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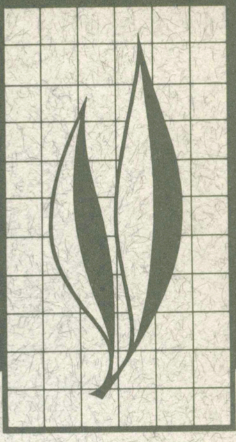

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Habitats and Dispersal of the Principal Leafhopper Vectors of Pierce's Disease Bacterium in the San Joaquin Valley

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The green sharpshooter (*Draeculacephala minerva* [Ball]) and redheaded sharpshooter (*Carneocephala fulgida* [Nott.]), important leafhopper vectors of Pierce's disease bacterium to grape and alfalfa, commonly inhabit permanent pastures and weeds alongside or in cropped fields. The species composition, stand, vigor, and persistence of grasses and other plants determine the extent to which sharpshooter populations can develop. Bermudagrass *(Cynodon dactylon)* is a highly preferred host of both sharpshooters and watergrass *(Echinochloa crusgalli)* is a favorite host of *D. minerva.* Irrigation and weed control practices that produce succulent stands of preferred host plants thus increase sharpshooter populations.

Conventional sweep net sampling was useful in phenological studies and for estimates of adult sharpshooter abundance in short, dry vegetation on warm days, but inadequate for estimates of nymphal densities. An analysis of the relationship of the average number of sharpshooters per sample and the number of samples to sampling reliability was made for both sharpshooter species. Discrete generations were determined most accurately by identifying the proportion of females with mature ovaries or the relative proportions of developmental stages, rather than by evaluating changes in the relative abundance of nymphs or adults.

Adult sharpshooters disperse throughout the growing season from breeding habitats. Flights occur predominantly from 30 to 90 minutes after sunset during summer evenings when the sunset temperature is above 70°F (21°C). *Draeculacephala minerva* is an active flier from April through September; *C. fulgida* has peak flights from May through mid-September. The green sharpshooter is attracted to lights during early evening. Nearly equal numbers of males and females are usually found in breeding habitats, but female *D. minerva* are about five times more dispersive than males. Populations and aerial densities of both sharpshooters varied enormously according to site and year, but changes in *C. fulgida* populations were much more volatile than those of D. minerva.

These studies suggest that the most productive strategy for preventing diseases spread by these sharpshooters is to eliminate and prevent habitats conducive to either sharpshooter, chiefly by weed control and irrigation practices.

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Alexander H. Purcell and Norman W. Frazier

Habitats and Dispersal of the Principal Leafhopper Vectors of Pierce's Disease in the San Joaquin Valley[1]

INTRODUCTION

PIERCE'S DISEASE (PD) has caused major losses of grapevines during periodic epidemics in California. Between epidemics, this usually lethal disease spreads less rapidly but individual vineyards can be seriously damaged. The pattern of occurrence of PD suggests that insect vectors were responsible for its natural spread (Hewitt et al. 1946), and xylem-feeding leafhoppers of the subfamily Cicadellinae (= Tettigellinae), commonly known as sharpshooters, were found to be capable of transmitting the causal agent of the disease (Frazier 1943; Hewitt et al. 1942, 1946). In the Central Valley of California two sharpshooter species, the green sharpshooter *Draeculacephala minerva* (Ball) and the redheaded sharpshooter *Draeculacephala fulgida* (Nottingham), are considered the most important PD vectors because of their abundance relative to other xylem-feeding species (Hewitt et al. 1942; Winkler et al. 1949). In coastal California grape-growing regions, the blue-green sharpshooter *Graphocephala atropunctata* Signoret (= *Hordnia circellata*) is the principal PD vector (Hewitt et al. 1942; Purcell 1975).

The same bacterium that causes PD also induces alfalfa dwarf disease (Frazier 1943; Hewitt et al. 1946; Goheen et al. 1973) and almond leaf scorch disease (Mircetich et al. 1976; Davis et al. 1979), and is pathogenic in other plant hosts such as white sweet clover (Freitag 1951). *Draeculacephala minerva* and *C. fulgida* are capable of inoculating alfalfa (Frazier 1943) and almond (Mircetich et al. 1976; Purcell 1980) with Pierce's disease bacterium and are considered important in the natural spread of alfalfa dwarf (Nielson 1968). *Draeculacephala minerva* may be involved in the spread of almond leaf scorch disease, but there is no clear evidence of the identities of the chief vectors responsible for natural spread (Purcell 1980).

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In the 1940s, the causal agent of Pierce's disease was thought to be a virus (Hewitt 1939). In 1967, evidence that some of the leafhopper-transmitted "yellows viruses" might be mycoplasmas or other procaryotes (Doi et al. 1967) prompted reinvestigations of the etiology of PD using antibiotic therapy (Hopkins and Mortensen 1971). Antibiotic and heat therapy and microscopy (Goheen et al. 1973; Hopkins and Mollenhauer 1973) suggested that a bacterium was the causal agent of PD. This hypothesis was confirmed by the culture and proof of pathogenicity of the causal bacterium (Davis et al. 1978). These findings allowed a new perspective of many aspects of PD. The proposed mechanism by which leafhopper vectors transmit the causal agent (Purcell et al. 1979), the lack of persistence through winter of many late season infections of grapevines (Purcell 1981b), and the very broad ranges of symptomless host plants (Freitag 1951) and vectors of the causal agent (Frazier 1944, 1965), make better sense in light of a bacterial rather than a viral etiology. This radical advance in understanding of the cause of PD, however, had little apparent effect on understanding the biology of PD vectors, but this new awareness should change some basic perspectives of disease epidemiology, such as climatic effects on disease spread and development (Purcell 1982).

Observations that the worst outbreaks of PD were invariably in vineyards or portions of vineyards near permanent pastures, alfalfa fields, or permanent irrigation ditches led early investigators to concentrate on these habitats as possible sources of insect vectors. The regular occurrence of PD-infectious green and redheaded sharpshooters in such locations was evidence of the importance of these two leafhoppers in the natural spread of PD (Frazier 1943). Neither *D. minerva* nor *C. fulgida,* however, was ever found frequently on grape. Grape apparently was only an occasional or "accidental" host plant (Winkler et al. 1949) that, nonetheless, could be infected after exposure to infective individuals of either species (Frazier 1943; Severin 1949). Sharpshooter dispersal, therefore, is important in the spread of PD. For these reasons, the principal objectives of our studies were to determine habitat preferences and dispersal behavior of the green and redheaded sharpshooters. This paper includes unpublished observations and experiments made during the 1940s by one author, Norman Frazier (NWF), and other results from 1976 to 1980 of research by Alexander Purcell (AHP).

REVIEW OF KNOWN BIOLOGY

The green sharpshooter, *Draeculacephala minerva,* is commonly abundant in the Central Valley and coastal valleys of California. It is recorded from northern California through Panama, as far east as southern Texas, and has been introduced into Hawaii (Young and Davidson 1959). Gibson's (1915) studies of *D. mollipes* (Say) in Arizona were probably of *D. minerva* (Young and Davidson 1959).

Although recorded from a large number of plant hosts, *D. minerva* is especially abundant in grasses and sedges in moist habitats, bermudagrass (*Cynodon dactylon* [L.] Pres.) being an especially favored host (Hewitt et al. 1942). Irrigated pastures, bogs, stream banks, or locations with a luxuriant but not dense growth of grasses were favored breeding habitats. This leafhopper was collected regularly from weedy stands of alfalfa and from weeds in vineyards (Winkler et al. 1949). On the basis of its abundance and widespread distribution, the green sharpshooter was considered to be the most important vector of Pierce's disease bacterium in central California (Winkler et al. 1949).

No mass movements of the green sharpshooter have been noted. Its dispersal seems to be quite localized, with the greatest activity during early evening (Winkler et al. 1949). No details of quantitative studies of dispersal have been published. High winds were noted to suppress flight activity (Gibson 1915).

Three generations were reported in the San Joaquin Valley. Eggs of the first generation were deposited in late February, the second generation in early May, and the third generation in mid-July. Apparently a small fourth generation was produced from eggs laid in August (Winkler et al. 1949). In southern Arizona, Gibson (1915) observed six generations in field cages that corresponded closely to field observations. Using Gibson's data for average egg development, a developmental threshold temperature of about 13.5°C (56°F) can be estimated for first generation eggs, using a regression of the reciprocal of development time against average temperature. The data are inadequate to estimate other developmental thresholds and rates. The total nymphal period varied from 20 to 51 days depending upon the season.

As in California studies (Hewitt et al. 1942; Winkler et al. 1949), the main overwintering form observed in Arizona was the adult stage (Gibson 1915); most were a brown color phase that subsequently produced typical green-colored progeny. Gibson's (1915) regular observations of brown adults leads to the supposition that he was working with *D. minerva* rather than *D. mollipes.* Only general summaries or conclusions of the seasonal occurrence of brown and green color forms have been published, however.

The redheaded sharpshooter *C. fulgida* is also common in the Central Valley of California. Four generations per year were reported in central California, with eggs hatching from March through August. Bermudagrass was reported as the most important host plant. However, *C. fulgida* seems to prefer habitats with sparser, less luxuriant plant growth than does *D. minerva* (Winkler et al. 1949). Based on its abundance and distribution, the redheaded sharpshooter is considered to be an important vector of Pierce's disease in California.

Estimates of sharpshooter abundance

Estimates of the relative abundance of *D. minerva* and *C. fulgida* were an essential part of extensive studies in the 1940s of the relation of sharpshooter populations to the incidence of Pierce's disease. Sweep net samples of adults and nymphs of the green sharpshooter and redheaded sharpshooter for a given year were compared to the incidence of PD in the same or succeeding year when the results for quarter-section vineyard blocks were analyzed. There was no significant correlation when data from 10 acre blocks was analyzed (Winkler et al. 1949). It is possible that samples taken from smaller plots showed no correlation because of basic inaccuracies in the sweep net method, inadequate sample size, or inappropriate analytical methods. Thus an evaluation of the accuracy and reliability of this traditional sampling method in estimating sharpshooter populations was needed to put into proper perspective the large amount of published and unpublished data derived from sweep net sampling of sharpshooters.

METHODS AND MATERIALS

Sampling methods for sharpshooters

A standard sample unit of 50 sweeps with a 38.1 cm diameter circular net was compared to 25 placements in the same location by a D-vac "vacuum insect net" suction sampler (D-vac Corp., Riverside, Calif.) with a 33.0 cm diameter intake. In D-vac samples, a plastic cone that increased suction pressure by reducing the intake to a 19.7 cm (7.75 in) diameter was used for most samples. The starting point of each sample was randomized within an established plot boundary. The sweeps were made with a pendulum-like swing with the rim of the net as close as possible to the ground at the low point of the swing. Sweeps were made with a steady rhythm about 1.2 m (5 ft) apart as the sampler walked at a slow pace. In taking D-vac samples, the intake was pressed flush to the ground for 2 to 3 seconds and then moved about 1.8 m (6 ft) to the next placement point for 25 total sucks. A variety of pastures, orchard or vineyard cover crops, and alfalfa fields were sampled from 1976 to 1980, taking from 8 to 12 samples with each method per site. Each sample was transferred to a plastic bag, heated overnight at approximately 40°C (104°F), sorted, and counted. Alternatively, some bags were inflated with carbon dioxide to anesthetize the insects prior to counting.

Phenological studies: *Draeculacephala minerva*

An old alfalfa field which consisted of approximately 70 percent grasses near the Kaweah River approximately 1 mile south of Woodlake, Calif. was sampled by sweeping in 1943 to 1945. The field was used as a pasture and periodically was lightly grazed but the site was never treated with insecticides. Samples were taken biweekly from November through February and weekly for all other months. Enough sweeps were made to capture at least 25 *D. minerva* on each date, except during winter months when it was sometimes not possible to collect this number. On the same day of capture, collections were sorted to record the numbers of each larval instar, male and female adults, and their color phase. Females were dissected under a microscope and the condition of the ovaries identified as either containing maturing eggs or not. Similar collections were made from roadside weeds 14 miles west of Fresno, Calif. where the redheaded sharpshooter could be consistently captured. On occasions during winter months when *C. fulgida* were not found in roadside weeds, one or more of several nearby sites were sampled. Sampling continued in this location and other pastures near Gilroy, Milpitas, and Geyserville.

Forty-three observation sites listed in table 2 were visited regularly from 1977 to 1978 for studies of sharpshooter ecology and to collect sharpshooters for infectivity testing. Each site was visited monthly—usually every 2 weeks from January through September 1977. Sites were located from 13 km (8 mi) north of Visalia to within a 10 km (6 mi) radius of Earlimart. Table grape vineyards were especially emphasized. During each visit, at least 200 sweeps were made of weeds, plant cover, or alfalfa, and the numbers of sharpshooters collected in each 50 sweeps were recorded. Weed growth and cultivation were also noted.

Weed control experiment

A long-term vineyard weed control plot at the University of California Kearney Horticultural Experiment Station at Parlier, Calif. provided an opportunity to investigate the occurrence of leafhoppers in different habitats created by different weed control treatments. The plot consisted of 'Thompson Seedless' grapevines planted in 1966 in a randomized complete block design with eight replications of five treatments. Each replicate consisted of three rows of 18 vines planted 1.8 m apart. The following five weed control methods were used.

1. Complete chemical: vine rows and middles (between rows) treated with chemical herbicides (1968-1970: Simazine, Paraquat, Trifluralin, Diuron; 1971-1978: Simazine, Nitralin Oryzalin, Glyphosate) with the objective of obtaining as complete weed control as possible.
2. Middles disced in spring only; vine row cultivated with a French plow.
3. Middles with a permanent rye grass cover crop periodically mowed in summer; vine rows sprayed with herbicides.
4. Middles with a barley cover crop in winter, disc-cultivated during the growing season; vine rows sprayed with herbicide.
5. Middles disc-cultivated during the growing season; vine rows sprayed with herbicide.

Sharpshooter populations in weeds or cover crop in each plot were sampled by sweep net. Twenty-five sweeps per row were made in two rows in each replicate. Samples were taken separately from the middles and the vine rows of each replicate in which enough weeds were present to sample. Plots without weeds were not sampled or only a few sweeps were made because of the scarcity of weeds on some sampling dates. Insecticides were usually applied in late May or early June to control the grape leafhopper *Erythroneura elegantula* Osborn, with second treatments in July in some years. A single application of 2.8 kg/ha (2.5 lb/acre) of Thiodan in a 1 percent (W/W) aqueous spray was applied on May 31, 1977.

Rotary nets

During studies of sharpshooter dispersal in the 1940s, four rotary nets were constructed by the Department of Agricultural Engineering at UC Davis, modified from the rotary net described by Barnes et al. (1939). Two nets of wire screen mesh cones 51.2 cm (20 in) wide at the mouth tapered to a 14 cm (5.5 in) diameter opening to which cloth bags were attached to collect captured insects. The outer rims of each net traveled a circle 4.2 m (13.8 ft) in diameter. The speed of the nets, usually about 36 revolutions per minute (rpm), was changed by selecting different pairings on doubly-grooved drive pulleys on the short and long axles. Two nets were powered by gasoline engines and were more prone to mechanical malfunctions than the two electrically-powered motors.

Net locations. Four rotary nets were positioned near vineyards within a 640 acre experimental area near Woodlake; described by Winkler et al. (1949). Net locations in these plots (Winkler et al. 1949) were as follows.

1. Northwest corner of block C-2, a vineyard with uncultivated land to the south and west. An electric-powered motor was used in 1944, replaced by a gasoline-powered motor in 1945, and moved to the center between blocks C5 and C6.

2. Northeast corner of block E10, an open field with a sump pond in 1943, planted to grapes in 1945. Gasoline power was used in 1943 and electric power in 1944, 1945, 1947, and 1948.
3. Southwest corner of block F9, an irrigated pasture. Gasoline-powered in 1944. In 1945, 1947 to 1948, an electric-powered net was sited across the avenue in the southeast corner of block F-12 at the margin of a vineyard with irrigated pastures, alfalfa, and uncultivated land to the east, south, and west.
4. Center of a 4 acre noncultivated area of sandy soil surrounded by vineyard blocks D6 and D7. Gasoline-powered.

Sticky mesh traps—1976

For studies of sharpshooter dispersal from alfalfa fields, large (1 W by 3.1 H m or 3.3 by 10 ft) vertical sticky traps were placed along each of the four sides of two alfalfa fields. These traps consisted of fiberglass 0.6 cm (0.25 in) mesh screens coated with Stickem Special (Michel & Pelton, Emeryville, Calif.) and suspended along 4 m metal pipe or wooden stakes. The traps were monitored throughout most of July and August 1976 along two alfalfa fields in Fresno County that harbored moderate populations of green and red-headed sharpshooters, and along two sides of an irrigated pasture several miles south of the alfalfa fields. At weekly intervals, captured sharpshooters were removed and counted in 25 cm (10 in) height intervals beginning at ground level. One field was cut 2 weeks before the other field, with cuttings made every 4 weeks in the same field, followed by irrigation 1 and 3 weeks after cutting.

RESULTS AND DISCUSSION

Comparison of D-vac and sweep net sampling

Over the entire range of values for average captures of adult *D. minerva* per sample, there was a significant correlation ($r^2 = 0.76$, 14 d.f., $p<0.001$) between sweep net and D-vac samples of the same site on the same date (fig. 1). The numbers of *C. fulgida* collected by D-vac were insufficient for statistical comparisons with sweep net samples.

Heavy morning dews made difficult the retrieval and processing of insects collected by either method. On two separate dates in August 1980, adult green sharpshooters were collected by sweep net ($n = 10$) in a 2 ha (5 acre) pasture east of Marysville in early morning, midday, and late afternoon. The average numbers (range 5.7 to 7.7) collected by each method were not significantly different (t-test, 14 d.f., $p>0.2$) among the three different sampling periods on either date over a range of temperatures of 17° to 39°C (64° to 102°F).

Overall, D-vac sampling collected 7.4 times as many nymphs as sweeping. There was no significant linear correlation ($r^2 = 0.33$, $p>0.1$) between the average numbers of *D. minerva* nymphs collected by D-vac and the average numbers collected by sweep net in 10 paired comparisons (fig. 2), but Spearman's rank correlation (Snedecor and Cochran 1967) of the same data was significant ($r_S = 0.77$, $0.05>p>0.04$). Although the numbers of other leafhopper species were not tabulated from these samples, the D-vac collection of nymphs of several leafhopper species was observed to be consistently many times higher than by sweep net, whereas sweeping often collected more adults. Moreover, D-vac often collected hundreds of saprophytic mites when only much lower numbers or none were obtained by sweeping. Apparently, very small (<2 mm) insects were collected less efficiently by sweeping. In the laboratory, *D. minerva* and *C. fulgida* caged on grasses, fed chiefly at the bases of the stems. We also have observed this behavior in the field, which would explain in part the disparity between the two methods in collecting nymphs. D-vac should collect a larger proportion of insects nearer the ground than sweeping, and thus approach measurements of sharpshooter density per area.

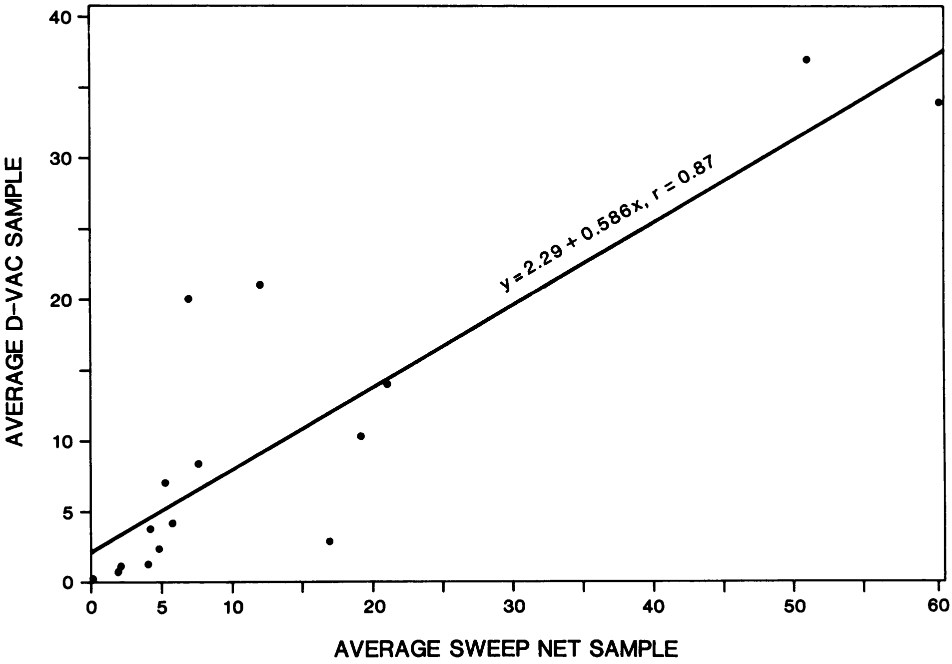

Fig. 1. Correlation of *D-vac* samples of adult *Draeculacephala minerva* with *sweep net* samples.

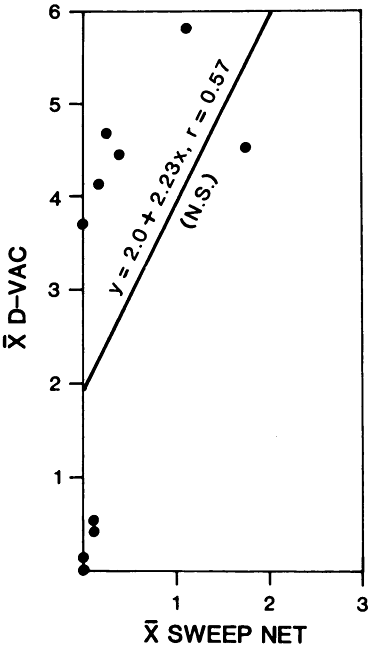

Fig. 2. Correlation of *D-vac* samples of *Draeculacephala minerva* nymphs with *sweep net* samples.

A cone adapter, which reduced the D-vac intake by 63 percent, increased collection efficiency, probably through increased suction. On six sampling dates in two pasture plots in 1980, there were no significant differences (t-test, 14 d.f., $p<.05$) between collections of adult *D. minerva* made with or without the adapter, even though the adapter reduced the area sample. Analysis of variance failed to reveal significant pasture-sampling method interactions. However, the excellent agreement between the two types of D-vac sampling tested ($r^2 = .87$, d.f. = 14, $p<0.005$) indicated that either method is a relative measure of *D. minerva* densities in low-lying vegetation. Sweep net sampling provided less reliable relative indices of adult populations that can be related to values obtained by D-vac sampling. The sweeping method was inadequate for estimating relative nymphal populations, except to the extent of recording their presence.

Sample reliability

The accuracy of relative sampling methods is determined by comparisons to absolute methods. Sampling reliability refers to the probability that the sample mean is representative of the true population density. Reliability can be gauged in terms of standard error of the mean ($S_{\bar{x}}$) relative to the mean ($\bar{x}$) (Southwood 1978), where $S_{\bar{x}} = Sn^{-1/2}$ (S = standard deviation, n = number of samples). Taylor's (1961) power law ($S^2 = a\bar{x}^b$) can be used to estimate the variance (S^2) as a function of the mean from the relationship:

$$S_{\bar{x}}/\bar{x} = (a/n)^{1/2}\,\bar{x}\,[(b/2)-1]$$

where a and b are coefficients of the regression equation described by $S^2 = a\bar{x}^b$. A wide range of values of $\bar{x}$ for *D. minerva* adults and *C. fulgida* from sweep net samples from pastures, alfalfa fields, and ditch banks from 1975 to 1980 is plotted against S^2 (log scales) in figure 3. The number of samples (n) required for a selected value of $S_{\bar{x}}/\bar{x}$ for each species is depicted in figure 4. A value of $S_{\bar{x}}/\bar{x}$ of 0.2 or less is considered adequate for many research uses (Southwood 1978). For *D. minerva,* this should be attained for 50-sweep samples of adults by taking an estimated 8 samples for $\bar{x} \geq 1$ and 3 samples for $\bar{x} \geq 10$. As $\bar{x}$ decreases to <1, the confidence limits (CL) that sample means closely estimate (i.e., within 20%) the "true" population mean, increase widely. Thus an $\bar{x}<1$ cannot be distinguished as significantly different from other small means unless large numbers of samples are taken. In most cases, however, such a small mean ($\bar{x}<1$) could be distinguished as significantly different from means greater than two by taking only eight samples. The confidence limits for treatment (or population) means ($\bar{x}_n$) can be estimated from the associated standard error ($S_{\bar{x}}$), which can be estimated from figure 4 for either species at the desired level of $S_{\bar{x}}/\bar{x}$), using the t-distribution: $CL = \bar{x} \pm t\,S_{\bar{x}}$. The distribution of variance relative to the mean (fig. 3) indicates an aggregated, hence non-normal, distribution. The correlation of log $S_{\bar{x}}$ with log $\bar{x}$ suggests that a log transformation of basic counts of sharpshooters should be made before using statistical methods of analysis based on the normal distribution.

The traditional and widespread use of the sweep net derives from its simplicity and speed of use. A large area of low-lying vegetation can be quickly surveyed or sampled by sweeping. Ideally, the numbers of insects collected by sweeping should be directly proportional to absolute densities. The basic problem with sweep net sampling is that this ideal is often not realized in practice, as many studies have shown (e.g., DeLong 1932; Gray and Treloar 1933; Beall 1935; Romney 1945; Fenton and Howell 1957; Nielson 1957; Saugstad et al. 1967; Byerly et al. 1978; Southwood 1978). The inaccuracies of the sweep net method derive from the influence of many variables on the number of insects captured by sweeping.

Temperature and wind may have substantial effects upon leafhopper catches in sweeps of low-lying vegetation (Romney 1945; Saugstad et al. 1967). Very short vegetation cannot be sampled effectively. In tall vegetation, sweeping collects arthropods only from the tops of plants taller than the net diameter (Southwood 1978). Our studies of sampling reliability and accuracy were based solely on short vegetation (<32 cm or 13 in) on dry, warm days without strong winds. Based on their correlation with D-vac sampling, sweep net samples provided a useful index for comparisons of adult populations for sample means greater than one sharpshooter per 50 sweeps, but could not be used where an accurate relative measure of nymphal densities or absolute densities were required.

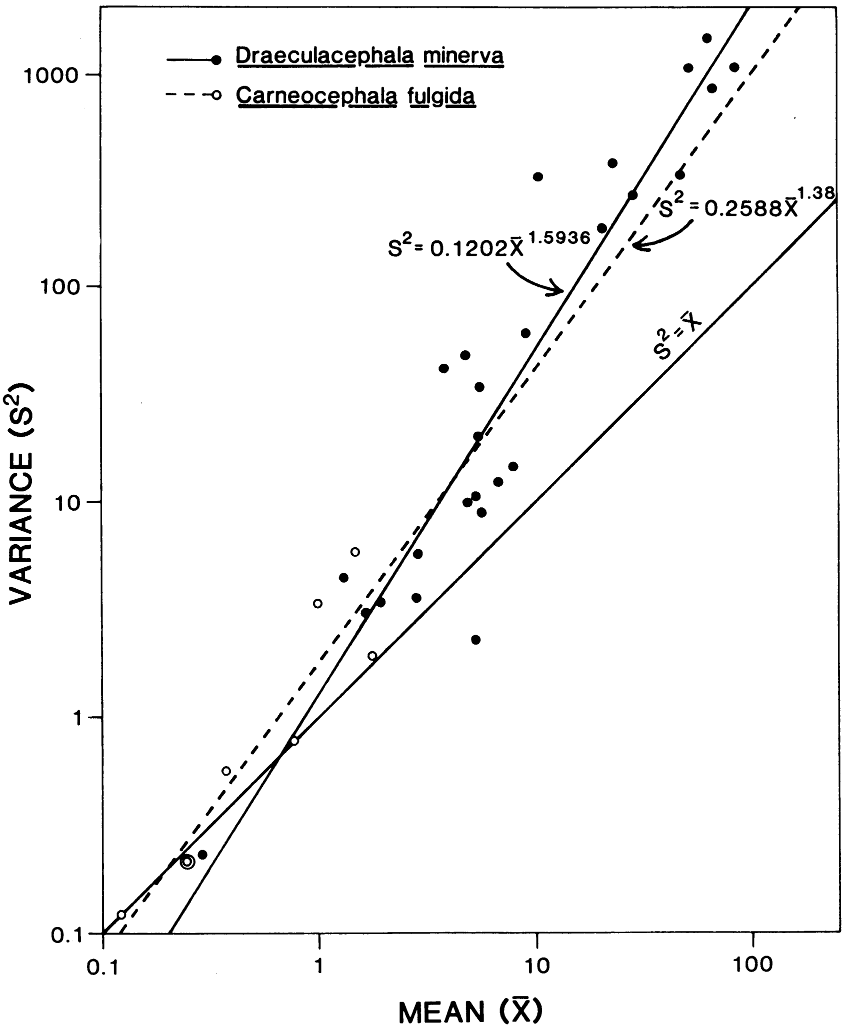

Fig. 3. Spatial distribution of adult sharpshooters in pastures according to Taylor's (1961) power law: a regression of the logarithm of the variance *(S^2)* against the logarithm of the mean *($\bar{x}$)* for *Draeculacephala minerva (solid circles)* and *Carneocephala fulgida (open circles)*.

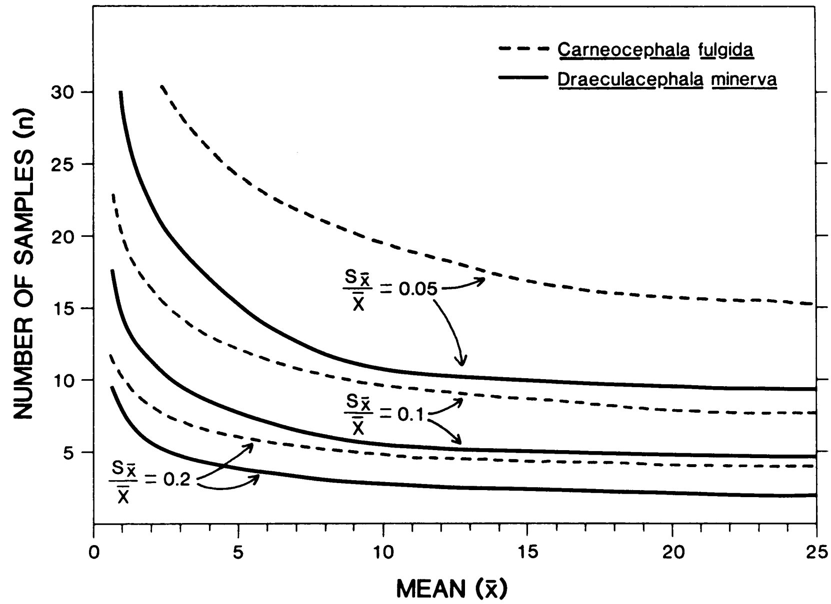

Fig. 4. Sample size required for selected values of the ratio, standard error (S.E.): mean *($\bar{x}$)* for *Draeculacephala minerva* adults *(solid line)* and *Carneocephala fulgida* adults *(broken line)*. Curves are derived from regression equations, figure 3.

Phenology: Seasonal life history

The number of generations per year of *D. minerva* and *C. fulgida* was deduced from periodic changes in the age structure composition of each species in samples taken routinely from several Central Valley sites over a three year period (1943 to 1945). *Draeculacephala minerva* had three major generations annually (fig. 5). Beginning in September the percentage of adult females that were gravid decreased sharply until February (fig. 6), which suggests that in the Central Valley this species enters reproductive diapause during autumn. Oviposition began in February and March, followed by the appearance of nymphs in March.

Brown-colored adults first appeared in late July (fig. 7). Apparently some nymphs of the second generation became brown adults, and a majority of the third generation matured into the brown color form. The brown form was rare or absent from collections made west of U.S. Highway 99 or from coastal locations. Intermediate colors varied from yellow-green or straw color to brown. The darker individuals are most common during late fall. Color polyphenism in the Hemiptera (including Homoptera) is commonly influenced by temperature, photoperiod, or host plant conditions (Müller 1979). The regular appearance of brown adults along the eastern side of the Central Valley and their absence on the western side, may have been caused by climatic differences between the eastern and western sides of central California during the late summer and early fall when these forms would be expected to be induced. Temperature especially might be expected to be a factor, but our observations do not offer any direct evidence on this question. The "citrus thermal belt" in the southeastern San Joaquin Valley is somewhat warmer during winter than more westerly portions of the valley. The brown color form has the obvious advantage of having better cryptic coloration to conceal it from predators against dead or dormant background

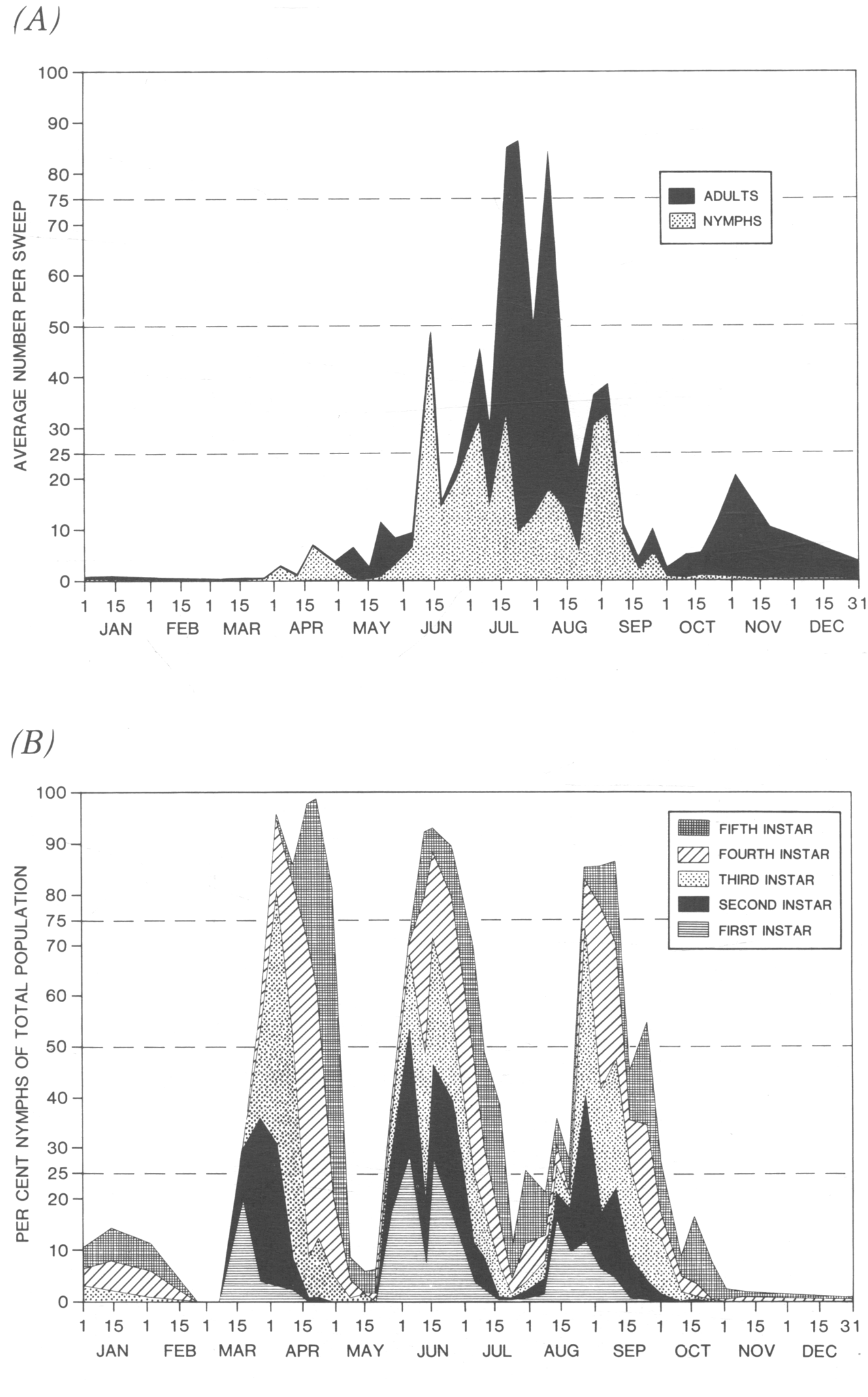

Fig. 5. *(A)* Seasonal abundance of adults and nymphs. *(B)* Age-structure of *Draeculacephala minerva* swept from a permanent pasture, Woodlake, Calif., 1943.

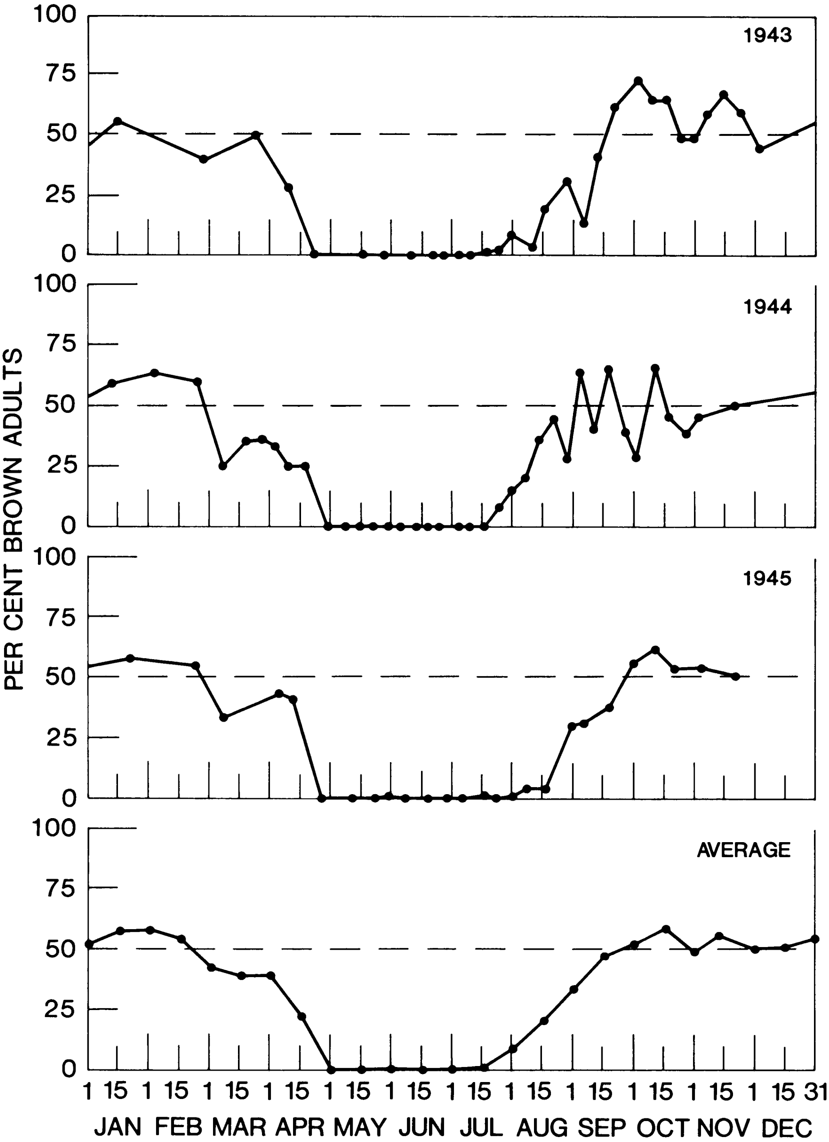

Fig. 6. Prevalence of brown color form *Draeculacephala minerva* adults, Woodlake, Calif., 1943 to 1945.

vegetation. The green color form is better camouflaged on live vegetation. The proportion of brown form adults remained relatively constant from October through February, however, so that any selective advantage of this color form of *D. minerva* during winter months was not evident from this study. A comparison of the data from figures 6 and 7 suggests that the adult color phase was not closely tied to ovarian diapause, because green adult females maturing in autumn were also in diapause.

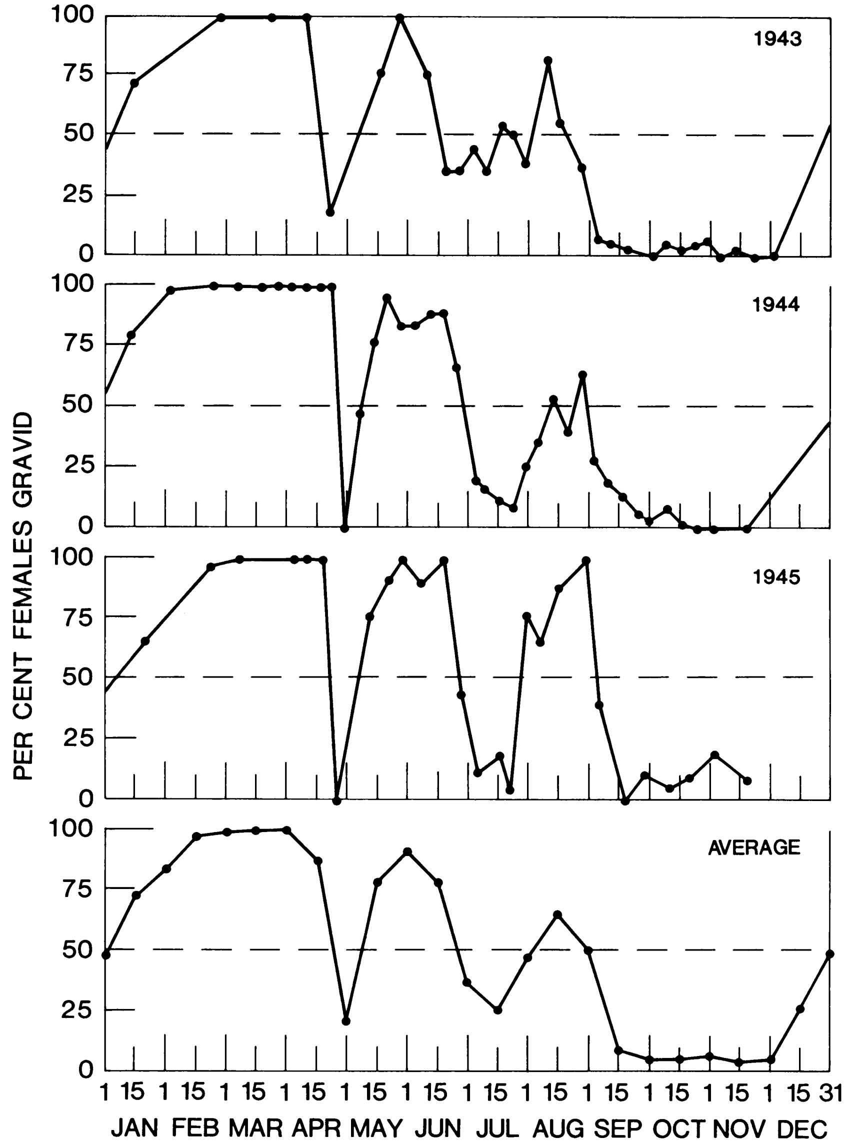

Fig. 7. Seasonal changes in ovary development (*gravid* = full of mature eggs) of adult female *Draeculacephala minerva,* Woodlake, Calif., 1943 to 1945.

Overwintering. Adults were difficult to collect during winter months, particularly during cold (below 7°C or 45°F) days, but adults were collected in higher numbers during warm days in late February and March, which suggests they are more active at warmer temperatures. Dissections of females revealed that brown-colored adults had larger fat bodies, which may be an adaptation to increase survival of overwintering adults during periods when food plants are scarcer. Third generation adults were noticeably less active than those of either the first or second generation. They were more inclined to "play dead" in the sweep net and were not as readily disturbed to flight from host plants during sweeping. The inactivity of overwintering adults may take advantage of the shelter that vegetation provides from frosts and rain.

Coastal generations. In north coastal locations (Gilroy, Milpitas, Geyserville) clear generational divisions were not as evident among populations of *D. minerva* (fig. 8) as in the Woodlake population. This may have resulted in part from the less frequent sampling and the fact that a wider area had to be sampled in order to obtain enough sharpshooters for dissections. The smaller populations could have also led to larger sampling errors (fig. 4). Nevertheless, the coastal populations clearly differed from Central Valley populations in the dates of generation peaks. In general, first generation nymphs appeared sooner but developed more slowly in coastal locations than did nymphs in the Woodlake plot. The evidence for reproductive diapause during autumn and winter months in coastal locations is blurred because sampling from these localities was less frequent and scattered over several sites. However, it is clear that in coastal locations ovarian development is delayed much less, if at all, during the winter than in the Central Valley.

The redheaded sharpshooter had four distinct generations per year (fig. 9). The appearance of each generation beyond the first could not be determined only from periodic changes in the abundance (per sweep density) of adults or nymphs. The periodic cycling in the age structure of the populations, however, indicates distinct generations, except that the beginning of the fourth generation probably was obscured by individuals surviving from previous generations.

The number of generations per year has been deduced for various leafhopper species from periodic changes in the abundance of adults (Rice and Jones 1972; McClure 1980; Purcell and Elkinton 1980). The pitfalls of this approach are illustrated by comparing our data for seasonal adult abundance (fig. 5*A*) with the population age structure for either *D. minerva* (fig. 5*B*) or *C. fulgida* (fig. 9). The seasonal changes in the percentage of adult females which were gravid were closely correlated with the periodic appearance in the Central Valley of new generations of both species. The rapid and short decreases probably result from the requirement for ovarian maturity after the adult molt in young female adults. However, this trend in ovarian development was not consistently noted in coastal localities for *D. minerva* (fig. 8).

Age structure analysis. Perhaps the most reliable indicator of generational distinctiveness was the seasonal periodicity of the various immature stages (figs. 5, 8, 9). Identifying and tabulating each instar is slightly more difficult and time-consuming than identifying a single instar, but the data provided by the more complete age structure analysis may avoid problems created by sampling artifacts. For example, it is logically impossible that the number of first instar leafhoppers is less than later instars of the same generation, but this appears to be the case from data shown in figures 5 and 8. As previously discussed, this is most likely the result of a sampling artifact: smaller instars are less efficiently sampled by sweeping than are larger instars, probably because of their smaller mass and the tendency of smaller instars to feed at the bases of plants. Differences in development times among larval instars would also influence the apparent abundance of that instar. Clearly, the abundance or density of each instar relative to other instars cannot be estimated from sweep net sampling. The regular seasonal changes of the composition of samples that are categorized as to instar, however, appear to be extremely useful in recording the number and time of appearance of distinct generations.

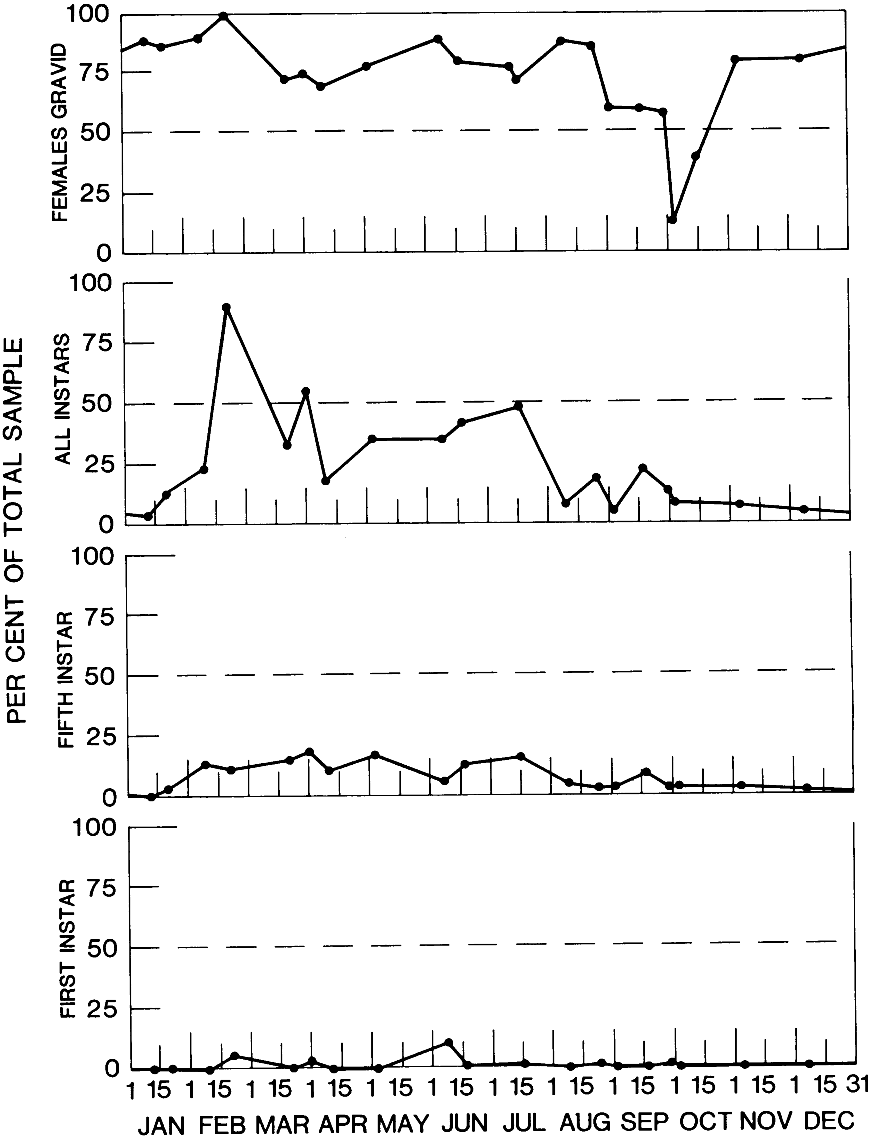

Fig. 8. Appearance of first and fifth instar nymphs, mature ovaries in adult females, and population density of *Draeculacephala minerva* from coastal localities; Gilroy, Milpitas, and Geyserville, Calif., 1943.

Major disruptive influences of insecticide applications or of cultivation were not factors in the sites in which the age structure of *D. minerva* and *C. fulgida* were observed. Such disturbances could complicate the analysis of life histories by either the age structure or adult abundance methods, although in most instances, the latter method would probably be more sensitive in assessing the effects on age structure of catastrophic events, such as insecticide treatment.

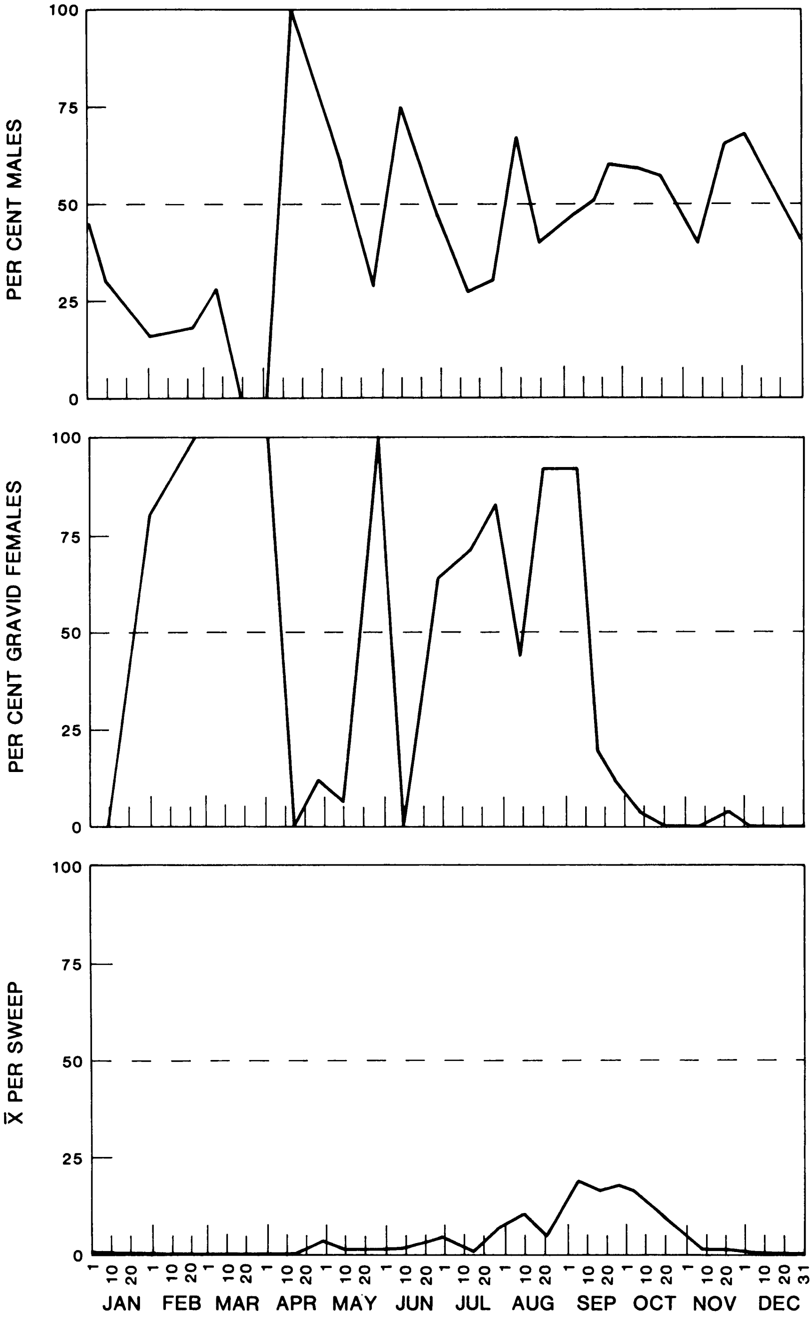

Fig. 9. *Carneocephala fulgida* seasonal sweep net sampling of adults and nymphs, males as percentage of adults, and percentage of gravid females from roadsides, ditches, and pastures, Rolinda, Calif., 1943 to 1945.

Host plant preference

Over the course of sweep net collections of *D. minerva* and *C. fulgida* from 1939 to 1948 (N. W. Frazier) and 1975 to 1980 (A. H. Purcell) from hundreds of localities in California, chiefly the Central Valley, an attempt was made to identify those plant species and habitat conditions in which populations of either leafhopper were greatest. Where nymphs were present, individual plants were examined for the presence of nymphs and eggs. Plant species from which eggs or nymphs were consistently noted were considered to be breeding hosts. Regular sampling in the same locations provided data on leafhopper preferences relative to the seasonal succession of plant growth.

The most important plant hosts of *D. minerva* recorded in this study are listed in table 1. *Draeculacephala minerva* was collected on one or more occasions from over 90 additional plant species not listed in table 1; these plants presumably were "occasional" hosts on which leafhoppers may have fed but did not visit regularly. It should be noted that both European grape *(Vitis vinifera)* and alfalfa *(Medicago sativa)*—pathological hosts of PD bacterium (Freitag 1951)—should be classified as occasional hosts of the green sharpshooter. As previously noted (Gibson 1915; Hewitt et al. 1942; Zimmerman 1948; Winkler et al. 1949), *D. minerva* has a wide host range but nonetheless shows definite host preferences. Extremely high populations can develop on stands of watergrass and bermudagrass (Hewitt et al. 1942). Permanent irrigated pastures seeded with perennial rye, fescue, or other grass mixtures also harbor high numbers of *D. minerva.*

The redheaded sharpshooter had a narrower range of plant hosts. Although bermudagrass was particularly preferred (Winkler et al. 1949), *C. fulgida* was found on other plants, particularly grasses. We have collected this sharpshooter from numerous pastures or grassy areas alongside ditches, roads, and drainage ponds where *D. minerva* is abundant. In general, however, *C. fulgida* prefers habitats with sparser plant growth in lighter textured sandy or gravelly soils that tend to dry more rapidly than those preferred by the green sharpshooter.

TABLE 1. COMMON PLANT HOSTS OF THE GREEN SHARPSHOOTER *(D m)*

Taxonomic grouping*	**Common name**	**Taxonomic grouping***	**Common name**
Breeding hosts			
Alismataceae*		*Festuca megalura*	foxtail fescue
Alisma triviale	waterplantain	*Hordeum leporinum*	farmer's foxtail
Echinodorus cordifolius†	burhead	*Hordeum glaucum*	wild barley
Cyperaceae		*Leersia oryzoides*	rice cutgrass
Cyperus acuminatus	taperleaf flatsedge	*Lolium perenne*	perennial ryegrass
Gramineae		*Paspalum dilatatum*	dallisgrass
Bromus rigidus	ripgut grass	*Poa annua*	annual bluegrass
Cynodon dactylon†	bermudagrass	*Setaria lutescens*	yellow bristletail grass
Distichlis spicata†	saltgrass	Juncaceae	
Digitaria sanguinalis†	hairy crabgrass	*Juncus bufonius*	toad rush
Echinochloa crusgalli	watergrass, barnyardgrass	Luthraceae	
Echinochloa oryzicola	rice watergrass	*Ammannia coccinea*†	red stem
Festuca elatior	meadow fescue	Portulacaceae	
		Calandrinia ciliata var. Menziesii†	red maids

Continued on next page.

TABLE 1. CONTINUED

Taxonomic grouping*	Common name
Feeding hosts	
Leguminosae	
Medicago polymorpha (hispida)	burclover
Melilotus indica	yellow melilot
Geraniaceae	
Erodium botrys	broadleaf filaree
E. cicutarium†	redstem filaree
E. moschatum	whitestem filaree
Malvaceae	
Malva parviflora	cheese weed
Lythraceae	
Lythrum paniculatum	panicled willow herb
Ludwigia repens	yellow waterweed
Boraginaceae	
Plagiobothrys stipitatus	—
Verbenaceae	
Lippia nodiflora†	garden lippia
Cyperaceae	
Cyperus acuminatus	taperleaf flatsedge
C. esculentus	yellow nutgrass
C. niger	umbrella sedge
C. rotundus	purple nutgrass
C. strigosus	umbrella sedge
Heleocharis montevidensis	mountain spike-rush
Scirpus americanus	three square
Gramineae	
Avena fatua	wild oats
Avena sativa	cultivated oats
Bromus rubens	red brome
Crypsis niliac (*aculeata* L.)	picklegrass
Eragrostis diffusa	diffuse lovegrass
Eriochloa gracilis	southwestern cupgrass
Hordeum geniculatum	Mediterranean barley
Hordeum brachyantherum	meadow barley
Leptochloa fascicularis	sprangletop
Lolium multiflorum	Italian ryegrass
Lolium temulentum	darnel
Paspalum distichum	knotgrass
Phalaris minor	Mediterranean canarygrass
Polypogon monspeliensis	rabbitfoot grass
Sorghum halepense	johnsongrass
Sorghum sudanense	sudangrass
Zea mays	corn
Salicaceae	
Salix spp.	willows
Polygonaceae	
Polygonum aviculare†	common knotweed
P. lapathifolium	willowweed
P. persicaria	ladysthumb
P. punctatum	water smartweed
Rumex acetosella	sheep sorrel
R. crispus	curly dock
R. pulcher	fiddle dock
Scrophulariaceae	
Scrophularia californica	figwort
Veronica peregrina	neckweed
Compositae	
Cotula coronopifolia	brassbuttons
Conyza bonariensis	flax-leaved fleabane
Gnaphallium chilense†	cotton-batting plant
Matricaria matricariodes†	pineappleweed
Xanthium strumarium	cocklebur

*Nomenclature follows Munz (1959) as amended by Munz (1969), with some common names from Jepson (1925).

†Breeding hosts also of *Carneocephala fulgida.*

Habitat preference

Sharpshooter populations were commonly observed to be higher in more heavily watered or poorly drained portions of fields. An illustration is the distribution of sharpshooters sampled in a permanent pasture 11 miles (18 km) east of Fresno, Calif. on July 1976. Standing water in the draining end of the pasture resulted in heavy growth of watergrass in this end. Twelve 50-sweep samples in each of three portions of the field yielded the following average number (± standard error) of adult *D. minerva:* (1) in the first 15 m (50 ft) from the drainage end of irrigated pasture (chiefly watergrass), $\bar{x} = 82.75$ (± 9.15); (2) in the next 15 m, consisting of a mixture of chiefly perennial tall fescue (*Festuca* spp. L.) and trefoil (*Lolium* spp.), $\bar{x} = 8.83$ (± 2.27); and (3) in a portion of the pasture 30 to 45 m (100 to 150 ft) from the drainage end, consisting of a solid stand of fescue, $\bar{x} = 5.67$ (± 0.94).

Another series of observations illustrated the degree of differences in sharpshooter densities among habitats close together but differing chiefly in the kinds of plants found in each habitat. Figure 10 depicts the average sweep net captures of *D. minerva, C. fulgida,* and other leafhopper species in 1975 in a permanent pasture and an alfalfa field separated by about 400 m (440 yd). In the 10 ha (25 acre) alfalfa field, raised irrigation checks ("weedy alfalfa") had a mixture of chiefly bermudagrass and alfalfa with some johnsongrass, whereas the stand of alfalfa between checks ("weed-free") had less than approximately 10 percent coverage of grasses. The nearby pasture consisted of tall fescue, perennial rye, and bermudagrass, with sedges growing in depressions that remained wet between irrigations.

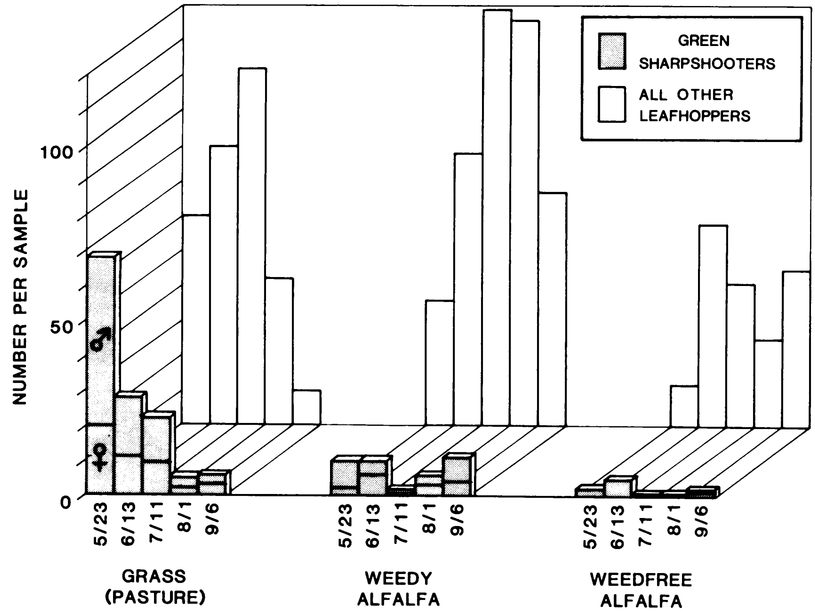

Fig. 10. Sweep net sampling of green sharpshooter adults (shaded columns) and other leafhoppers in a permanent pasture, and two portions of an alfalfa field near Raisin City, Calif., 1975. The proportion of male and female green sharpshooters is indicated for each sample date.

Both fields were periodically flood irrigated. Both *D. minerva* and *C. fulgida* were much more numerous in the pasture, followed by weedy alfalfa and relatively weed-free alfalfa; however, *C. fulgida* was relatively rare in these samples (fig. 10). The male:female ratio of *D. minerva* was usually greater than one. Other leafhopper species were more numerous on most dates in weedy alfalfa checks compared to permanent pasture grasses. The most common leafhoppers were *Amblysellus grex* Oman, *Graminella sonora* (Ball), and *Empoasca* spp. In alfalfa, *Aceratagallia* was occasionally abundant. These results reflect the importance of the frequency and state of growth of preferred host plants as important determinants of sharpshooter abundance.

Vineyard weed control experiment

Periodic sampling of a long-term vineyard weed control plot at Kearney Field Station revealed that sharpshooters were most prevalent on preferred hosts, in this case watergrass and bermudagrass. On August 31, 1976, an average of 5.87 adult sharpshooters per 50 sweeps was collected from the centers of plots that had been mowed for summer weed control. *Carneocephala fulgida* was the more abundant sharpshooter ($\bar{x} = 4.12$). These plots had a cover of chiefly watergrass and bermudagrass. In contrast, in three weed treatments that involved summer cultivation by discing, averages of 0.75 to 1.13 adult *D. minerva* were collected per 50 sweeps. In these three plots, the chief weeds were Mexican lovegrass (*Eragrostis mexicana* [Hornem.]), southwestern cupgrass (*Eriochloa gracilis* [Fourn.]), and crabgrass *(Digitaria sanguinalis).* Very few weeds and no sharpshooters were observed or collected from the complete herbicide treatment replicates.

At monthly or biweekly intervals from mid-February until late August 1977, further sweep net samples were taken in all plots. *Draeculacephala minerva* was again much more abundant in mowed plots than in other treatments, particularly in those replicates in which watergrass was abundant (fig. 11). There were no significant differences among weed control treatments in the average number of *D. minerva* collected until mid-May, when the numbers of *D. minerva* in mowed plots increased sharply. An insecticide treatment on May 31, 1977, with Thiodan for grape leafhopper control apparently reduced sharpshooter numbers dramatically. The numbers of *D. minerva* increased in July and August in mowed replicates compared to other treatments (fig. 11). Also during August, larger numbers of *D. minerva* were collected in the complete herbicide treatment plots compared to the previous year. The degree of weed control noted in 1976 in these plots was excellent, but by July 1977, watergrass and cupgrass covered from 15 percent to 40 percent of the complete herbicide treatment plots and sweep net captures of sharpshooters corresponded closely to weed cover. Probably for this reason, sweep net collections in the complete herbicide and summer-mowed plots were similar in August 1977 (fig. 11). The Kearney Field Station field superintendent suggested that weed control with glyphosate in 1977 was poor because of the winter rainfall shortage in 1976 to 1977, a record drought year for northern California (Earl Shaw, personal communication). Although *C. fulgida* was relatively abundant in mowed plots at Kearney in 1976, only a few adults and no nymphs were recorded in 1977 from the mowed or complete herbicide plots.

Observations of sharpshooter densities in vineyard weed control plots illustrated the effect of the type and persistence of weed cover on sharpshooter abundance. The relatively small size of plots, however, may have contributed a sizeable cryptic error (van der Plank 1963), that is, a spillover of adult sharpshooter from heavily populated plots to nearby or adjacent sparsely populated ones. In commercial vineyards, weed cover (or bare soil) usually is more uniform over larger contiguous areas, which should minimize spillover effects upon sharpshooter densities within large vineyards.

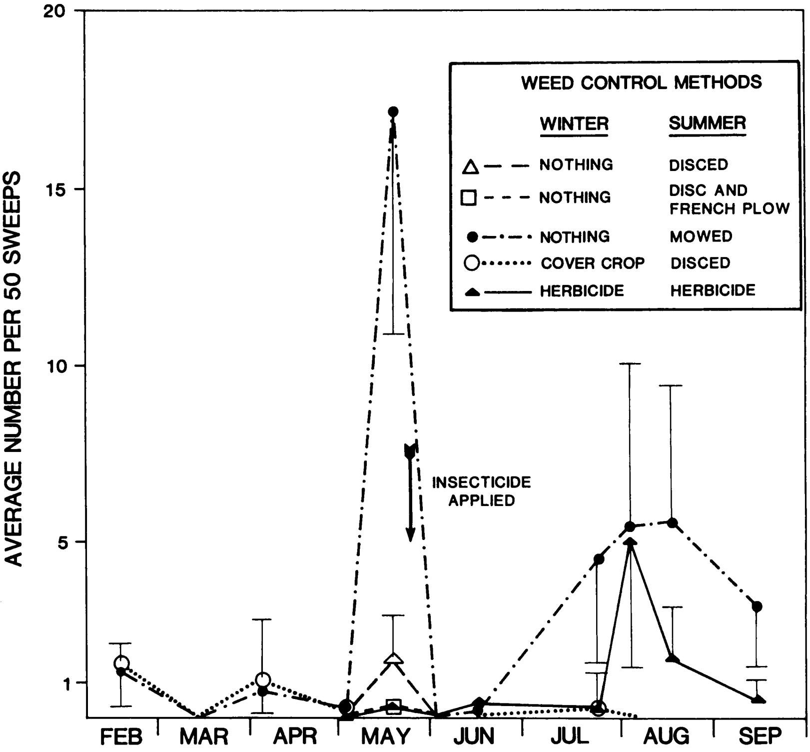

Fig. 11. Adult sharphooter densities sampled in five weed control treatments, Kearney Horticultural Field Station, Parlier, Calif., 1977. Vertical brackets are 95% confidence limits (t-distribution, n = 8). (See text for weed control treatments.)

Site surveys

The ranges of *D. minerva* in regular surveys in Tulare County, 1977, are summarized in table 2. Although sweep net sampling was not an adequate index of nymphal populations and the 8 to 12 samples per site did not provide adequate precision to statistically distinguish small (<2) average numbers of adult sharpshooters (see fig. 4), the influence of habitat on adult densities was clearly indicated in some types of habitats. Permanent pastures consistently yielded the highest densities, followed by weedy alfalfa fields, and two plum orchards that had a permanent cover of bermudagrass. Relatively weed-free alfalfa had very few sharpshooters. During this survey, *C. fulgida* was especially rare and was collected regularly only in several pastures. It was occasionally the only sharpshooter collected in strips or patches of bermudagrass along roadsides. The years 1976 to 1977 were record drought years for most of northern California; the overall low numbers sampled in the 1977 survey were much below those recorded in studies in the early 1940s (Winkler et al.

1949). The 1977 survey confirmed previous findings that grasses, especially bermudagrass, watergrass, and perennial forages in irrigated pastures, supported the highest numbers of *D. minerva* and *C. fulgida.*

A major concern of the 1977 survey was to investigate changes in sharpshooter populations on cover crops or weeds within vineyards and orchards. Only perennial grass cover of annual (e.g. watergrass) and perennial (e.g. bermudagrass) grasses supported high populations of sharpshooters at any time of year. Thus, alfalfa fields, pastures, and orchards with permanent bermudagrass cover were the only sites in which sharpshooters were collected throughout the year or in relatively high numbers on one or more occasions. Sharpshooters were rare in vineyards or orchard weeds and grasses (table 2), probably because these habitats provided suitable forage for populations of *D. minerva* or *C. fulgida* only for periods after June. This implies that both sharpshooters are either slow to disperse to new habitats or find acceptable only relatively stable plant communities that contain acceptable hosts. Such behavior fits Southwood's (1962) proposal that dispersal is attuned to the pace of change in the location of suitable habitats.

TABLE 2. HABITAT SURVEY FOR *DRAECULACEPHALA MINERVA*, TULARE COUNTY, 1977

		Range of *D. minerva* captured in 50-sweep samples		
Sites	**No.**	**(Jan-Mar)**	**(Apr-Jun)**	**(Jul-Sept)**
Vineyard clean cultivation	5	0	0	0-0.1
Vineyard weed cover	10	0-0.3*	0-0.5*	0-0.5
Orchard clean cultivation	3	0-0.2	0	0
Orchard winter cover crop	4	0-0.5	0-0.4	0
Plum orchard permanent cover	2	0.5-1.8	1.1-3.8	1.3-3.7
Pasture	4	0-3.1	3.2-27.9	1.4-19.1
Alfalfa	6	0-0.7	0-2.7	0-1.4
Roadsides	7	0-0.2	0-0.1	0
Drainage ponds	2	0-0.1	0-0.3	0-0.2

*In one vineyard, *D. minerva* were detected in bermudagrass during each 3-month period. Adults were rarely collected from vineyard weeds in 4 other sites during April-September and not at all from 5 other "weed cover" vineyards.

Management practices. Plant communities most suitable for *D. minerva* or *C. fulgida,* such as irrigated pastures, ditchbanks, and weedy alfalfa fields, retain plants succulent enough to be favorable for sharpshooters only through continuous human management—chiefly in the form of regular irrigation and mowing or grazing. The chief "undisturbed" habitats in which either sharpshooter occurs regularly are in grasses along streams or marshes. These may have been the original or primeval habitats before the rapid changes in the Central Valley ecology, brought on by the era of expanded agriculture. At present, abundant populations of either *D. minerva* or *C. fulgida* are mostly the result of human activities—cultivation practices that produce perennial plants preferred by these insects. The implications for Pierce's disease management are that dense vector populations in the San Joaquin Valley are chiefly the result of agricultural practices.

Unfortunately, succulent pastures that result from skilled pasture management may create a potential source of sharpshooter vectors to neighboring vineyardists. Furthermore, it should be evident from the results already presented, that relatively small areas of weeds such as those commonly found along roadsides, ditches, or field margins, are sufficient to produce many hundreds or thousands of *D. minerva* and *C. fulgida.* Thus where such sites are numerous or extensive, the degree of weed control necessary to reduce sharpshooter populations could be impractical, from the standpoint of disease management (Purcell 1981b).

Alfalfa dwarf disease. Weed growth may be an extremely important feature of the spread of alfalfa dwarf disease (AD), which the PD bacterium causes. Early studies of the spread of AD (Weimar 1933, 1937) concluded that the frequency of irrigation exerted a "marked effect" in increasing the incidence and "severity" of AD. Large plots irrigated twice a month suffered a rapid loss of alfalfa plants to AD compared to plots watered monthly. Plots which were not watered for 3½ months for seed production had even less dwarf, except for a single seed production plot located at the water inlet source and irrigation ditch (Weimar 1933). These observations and the conclusion that soil moisture has a profound effect on the spread of dwarf have never been satisfactorily explained. The most plausible explanation is that frequent irrigation produces luxuriant stands of grass weeds, probably including *Echinochloa crusgalli* and *Cynodon dactylon,* that produce high populations of *D. minerva* or *C. fulgida.* Weimar's (1937) photographs of experimental alfalfa plots clearly depict rank weed growth in the plots decimated by AD. It was proposed (Purcell 1979) that AD spread is accelerated by weed growth that produces higher vector populations. In turn, increased AD incidence reduces the vigor of alfalfa regrowth, thus promoting further weed growth, more vectors, and more inoculum (infected plants) at an accelerating pace (fig. 12). Mature stands of alfalfa that are relatively free of weeds strongly resist further weed encroachment; good weed control in alfalfa depends upon initial stand establishment and continued attention to weed control in normal cropping procedures such as irrigation and harvesting (Norris et al. 1981).

Dispersal

The abundance of insect vectors within or outside a crop is of obvious concern in the epidemiology of vector-borne plant diseases, but vector activities are equally important to disease spread. In a broad sense, "vector activity" relative to the spread of plant diseases includes not only vector movements and feeding behavior but vector-pathogen interactions as well. In this section studies of the movements of *D. minerva* and *C. fulgida* in or near breeding habitats and vineyards are summarized.

The spatial patterns of the occurrence of Pierce's disease in vineyards (Hewitt and Houston 1941; Winkler et al. 1949; Purcell 1974) relative to vector breeding habitats in Central Valley pastures and alfalfa fields (Purcell 1981a), or to riparian vegetation in coastal valleys (Winkler et al. 1949; Purcell 1975), suggests that the disease is spread mostly by vectors originating outside the vineyard (Winkler et al. 1949; Purcell 1974, 1975, 1979). The sharply focused pattern of some PD outbreaks in the Central Valley can be traced to relatively small patches of weeds (e.g., fig. 1B in Purcell 1979). In other cases, a larger entire pasture or field (e.g., Hewitt and Houston 1941; Purcell 1981a) can serve as a vector source for spread from a "line or area source" (Thresh 1976). In all these cases, the preponderance of evidence suggests that most PD spread requires vector dispersal from outside breeding habitats. Time and height of flight of sharpshooters in or near breeding habitats using rotary net was studied from 1943 to 1948 (NWF). Sticky mesh panels were used in 1976 (AHP) to estimate changes in dispersal rates following the cutting and drying of alfalfa.

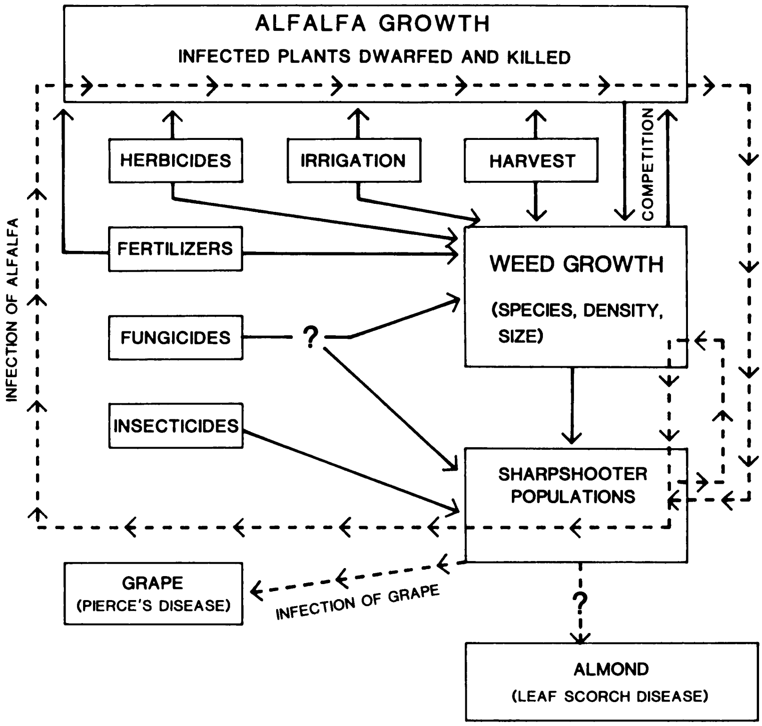

Fig. 12. Alfalfa dwarf epidemiology (modified from Purcell 1979) emphasizes the role of weeds. *Solid lines* represent substantial direct effects or interactions. *Broken lines* represent infection by Pierce's disease bacterium of sharpshooter vectors or plants. Pierce's disease in nearby vineyards represent "dead end" infections.

Rotary net collections

In observing collections of the rotary net in 1943, it soon became apparent that most sharpshooters were captured by rotary nets during early evening. When the rotary net was inspected every 10 to 15 minutes, from 30 minutes before sunset until 1½ hours after sunset, the peak capture rate occurred from 15 to 45 minutes after sunset, table 3. On 23 other separate dates during July and August 1943, when traps were checked at 10 to 30 minute intervals near sunset and less frequently from an hour after sunset until dawn, the same pronounced concentration of flight activity occurred from 20 to 40 minutes after sunset. When rotary net number 1 was inspected 3 times per day: about 1 hour after sunrise, 1 hour before sunset, and 1½ hours after sunset from August 4 through August 12, 1944, no sharpshooters were captured during the daylight period. In contrast, 49 *C. fulgida* and 4 *D. minerva* were collected in the 90 minutes after sunset and 15 additional *C. fulgida* in the late evening through early morning. These data demonstrate that flight activity for both sharpshooters peaks about an hour after dark.

TABLE 3. ROTARY NET CAPTURES OF *DRAECULACEPHALA MINERVA* AND *CARNEOCEPHALA FULGIDA* RELATIVE TO TIME OF SUNSET

Species*	**Minutes before (−) or after (+) sunset**								
	−20	−10	+10	+20	+30	+40	+50	+60	+70 to 90
I *C. fulgida*	0	1	1	12	105	88	41	7	7
D. minerva	0	0	0	0	5	6	6	1	1
	−30	−15	+15	+30	+45	+60	+75	+105	
II *C. fulgida*	0	0	1	86	27	2	2	0	
D. minerva	0	0	0	1	3	0	0	0	

*Net #3 during (I) 10 minute intervals of 5 nights, or (II) 15 minute intervals for 3 nights, between July 31 and August 14, 1944, Woodlake.
Male:female ratios for *C. fulgida:* (I) 1.03, (II) 1.57; and for *D. minerva:* (I) 0.538, (II) 0.33.

The percentage of sharpshooters collected during the day exceeded nightly catches only from October through mid-April, when total daily catches in the rotary-nets were very low: from 0 to 3 per week for *fulgida* and 0 to 26 per week for *minerva* for net number 3. Presumably evening temperatures were too cool for flights but daylight hours were warm enough for flight.

Rotary nets captured sharpshooters at all heights tested (3 to 123 cm). The male:female ratio of *C. fulgida* captured by rotary nets was 0.99 in 1947 for net number 3, which collected the greatest numbers of both sharpshooter species. Of the 16 weekly periods for which the total catch exceeded 28, the male:female ratio ranged from 0.41 to 1.61 and averaged 0.98, with only 4 of the 16 periods deviating from a 1:1 ratio by more than 20 percent. Captures of *D. minerva* in the same rotary net site yielded a much higher percentage of females. The male:female ratio of all collections of *D. minerva* in 1947 (net number 3) was 0.17 and ranged from 0.02 to 0.91 with a median ratio of 0.13 and an average of 0.21. We interpret this to mean that female *D. minerva* are 5 to 6 times more likely than males to fly. Sweep net collections of *minerva* consistently yielded as many or more males than females (figs. 9, 10) except during the winter months (fig. 9).

Rotary net catches of sharpshooters varied enormously with season and net location. In 1944, net number 3, located in an irrigated pasture, a very favorable habitat for both sharpshooter species, collected the greatest numbers of both green and redheaded sharpshooters (fig. 13). This was a year of greater overall abundance of both sharpshooters compared to the following years. The aerial densities of adult sharpshooters were much greater in an irrigated pasture (net number 3) than in uncultivated land (net number 2) or vineyards (net numbers 1 and 4). Seasonal changes in sharpshooter collections at these last three sites were similar (fig. 14) and presumably reflected dispersal flights from nearby breeding habitats. Peak flights of *C. fulgida* occurred in early July in all years studied (1944 to 1947), but with substantial flight activity from late May through August. In contrast, *D. minerva*'s flight activity during March through early May (1944, 1945, 1947) was sparse but consistently greater than *C. fulgida*'s during this period. *Draeculacephala minerva* flew in substantial numbers from May through August, but was far outnumbered in aerial density by *C. fulgida* in midsummer. The numbers of *C. fulgida* trapped per season were consistently higher than that of *D. minerva* in 1944, 1945, and 1947 to 1948 in the ratios of 20.7, 3.4, and 1.7 respectively. The spectacular balancing out of relative aerial density may have resulted from increasingly efficient elimination of bermudagrass from vineyards and environs near the Woodlake plots.

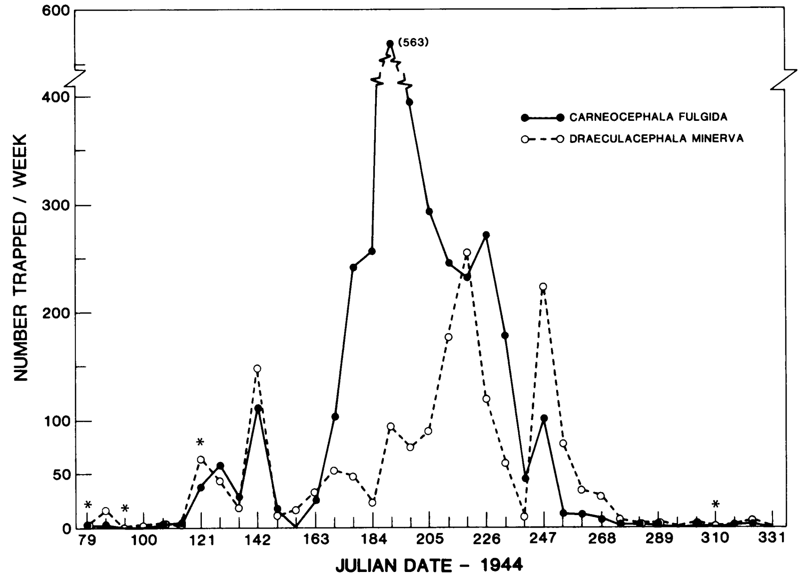

Fig. 13. Rotary net collections of green *(open circles, dashed line)* and redheaded *(dots, solid line)* sharpshooters in 1944 from net #3, in an irrigated pasture near a vineyard. *Asterisk* indicates incomplete operation for one or more days during a 7-day period because of mechanical malfunctions.

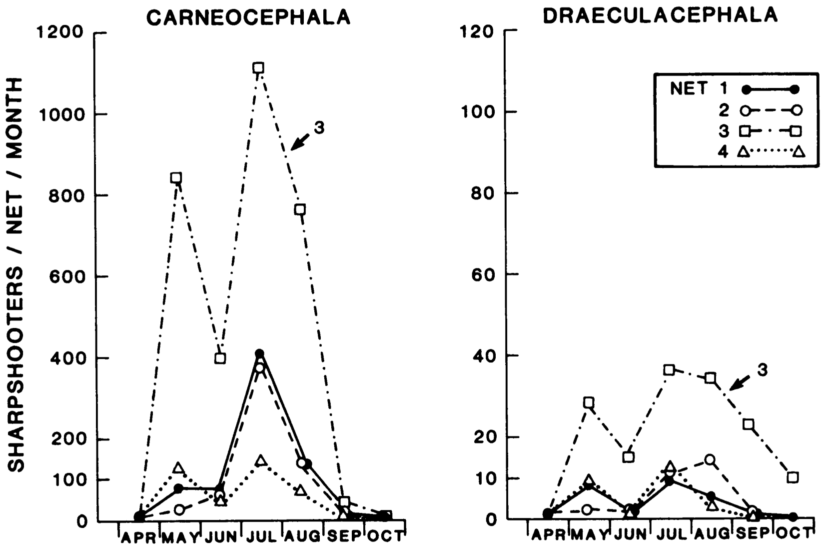

Fig. 14. Comparison of sharpshooter collections for four rotary nets in different locations in the Woodlake experimental plot (see text). Thirty day totals beginning April 4, 1944. Note scale for *Carneocephala fulgida* is 10 times that of *Draeculacephala minerva.*

The number of sharpshooters captured at night relative to average weekly temperature at sunset (fig. 15) suggests a flight threshold temperature below 70°F (21°C). Of 118 dates in 1947 to 1948 that had a high daytime temperature below 70°F (21°C) a total of 89 sharpshooters were caught in daylight collections in net number 3. No sharpshooters were caught on days with a maximum daily temperature of 62°F (17°C). Many of the low weekly catches shown in figure 15 represent sparse winter populations as well as low temperatures.

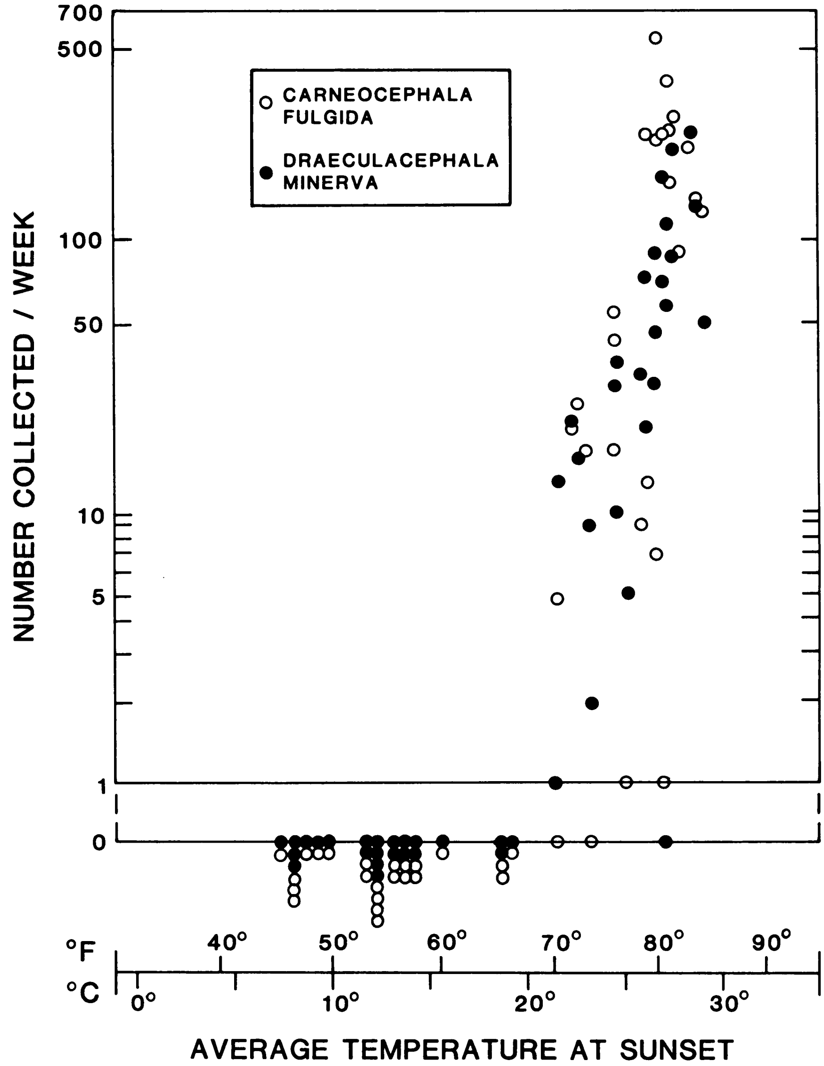

Fig. 15. Weekly rotary net catches of sharpshooters at night and the corresponding average temperature at sunset, April 11, 1947, to March 11, 1948, net #3, Woodlake, Calif.

Sticky trap collections near alfalfa

Large, sticky mesh traps were used to detect sharpshooter dispersal from breeding habitats. Very few sharpshooters were caught in preliminary field studies in 1975 to 1976 that used yellow can sticky traps (Purcell 1975) near a pasture with high natural populations of both *D. minerva* and *C. fulgida.* The apparent lack of attractancy of yellow to insects that fly after dusk is not surprising for nocturnally active insects (Prokopy and Owens 1983).

Sticky traps erected along alfalfa fields caught sharpshooters in numbers proportional to the numbers collected by sweeping within 50 m (or 50 yd) of the traps on dates at the beginning and end of the trapping period ($r = 0.76$, d.f. $= 6$, $p < 0.03$). The average weekly catch of traps near each field (fig. 16) did not change significantly in response to harvest or irrigation of the adjacent fields. In both fields, a slightly larger proportion of *D. minerva* females were caught at higher locations on the sticky mesh traps following harvest, compared to dates before cutting (fig. 16). This greater height could be indicative of a larger number of longer flights. Captures below 25 cm (10 in) probably reflect short-range foraging activity, thus their relevance as an indicator of dispersal is doubtful. In summary, these studies indicated that sharpshooters could disperse more or less continuously from breeding habitats in alfalfa, regardless of the field conditions.

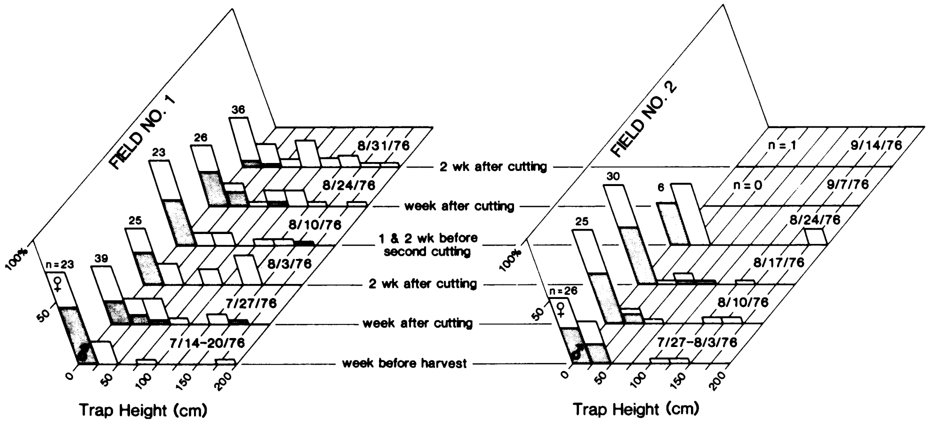

Fig. 16. Captures of *Draeculacephala minerva* at different heights on sticky mesh panels along each side of two alfalfa fields. Field 1 was harvested July 20, 1976, 2 weeks before field 2. *Shaded columns* represent the percentage of males, and *unshaded columns* the percentage of females per field per period; *n* = total number caught on four traps per week.

Attraction to lights

Species of *Draeculacephala* are attracted to lights in large numbers in the midwestern states (Young and Davidson 1959). We have also noted numerous *D. minerva* at fluorescent lights east of Marysville during July, August, and September 1980 and 1981. An 8-watt ultraviolet lamp (BioQuip Products, Santa Monica, Calif.) attracted numerous *D. minerva* females from a nearby pasture shortly after dark in a 1-day study on August 8, 1980.

Sweep net samples ($n = 10$) of *D. minerva* adults in two nearby fields averaged 5.7 and 6.7 with a male:female ratio of 1.47 ($p < 0.05$ for t-test of significance of dependent mean difference between males and females). The male:female ratio of 87 sharpshooters aspirated from the ultraviolet lamp was 0.12. It appears that females are either more strongly attracted to lights or more active fliers than are males. Similar male:female ratios from rotary net traps support the latter hypothesis.

Observations of *D. minerva's* response to lights suggest that the attraction to lights is highly seasonal. Similar seasonal fluctuations were observed in rotary net captures (figs. 13, 14), but these have not been related to wind, temperature, lunar phase, or other factors that might influence flight activity. Further study would be needed to evaluate light traps as either a cause or a measure of sharpshooter dispersal.

The attraction of sharpshooters to lights may have some consequences for the spread of PD. It was noted in 1940 that blue electrocuting light traps that had been evaluated for grape leafhopper control, 1938 to 1939, were foci of Pierce's diseased grapevines (Frazier 1943). This observation was an important clue leading to the identification of sharpshooters as PD vectors. *"Carneocephala fulgida* was very markedly more numerous directly under the 250-watt traps than anywhere else in the 10 acre (4 ha) block of vines" (Frazier 1943). The same study also indicated that *D. minerva* was "noticeably...more numerous under the same lights..." Our studies yielded no consistent observations of the attractancy of lights to *C. fulgida* because light traps were not monitored near sites with high populations of *C. fulgida.*

CONCLUSIONS

Both *Draeculacephala minerva* and *Carneocophala fulgida* reach their greatest densities on rapidly growing weeds, particularly bermudagrass and watergrass. The concentration of PD near such foci has been well-documented (reviewed in Winkler et al. 1949; Purcell 1979, 1981a). The elimination and prevention of habitats that promote sharpshooter development should be a major concern in reducing the spread of Pierce's disease or alfalfa dwarf. Where sharpshooter habitats are within the management or control of growers, elimination of weeds during early spring before grapes begin to leaf out is perhaps of greatest importance. The destruction of sharpshooter habitats by clean cultivation or herbicide treatment in late summer or autumn also eliminates sharpshooter reproduction and development so that subsequent sharpshooter populations usually will not develop by the following growing season. Perennial cover crops or weeds, however, may provide a significant source of infectious sharpshooters.

Substantial PD spread can occur with very little if any detectable sharpshooter feeding on grapevines. In theory, relatively few active vectors could quickly infect a high percentage of vines in vineyard, depending upon: the number of vectors, their pathogen transmission efficiency, and plant-to-plant movement (Purcell 1981b). In considering what level of sharpshooter abundance might constitute an "economic threshold" (Stern 1973), it is perhaps most prudent to attempt by means of crop and weed management to prevent sharpshooter populations from developing at all, rather than to attempt to control established vector populations. Numerous observations of rebounds in sharpshooter populations following insecticide treatment (e.g., fig. 11) demonstrate that pesticides depress populations only temporarily. Similarly, the potential of biological or natural control of *D. minerva* and *C. fulgida* is severely limited by the high degree of vector control required to suppress disease spread. Reducing sharpshooter populations with insecticides is a temporary measure that would probably be useful only in special circumstances, such as the rapid control of previously unrecognized sharpshooter populations during the spring months when grapevines infected by PD bacterium are most likely to remain chronically diseased (Purcell 1981b).

Continuous dispersal of *C. fulgida* and *D. minerva* from breeding habitats suggests that selective and staggered harvest of hay or pastures would not reduce the numbers of dispersing vectors enough to recommend these practices to control PD in vineyards near alfalfa hay fields. A far more effective approach would be to prevent the immediate contact of vineyards with vector source areas. Because Pierce's disease is very much an "edge effect" disease (Hewitt and Houston 1941; Purcell 1974, 1981a), the increased average size of grape plantings over the past few decades may have reduced the overall incidence of PD by reducing the fraction of vineyard area that is made up of "edge." Furthermore, larger fields may have reduced the diversity or heterogeneity of cropping patterns in central California so that there are fewer vector source areas (pastures and alfalfa hay fields) within the vicinity of commercial vineyards. Perhaps the most important change in the agroecosystem of the Central Valley since the 1940s to affect the spread of Pierce's disease is improved weed control made possible by chemical herbicides. The breeding habitat for sharpshooters would be greatly reduced by good weed control.

Major epidemics of Pierce's disease have tended to follow a succession of wet years (Winkler et al. 1949). Although not proven, the most likely explanation of this trend is that winter rainfall leads to expanded areas of vegetation that are suitable sharpshooter breeding habitat and remain suitable for longer than usual periods during the spring and early summer months. This leads to larger vector populations spread over a wider area. The average number of sharpshooters noted in our studies during the 1970s were generally very much lower than comparable observations in the early 1940s. In successive drought years, *C. fulgida* was especially rare. Although Pierce's disease is a continual threat to California vineyards regardless of annual weather, it seems likely that the potential remains for climate-induced epidemics in which PD is more widespread and intensive than has been the case since the 1940s.

The epidemiology of alfalfa dwarf disease (AD) is much less understood than that of Pierce's disease. It is puzzling that AD can be severe in the southern Central Valley but has never been detected in the northern Central Valley (Purcell 1980) despite the abundance of sharpshooters and of alfalfa throughout this part of the Central Valley. AD also was absent from the Antelope Valley in the Mohave Desert, despite substantial plantings of alfalfa. Intensive surveys for AD were made in both areas (Harris and Schlocker 1943). Conversely, almond leaf scorch disease (ALS), which also is caused by the PD bacterium (Davis et al. 1979), has been quite severe in some parts of northern Central Valley and in the Antelope Valley, but is absent in southern Central Valley, suggesting a possible strain difference in the pathological characteristics of PD bacterium (Purcell 1980) in different parts of California.

The range of plants acceptable for feeding by *D. minerva* or *C. fulgida* is quite wide and many sharpshooter host plants are hosts of PD bacterium (Freitag and Frazier 1954). Studies are needed of the relative importance of symptomless plant hosts of PD bacterium as sources of inoculum for diseases caused by this bacterium.

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