associated with the leafhopper through rearing from plant samples containing leafhopper eggs. Approximately 1/2 gallon of plant material was collected in the field and brought back into the laboratory. This material was then placed into a 1-gallon ice cream container which was fitted with three holes in the lid into which were placed three dram patent lip glass vials. The container was then placed on its side in a room with high light and 85°F temperature. Emerging insects were attracted to the light and were trapped in the glass vials.

The population curves for the parasites are based upon the same samples as those used in population studies of *E. solana*. Predators were associated with *E. solana* through direct observation in the field. No other studies were conducted upon predators.

Population levels of the nymphs were determined by using the same samples used for the study of the adult leafhopper populations. The numbers of nymphs of *E. solana* present in the samples are used only as indicators of relative abundance of the nymphs, because the method does not yield an accurate measurement of this stage during the entire growing season. Early in the season the plants are small and an entire plant can be sampled with one suction, but as they grow larger progressively less and less of the plant is sampled. Because nymphs favor the lower less accessible area of the plant, a less representative sample of the nymphs results as the season progresses.

The migration and flight patterns of *E. solana* adults were studied by capturing on sticky board traps. Each trap consisted of one 2 inch × 4 inch post painted yellow on both 4 inch sides and coated with “Stickem special” which served as an adhesive and preservant. Each trap was placed between the two fields (one of cotton and one of sugar beets) with the prepared sides facing the fields and with 6 feet of trap surface extended above ground level. Four such traps were placed 75 feet apart in a line between the two fields. Each side of the trap was marked off into 1-foot lengths to help determine the height of flight.

### Life History Studies

Presence or absence of mature eggs in a female of *E. solana* was determined by infiltration with cedarwood oil and making an examination under low power on a microscope using transmitted light. Eggs present are easily seen by this method (fig. 7).

One hundred females were taken from each sample and put directly into cedarwood oil in a small Stender dish which was then placed in an oven heated to 90°F and left there for 10 to 14 days. After this, the insects were sufficiently cleared so that they could be examined for eggs. (Specimens can be stored indefinitely in the oil at room temperatures.) Location of individual eggs in plant tissue was determined by clearing the plant parts in a hot lactophenol-glycerine solution and examining them as previously described for the laboratory studies. Entire plants were brought into the laboratory. Results from leaves occupying the same position on different plants were pooled and the results averaged. In this manner, not only the plant parts favored but their position on the plant was determined.

One hundred adults were selected at random from the samples taken from several fields and the sex of each individual recorded. When less than 100 adults were present in the sample, all were sexed and counted.
Fig. 7. Body of female of *E. solana* infiltrated with cedar wood oil showing eggs in place in abdomen.
Temperature and Precipitation Records

Temperature and precipitation records were obtained from the U. S. Weather Bureau Climatological Summaries (1964, 1965) and mean temperatures were calculated for the periods between samples. Precipitation data are presented as monthly averages.

RESULTS AND DISCUSSION: LABORATORY STUDIES

Life History Studies

Adult longevity. In the laboratory, the maximum life span of a mated, actively ovipositing female was found to be 120 days at 80° F (table 1). At 70° F the maximum span was reduced to 78 days, and to only 30 days at 90° F. Average life span was 84.0 days at 80° F, 51.2 days at 70° F, and 25.0 days at 90° F. No determination of the adult life span or other characteristics of the adult were made under greenhouse (75 to 85° F) conditions.

No significant differences in mortality were noted between the sexes.

Oviposition. At 70° F the pre-oviposition period of E. solana was quite long, ranging from 11 to 23 days with a mean of 16.8 days. This period decreased at 80° F to a mean of 9.8 days with a range from 8 to 11 days, while at 90° F it decreased to a mean of 7.5 days with a range from 6 to 9 days.

At 80° F the total number of eggs laid per female was more than that occurring at either 70° F or 90° F. A maximum of 104 eggs was produced by a single female at 80° F while maximums of 59 and 14 were produced at 70° F and 90° F, respectively. The mean numbers of eggs produced per female were 83.5 at 80° F, 32.3 at 70° F, and 10.2 at 90° F.

The reproductive rate, i.e., the mean number of eggs/female/day, varied only slightly among the three temperatures employed. This ranged from 1.4 eggs per female per day at 70° F to 1.5 eggs at 80° F and to 1.6 at 90° F. As with many of the other parameters measured, a temperature of 80° appeared to result in a longer ovipositional life of actively producing females than did either 70° or 90° F. The maximum egg-laying period recorded at 80° F was 66.0 days with a mean of 57.3 days. This period was reduced at 70° F to a maximum of 42.0 days with a mean of 23.0 days. At 90° F, this period was reduced to a maximum of 8.0 days with a mean of 6.5 days.

The females of Empoasca solana are equipped with a strong ovipositor with which the egg is inserted into the plant tissue. The egg is embedded inside the plant tissue (figs. 8–9) with at most only a small slit externally marking the site. Where eggs are deposited in the leaf-blade tissue between the veins, a small swelling may be visible. The egg is oriented with its long axis parallel to the longitudinal axis of the vein and petiole when deposited in these plant parts. The same is also generally true for those eggs deposited in the tissue of the leaf blade in that they are generally oriented parallel to the nearest vein.

While studying the ovipositional habits of the female, site preferences for deposition of the egg were also determined. The three areas made available to the female for egg deposition were the leaf-blade area between the veins, the leaf veins, and the leaf petiole. By far the greatest number of eggs were deposited in the veins (table 2). Over 90 per cent of the eggs were deposited in this area of the leaf while the remainder were divided between the leaf blade and the petiole.

Development from Egg to Adult

On cotton leaves the shortest incubation period, a mean of 5.9 days, was
observed at 90° F (fig. 10). At 80° F the mean was 7.3 days, while at 70° F the mean was 13.2 days. Under greenhouse conditions with temperatures ranging between 75° F and 85° F, a mean incubation period of 7.7 days was observed. On sugar beet leaves at 70° F the mean incubation period was 13.1 days, while at 80° F the mean was 8.9 days. No data was taken from sugar beet leaves at 90° F.

Another effect of increasing temperatures upon the developing egg was the compression of a greater part of the emergence into a shorter period of time. At 70° F emergence was more or less evenly spread over a period of 4 days, at 80° F 2 days, and at 90° F 1 day.

On cotton leaves the first instar nymph took almost one day longer to develop at 70° F, than at 80° F, 90°F or in the greenhouse (75° F to 85° F) (table 3). At the latter three temperatures, the period of development of the first instar was essentially the same. The same situation also holds true for the second, third and fourth nymphal instars.

However, duration of the fifth nymphal instar is roughly a day longer (table 3) than any of the preceding instars at the same temperature. At 70° F the duration of the fifth instar is more than 2 days longer than any of the preceding instars at this temperature.

The mean time required for total nymphal development at 70° F was 14.9 days, considerably longer than at any of the other temperatures employed. This trend of longer developmental periods is also evident in the time elapsing from deposition of the egg to the emergence of the adult. When reared on sugar beet leaves, no major differences between developmental times at 70° F and 80° F were noted except an increase in the duration of the first instar nymph at 70° and an increase in the incubation period of the egg at 80° F (table 4). In both cases, the developmental time was about
Fig. 8. Egg of *E. solana* inserted into vein of cotton leaf.
Fig. 9. Egg of *E. solana* inserted into leaf-blade tissue.
TABLE 2

EGG DEPOSITION SITE PREFERENCES OF *EMPOASCA SOLANA* ON COTTON LEAVES UNDER CONTROLLED CONDITIONS

<table>
<thead>
<tr>
<th>Temperature (°F)</th>
<th>Number and per cent of eggs deposited in:</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Vein</td>
<td>Leaf blade</td>
<td>Petiole</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Number</td>
<td>Per cent</td>
<td>Number</td>
</tr>
<tr>
<td>70</td>
<td></td>
<td>176.0</td>
<td>90.3</td>
<td>8.0</td>
</tr>
<tr>
<td>90</td>
<td></td>
<td>51.0</td>
<td>92.4</td>
<td>2.0</td>
</tr>
</tbody>
</table>

1 day longer on beet leaves than on cotton. The time required to complete a generation, that is, the elapsed time from deposition of the egg to the deposition of the first egg by the resulting female, was found to be 21.7 days at 90° F, 26.5 days at 80° F and 44.9 days at 70° F (table 5).

Discussion

On the basis of the results obtained in the laboratory studies, a temperature of 80° F appears to be more nearly optimal for development of *Empoasca solana* than either 70° F or 90° F. Time required for development at 70° F is greatly extended in relation to that observed at both 80° F and 90° F, while the major differences between 80° F and 90° F were in those stages of the insect concerned with oviposition.

Even though the times required for the development of the egg and nymph and the duration of the pre-oviposition period are shorter at 90° F than at 80° F, the reproductive capacity is far greater at 80° F due to the much longer oviposition life of the female.

At 80° F the female lays an average of 83.5 eggs over her egg-laying life of 57.3 days, while at 90° F she lays an average of 10.2 eggs during an egg-laying life of only 6.5 days. Thus, even though a temperature of 90° F decreases the developmental time required for the immature stages, the far greater reproductive capacity evident at 80° F would appear to more than offset the slightly longer life cycle.

A point of some concern here is that the reproductive rate, i.e., the number of eggs laid per female per day, was essentially the same at the three temperatures employed. Within certain limits, the reproductive rate of insects increases as temperature increases (Wigglesworth, 1950; Patton, 1963). It is not felt that these limits for this insect were reached at the temperatures employed in this study. Thus, the apparent lack of a change in reproductive rate in this study may be due to a lack of sufficient numbers studied rather than to limits imposed by temperature. Only further study would clarify this point.

A few observations on the biology of *E. solana* were made in an insectary by Poos (1932) who reported that the incubation period of the egg ranged from 9 to 17 days and nymphal development from 9 to 11 days; one female lived for 88 days. These observations fall within ranges indicated by the current laboratory studies.

It would also appear that *E. solana* is less prolific than either *E. abrupta* or *E. fabae* (Poos, 1932; DeLong, 1938). No data on the reproduction of *E. arida*, *E. filamenta* or *E. mexara* were found in the literature. A comparative study of the biologies of the species of *Empoasca* associated with cotton in California would help clarify the status of their economic importance.
Only recently have there been studies reported on the effects of temperature upon the oviposition and development of *E. fabae* under constant conditions in the laboratory. Kieckhefer and Medler (1964) found that oviposition by *E. fabae* was apparently at its maximum at a constant temperature of 75°F. No nymphs emerged from plants held at 60°F or 90°F. Kouskolekas and Decker (1966) found that the maximum rate of development occurred at temperatures between 83°F and 88°F. Above 88°F the developmental rate and survival declined.

These data correspond somewhat to those obtained in the current study in that maximum oviposition occurred at 80°F and reproduction declined, both in laboratory and field, as mean temperatures rose to or exceeded 90°F.

**Symptoms of Feeding**

The first symptoms of feeding by *E. solana* to appear were fine white scratches on the upper surface of the leaf (fig. 11). Considerable wilting of the plants was then often observed. Next, the leaf margins became chlorotic and the chlorosis shortly involved most of the leaf tissue except the vein and the immediately adjacent tissue (fig. 12). The chlorotic areas then became necrotic, which resulted in the leaf margins curling upward and gave a dried, burned appearance to the leaf. Considerable stunting of the plants was also observed (fig. 13).

No yellow or red discoloration such as occurs in the field appeared under greenhouse conditions. To further investigate this point, caged plants were infested with leafhoppers and held in
### Table 3

**EFFECT OF TEMPERATURE ON NYMPHAL DEVELOPMENT OF *EMPOASCA SOLANA* ON COTTON**

<table>
<thead>
<tr>
<th>Instar</th>
<th>Days required for nymphal development at various temperatures</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>70°F</td>
</tr>
<tr>
<td></td>
<td>Number of insects</td>
</tr>
<tr>
<td>1</td>
<td>47</td>
</tr>
<tr>
<td>2</td>
<td>46</td>
</tr>
<tr>
<td>3</td>
<td>42</td>
</tr>
<tr>
<td>4</td>
<td>35</td>
</tr>
<tr>
<td>5</td>
<td>29</td>
</tr>
<tr>
<td>Total</td>
<td>150</td>
</tr>
</tbody>
</table>

*Theoretical minimum and maximum nymphal developmental period calculated from the shortest observed duration of each instar.
†Minimum and maximum nymphal developmental period observed for a single individual.
TABLE 4
EFFECT OF TEMPERATURE ON NYMPHAL DEVELOPMENT OF EMPOASCA SOLANA ON SUGAR BEETS

<table>
<thead>
<tr>
<th>Instar</th>
<th>Days required for nymphal development at two temperatures</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>70°F</td>
</tr>
<tr>
<td></td>
<td>Minimum</td>
</tr>
<tr>
<td>1.</td>
<td>11</td>
</tr>
<tr>
<td>2.</td>
<td>8</td>
</tr>
<tr>
<td>3.</td>
<td>7</td>
</tr>
<tr>
<td>4.</td>
<td>7</td>
</tr>
<tr>
<td>5.</td>
<td>6</td>
</tr>
<tr>
<td>Total</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>—</td>
</tr>
</tbody>
</table>

*Theoretical minimum and maximum nymphal developmental period calculated from the shortest observed duration of each instar.
† Minimum and maximum nymphal developmental period observed for a single individual.

In the greenhouse under constant controlled conditions, cotton leaves do not harden and mature as they do under field or outdoor conditions. This may account for the lack of appearance of the pigments necessary for the development of the yellow and red discolorations.

E. solana is a member of the phloem-feeding group of Empoasca. This group of species feeds upon the phloem tissues of the leaf, resulting in a characteristic type of damage commonly termed “hopperburn” (Smith and Poos, 1931; Carter, 1962). Hopperburn is usually manifested by a wrinkling of the leaf followed by an upward rolling and necrosis of leaf margins. Necrosis along the leaf margins increases in size until most of the leaf area is involved except for a narrow strip along the mid-vein. When feeding is heavy, all the leaves may curl and dry up, the petioles wither, and defoliation may occur. Plant stunting and leaf color changes may also occur (Carter, 1962). Hopperburn may differ in appearance from crop to crop.

TABLE 5
TOTAL DEVELOPMENTAL TIME REQUIRED FOR EMPOASCA SOLANA ON COTTON FROM EGG TO EGG (I.E. ONE GENERATION); EXPRESSED AS MEAN NUMBER OF DAYS REQUIRED FOR EACH LISTED STAGE

<table>
<thead>
<tr>
<th>Stage</th>
<th>Temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>70°F</td>
</tr>
<tr>
<td>Egg</td>
<td>13.2</td>
</tr>
<tr>
<td>Nymph</td>
<td>14.9</td>
</tr>
<tr>
<td>Preovipositing female</td>
<td>16.8</td>
</tr>
<tr>
<td>Total</td>
<td>44.9</td>
</tr>
</tbody>
</table>
Fig. 11. Scratches on upper surface of cotton leaf produced by feeding of *E. solana*. Right: scratches due to feeding. Left: no scratches, not fed upon.

Fig. 12. Effects of *E. solana* feeding on cotton leaf in greenhouse. Left: fed upon (note extensive chlorosis). Right: not fed upon, no symptoms.
Fig. 13. Effects of feeding of *E. solana* upon cotton seedlings in the greenhouse. Right: infested. Left: uninfested. Note stunting of infested plants.
Feeding by *E. abrupta* on cotton leaves in the greenhouse or lathhouse produces a fairly large stipple, or spot, on the upper surface of the leaf (fig. 14). When feeding is extensive, numerous stipples are present and when several stipples are close together, they may coalesce, giving a whitish blotchy appearance to the leaf. Other symptoms of heavy feeding by *E. abrupta* may include a rolling-under of the leaf margins and a partial necrosis of the leaf tissues. *E. abrupta* is a member of the mesophyll-feeding species of *Empoasca*, following the grouping of Smith and Poos (1931). These workers found that the mesophyll-feeding species of *Empoasca* confine their feeding to these tissues of the leaf and die after a few hours' confinement to stems, petioles, and mid-veins of the leaf.

### RESULTS AND DISCUSSION: FIELD STUDIES

#### Life History Studies

**Habits of Adults and Nymphs**

The adults of *Empoasca solana* are found generally over all the foliage of the plant and feeding appears to occur on all leaves except the newer growth of the terminals and laterals. Feeding is done from the lower surface of the leaf where the insect feeds primarily in the phloem tissue. Early in the morning, when temperatures are lower, the adults are found on the lower portions of the plant and are not easily induced to move about or to fly. As the temperature rises, the adults move around more readily and take flight when disturbed. Under such conditions, a person walking through a heavily infested field at midday may be surrounded by a cloud of leafhopper adults.

*Empoasca* adults are fragile insects and will not survive rough handling but, as has been demonstrated with *E. fabae*, members of this genus are capable of traveling long distances (Pienkowski, 1962; Pienkowski and Medler, 1962, 1964). In the field the flight of *E. solana* is somewhat short and erratic. The total distance covered in a single flight may be quite short but a number of successive flights undoubtedly are one of the means by which longer distances are covered. When disturbed the adult moves over the leaf surface with a very rapid oblique movement, or else it takes flight.

Even though the adults are found on all areas of the plant, egg deposition occurs primarily in the leaves on the lower half of the plant (fig. 15). On 10 plants examined in mid-June, a total of 4439 eggs were found. A summary of egg distribution of *E. solana* on cotton in mid-June, Imperial Valley, showed the following average value for 10 plants:
Plant height (cm) ........... 33.7
Number of main stem leaves .. 16.0
Number of eggs deposited .... 537.7
Main stem leaves (per cent) .. 65.4
Lateral branch leaves
(per cent) ................... 34.6
Lower half of plant
(per cent) ................... 77.4

A mean value of eggs deposited for each leaf position was calculated and plotted on a schematic diagram of a cotton plant. Figure 15 represents the distribution of eggs on a typical plant in mid-June; the plant was 33.7 cm in height and had 16 main stem leaves. On this typical plant, 66.4 per cent of the eggs were deposited in the main stem leaves and 43.6 per cent in lateral branch leaves. Over 75 per cent of the eggs were deposited in leaves on the lower half of the plant, and 85 per cent of these eggs were deposited on main stem leaves and the first leaves of lateral branches.

The general distribution pattern of the eggs thus appears to be centered in older, more mature leaves of lower parts of the plant; as newer leaves mature, they become more acceptable for oviposition. This is somewhat similar to the preferences exhibited by E. fabae on various clones of Solanum tuberosum (Miller and Hibbs, 1963). These authors found that while E. fabae would oviposit in both the very young and fully mature plant tissue, a decided preference for tissue of medium maturity was exhibited. The factors governing acceptance are not known but undoubtedly are quite complex.

Like the adult, the nymph feeds primarily upon the phloem tissue from the lower surface of the leaf (fig. 16). Field observations indicate that the nymph spends most of its life on the leaf from which it hatched. Some movement from leaf to leaf takes place, but most of such movement occurs when the leaf becomes unfavorable for further feeding—this generally occurs when feeding has been extremely heavy and the leaf is severely affected or when some other factor has made the leaf unfavorable. During the heat of the day the nymph is extremely active and, when disturbed, moves very rapidly over the surface of the leaf.
Plate II. Symptoms induced by feeding of *E. solana* upon cotton leaves in lathhouse and field. Upper left: no symptoms, not fed upon. Upper right: light blotching and discoloration. Lower right: extensive discoloration involving most of leaf. Lower left: severe discoloration involving all of leaf, left side of leaf is somewhat senescent.
Sideways movement (as noted for the adults) is also a characteristic of the nymph. Later instars, especially the fourth and fifth, are able to jump considerable distances when disturbed. Several leaps of 4 to 6 inches were observed.

The distribution pattern of a nymph population of a cotton plant appears to follow that observed for eggs. The greater numbers of nymphs are found on the older, more mature leaves of the lower half of the plant. When populations are extremely high, the nymphs can be found higher on the plant. It would appear that feeding preferences and site of egg hatch play major roles in this distributional pattern.

**Symptoms of Feeding**

During the course of this study, the symptoms of feeding by *E. solana*, *E. fabae*, and *E. abrupta* on cotton and *E. solana* on sugar beets were observed in the field. The first evidence of feeding by *E. solana* on both cotton and sugar beets was the appearance of fine white scratches on the upper surface of the leaf (fig. 11, 17). On cotton, as the feeding continues, the margins of the leaf turn yellowish in color and soon to a deep red. This discoloration may be evenly distributed about the leaf but most often it is uneven in distribution, resulting in a somewhat blotchy appearance. As the injury progresses, the blotches appear also in the center of the leaf eventually involving most of the leaf tissue except the veins and that tissue immediately adjacent to them (see color plates, pages 270–271). The leaves by this stage have also assumed a thickened, leathery appearance. Under typical field conditions, much of the injury is confined to the older, more mature leaves of the lower one-third to one-half of the plant, the area where the nymphs are concentrated. In cases of extremely heavy population levels and severe damage, the leaf injury may extend to the top of the plant. No wilting or obvious stunting of the plants was observed in the field.

In 1952, when populations of *E. solana* were first found to be seriously damaging cotton in the Imperial Valley, it was found that when leafhoppers were abundant on cotton plants fruiting was severely affected—squares and small bolls were shed and larger bolls became soft and spongy (Reynolds and Deal, 1956). It was also reported that hopperburn was in evidence in that the leaf margins turned yellow or reddish and often became thickened and leathery. Wilting was not observed on infested cotton in the field.

Symptoms produced on cotton by the feeding of *E. fabae* are very similar to those produced by *E. solana* (see color plates, pages 270–271). Feeding by *E. fabae* results in the leaves becoming somewhat thick and leathery with reddish and yellowish blotches. The margins of the leaf tend to curl downward and become discolored. Smith (1953) also reported a decrease in length of internodes resulting in compact and bushy plants. Heavy feeding by *E. abrupta* on cotton causes a general loss of green color due to the loss of chlorophyll from the fed-upon cells. No other symptoms of significant damage to cotton were observed.

Feeding symptoms of *E. solana* on sugar beet leaves are somewhat different from those produced on other plants. Injury to sugar beets was first manifested as a light, fine stippling on the leaf surface, often appearing as fine scratches. As feeding and resulting injury intensified, margins of the leaf curled upward slightly, the yellowing or chlorosis encompassed most of the leaf tissue, and the leaves assumed a somewhat thickened and leathery appearance. The gross discoloration and necrosis (i.e., hopperburn) of the leaf
tissue exhibited on other injured species of plants did not occur on sugar beets even under extremely high populations.

In studying the effects of *E. solana* upon yield of sugar beets grown for sugar in the Imperial Valley during 1954–1960, Reynolds et al. (1967) reported as symptoms of feeding only severe wilting of the leaves. They also found a resulting increase in the amount of root rot present, a decrease in sugar content, and a decrease in root yield due to extensive feeding by this species.

Hills et al. (1944) found that populations of *E. solana* materially reduced the yield of sugar beet seed in Arizona. They concluded that *E. solana* fed largely on the vegetative parts of the plant and reduced the seed yield primarily through devitalization of the plant. Infested plants were reported to be dwarfed and to produce less seed.

**Seasonal Occurrence and Ecology**

Periodic sampling served to establish the seasonal occurrence and abundance of *Empoasca solana* and its parasites and predators and also the relationships of various cultural patterns to these parameters. It was noticed early that sugar beets appeared to play an important role in the seasonal occur-
rence and abundance of *E. solana* on cotton (Reynolds and Deal, 1956). In order to explore the role that sugar beets may play, cotton fields adjacent to sugar beets and cotton fields far removed from sugar beets were utilized in the study. The seasonal growing patterns of these two crops in the interior desert valleys of southern California are such that one or the other is available to the leafhopper throughout the year as cotton is usually grown from February through October and sugar beets from September through June. Sugar beet production in the Coachella Valley has declined in recent years and in 1964 few fields were planted and carried through to harvest. In 1965, no sugar beets were grown in that part of the Coachella Valley in which a portion of these studies were conducted.

Analysis and interpretation of population curves obtained during the course of this study include consideration of a number of factors such as the use of insecticides. As most of the fields utilized were grower-owned, some use of insecticides was unavoidable. In the following discussions, insecticide treatments are indicated where applicable.

As mentioned previously, the samples became less indicative of the true level of the nymphs present on cotton as the season progressed. For this reason, most of the discussion of population curves is based upon the adults. The curves representing the nymphs are brought into the discussion when deemed advisable.

**Population Curves, Coachella Valley**

**Kennedy (1964).** This cotton field was approximately 10 miles from the nearest sugar beets and was located on the extreme western edge of the valley. Adult *E. solana* were present in the field in minute numbers through May, but an increase became evident at the first of June and continued through July (fig. 18). The population then began a rapid rise to a peak of some 5700 adults per sample in the latter part of July. At this time, an insecticide application directed toward *Lygus hesperus* Knight was applied and the leafhopper population was reduced drastically. This insecticide-induced reduction lasted only a short time, after which the leafhopper population again increased and peaked in mid-August. Minor increases were again evident in late August and September, but the general trend from late July through to defoliation in early November was downward.

What shape the population curve would have taken in the absence of insecticides can only be surmised. On the basis of other curves obtained for fields where insecticides were not a factor, it is believed that the higher population level of mid-July would have endured through late July and August if insecticides had not been used. This is indicated by the number of nymphs present before insecticide usage. These nymphs would have been expected to become adults about the first of August. With insecticide usage, these nymphs were killed and the peak of adults occurring in mid-August is thus probably a result of eggs which were not affected by the insecticide.

**Rummonds (1964).** This cotton field was adjacent to sugar beets and was located in the southeaster portion of the valley, about 10 miles from the Kennedy field. The sugar beet field was immediately to the south of the cotton field and separated from it by a narrow dirt road.

*Empoasca solana* adults were quite abundant on the sugar beets at the end of April when sampling was initiated (fig. 19). The population level rose quickly to a peak of 2400 adults per sample in early May and maintained itself with only a minor decline through the first of June. At this time,
a rapid decline took place with the population reaching a very low level by the end of June. Another low peak occurred in early July but the population again declined until early August when the sugar beets were harvested for cattle feed.

In the adjacent cotton field very few adult leafhoppers were present until June 1, at which time the sugar beets had become unfavorable for further development of the leafhopper. The population level in this cotton field rapidly rose to a peak in June. This high pop-

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**Fig. 18.** Population curves (1964) for *E. solana* in the Kennedy cotton field, Coachella Valley.

**Fig. 19.** Population curves (1964) for *E. solana* in the Rummonds cotton and sugar beet fields, Coachella Valley.
ulation level was maintained through July. After reaching the peak of 6800 adults per sample in late July, the population level rapidly declined to a low level which persisted until defoliation took place in early November.

Rummonds (1965). This cotton field was the same as that utilized in 1964. The situation was different from that prevailing in 1964 in that sugar beets were not grown in the area and a different variety of cotton was grown. The effects of this variety change upon \textit{E. solana} are not known, but previous observations (Reynolds, 1967) have not indicated major differences in leafhopper populations between the two varieties Deltapine Smooth Leaf (1964) and Acala 4-42 (1965). The variety of cotton in this field was slow to reach a stage of growth large enough to make sampling with the suction device feasible. As a result, sampling was not initiated until early June.

Adult \textit{Empoasca} were present at this time but in low numbers (fig. 20). Beginning on the first of July, an increase in numbers was noted which continued to a peak of 2000 adults per sample in early August. This population level was maintained with a downward trend through late August when it declined sharply. The population level continued to decline until defoliation took place in mid-November.

Population Curves, Imperial Valley

Elmore (1964). This cotton field was located in the northern portion of the Imperial Valley approximately 7 miles from the nearest sugar beets. The initial rise in numbers of \textit{E. solana} took place in early June and the population level rapidly rose to a peak of 3400 adults per sample in the third week of July (fig. 21). A sharp decline took place the last week of July, but the population level again increased sharply to 3200 adults per sample in early August. After this increase, the population level declined through to the end of October when defoliation took place.

Elmore (1965). This cotton field was in the same location as in 1964 and again far removed from sugar beets.
Adult *E. solana* were present in low numbers in the field when sampling was initiated in early May (fig. 22). The population level rose rapidly through mid-June to 5500 adults per sample in late June. The population then began a decline which was greatly accelerated by an insecticide application the second week of July. This decline resulted in a very low population level in mid-July. Later two moderately high peaks occurred, one in late July and one in early August. Both of these population increases were halted by insecticide applications resulting in a low population level through late October when defoliation took place.

Here again, as in the Kennedy (1964) field, the shape the population curve would have taken in the absence of insecticides can only be surmised from population curves obtained from fields where insecticides were not a factor. In the absence of insecticides, this population would probably have remained at a higher level through late July and into early August. The nymphs which were killed by the insecticide application on July 12 would likely have given rise to higher peaks of adults than occurred in late July and early August. Those adults contributing to the peaks in late July and early August may well have resulted from migration into the field, and from resident eggs not affected by the insecticide.

**Jack (1964).** This cotton field was located in the northcentral region of the Imperial Valley approximately 10 miles southeast of the Elmore location. The field was separated from a sugar beet field on the west by a small irrigation canal and a narrow dirt road.

*Empoasca solana* adults were present in very low numbers in both cotton and sugar beets until the first week in June (fig. 23), at which time a population increase was evident in both fields. This increase accelerated in both fields the latter part of June and continued to a peak in the cotton field in late July. The increase did not result in nearly as high a peak in sugar beets as in cotton. After reaching a peak of 1100 adults per sample in the sugar beet field on June 25, the numbers fell off rapidly to a low level a week before harvest in mid-July. In cotton, the higher population level

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**Fig. 21.** Population curves (1964) for *E. solana* in the Elmore cotton field, Imperial Valley.
with a peak of 7300 adults per sample held until August 1 when an insecticide application was made. After insecticides were applied the population level began a decline which continued through August. Several more insecticide applications were made, and after these were made the population remained at a low level to the end of October when defoliation took place. Here, as in the other fields where insecticide applications were made, it is felt that the higher level of the population would have been maintained for a longer period of time in the absence of insecticides.

Jack (1965). This cotton field was in the same location as the previous Jack (1964) field. The situation was changed somewhat in that sugar beet fields were separated from the cotton field on both the north and east sides by small irrigation canals and narrow dirt drives.

Adult *E. solana* were present in relatively low numbers in both sugar beet fields when sampling was begun, in early November 1964 for the east field and in mid-March for the north field (fig. 24). In the east field, the population level remained low through mid-March when it began to rise in early April. This level remained fairly constant until early May when a rapid rise took place which was terminated by harvest in mid-May. At this time, the level had reached 8800 adults per sample. In the north sugar beet field, no increase was evident in April, as occurred in the east sugar beet field. However, there was a rapid increase in early May which continued through to mid-June to a peak of 16,400 adults per sample when harvesting began on June 15. The population then declined through to the end of harvest at the first of July.

The population level in the cotton field was extremely low through the first 2 weeks in May but then rose rapidly in early June. From this initial peak, the level rose to a peak of 35,500 adults per sample in late June. A major decline then occurred and was further accelerated by an insecticide application in early July. After this insecticide application, a low population level was
maintained through to early November when defoliation took place. Here again, it is probable that in the absence of insecticides this population would have again increased to a high level which would have been maintained through July rather than declining to a lower level which was maintained the remainder of the season.

Meloland (1965). This cotton field was located in the southeast portion of the Imperial Valley approximately 20 miles southeast of the Jack field. Although no sugar beets were immediately adjacent to the cotton field, a number of sugar beet fields were within 0.5 mile. The first samples in early June showed that the population of _E. solana_ was undergoing an initial increase which continued through July (fig. 25). After the peak in July of 25,300 adults per sample, a decline set in which carried through to early September when two insecticide applications directed toward stink bugs, _Euschistus_ sp., were made. Sampling was discontinued after insecticides were used, but it is felt that such usage did not drastically affect the population curve as they were applied late in the season when the population level is normally low.

**Influence of Sugar Beets upon Leafhopper Populations on Cotton**

Reynolds and Deal (1956) reported that large populations of _Empoasca solana_ build up in sugar beets and migrate into the breed on cotton when conditions become unfavorable in the sugar beets. As was previously noted, the growing patterns of the two crops in the Coachella and Imperial Valleys have been such that one or the other crop is available to the leafhopper throughout the year.

The data obtained during the current study substantiate the observations reported by Reynolds and Deal (1956). However, the influence of sugar beets has been found to vary greatly from situation to situation.

The most obvious situation was when the proximity of sugar beets lent directly to the development of the leafhopper population in the adjacent cot-
ton field. This is shown most clearly in figure 19 (Rummonds, 1964).

Population curves presented in figure 19 show a decline in numbers of adult *E. solana* in sugar beets in early June, and a corresponding increase in adults present in the cotton. Insufficient numbers of nymphs were present in cotton at this time to give rise to such a sustained increase in the numbers of adults. Therefore, the initial increase must have been due mostly to movement of adults into the cotton. The only source in the area of large numbers of adults was the adjacent sugar beet field. A direct correlation thus appears to exist between population decrease in sugar beets and population increase in cotton.

On comparing situations with cotton adjacent to sugar beets (Rummonds, 1964) with cotton far removed from sugar beets (Kennedy, 1964, Rummonds, 1965) in the Coachella Valley, it is found that not only did the leafhopper population build to a higher level earlier in the season when sugar beets were a factor but that the higher level was also maintained for a longer period of time. The population curve presented in figure 20 (Rummonds, 1965) represents one of the above cotton fields in 1965 when no sugar beets were grown in the area as opposed to 1964 (fig. 19) when sugar beets were adjacent to it. As is shown, much lower population levels were reached in 1965 than in 1964. It appears logical to conclude that a large portion of the differences was due to the absence of sugar beets, although some may be attributed to differences between seasons and other factors. Population curves obtained in the Imperial Valley do not present as distinct a picture as those obtained in the Coachella Valley. However, even though the picture is not as distinct as may be desired, it would appear that a greater influence was exhibited by sugar beets here than in the Coachella Valley.

Another factor which may have contributed to the indistinctness of this picture is that in the Imperial Valley cotton and sugar beets have had a much longer and closer association than they
have had in the Coachella Valley. As a consequence, *E. solana* may have achieved greater independence from a single crop host. In this respect, it was early noted (Reynolds *et al.* 1965) that *E. solana* had become abundant on sugar beets several years before becoming a problem on cotton. It may well be that this insect has become less dependent upon sugar beets over the intervening years and has adapted to cotton as another favored host. Supporting this hypothesis are the occurrence of damaging populations of *E. solana* in cotton fields far removed from sugar beets, the occurrence of *E. solana* in the cotton earlier in the season than previously noted (Reynolds 1967), and the maintenance of moderate populations in the cotton later in the season after sugar beets have been harvested and ceased to be a factor.

Population curves presented in figure 24 (Jack, 1965) present two different situations in the same location: one where sugar beets contributed directly to population development on cotton, and the other where the contribution was less direct. The east field of sugar beets quite possibly contributed directly to the development of *E. solana* populations in both adjacent cotton and sugar beets. The population in this sugar beet field increased earlier than either of the other two fields, and was harvested earlier than the sugar beets in the north field. As a result of the harvesting operation the leafhopper adults were forced to find new host material, and this was readily available in adjacent cotton and sugar beets.

In the latter two fields, populations increased at approximately the same time and rate. However, the population in the sugar beet field (north field) declined during the harvest period. During this same time, the population in the cotton continued to increase, reaching a level some five to six times the level reached in most of the other fields studied.

The three population curves show that nymphs of *E. solana* did not appear in numbers in the cotton field until mid-June after the first peak of adults had been reached. Therefore, the adults forming the major part of this first peak had to originate outside the
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cotton field. It also appears that the adults comprising the first peak in the north field of sugar beets for the most part originated in the east field as nymphs appeared in the north field concurrently with the adults. Thus, the east field contributed directly to the development of leafhopper populations in both the north field of sugar beets and the cotton by contributing large numbers of adults to both fields.

The relationship of the north field of sugar beets to the cotton is less distinct. A large portion of the major peak in population in cotton may well be due not to breeding within the cotton field but, rather, to movement of adults into the field from the north field of sugar beets—a decline in numbers in the sugar beets took place during harvest while a sharp increase in adults in cotton took place at the same time. It would appear that the numbers of nymphs present in the cotton field prior to this major peak were not sufficient by themselves to support such a high level of adults.

A third situation is represented in the population curves presented in figure 23 (Jack, 1964). Here, sugar beets were present but appeared to play a small role in the development of the population of E. solana in the adjacent cotton field. The sugar beets may possibly have contributed leafhopper adults to the first peak in the cotton; however, in the absence of measurements of the movement between these

Fig. 26. Numbers of adult E. solana caught on sticky board traps placed between a cotton field and a sugar beet field, Jack (1965) area, Imperial Valley. Traps installed 27 May 1965. Each bar represents the catch during period between counts. Figures at end of bar are numbers of adults caught.
Fig. 27. Population curve proposed for *E. solana* in cotton fields far removed from influence of sugar beets, Imperial Valley.

Of the eight population curves representing *E. solana* in cotton fields, only two reached levels above 8000 adults per sample. In the Jack 1965 field (fig. 24), the level reached was near 32,500 adults per sample, while in the Meloland 1965 field (fig. 25), the level reached was near 25,200 adults per sample. Both of these fields were in areas of intensive sugar beet culture. “Normal” population curves for *E. solana* as used here refer to those population trends exhibited in cotton fields far removed from the influence of sugar beets. In areas of intensive farming (such as the Imperial Valley) normal curves may be the exception rather than the rule.

In 1964 and 1965, cotton fields far removed from sugar beets were surveyed in both the Coachella and Imperial Valleys (figs. 18, 20–22, 25). If a composite curve, representing the data presented for those fields far from the influence of sugar beets were drawn it is believed that it would be similar to that presented in figure 27. Adults would be present in low numbers in the field through May, at which time a gradual increase would take place and would continue through mid-June into July. A rapid increase to a peak of 4000-5000 adults per sample would occur in late July. A somewhat gradual decline would then occur, resulting in a low population level from the latter two fields, supporting data is not available.

Measurements were made of the relative amount of movement of adults between the Jack (1965) cotton field and the sugar beets to the north. This study showed (fig. 26) that through late May and early June the major portion of the movement was from the sugar beets into the cotton, even though the prevailing winds were blowing in the opposite direction. This trend was reversed in late June, but this reversal is believed to represent random movement, as it was in the direction of the prevailing winds and the sugar beets in that area of the field had been harvested. Even considering the period of the reversal, total movement favored the cotton over the sugar beets.
part of August to the time of defoliation at the end of October.

**Influence of Temperature upon Abundance of E. solana**

Interpretations of the influence of temperature upon leafhopper abundance are based upon comparison of the population curves previously presented in figures 18 through 25, and upon ambient mean temperatures. It is realized that ambient temperature varies somewhat from the temperature prevailing in the microclimate of the insect, but it is believed that the temperature-abundance relationships will nonetheless hold true.

No obvious correlations between precipitation and the abundance of *Empoasca solana* in desert valleys were present. The Coachella and Imperial Valleys receive little rainfall, the yearly average in both areas being near 2 inches (U. S. Weather Bureau 1964, 1965). Most of this occurs in November and December—a time when leafhopper are at a low population level due to factors other than precipitation. Monthly precipitation figures are included with the temperature data (figs. 28, 29) for comparison with each population curve. In the cotton fields studied, the general pattern appears to be an initial increase in the population of *E. solana* in June and early July after a period of time when the mean temperatures have been near or above 80° F. In all the cotton fields except one, the higher population levels occurred during the warmer summer months when mean temperatures were at or above this level.

In two fields (figs. 19, 23), there were indications that high temperatures, as shown by mean temperatures near or above 90° F, adversely affected reproduction. In these fields numbers of nymphs declined sharply as mean temperatures neared, or rose above, 90° F. Adverse effects of high temperatures were manifested in the laboratory as reduced longevity and fecundity. The population levels, both nymphs and adults, in all cotton fields studied invariably declined by mid- or late August regardless of prevailing mean tem-
Fig. 29. Mean temperatures and monthly precipitation, Brawley, Imperial Valley.

temperatures which often were still in the favorable range. This would indicate that other factors, such as host suitability and photoperiod, may be exerting a more powerful influence upon population levels in the latter part of the season than in early and mid-season.

A somewhat different picture is presented in sugar beet fields. Sugar beets are not grown in lower desert valleys during July and August because higher temperatures are not favorable for good root growth, and also because it is desirable to provide a host-free period for combating the beet leaf hopper, *Circulifer tenellus* (Baker), the vector of curly top virus of sugar beets. Therefore, population increases of *E. solana* in sugar beets are terminated before their peak by harvesting beets grown for sugar, as well as by poor growth of beets grown for cattle feed. Most population curves representing *E. solana* in sugar beets may, therefore, well have shown further increases if conditions had remained favorable. Under prevailing conditions, increases in the population of *E. solana* in sugar beets first became evident when mean temperatures were in the high 60’s. The major increases occurred during periods when the mean temperatures ranged in the 70’s. The influence of higher temperatures could not be studied in sugar beets because of harvest before such temperatures occurred.

In summation, it was found that population increases in the field were closely correlated with the mean temperature. Population levels showed slight increases when the mean temperatures ranged between 60° to 70° F, greater increase when the range was 70° F to 80° F, and greatest increase when the mean temperatures were in the 80’s. Mean temperatures near or above 90° F, appeared to inhibit reproduction, as evidenced by a decline in the number of nymphs when mean temperatures reached this level.

**Overwintering**

According to Oman (1949), some species of the genus *Empoasca* overwinter as adults while other species overwinter in the egg stage. Of the six species associated with cotton in California, *E. abrupta*, *E. fabae*, *E. filamenta*
and *E. solana* are reported to overwinter as adults (Manis and Turner, 1942; Smith, 1942; Michelbacher *et al.*, 1955; Ross *et al.*, 1965). No information on the overwintering condition of *E. arida* or *E. mexara* is available. Ross *et al.* (1965) reported that *E. solana* occurs throughout both the tropical and subtropical regions and, in summer, may occur as far north as the Canadian border. They also state that in winter most individuals in the temperate region are killed by cold temperatures, although a few survive at the southern edge of this region. This is evidently the case in the Imperial Valley, as these authors place the northernmost winter record for this species at about 31° latitude, while the Imperial Valley lies at approximately 33° latitude.

Adults and nymphs of *E. solana* were found (fig. 30) throughout winter (November–March) on sugar beets, with the exception of February 12 when the adults but no nymphs were found. Although both stages were present in low numbers during this time, rapid population increases occurred when conditions became favorable in early spring. This agrees with the observation of Hills *et al.* (1944) who reported that *E. solana* occurs and breeds in sugar beet fields throughout the winter months in Arizona, but that the numbers are somewhat reduced during January and February. In another study it was also determined that when adults were present mature eggs were present in at least some of the females (figs. 30 and 31). This information, together with the presence of nymphs throughout the winter, would indicate that some reproduction occurs during winter when temperatures become favorable. The sex ratio during this time was also determined (figs. 30, 31). No direct correlations between sex ratio, per cent females with mature eggs, and abundance of the adults or nymphs are apparent.

*E. fabae* is reported (Ross *et al.* 1965) to overwinter as the adult in the more southerly parts of the U. S., with its more northern distribution due to
migration of adults each spring. The western population of *E. fabae* apparently is confined to warmer areas of the state where winter temperatures are moderate. However, it appears that in the desert valleys of southern California *E. fabae* may be replaced by *E. mexara*. Records of *E. fabae* from these areas have not been verified and may involve confusion of the two species, as they are similar morphologically and biologically. *E. filamenta* has been reported as overwintering as adults on such plants as orange, winter crops, and weeds in California (Smith, 1942) and as adults in trash and debris along fence rows in Idaho (Manis and Turner, 1942).

**Effect of Chemical Controls Directed towards *Empoasca solana* upon the Integrated Control Program**

The pest control program on cotton in the Coachella and Imperial Valleys is one which has evolved to its present state over a number of years (Reynolds, 1967). This integrated control program is based primarily upon careful field evaluation of insect populations, judicious use of insecticides, and preservation of native predators and parasites. Cultural methods also play an important role in the program (Stern et al., 1959). A major factor contributing to its efficiency is the reduction or elimination of early- and mid-season insecticide applications. Chemical controls aimed towards *E. solana* on cotton are generally applied during this period. Injudicious choice or application of insecticides at this time could seriously disrupt the program.

Recognizing that chemical controls for *E. solana* on cotton in southern California are generally necessary, we must nevertheless disrupt the over-all program as little as possible. Accordingly, selective insecticides such as demeton and trichlorfon are currently recommended for control of *E. solana*.
on cotton in the Imperial Valley (Reynolds, 1964; Reynolds et al., 1965).

Continued research on selective insecticides and the biology and ecology of the arthropod fauna of cotton fields would further the understanding of the bases and processes of integrated control on cotton. Such information is necessary for further implementation of integrated control programs (Smith and Reynolds, 1966).

Natural Enemies of *Empoasca solana*

Studies on natural enemies of *Empoasca solana* were confined to the association under field conditions of various predators and parasites with the leafhopper, and to determination of the seasonal occurrence and abundance of several hymenopterous egg parasites. No studies were conducted on the biologies or efficiencies of these natural enemies.

Predators

A number of predators were observed feeding upon the adults or nymphs, or both, of *E. solana* in the cotton fields. Many of these predators reach high population levels in the fields and undoubtedly exert some influence upon leafhopper population levels. The nature and extent of this influence was not determined, as studies were confined to casual observation in the field. Most of these predators are general feeders (van den Bosch and Hagen, 1966) and prey upon such other insects in the cotton fields as the cotton leaf perforator, *Buccalatrix thurberiella* Busck, the bollworm, *Heliothis (= Helicoverpa) zea* (Boddie), *Lygus* spp. and many others. Predators observed feeding on *E. solana* in Coachella and Imperial Valleys were:

- **Neuroptera**: Chrysopidae
  - *Chrysopa* sp., probably *Chrysopa carnea* Stephens.

- **Hemiptera**: Anthocoridae
  - *Orius* sp., probably *Orius tristicolor* (White).

- **Hemiptera**: Lygaeidae
  - *Geocoris* sp., probably *Geocoris punctipes* (Say).

- **Hemiptera**: Nabidae
  - *Nabis* sp., probably *Nabis americoferus* Carayon.

- **Hemiptera**: Reduviidae
  - *Zelus* sp., probably *Zelus renardii* Kol.

- **Sinea** sp.

- **Arachnida**: Araneida
  - Thomisidae: crab spiders.
  - Lycosidae: wolf spiders.
  - Miscellaneous spiders.

Parasites

Emphasis in this aspect of the study was placed upon the hymenopterous parasites of the eggs of *E. solana*. Three of these parasites were found in the area, *Anagrus giraulti* Crawford (Mymaridae), *Abbella subflava* Girault (Trichogrammatidae) and *Aphelinoides plutella* Girault (Trichogrammatidae). Population curves for these three parasites in two sugar beet fields and five cotton fields in the Coachella and Imperial Valleys are presented in figures 32 through 38. These curves are based upon the abundance of the adult only.

*Anagrus giraulti* was by far the most abundant of the three egg parasites included in this study. It was found quite commonly in cotton and sugar beets in the Coachella and Imperial Valleys. In every field the population level of *A. giraulti* responded to increases and decreases in the numbers of *E. solana* indicating a close relationship between the two insect species. *A. giraulti* may not exert a great influence upon the population levels of *E. solana* even though a close relationship between the
Fig. 32. Population curves for Anagrus giraulti, Abbella subflava, Aphelinoides plutella and Empoasca solana in the Rummonds (1964) sugar beet field, Coachella Valley.

Fig. 33. Population curves for Anagrus giraulti, Abbella subflava, Aphelinoides plutella and Empoasca solana in the Rummonds (1964) cotton field, Coachella Valley.
Fig. 34. Population curves for *Anagrus giraulti*, *Abbella subflava*, *Aphelinaeidae plutella* and *Empoasca solana* in the Rummonds (1965) cotton field, Coachella Valley.

Fig. 35. Population curves for *Anagrus giraulti*, *Abbella subflava*, *Aphelininaeidae plutella* and *Empoasca solana* in the Jack (1964) cotton field, Imperial Valley.
Fig. 36. Population curves for *Anagrus giraulti*, *Abella subflava*, *Aphelinioidea plutella* and *Empoasca solana* in the Jack (1965) cotton field, Imperial Valley.

Fig. 37. Population curves for *Anagrus giraulti*, *Aphelinioidea plutella*, and *Empoasca solana* in the Jack (1965) sugar beet field, north field, Imperial Valley.
two appears to exist. The numbers of *A. giraulti* are generally in the low hundreds while *E. solana* may number around 5000 to 7000 per sample at the same time. The highest number of *A. giraulti* recorded during this study was 1312 per sample at a time when *E. solana* was numbering over 15,500 per sample.

*A. giraulti* overwinters in sugar beet fields in the Imperial Valley but it is present only in low numbers from November through February. The occurrence of adult *A. giraulti* in the Imperial Valley is contrary to the findings of Flock *et al.* (1962) who found no *A. giraulti* present in the area during the winter months and thus concluded that it must re-enter the area each spring. *A. giraulti* is a parasite of the eggs of *C. tenellus*, as are *A. subflava* and *A. plutella* (Muesebeck *et al.*, 1944; Flock *et al.*, 1962; Peck, 1963).

*Aphelinoidae plutella* was found during the growing season on sugar beets and cotton in somewhat greater numbers than *A. subflava*. In general there was little change in the popula-

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**Table 6**

ABUNDANCE OF EGG PARASITES OF *EMPOASCA SOLANA* DURING THE WINTER AND SPRING (1965), JACK SUGAR BEETS, EAST FIELD, IMPERIAL VALLEY

<table>
<thead>
<tr>
<th>Date</th>
<th>Numbers per 100 sample of parasites†</th>
<th>A. subflava</th>
<th>A. giraulti</th>
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<tr>
<td>11-6-64</td>
<td>1</td>
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<td>0</td>
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<td>24</td>
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†Insecticide treatment March 18, 1965.

*In Aphelinoidae plutella absent from all collections.*
tion level of A. plutella, but in four of the seven fields a population increase was evident in early- and mid-season. This increase most commonly occurred in late June or early July but also occurred as early as early May and as late as late July.

In three of these fields this increase in the numbers of A. plutella coincided with periods of increase in E. solana. In the fourth field this increase of A. plutella occurred in late May before any buildup of E. solana occurred in the field.

A. plutella is also a parasite of Aceratagallia sp. and C. tenellus, both of which can become abundant on certain plants in the area (Flock and Deal, 1959; Flock et al., 1962). A portion of the asynchrony evident between this parasite and E. solana may be due to buildup of the parasite upon the other leafhoppers. Adult A. plutella were not found in sugar beet fields during the winter months.

Abella subflava was found during most of the growing season in cotton and sugar beet fields but only in minute numbers. Adult A. subflava were found in extremely low numbers in sugar beet fields during the winter months. No evidence of a response by A. subflava to increases in numbers of E. solana was obtained.

More information on the biology and efficiency of the natural enemies of E. solana is necessary before a more complete integrated control program can be implemented in the Coachella and Imperial Valleys of California.

SUMMARY

1. On the basis of the type of injury inflicted by Empoasca solana upon cotton and sugar beets and the resulting decreases in crop quality and quantity, this species is determined to be a serious pest of these crops in the Coachella and Imperial Valleys of California.

2. The present distribution of E. solana includes the southern portions of the U. S. but apparently is of importance to cotton only in the desert valleys of southern California.

3. Of the six species of Empoasca associated with cotton in California, E. fabae and E. solana are phloem-feeders and E. abrupta, E. arida and E. filamenta are mesophyll-feeders. E. mexara is not assigned to either of these groups because of lack of information on its feeding habits and injury.

4. These six species of Empoasca can at present be separated only by characters of the male genitalia.

5. Hopperburn caused by E. solana upon cotton is described and appears similar to that caused by E. fabae.

6. The adult of E. solana is relatively long-lived and prolific at a constant temperature of 80° F in the laboratory. Temperatures of 70° F and 90° F are less favorable for the adult and reproduction.

7. In the field, abundance of E. solana is apparently correlated with mean temperature. Populations reach their highest levels when the mean temperatures are between 80° F and 90° F. Some population increase occurs when the mean temperatures are between 65° and 75° F, but as mean temperature nears or exceeds 90° F reproduction appears to be adversely affected.

8. No correlation of abundance of E. solana with precipitation was evident.

9. Adults of E. solana occur generally over the plant, while nymphs favor the undersides of older, more mature leaves of the lower portion of the plant.

10. Egg deposition also occurs primarily
in older, more mature leaves of the lower portion of the plant. Eggs are inserted into the tissues of the veins of the leaf, or in the leaf blade between veins. A few eggs may be inserted into the leaf petiole.

11. In the absence of adjacent sugar beet fields, the population curve takes the general form of a normal distribution curve. A slow increase in numbers through April and May gives way to a rapid increase in June, culminating in a peak in late June or early July. The population level in general rapidly declines through the latter part of July and August, with low numbers present in the field through the remainder of the season.

12. In cotton fields where adjacent sugar beet fields are exerting an influence upon the development of leafhopper populations, populations build up earlier in the season and reach higher levels than in cotton fields where sugar beet fields are not a factor. This is due to movement of the leafhoppers into the cotton fields from the sugar beet fields.

13. Much of the flight of E. solana between sugar beet and cotton fields in spring appears to be from sugar beets toward cotton.

14. Sugar beets are the primary overwintering site for E. solana in the Imperial Valley. Some reproduction and development takes place throughout the winter on this crop.

15. A number of insects and spiders were found to prey upon nymphs and adults of E. solana in cotton fields. Three hymenopterous parasites were found to parasitize the eggs of this leafhopper. Of the three egg parasites, only Anagrus giraulti appeared to be directly correlated with the abundance of E. solana.

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To simplify the information, it is sometimes necessary to use trade names of products or equipment. No endorsement of named products is intended nor is criticism implied of similar products not mentioned.
The symptoms of feeding by \textit{E. solana} on cotton include chlorosis and reddening of lower leaves of the plant. As a result of heavy feeding, young bolls and squares are shed and older bolls become soft and spongy. Yields are thus drastically affected.

Three hymenopterous parasites were found to attack the egg of \textit{E. solana}. They are: \textit{Abella subflava} Girault, \textit{Aphelinoidea plutella} Girault (Trichogrammatidae), and \textit{Anagrus giraulti} Crawford (Mymaridae). Only \textit{giraulti} exhibits an increase in numbers with an increase in the numbers of \textit{E. solana}.

Under controlled environmental conditions, \textit{E. solana} exhibits its maximum reproductive capacity at 80°F. The developmental period is shorter at 90°F than at 80°F, but the number of eggs produced at 90°F is also drastically reduced.

Six species of \textit{Empoasca} occur on cotton in California. These are \textit{E. abrupta} DeLong, \textit{E. arida} DeLong, \textit{E. fabae} (Harris), \textit{E. filamenta} DeLong, \textit{E. mexara} Ross and Moore, and \textit{E. solana} DeLong. \textit{E. abrupta}, \textit{E. mexara} and \textit{E. solana} occur on cotton primarily in the southern desert valleys while \textit{E. arida}, \textit{E. fabae}, and \textit{E. filamenta} occur on cotton primarily in the San Joaquin Valley. \textit{E. abrupta} and \textit{E. solana} are found on cotton in both areas. These species are differentiated on the basis of various morphological characters associated with the male genitalia.

Of these species \textit{E. abrupta}, \textit{E. arida}, and \textit{E. filamenta} are primarily mesophyll feeders, while \textit{E. fabae} and \textit{E. solana} feed primarily upon phloem tissues. Species causing the most damage, and thus of greatest economic importance on cotton in California, are \textit{E. fabae} and \textit{E. solana}, both primarily phloem-feeders.
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