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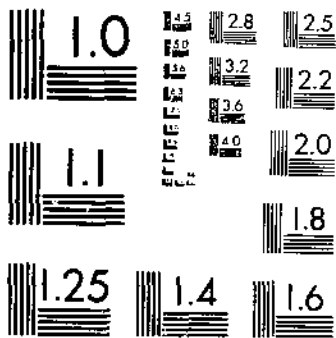
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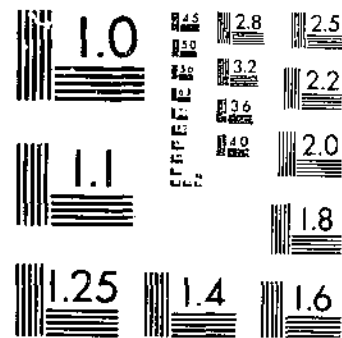
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Insect Transmission of *PHONY PEACH DISEASE*

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Since 1900 phony peach has caused the loss of thousands of peach trees in the Southeastern United States. As there is no known cure for this virus disease in plants, the only feasible control program has been to destroy diseased trees as rapidly as they could be identified, a method not sufficiently effective to accomplish eradication. This bulletin describes the studies that were undertaken to discover the insect vectors of the disease and how they perform, as a basis for developing a more effective control program.

THE DISEASE

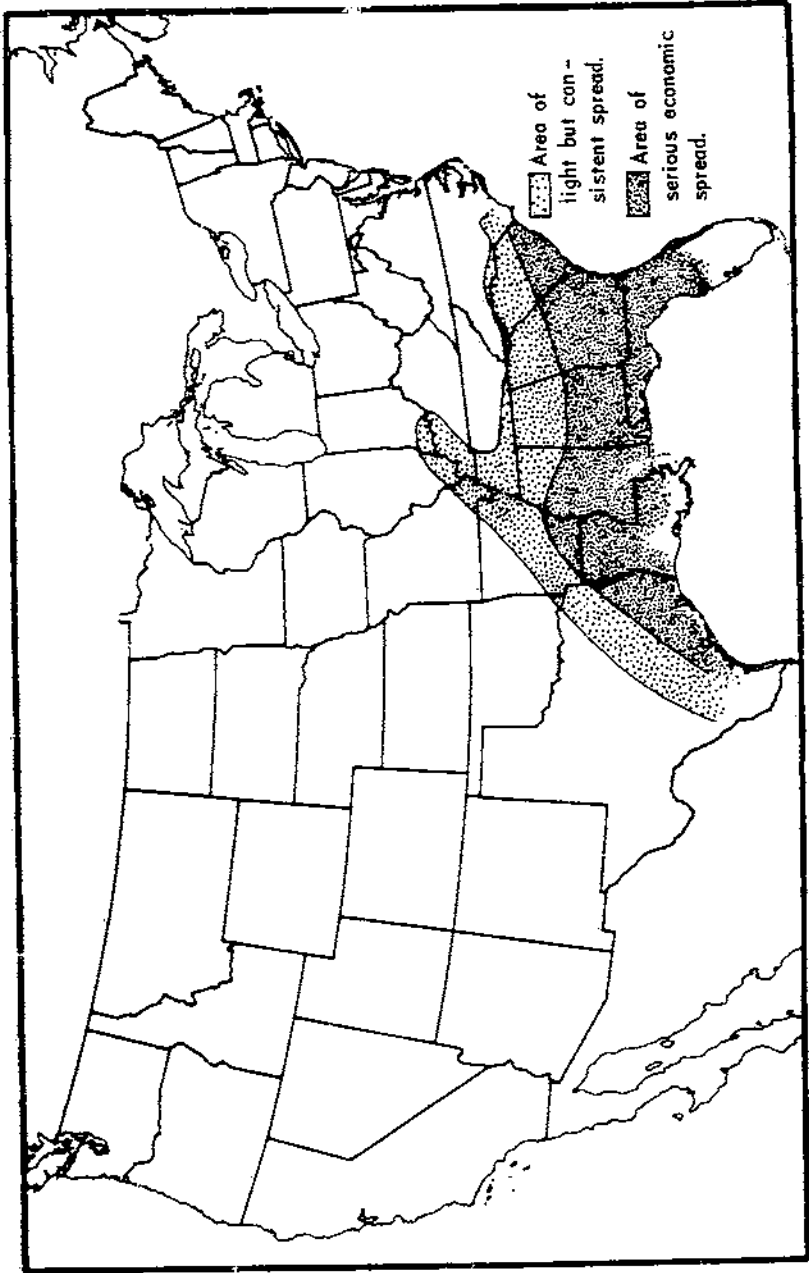
Phony peach affects various members of the genus *Prunus*. This virus disease appears to have been first observed about 1890 (10).² At that time a few stunted trees were noted in a peach orchard near Marshallville, Ga. Phony trees are characterized by shortened internodes, rather profuse lateral branches, and flattened dark-green leaves. Decided dwarfing of new growth results, and the periphery of the upper crown takes on a uniform, rounded appearance. In the spring phony trees flower and leaf earlier than normal ones of the same variety, and they hold their foliage later in the fall. They bear fewer and smaller fruits that are earlier ripening and generally more highly colored than those on normal trees.

For several years dissemination of the disease seems to have been strictly local, but gradually the malady began to spread. By 1915 it was generally distributed through orchards of the 5 or 6 counties of south-central Georgia known as the Fort Valley area. By 1935 the disease had spread as far west as eastern Texas, north to central Illinois and northern Kentucky, and along the Atlantic seaboard as far north as North Carolina.

Surveys made between 1929 and 1935 indicated that the situation had become static. Annual local spread was rapid in the Coastal Plain from South Carolina to eastern Texas. It was slower in the Piedmont area of the Gulf Coast States and in the upper Mississippi and lower Ohio river basins. Although occasionally the disease had been reported from south-central Illinois, southern Indiana, Maryland, and Pennsylvania, it did not appear to spread locally in those areas or if so, very slowly (fig. 1).

¹ Retired May 31, 1957.

² Italic numerals in parentheses refer to Literature Cited, p. 26.



16-0484

FIGURE 1.—Distribution of phony peach disease.

Investigations into the nature of the disease were begun in 1921. For several years progress was dishearteningly slow. Although periodical surveys demonstrated clearly that the disease was spreading constantly, no fungus or bacterial organism could be associated with it. Early attempts to transmit it by means of buds or by grafts made with top wood were unsuccessful. Thus its infectious character could not be demonstrated. Finally it was found that the disease could be transmitted readily by means of root grafts (10).

For many years phony peach was recognized only as it affected peach. After a method of artificial transmission was discovered, pathologists soon determined that numerous species of wild plums, as well as apricots and almonds, could be infected, and that most of these species of *Prunus* showed symptoms similar to those in peach (10). In a few species of plums the symptoms were not pronounced or were even masked.

After various species of plums were successfully inoculated, further studies soon indicated that most of these species are subject to natural infection when the trees are grown in areas where the disease spreads freely (18). In particular, *Prunus angustifolia*, the common wild plum of the Southeast, has been shown to be generally infected wherever the disease is active in peach (3, 4, 7, 15, 19). Unfortunately *angustifolia* is one of the hosts in which the disease is masked or displays very doubtful symptoms, and for this reason its role in the natural dissemination of phony peach was underrated until recently.

VECTOR RESEARCH

Methodical search for a vector of phony peach was begun in the spring of 1936. By then pathologists had learned that the disease was readily graft transmitted from root to root of peach, from roots of peach to those of many other species of *Prunus*, and reciprocally among these members of the genus. However, they had not demonstrated transmission of the disease by budding or grafting when top wood was used. It was reasonable to infer that the disease was confined to the roots of the trees and hence to presume that the natural vector was a root-feeding arthropod.

Most of the vectors of plant viruses that had been detected by 1936 were insects, most of which belonged to the Homoptera. Thrips were known to transmit a few diseases, there was evidence that beetles transmitted 1 or 2 viruses affecting annuals, and mites were suspected at least once.

Little information was available regarding the insect fauna of peach orchards. One report on the results obtained from jarring trees (18) listed many species of Coleoptera but included few Hemiptera (Heteroptera and Homoptera). There was even less published information regarding the soil fauna of the Southeastern United States and none concerning the soil insects that might be particularly associated with peach orchards. One aphid was known to feed on peach roots, but its distribution compared with that of the disease made it appear doubtful that it could be implicated.

SURVEYS

Obviously any orderly search for a root-feeding vector must be based on a comprehensive list of all soil-infesting insects found in peach orchards within the area in which phony peach was spreading. This called for systematic collections of soil insects from several widely scattered orchards where phony peach was spreading rapidly, from orchards where it was spreading very slowly, and from orchards where local spread did not occur. It was anticipated that many species would automatically be eliminated as suspects by comparing their prevalence with the behavior of the disease.

Ideally each collecting station would be visited four times a year, and the survey would be repeated a second and possibly a third year, as results might dictate. It was not possible to follow entirely the ideal schedule, but most of the stations were visited at least once in each of the four seasons. Collections were made at 30 stations in 15 localities in 12 States. Of the 15 localities, 6 were in areas of rapid spread of the disease, 4 in areas of moderate to light spread, and 5 in areas where local spread was very light or did not occur. Supplemental surveys were made at 69 stations in 16 additional localities.

Methods and Equipment

Since the best known method for collecting soil insects was with Berlese funnels (5), a cabin trailer was equipped with a battery of six of these instruments. Current for operating the funnels was provided by a portable generator mounted in the pickup truck that pulled the trailer. The trailer was also equipped with cupboards, desks, a sink, microscopes, collecting supplies, stationery and record forms, and reference books (6). Thus the outfit was entirely independent. It could be parked anywhere, and investigations could proceed with a minimum of complications.

After each visit to a collecting station, the material was sorted as to species insofar as possible and was preserved in 70-percent alcohol in $\frac{1}{2}$ -dram vials. It was then forwarded to the former Division of Insect Identification for determination.

Expansion of Survey Objectives

Shortly after the survey was started, the pathologists advised us that they had evidence that the virus of phony peach did occur in the tops of wild plum trees. With new techniques they were soon able to demonstrate the erratic presence of the virus in the tops of peach trees (12). Consequently, the survey objectives were expanded to include insects found in the tops of peach trees and on ground cover within the orchard area. Some collections were also made from wild plums growing in the vicinity of collecting stations. Collections of aerial insects were mostly culled, and only those insects with sucking mouth parts were preserved for identification. This was particularly true for all material collected on ground cover.

Records

Records were made to cover all activities of the survey. They included (1) a collection record of all material collected at each visit to each station and pertinent data on the conditions surrounding each collection; (2) a species record, in which every collection of a species

was recorded, together with geographical, seasonal, and ecological data on each capture; and (3) an accessions record, in which every collection was listed numerically, with references to the proper station and visit.

Progress

By the end of 1938, 3,360 collections of sucking insects had been made. They included 282 species of Homoptera, 176 species of Heteroptera, and 24 species of Thysanoptera. An analysis of the data covering this material, based on such factors as geographical distribution, known absence in some orchards heavily infected with phony disease, and positive association with peach trees, reduced the overall list to a preliminary list of 34 suspected species of Homoptera and 42 of Heteroptera. This list included all four of the native species of Cicadellidae that were later convicted as efficient experimental vectors.

A study of collection records cast serious doubt on the probability that any soil insect transmitted phony peach. Only a small group of burrowing bugs (Cydninae) and a few root-infesting aphids warranted any consideration. Since the burrowing bugs were scarce or entirely absent in some orchards where the disease was extremely active, they were ruled out. Of the soil aphids, only the black peach aphid (*Amuraphis persicae-niger* (Smith)) could be definitely associated with peach, yet its distribution was the exact opposite of that of the disease. Whereas it decreased in abundance southward, the incidence of disease spread increased. For these reasons and because the pathologists had found that the virus might be present in the aerial parts of the trees, particular attention to soil insects appeared to be no longer justified.

After attaining a preliminary list of suspected vectors, survey methods were modified appreciably. The formalized survey was steadily curtailed, both as to the number of stations visited and to the types of collecting followed. Few soil collections were made, and the program gradually developed into a search for a limited group of Homoptera in a few orchards that had a consistent history of rapid disease spread. The trend toward specialization was further encouraged upon publication of evidence that the virus of phony peach was confined to the woody cylinder of the host plant (11). Discovery of this characteristic of the disease called for a sharp curtailment of our list of most promising suspects.

Distribution data concerning several of the species that were then of greatest interest proved to be inconsistent, and there was for a time considerable uncertainty as to the rank of such species as suspects. It soon became apparent that these species had only seasonal association with peach orchards and that we had not always timed our visits properly. Consequently, a new survey method was adopted. This consisted in exposing sticky-board traps (14) in peach orchards for which we had incomplete or unsatisfactory data. The traps were visited once each month when possible, but even when not visited for 2 or 3 months they furnished valuable information. Continuous trapping throughout the year confirmed our conclusion as to the seasonal behavior of several species of Cicadellidae and demonstrated the occasional presence of our principal suspects in all survey orchards having a high incidence of annual disease spread.

By 1942 circumstantial evidence—abundance of the insects as compared to the behavior of the disease, positive association of the insects with peach trees at some period of the year, and feeding habits of the insects—led us to select four sharpshooters as the most probable suspects. These were *Homalodisca coagulata* (Say),³ *Oncometopia undata* (F.), *Graphocephala versuta* (Say), and *Cuernia costalis* (F.). The first two species seemed to meet all our requirements, with *coagulata* in the strongest position because it is strictly a southern species and because it was found in greater abundance on peach twigs than were the others. *G. versuta* often feeds on foliage perhaps mainly on midribs of leaves, but it can feed on stems if confined on them. It is frequently taken on several species of wild plums. *C. costalis* held the lowest rank, because it is primarily a grass feeder. It is taken occasionally on very small peach trees and is sometimes found on low-hanging twigs of large trees. In confinement it feeds readily on peach twigs. Thus by 1942 the survey method had furnished four species of Cicadellidae that we were confident included the vector of phony peach. The evidence was impressive, but it was still only circumstantial. Definite proof of the role of these four species was not obtained until 1949.

TRANSMISSION STUDIES

At Chattanooga

In 1939 a laboratory was established at Chattanooga, Tenn., for conducting experiments on insect transmission of phony peach. This location was selected because it was in an area where the disease was endemic but was spreading so slowly that it was not likely to reach the experimental trees. This factor was especially important, since the disease has a 2- to 3-year incubation period. In addition, no commercial peach orchards were located in the immediate vicinity; consequently, maintenance of diseased trees would not jeopardize an established industry. Climatological conditions were presumed to be favorable for the normal performance of the vectors.

Work during 1939 was limited to feeding tests. They provided information as to the ability of several species of Homoptera and Heteroptera to live on peach for periods of considerable duration. In the following winter 12 phony trees, artificially infected by means of root grafts, were planted at the laboratory. They were covered with 16 mesh screen cages to minimize the danger of natural spread from them to test trees.

Transmission tests were conducted from 1940 until 1945. As test trees, June-bud Elbertas were planted each winter for use during the ensuing spring and summer. These trees were set in the open, 4 feet apart in 10-foot rows. Alternate trees were used for the tests, every second tree being left untreated and used as a check on the natural spread of phony peach. Of 603 tests made at Chattanooga, 108 involved *coagulata*, 43 *undata*, 39 *versuta*, and 50 *costalis*. Of the

³ Until recently the species of *Homalodisca* commonly found in the Southeast has been designated as *triquetra* (F.). Current studies by D. A. Young, formerly of the Entomology Research Division, demonstrate that *triquetra* is a South and Central American species that is not found within the continental United States.

remaining 363 tests, 73 dealt with 22 other species of Cicadellidae, 38 with 8 other species of Homoptera, 214 with 7 species of Cydninae, 28 with 6 other species of Heteroptera, and 10 with the peach tree borer.

For various reasons, some of which are not entirely clear, the selection of Chattanooga as a site for transmission work on phony peach proved to be disappointing. Among the more obvious factors was the need to travel about 200 miles south to collect adequate supplies of the primary suspect, *coagulata*, which is not found in Tennessee and is very scarce in the northern third of Georgia. Many methods for transporting the insects were tried, but none were satisfactory. Usually 50 percent or more were dead on arrival at the laboratory or died soon afterward. Even worse, many of the insects that survived for some time did not perform normally. The efficacy of root-inoculated trees as sources of inoculum was questionable. Finally, because we were away from the area in which the disease was most active, we could not adequately study the habits and behavior of several species of insects that were under test. This delayed acquiring desirable evidence not only concerning probable vectors but also regarding seasonal abundance of the various insects, which in turn interfered seriously with attempts to obtain adequate numbers for experimental use.

Out of 240 attempts at transmission with insect species that later proved to be capable vectors of the disease, only three tests were possibly successful. In 1943 three phony trees were found within a few feet of each other in the block that had been used for transmission work in 1941. One tree had been inoculated by *costalis* and another by *versuta*. Unfortunately the third tree was an untreated check. There was much evidence that the first two tests did represent successful transmissions. They were made concurrently, the same phony tree served as a source of inoculum in both tests, the proximity of the two phony test trees was a natural result of simultaneous tests, and finally, both insect species belonged to the Tettigellinae. Yet the occurrence of the disease in an untreated control tree nearby prevented drawing positive conclusions from these results.

In 1944 one tree that had been inoculated by *coagulata* in 1942 had phony peach. Since *coagulata* is also a member of the Tettigellinae, this phony tree strongly supported the suspicion that the correct group of insects had been chosen for particular attention. Conclusive proof was still lacking, and the very low percentage of infections resulting from 2 years' effort made it appear that progress at Chattanooga would be very slow indeed. It was therefore decided to move the laboratory to some point within the area in which the disease displayed major activity. The propriety of this decision was subsequently confirmed, in that no transmission resulted from a total of 107 tests with members of the Tettigellinae made at Chattanooga between 1943 and 1945.

At Fort Valley

In 1945 transmission tests were started at the Horticultural Field Laboratory near Fort Valley, Ga. The following year our laboratory was transferred to Fort Valley, and all subsequent transmission work was conducted there.

This location is in the heart of the middle Georgia peach belt, where phony peach is of greatest economic importance. Because of the rapidity with which the disease spreads in central Georgia, it was necessary to protect all experimental material from natural infection. With few exceptions, the trees used in the transmission tests were June-budded trees procured from nurseries in Tennessee or northern Alabama, where the disease does not occur or is of minor importance. Different varieties were used, but only one variety in any one year. Visual diagnosis for phony peach is based largely on comparative symptoms rather than on positive ones, and a mixture of varieties or the inclusion of seedlings adds materially to the difficulty of making an early diagnosis.

At Fort Valley the test trees were planted in large screen houses, usually about 40 by 100 feet and 8 feet in height. During 1945-48 the trees were set 1½ feet apart. At the end of each season they were transported to an area where little local spread occurred and planted 4 feet apart in 12-foot rows in the open. This plan proved to be unsatisfactory. Each year difficulties arose that culminated in a severe mortality among the test trees. In addition, transplanting tended to retard the appearance of symptoms for about a year. Beginning in 1949 the test trees were planted 3 or 4 feet apart and left in the screen house until final readings could be made.

From 1949 to 1952 half the trees were kept as checks, the planting arrangement being T (test) X (check) T X in the first row, X T X T in the second, and so on for the entire planting. Wider spacing and the necessity for holding the trees in the cages for as long as 3 years put space at a premium. Consequently, thereafter only a third of the trees were kept as checks. Then the arrangement was as follows: T T X T T X in the first row, T X T T X T in the second, X T T X T T in the third, and so on. From the standpoint of protection from natural spread our procedures were fully adequate. No check tree became infected.

The insects were handled usually in two types of cages. One type consisted of cloth bags of various grades of muslin sheeting or of cheesecloth, about 18 inches long by 14 inches wide, with a long, oval spreader, 10 by 3 inches, in the closed end. The spreaders were made from baling wire. These bags were tied over the ends of twigs or slender branches. The weight of the material appeared to have no appreciable effect on the survival of the caged insects. The other type was sleeve cages of plastic screening, 12 inches long by 6 inches in diameter, with 11-inch cuffs of muslin sheeting attached to each end. Wire rings at each end of the plastic section kept the cages properly distended. The sleeve cages could also be placed over the ends of branches or could be used farther down on the branches if desirable. Their principal advantage was that they permitted considerable visibility, so that the condition of the insects could be observed without removing the cages from the trees. Survival did not appear to be any greater in the sleeve cages than in the cloth bags.

Vectors

In the first year (1945) at Fort Valley 138 transmission tests were made, attention being confined to the four species of Tettigellinae considered as primary suspects. Unfortunately many of the experi-

mental trees died during the incubation period, but 86 of them were maintained long enough to permit dependable diagnosis. Twelve positive cases of phony peach developed in this group on trees that had been inoculated by *coagulata*, *undata*, and *versuta*. No disease appeared in any of the check trees. The figures were large enough to assure us that we were working with the correct group of leafhoppers. Transmission tests made in 1946 confirmed the role of the first two species, very few tests being made with *versuta* that year, and *costalis* was added, with a record of 6 successful infections out of 59 inoculations (22).

Draeculacephala sp. was used in 17 primary tests in 1946 and 1950. One of the trees inoculated in 1950 had phony peach in 1953. Many of the trees inoculated in 1950 took 3 years before symptoms appeared. The group of insects that effected this transmission were caged serially on six test trees but infected only the fourth one in the series.

During 1953, 33 primary tests were made with *Homalodisca insolita* (Wlk.), a species that had recently migrated into the Southeast from the Southwestern United States. Of the 33 inoculated trees, 14 had phony peach in 1955 (23).

Through 1955 positive transmissions were effected by six species of the Tettigellinae. The efficient vectors were *costalis*, *versuta*, *insolita*, *coagulata*, and *undata*, and the inefficient vector was *Draeculacephala* sp. Probably any of the Tettigellinae can transmit phony peach to some degree, although several species may be as inefficient as *Draeculacephala* sp. appears to be.

From 1947 through 1955 a total of 779 primary tests with the five efficient species were completed. Because of the 2- to 3-year incubation period, this total includes only those tests that were made between 1945 and 1953. It does not include repetitive tests made during the serial transmission tests or tests with nonviruliferous insects fed on source trees other than peach or plum. On the other hand, it does include all other primary tests regardless of season of operation, condition of source trees and test trees, variations in latent periods, source of experimental insects, and all tests in which wild vectors were caged immediately on test trees without previous caging on infected source trees.

From the 779 tests, 153 positive infections resulted—an overall experimental efficiency of 19.6 percent. The indicated comparative efficiency by species (table 1) based on all tests is misleading, since both *costalis* and *coagulata* were employed under far more variable conditions than were the other three species. The records show that no successful inoculations were made during February and March. Attempts at transmission after September 1 were mostly unsuccessful. Of 185 such tests, only seven positive infections resulted from primary inoculations. Since all but two of the winter and fall tests dealt with *coagulata* or *costalis*, obviously these tests cannot be included in calculations made to determine the comparative efficiency of the five species under consideration. Also, since the figures are intended to deal only with the transmissive abilities of the insects under experimental procedures, the data on natural transmission should be excluded. Elimination of these various tests leaves a total of 469 tests made between April 1 and August 31. Of these, 130 resulted in positive infections, an average efficiency of 27.7 percent.

TABLE 1.—Efficiency of five species of leafhoppers as vectors in phony peach transmission, 1947–55

Species	All tests		Tests made under comparable conditions (April 1–August 31)	
	Number of tests	Percent efficiency	Number of tests	Percent efficiency
<i>Homalodisca coagulata</i>	445	14.8	217	24.4
<i>Oncometopia undata</i>	117	33.3	100	33.0
<i>Cuerna costalis</i>	148	17.6	101	24.7
<i>Homalodisca insolita</i>	33	42.4	23	47.8
<i>Graphocephala versuta</i>	36	22.2	28	28.6

In view of the widely varying numbers of tests performed with the different species and, even more, of the strongly disparate conditions during the optimum period for experimental transmission, it seems doubtful that there is any real difference in the efficiency of these species as experimental vectors. The results with *insolita* might be questioned. However, the figures for this species represent the results of only 1 year's work. Three of the other species were even more effective during single years, and further testing will undoubtedly lower the success ratio of the *insolita* findings.

Nonvectors

In addition to the 6 proved vectors, 36 other species of Homoptera, 13 species of Heteroptera, and 1 species of Lepidoptera were tested. Only 1 to 5 tests were made with some species and 10 to 77 tests with others. However, nearly all this work was performed at Chattanooga prior to the incrimination of any vector. Because of the very poor success, even with actual vectors, of our efforts in that locality, the negative results with other species do not appear worthy of consideration.

At Fort Valley during 1945–53 one or more tests were made with 14 species of Homoptera, other than the 6 proved vectors, and also with two groups of insects that could not be identified specifically. The names of these species and the number of tests made with each are as follows:

Species	Number of tests
Cicadellidae (Tettigellinae):	
<i>Aulacizes irrorata</i> (F.).....	12
<i>Carneoccephala flaviceps</i> (Riley).....	1
Other Cicadellidae:	
<i>Agallia constricta</i> Van D.....	1
<i>Chlorotettix viridis</i> Van D.....	8
<i>Cyponana fastiga</i> De L.....	11
<i>Cyponana</i> sp. (probably <i>fastiga</i>).....	2
<i>Paraphlepsius irroratus</i> (Say).....	3
<i>Paraphlepsius</i> sp. (probably <i>irroratus</i>).....	3
<i>Scaphytopius acutus</i> (Say).....	1
<i>Texananus ercullus</i> (Uhler).....	1
<i>Tylozygus bifidus</i> (Say).....	1

	Species	Number of tests
Cercopidae:		
	<i>Tomaspis bicincta</i> (Say).....	2
Dictyophoridae:		
	<i>Scolops pungens</i> (Germ.).....	1
Membracidae:		
	<i>Spisistilus festinus</i> (Say).....	3

Although all attempts at transmission with these species failed, it is obvious that too few tests were made to warrant their definite classification as nonvectors. The tests with *A. irrorata* were particularly unsatisfactory. This large sharpshooter has habits similar to those of *coagulata* and *undata*. Like them, it includes peach among its favored woody host plants. Only 12 tests were made with this species, because it is scarce in the Fort Valley area and seldom are more than 1 or 2 individuals found at any one time. Consequently, in most tests only 2 or 3 insects were used. If this species could have been adequately tested, we believe that it would have been as effective a vector as the other members of the tribe Proconiini.

Probably *Graphocephala coccinea* (Forst.) can transmit phony peach experimentally. In the Fort Valley area the species was taken occasionally on sticky-board traps in peach orchards, but it confined its activities almost exclusively to wooded areas, never migrating generally to the open fields as does *versuta*. The species is not common in the Gulf States, and we never succeeded in collecting live specimens in numbers adequate for satisfactory transmission tests.

Role of Donors

Studies of the behavior of virus diseases affecting trees and shrubs have many complicating or conditioning factors in addition to those pertaining to investigations of viruses in annuals. In the transmission of phony peach, these include such variables as the season of testing as it may affect the performance of both the vectors and the test trees, possible irregular distribution of the virus within the source plant, and the long but indefinite incubation period of $1\frac{1}{2}$ to 3 years.

The first marked effect of these confusing factors is that the experimenter enters on each new transmission study in an uncertain frame of mind. When he must wait for 2 or 3 years before he can obtain positive results from an experiment, questions loom very large, such as whether a particular diseased tree can furnish virus to the vectors, whether the test trees are in condition to become infected, or whether individual insects can act as vectors. Results from many tests on the transmission of phony peach were vitiated by some of these factors that were not recognized at the time the tests were made.

From the inception of experimental work on phony peach there has been much uncertainty as to the distribution of the virus in the host plant. About 1935 Hutchins (*11*) tested both the wood and bark of roots as sources of inoculum, and he concluded that the virus is not present in the phloem but is confined to the woody cylinder of the host plant. Subsequent experimentation failed to furnish any contradictory evidence, and the finding that the known vectors are all xylem feeders adds much confirmatory evidence.

With this new aspect of distribution as a guide, the possibility that transmission might be obtained through the medium of top wood was canvassed. Employing modified types of inoculum, it was found

that the disease could be transmitted readily from the tops of infected wild plums and occasionally from affected peach trees. Through the use of heel spurs and stalked buds, considerable success was attained in transmission from peach to peach (12), and apparently equal results follow the use of approach grafts. Even so, the percentage of failures that follow attempts to achieve transmission by means of top wood pose a serious question, as yet unanswered, as to the distribution of the virus in peach tops, both spatially and seasonally.

Plum twigs appear to be much more efficient sources of infection than peach twigs. This leads to the conclusion that the virus is more uniformly distributed in plum tops and suggests the possibility that it may be present in higher titer in plum than in peach.

In 388 transmission tests with insects of known transmissive capability, 86 trees were used as possible sources of inoculum—74 were peach, 11 were plum, and 1 was a peach tree bearing a plum branch, both parts being used as sources. Many trees were used only once, although a few served as donors for numerous tests. Positive inoculations resulted with insects that were caged on 43 of these trees—32 peach, 10 plum, and 1 peach with a plum branch. Of the 43 trees that gave negative results, 24 were used only once and 10 were used twice. Success might have followed repeated use of at least some of these trees. Seven of the nondonors were used three times, one served in 4 tests, and one in 6. As compared with the nondonors, the donors were used as follows: 9 trees were used once, 8 twice, and the remaining 26 from 3 to as many as 89 times.

It must be understood that not all tests with donors were successful. During the experiments operators received a strong impression that some of the source trees were much less efficient than others. However, so many variables were involved in the experimental procedure, such as number of tests per source tree, season of testing, and source of the insects, that no definite conclusions can be drawn. This is true concerning possible differences not only among peach trees but also between peach and plum trees.

However, one series of experiments does furnish definite data regarding possible differences between peach and plum as sources of inoculum and, by reasonable extension, regarding possible differences in the distribution of the virus in the two hosts. In the summer of 1942 a Hiley peach tree in its first growing season was inoculated by means of a short scion from a phony wild plum. The scion itself lived and developed into a good-sized branch. From May 1946 to July 1950 this tree was used as a source of inoculum in 89 transmission tests. The results in table 2 indicate that plum is a more effective donor than peach, regardless of the vector. Elimination of 11 tests of *coagulata* on peach and 7 on plum, initiated during the periods of hot weather that killed the insects before the latent period of the virus was complete, strengthens the conclusions.

Even more directly comparable figures are available from a few tests. On June 10, 1949, 59 sharpshooters were collected from Albizia and tung trees. These were caged on the branches of the source tree as follows: On peach, 22 *coagulata* adults; on plum, 18 *coagulata* adults, 11 nymphs of the same species, and 8 *undata* adults. Some of the nymphs transformed to adults while caged on the inoculum. After feeding on the donor for 3 days, the living insects were trans-

TABLE 2.—Comparative adequacy of peach and plum branches of a diseased tree as donors of virus for insect transmission of phony peach, 1946-50

Species	Peach		Plum	
	Number of tests	Number of positive infections	Number of tests	Number of positive infections
<i>Homalodisca coagulata</i>	29	2	19	11
<i>Oncometopia undata</i>	6	0	9	7
<i>Cuernia costalis</i>	11	2	10	10
<i>Graphocephala versuta</i>	4	3	1	1
Total.....	50	7	39	29
Percent efficiency.....	14.0		74.4	

ferred to test trees as follows: 16 *coagulata* adults from peach, 16 *coagulata* adults from plum, 3 *coagulata* adults and 7 nymphs from plum, and 5 *undata* adults from plum. All the insects from the plum branch transmitted the disease, but those from the peach branch failed to do so.

On June 15, 1949, 50 *coagulata* adults, collected from Albizzia and tung, were divided into two equal lots. One was caged on the peach branch of the source tree and the other on the plum branch. Mortality was high, but on June 21, 8 adults from the plum and 12 from the peach branch were caged on test trees. Those from the plum transmitted the disease, but those from the peach did not.

Again on June 15, 94 *coagulata* adults, collected on sunflowers, were divided into four lots. Three lots were caged on the peach branch and the fourth on the plum branch. At the same time a small lot of *undata* from the same source was caged on the plum. On June 21 they were transferred to test trees—lots of 15, 13, and 13 *coagulata* adults from the peach and lots of 14 *coagulata* and 6 *undata* adults from the plum. Both lots from the plum transmitted the disease, but the three lots from the peach did not.

Although these data do not furnish any light on such factors as abundance of inoculum or prevalence of the virus in the plant host, they do indicate that the virus behaves differently in plum than it does in peach.

An interesting feature of the work with the plum branch may be noted here. On September 5, 1950, 4 lots of *coagulata* and 1 lot of *undata*, all collected from a small planting of okra, were caged on the plum branch. At that time the branch had shed all its leaves, many of the twigs had died, and the entire branch appeared to be dying. The insects were left on the plum for 18 hours and were then transferred to five test trees. The 1 lot of *undata* and 2 lots of *coagulata* transmitted the disease. Failure of the other 2 lots of *coagulata* to transmit appears to be due to the condition of the test trees (see p. 14). Although the plum branch appeared to maintain some life into the ensuing winter, it was dead and drying out by the middle of March 1951.

Condition of Test Trees

Throughout the experimental work on insect transmission of phony peach, the tests made during the spring were highly successful. In some years the tests in July and August also resulted in a considerable proportion of positive inoculations. In order to obtain comparable figures, it is necessary to eliminate all comparisons of tests with different species, as well as all those with different source trees. Such figures are available only for *coagulata*, except in 1949 when enough tests were made with *undata* to support comparisons. The totals are less than desirable, especially when considered on a yearly basis. Nevertheless, the general trend is sufficiently consistent to warrant consideration for the 3 years for which comparisons were made. The data in table 3 show that transmissive efficiency in July was only two-fifths of that for June, and the efficiency in August was two-thirds of that for July and less than two-sevenths of that for June.

TABLE 3.—*Monthly efficiency of leafhoppers as vectors of phony peach in certain years at Fort Valley, Ga.*

Species and year	June		July		August	
	Number of tests	Number of positive infections	Number of tests	Number of positive infections	Number of tests	Number of positive infections
<i>Homalodisca coagulata</i> :						
1946.....	2	1	13	4	17	1
1947.....	7	4	29	3	7	1
<i>Homalodisca coagulata</i> and <i>Oncomelopia undata</i> , 1949.....	29	12	37	7	17	3
Total.....	38	17	79	14	41	5
Percent efficiency.....	45		18		12	

Several reasons have been suggested for this decrease in experimental efficiency during the summer. In particular, there has been speculation that high temperatures may inactivate the virus in the top of the plant or in the insect. That this is not true for the trees is indicated by the highly successful inoculations made by budding with beeled spurs or short scions during the late summer. As for the insects, some of the highest summer temperatures during the experiments were in June, when efficiency in experimental transmission was at its peak.

Possibly the results may be caused by seasonal variations in the condition of the test trees, and a few small-scale experiments seem to support this hypothesis. For the work on experimental transmission, June-bud trees of one variety were planted each winter in a large screen house. The trees were usually fertilized in early spring and generally received no further fertilization. Growth was usually very vigorous throughout the spring and continued at a retarded rate into July. Then growth was checked very sharply or ceased entirely and

the wood began to mature. During some summers when rains were abundant, growth was resumed, at least in some trees. This behavior was only general. Individual trees varied greatly in their reactions, both as to the time and amount of growth.

To test the possibility that the virus might have more difficulty in establishing itself in trees that had checked growth, several trees were cut back heavily on August 8, 1950, in order to shock them into a resumption of growth. They responded satisfactorily and by September 5 had produced new shoots up to 20 cm. or more in length and were still growing vigorously. On that date *coagulata* adults were caged on a source tree that had been a successful donor of the virus. After 3 days on this tree the insects were transferred to test trees. Two lots of 10 insects each were caged on two vigorously growing trees. Two other lots of 7 and 14 insects were caged on two trees that had not been cut back and had made no new growth since July. The vigorously growing trees were infected; the other two trees were not. Because it was a small-scale experiment further work is needed, but the results are certainly suggestive.

Details of Transmission

During the early experiments every attempt was made to avoid foreseeable qualifying factors that might interfere with successful transmission. Consequently, most of the tests were made with groups of as many as 15 to 25 insects, they were caged on inoculum for 3 days or more, and they were left on the test trees for 20 to 30 days or, if for a shorter period, at least as long as any survived. Later, many refinements were introduced. Smaller groups of insects were employed, and the periods on the inoculum and the test trees were sometimes as short as 1 and 5 days, respectively.

Because of the great difficulty in rearing members of the Tettigellinae in confinement (8, 9), and because the objective was merely to determine the ability or disability of certain species of insects to transmit phony peach, all the early experiments were made with wild insects. Apparently most of them were innocuous when caught, since it was possible to demonstrate natural transmission only when the insects were caught on diseased trees or under certain special conditions. However, the faint possibility that occasional individuals might have been naturally infective precludes the use of data from any tests with wild insects when considering such features as length of the latent period. Furthermore, it is necessary to qualify any conclusions regarding such features as comparative ability of various naturally infected trees to serve as donors. For this reason, few inferences can be drawn from the early experiments or from any tests with *coagulata* or *undata*. In later experiments some success was achieved in rearing the two grass-feeding species *costalis* and *insolita*, and most of the conclusions regarding transmission must be drawn from experiments with these two species.

Acquisition Feeding Period

Because of the scarcity of reared, noninfectious insects, no attempt was made to determine exactly the minimum acquisition feeding periods. Periods of 3 or 4 days were entirely adequate and as satisfactory as considerably longer periods. One lot of *undata* and one of *versuta*, collected in northwest Georgia, transmitted the disease

after 1 day on the source tree. One lot of *costalis* and two of *insolita* that were reared on Johnson grass also transmitted the disease after an acquisition period of 1 day.

Nevertheless, there is evidence that 1 day is not always long enough to acquire the virus. On June 12 and 26, 1953, two lots of *insolita* were caged on a small phony peach tree for 3 days. Both lots transmitted the disease. Another lot of *insolita*, caged on a phony Methley plum tree for 3 days beginning June 30, was successful in infecting a test tree. In contrast, only 1 lot out of 3 caged on the same plum and 1 lot out of 4 caged on the same peach for 1 day transmitted the disease. The 1-day lots were caged on inoculum on July 2 and 8. The seasonal element does not appear to be a factor in these tests, since the two 1-day lots transferred to test trees on July 3, the same date as one of the 3-day lots, failed to transmit, whereas two of the 1-day lots transferred on July 9 were successful. The total acquisition periods appear to have been adequate. The 3-day lot and the two 1-day lots that were transferred on July 3 were on the test trees for 14 days. All the July 9 transferees were on the test trees for 19 days.

All insects in these tests were reared on Johnson grass in an insectary. One lot consisted of only 4 insects, the others of 9 or more. These numbers were adequate, because the two 1-day lots containing the fewest insects were the only ones that infected their test trees.

Latent Period

It has long been recognized that the transmission of a plant virus by a leafhopper requires a latent period⁴ of appreciable duration. For some years there was uncertainty as to the exact nature of this interim between acquisition of the virus and ability to infect a new plant host. Since 1940 various workers (2, 17) have demonstrated that sometimes the phenomenon is actually one of incubation, with the virus multiplying within the body of the host, and that some viruses appear to be diseases of their insect vectors as well as of their plant hosts.

Because most of our work has been done with wild insects, few data have been obtained regarding the latent period, but there is some evidence that it is required for the transmission of phony peach. For some of the pertinent tests, the insects were collected on garden annuals or perennials, or on grasses in northwest Georgia. Since no phony peach trees have ever been observed in the area, the possibility that the insects could have been infective when caught is extremely remote. In other tests the vectors were reared from eggs, either on Johnson grass or sunflowers, in an insectary.

On June 22, 1950, three *costalis* adults were caged on inoculum. Eight days later they were transferred to a test tree for 5 days. They failed to infect this tree. On July 5 the two living insects were moved to a second test tree, where they remained for 23 days. They infected the second tree. There is evidence that vectors of phony peach can acquire a starting dose of the virus in 1 day or less. However, it is not known that they always do so. The only positive information

⁴ For clarity, it appears best to use the terms "latent period" to cover the behavior of the virus in the insect's body and "incubation period" to designate the interim between infection and appearance of symptoms in the plant host.

furnished by this test is that the latent period was more than 5 days and possibly as long as 12 or more.

In other tests two *undata* nymphs collected on dahlias at Dahlonga, Ga., were caged on inoculum for 3 days. On July 24, 1950, they were transferred to a test tree. Both died on the test tree prior to August 8, but they transmitted the disease. In this test the latent period could not have been more than 15 days. On July 11, 10 *versuta* adults collected on weeds and grass in Catoosa County, Ga., were caged on inoculum for 1 day and then were transferred to a test tree. The insects all died on the test tree within 16 days. However, they transmitted the disease. The latent period must have been less than 17 days.

Results of tests with some wild vectors of all species suggest that under optimum conditions the requisite latent period may be definitely shorter than is indicated by the above tests, and a few tests in 1953 with nonviruliferous *costalis* and *insolita* confirm this belief. One lot of *costalis*, reared on Johnson grass, was allowed an acquisition period of 1 day and a transmission period of 7 days. This lot transmitted the disease after a maximum possible interval of only 8 days. Two lots of *insolita*, given 3-day acquisition periods and 7- and 8-day transmission periods, successfully infected their test trees after maximum latent periods of 10 and 11 days, respectively.

On the other hand, in five tests in which the vectors were caged on two test trees in succession, the insects failed to infect the first test trees after possible latent periods of 10 to 20 days, but they did infect the second test trees. One lot of *costalis* failed to transmit during a possible latent period of 11 days, but it did succeed when permitted a possible maximum of 21 days. Two lots of *insolita* did not transmit in 10 and 14 days, and two other lots failed to do so in 20 days. All four lots succeeded when given additional time. Unfortunately since all died after an indeterminate period on their second test trees, no figures are available on the maximum possible latent periods for successful transmission.

It must be recognized that varying tree response may be a factor in some if not all the tests cited above. For example, one lot of 14 *costalis* insects infected the first test tree after a maximum possible latent period of 8 days. Two insects died on this tree. The remaining 12 failed to infect a second tree on which they were confined for 4 additional days, but they did infect a third tree during an indeterminate additional period. These results may be considered in two ways. Either fully infective insects do not always achieve transmission, or in group tests some individuals may require a longer period to build up an infective dose than do others. This latter hypothesis would demand that 1 or 2 individuals (those that died on the first test tree) were fully infective within 8 days but that the other 12 insects required over 12 days to reach the infective threshold.

During the fall of 1947 *coagulata* was taken in great abundance on peach trees in the Fort Valley area. Three series of transmission tests were set up. In the first series conducted between October 21 and December 8, 79 tests were made. In the second series between December 1 and January 6, the insects were transferred to a second set of test trees for 59 tests, and in the third series between January 6 and 23, the insects were again transferred to a third set of test trees

for 18 tests. In making the first transfer from the first test trees to the second set, single lots of insects were usually moved. Insects used in 2 or 3 first-series tests were combined to make an adequate lot for three of the second-series tests. In the third series direct transfers of single lots were made for 13 tests, whereas for 5 tests transfers were made with composite lots of insects used in 2, 3, or 5 second-series tests.

Insects for all but 8 tests of the first series had been collected from peach trees in commercial orchards, many of them from phony trees. In 16 tests insects from obviously phony hosts were caged directly on the test trees. In the other 63 tests the vectors, regardless of source, were given a preliminary feeding on some particular source tree before being tested. All trees used in the first- and second-series tests were 1 year old since leaving the nursery. All had mature wood. A few of the trees used in the first series still bore 3 or 4 terminal leaves, but the others were bare, as were all the trees used in the second series. Tests in the third series were made with newly planted June-bud whips that were fully dormant.

The demonstrably possible latent period for the first series ranged from 34 to 50 days for insects given the full treatment and from 30 to 36 days for insects collected on diseased host trees and caged directly on test trees. From the 79 tests in this series only one positive transmission was obtained, or an efficiency of only 1.3 percent. This result was accomplished by a lot of 20 insects collected from peach trees on October 28, caged on a phony wild plum tree for 3 days, and transferred to the test tree on October 31. Seven of the twenty insects lived for 31 days on the test tree and were then transferred to a second tree, which they failed to infect. All insects died on the second tree, and it is not known how long they lived on it. All the infectious insects on the first test tree may have been among the 13 that died on that tree. The demonstrably possible latent period was only 34 days. Failure of any insects in the other 78 tests to transmit the disease, even after possible latent periods of as long as 50 days, suggests that some insects in the successful group may have been already infectious when caught.

In the second-series tests the demonstrable latent period ranged from 58 to 85 days. Transmission occurred in 4 of the 59 tests, or an efficiency of 6.8 percent.

In the third-series tests all insects died in 13 out of the 18 tests, and there is no record of the length of their survival. The possible latent period cannot be determined except that it was at least as long as the sums of the previous periods of confinement. These totals ranged from 67 to 84 days. Insects in five tests had possible latent periods of 86 to 110 days.

From the 18 tests in this series only one positive transmission occurred, or an efficiency of 5.6 percent. This figure may well be unfairly low. Cold weather prevailed during the test period, and probably the insects did little if any feeding. However, the one transmission was effected by a group of insects that died on the test tree. The possible latent period was over 83 days. The group was composed of insects that had been used in 3 first- and 2 second-series tests. None of the five trees used in earlier tests were infected.

It must be recognized that these tests had some obvious and some

unknown complicating factors. Among these were the physiological condition of the individual test trees and of the individual donors, possible infectiousness of some of the insects when collected, and varying degrees of activity in different lots of insects or even in individual insects. This last factor should not be discounted, since feeding activity was certainly less in late December and January, when the second- and third-series tests were made, than in November and early December, when the first-series tests were under way. Probably any of these complicating factors would become more and more consequential during cold weather and the concurrently progressive dormancy of both plants and insects and thus would be more important in the second- and especially in the third-series tests. This strengthens the evidence that the increased transmission efficiency in the second- and third-series tests indicates a marked lengthening of the requisite latent period, which was due to low temperatures (16).

Retention of Virus

On April 7 and 11, 1950, three lots of *costalis* were each caged on a test tree after confinement on inoculum for 19 to 67 days. All lots were left on the trees for 7 to 10 days and then transferred to a second set for 10 days. This process was continued until all the insects died. One lot was transferred serially to 4 test trees, infecting all 4; the second lot to 7 trees, infecting the first 5; and the third lot to 9 trees, infecting only the first 8.

Only 3 out of 9 insects in the second lot lived to be caged on the sixth and seventh trees. Only 1 out of 15 insects in the third lot lived to be caged on the ninth tree. It died on this tree and there is no positive evidence that it ever fed on it.

The longest period between caging on the first tree and on the eighth was 89 days. The infective insects retained the virus for 91 days or more.

On April 20, 1951, a lot of 8 *costalis* insects was caged on a test tree, after having fed for 44 days on a source tree. After 3 days on the test tree, these insects were transferred to Johnson grass for 7 days. They were then caged on a second test tree. This process was repeated once more before they all died. The vectors failed to inoculate the first test tree, but they did inoculate both the second and third trees. The period between caging on the first and last test trees was 21 days. In this period they spent 14 days on nonsusceptible plants.

In October 1952 large numbers of *costalis* were collected from grasses and caged on three phony trees for 6 to 10 days. On October 21 and 30 they were removed and introduced into a small cage placed in the open over a heavy growth of Bermuda grass. After at least 144 days six insects were taken from the cage on March 23 and confined in the greenhouse on a potted Hiley June-bud tree for 8 days. They were then transferred to a similar tree planted in a screen house, where they were left for 44 days. The insects did not infect the first tree but did infect the second, having retained the virus for at least 152 days. It should be noted here that all attempts to infect potted trees in the greenhouse in March failed.

Seventeen *costalis* insects were caged on a phony tree from November 25, 1952, until February 9, 1953, when they were transferred to potted Johnson grass in a greenhouse. On April 4 the insects were

caged on a Hiley June-bud tree in a screen house, where they remained for 37 days. They infected this tree, having retained the virus during at least 54 days of active life on a nonsusceptible host plant.

Attempts to ascertain the ability of other species of vectors to carry the virus over the winter failed because of our inability to maintain these species through the semihibernation period. All the vectors become active during warm periods throughout the winter. *C. costalis* feeds on stems of grasses, under which it seeks shelter during cold weather, but the other species normally fly about on warm days, seeking food at considerable distances from where they hibernate. Such insects are as difficult to handle in cages during the winter as they are during the summer.

Transmission by Nymphs

In a single test two noninfectious *undata* nymphs, after being confined for 3 days on a source tree, transmitted the disease to one test tree. Since the nymphs died on this tree in less than 15 days, the latent period must have been less than 18 days.

This test is of additional interest in that two other noninfectious *undata* nymphs, confined on the source tree in the same cage with the first two, transformed to adults on the source tree. They failed to infect either of two test trees to which they were transferred serially, although both lived long enough to permit a latent period of over 18 days.

Minimum Number of Vectors (Infective Dosage Level)

Transmission did not occur when single vectors were used in 17 tests with four species. Five infections were obtained with two vectors—one infection each with *costalis*, *insolita*, and a combination of one *undata* and one *coagulata*, and two with *undata*. Eight infections were obtained with three vectors—three infections each with *costalis* and *coagulata* and one each with *undata* and *insolita*.

Nevertheless the patterns of primary infections in young orchards often suggest that they were achieved by single insects. In many orchards the initial infection in a planting of 1,000 or 2,000 trees has been limited to 2 or 3 trees growing in a very restricted area—frequently immediately adjacent to each other. In other orchards there have been 2 or 3 foci of initial infection, each affecting from 2 to 4 trees. It is difficult to imagine that such patterns can result from the activities of a group of insects traveling from tree to tree. Yet, unless individual insects can transmit infection, the situation can be explained only by assuming the occurrence of a general, heavy invasion of the young orchard by the sharpshooters and the chance association of 2 or 3 infectious insects on individual trees. Not only is the major premise contrary to observed behavior, in that the sharpshooters are seldom found in abundance in very young, healthy orchards, but the odds appear overwhelming against such fortuitous associations occurring in such extremely limited areas.

Diversity in Infective Ability

Since attempts to transmit phony peach with single vectors have not been successful, there are no data by which to compare the capabilities of individual insects as vectors. It has been demonstrated

that some groups of vectors can acquire the virus from infected trees and that they can infect other trees for long periods, in comparison with their normal life span. Moreover, they may maintain this ability when they are confined on nonsusceptible hosts. It appears reasonable to conclude that not only can some sharpshooters acquire dosages of the phony peach virus but that it multiplies within their bodies.

During transmission studies a decreasing population of vectors commonly reached a level at which infection was no longer transmitted. In one test two *costalis* adults transmitted the disease, one insect dying on the test plant. When transferred to a second test plant, the remaining insect failed to transmit. In another test three insects infected the eighth test plant in a series, but a single survivor failed to infect the ninth. In another test five insects infected the fifth test plant, but three survivors failed to infect the sixth and seventh plants. In a serial test with *versuta*, lots of 16, 15, and 8 insects successfully inoculated the first, second, and third trees, respectively, but lots of 5 and 2 remaining insects failed to infect the fourth and fifth trees. Finally, in a test with *coagulata*, lots of 19 and 12 insects infected the first and second trees in a series, respectively, but 6 remaining individuals did not infect the third tree.

By themselves the first two tests cited might suggest the inability of single vectors to furnish infective doses of virus. However, the other three tests show clearly that other factors were entailed and that for some reason certain vectors could not transmit the disease. Several possible causes are apparent. These nonvectors may have failed to imbibe any virus while feeding on the donor. This would be expected and is possible if the virus was distributed unevenly in the host plant.

On the other hand, inability to transmit may stem from some factor operating within the insect. This may be of a negative character, such as the inability of the virus to move from the digestive tract to the salivary glands, a condition that appears to occur in some other leafhopper vectors (1, 20, 21). Inability to transmit may be of a positive character, such as the ability of some vectors to inactivate or to destroy the ingested virus before it can multiply within their bodies. This would suggest that the virus induces a disease in some insects, as well as in some plants, and that some insects can overcome the infection just as other animals overcome infections by other viruses. The infective insects would be sick insects. This situation is suggested because the infective insects of a given population do not live so long as the noninfective, as indicated in three of the tests cited.

NATURAL VECTORS

Several species of the Tettigellinae, regardless of their natural feeding habits, are able to exist for long periods on peach and plum. At least five species transmit phony peach experimentally with equal facility. This experimental parity does not in any way indicate an equality in importance as natural vectors. In fact one species that was most successful as an experimental vector probably rarely serves as a natural vector.

C. costalis lays its eggs in the blades of various grasses and commonly hibernates under matted grasses in the open. The adults as well as

the young feed primarily on grasses, but at times considerable numbers are found in early spring on low-growing weeds, such as *Oenothera*. Occasionally the adults are taken on taller plants, such as sunflowers and okra, where they may be located as high as 5 or 6 feet aboveground. There is no definite association with peach or any other trees or shrubs. Both the adults and the larger nymphs sometimes feed on young peach seedlings in areas where the insects are locally abundant, but the species is seldom found on older trees, although an adult may rarely feed on low-hanging twigs of trees in grassy areas. Most such associations have been observed on dehorned trees that have a few twigs arising from the bases of the main limbs. Obviously the habits of this species obviate any importance as a natural vector of phony peach.

Much the same may be said of *insolita*. Its general feeding habits appear to be even more restricted than those of *costalis*. In the Fort Valley area *insolita* has been found, with few exceptions, on only two grasses, Johnson grass and Texas millet. However, specimens have been taken on low-hanging twigs of dehorned peach trees, and once an adult was observed feeding on a peach twig about 6 feet aboveground. Since Johnson grass is an introduced plant, *insolita* must have changed its feeding habits recently, and further changes may occur in its new habitat in the Southeast. However, *insolita* probably will never become a natural vector of phony peach.

G. versuta, *H. coagulata*, and *O. undata* are much more closely associated with woody plants or with stout-stemmed annuals and perennials. *G. versuta* prefers the latter. It is seldom found on peach trees, and then usually on the leaves. Its habit of feeding on large veins rather than on twigs and stems appears to be common. The insect is found rather generally, in low populations, on wild plums and may transmit phony peach from infected wild plums to nearby plantings of young peach trees. It appears to play little or no part in spreading the disease from peach to peach.

H. coagulata and *O. undata* not only feed freely on the stems of woody plants but are particularly associated with trees and shrubs during the spring and fall. Moreover, peach trees are one of their favored hosts during those periods, and some association with peach occurs throughout the growing season. The habits and behavior of these two species make them logical suspects as primary natural vectors of phony peach.

As a check on the probable infectiousness of wild populations of leafhoppers used as vectors in transmission work, several direct tests were made. Collected insects were caged immediately on test trees without an interim on a phony tree. As with many other types of tests, the results, which were negative, are not available for comparison, because the tests were made early in the spring or during other periods in which we learned later that transmission either does not occur or occurs only occasionally.

In the spring of 1950 and 1952 *costalis* was collected on and under grasses in orchards heavily infected with phony peach. Sixteen lots of from 14 to 25 insects each were caged directly on test trees. No infection resulted.

During 1950 and 1952 seven lots of *versuta*, with 11 to 47 insects per lot, were collected from sunflowers growing among infected trees.

They also were caged directly on test trees. All results were negative.

Two lots of *undata* and one of *coagulata*, with 14 to 21 insects per lot, were collected on sunflowers growing near Fort Valley but at some distance from peach orchards. Results of direct tests with these insects were negative. A third lot of nine *undata* insects, collected on *Albizzia* growing at the laboratory, also gave negative results.

For several years there was, near Fort Valley, a small ornamental nursery bordered on two sides by a peach orchard that was heavily infected with phony peach. *O. undata* was notably abundant in this nursery during April and early May of 1949 and 1950. The species appeared to prefer ash and redbud as food hosts. Fifteen lots of 11 to 25 insects each were collected, mainly from ash, and used in direct tests. Six of the fifteen lots induced infections in the test trees. Since this species was generally present on the peach trees in the adjacent orchard during the same period, it is suspected that the infectious insects had fed on phony peach trees and had then moved from the orchard to the nursery.

Five lots of *coagulata*, with 5 to 15 insects per lot, were also collected on the nursery trees during the same period. On direct test none of them transmitted the disease. These results are plausible, since *coagulata* is 4 to 6 weeks behind *undata* in moving from hibernation areas into the open. By the time this species invaded the fields, the ash and other nursery trees were acceptable as food hosts, and *coagulata* probably flew directly to the nursery without an interim in the peach orchard.

As part of an experiment on the eradication of wild plums, some bushes in a thicket at the edge of the laboratory grounds were sprayed with ammonium sulfamate in June 1949. Shortly afterward the foliage on the treated bushes turned brown and the bushes were in an obvious state of decline. *H. coagulata* was attracted to these sick plants in large numbers. However, none could be found on the untreated bushes even when they were growing close to the treated ones. Because of the proximity to infected peach plantings, some of the plum trees were suspected of being phony, although none showed any visual evidence. Six lots of insects, with 8 to 25 per lot, were collected from the treated plums and caged directly on the test trees. Two lots successfully transmitted phony peach.

For about 25 years a Federal-State cooperative service has provided for annual inspections of peach orchards in areas where phony peach causes serious economic losses and for marking all trees that show disease symptoms. It is customary to cut off the scaffold branches of the diseased trees, leaving only enough wood for easy removal of the stumps with a chain and tractor. Ideally all twig growth should also be removed, since a considerable period frequently intervenes between marking and removal. Not only do such twigs tend to maintain life in the stumps but also they are notably attractive to vectors of phony peach. Unfortunately the inspections must be made during hot weather. Dehorning of trees is strenuous, and in old orchards containing many phony trees the laborers who cut the trees become tired and careless. As a result, removal of twigs from the stumps is sometimes neglected.

Old twigs on dehorned stumps begin to attract the vectors about 7 to 10 days after the trees are cut. During July and early August in

1949 and 1950 ten lots of *coagulata*, with 8 to 16 insects each, were collected on phony stumps and caged directly on test trees. Eight of these lots caused infections. Four similar lots collected in September failed to transmit the disease. During the July-August period 2 out of 4 lots of *undata*, with 3 to 10 insects each, included infectious individuals. It should be noted that *undata* is far less abundant on peach trees during the summer than is *coagulata*. One out of two lots of *costalis* from phony stumps infected a test tree. This lot consisted of only three individuals. This species occurs only rarely on phony stumps.

These tests indicate clearly that *coagulata* and *undata* are important natural vectors of phony peach. *C. costalis* might be a primary vector except for its habits. Even when this species becomes infectious from feeding on phony stumps, there is little likelihood that it will move to other peach trees. The noninfectiousness of either *costalis* or *versuta* collected in diseased orchards, but not directly from peach trees, again indicates the improbability that these species play any serious part in natural transmission.

The large number of failures resulting from attempts to transmit the disease by means of wild insects from certain phony trees, suspected of being nondonors or very inefficient donors, seems to indicate that only a small percentage of individuals of all species captured at some distance from peach orchards are infectious.

Much collateral evidence indicates that *coagulata* is the outstanding primary vector. However, during a period of 4 to 6 weeks in early spring *undata* has been taken in much greater numbers. The sole explanation appears to lie in their contrasting spring behavior, since *undata* moves from hibernation quarters to open fields much earlier than does *coagulata*.

After June 1-15 *coagulata* is much more common than *undata*, not only on peaches but on such favored summer hosts as sunflowers and okra. It is much more abundant than *undata* in the Coastal Plain and extreme lower Piedmont of the Gulf States.

Final evidence for the superiority of *coagulata* as a natural vector is furnished by a comparison of the distribution of that species with that of the disease. Although phony peach may spread locally wherever *undata* is present, the incidence of spread coinciding rather closely with the comparative abundance of the insect, serious epidemics are known only in areas where *coagulata* is found.

SEASON OF SPREAD

Several attempts have been made to determine when phony peach spreads naturally or is most active. In the early experiments small peach trees growing in 10-inch pots were suspended in trees in commercial orchards where the disease was particularly active. Between 1945 and 1949 a total of 680 trees were exposed. Usually three exposure periods were used, approximately from March through May, June through August, and September until January. Only 1 of the 680 trees ever exhibited disease symptoms. This tree had been exposed in a phony orchard tree from June 15 until September 16.

In addition to the failure to obtain adequate infections at any season, the use of potted trees proved to be unsatisfactory. Much

time and labor were spent watering the trees, and they grew very poorly. There was evidence also that the vectors were not attracted to the twigs of the small trees, even when they were closely intermingled with the tops of the mother trees. Although large numbers of *coagulata* were noted at times in the test trees, few adults were ever observed feeding on the potted trees.

An experiment was planned³ to provide periodical exposures of peach trees planted in the ground, the exposures to be repeated for at least 3 years. It was thought that this method would increase the probability of infection of at least some of the exposed trees, since it had been observed that orchard trees are seldom infected during the first year but that they are increasingly susceptible, because of greater attraction to the vectors, during the second and third years. Unfortunately this experiment was started in the spring of 1950 when the rate of disease spread was beginning markedly to recede, mainly because of great decreases in vector populations. Through the 3 years of testing only 38 of the 1,009 test trees became infected and 31 of these were in controls that were continuously exposed. Results of the periodically exposed lots are shown in table 4.

TABLE 4.—Season of natural spread of phony peach in peach trees, Fort Valley, Ga., 1950-55

Exposure period	Number of trees exposed	Percent diseased
March-May	192	0.5
June-July	197	2.0
August-September	173	1.1
October-February	188	0

Unsatisfactory as the results proved to be, they seem to indicate that spread occurs from May through August and that June and July are the months of greatest activity. They agree largely with the results of experimental transmission during varying periods of the year.

SUMMARY

The search for insect vectors of phony peach was initiated in 1936 by means of extensive surveys in the Southeastern United States. These included the collection and identification of Hemiptera (Heteroptera and Homoptera) and Thysanoptera from peach trees, weeds and grasses, and soil in peach orchards. Surveys were made in orchards where the disease was spreading rapidly, where spread was slow, and where local spread did not occur. Analysis of the survey records suggested a small group of Cicadellidae as the culprits, and the species finally incriminated were contained in this group.

Transmission studies demonstrated that the following leafhoppers are capable of transmitting phony peach under experimental pro-

³ In cooperation with Glenn KenKnight and L. C. Cochran, pathologists, Crops Research Division, Agricultural Research Service.

cedures and all are about equally efficient (24 to 33 percent): *Homalodisca coagulata* (Say), *Oncometopia undata* (F.), *Cruerna costalis* (F.), *Graphocephala versuta* (Say), and *H. insolita* (Wik.).

Phony peach is a persistent virus disease. The virus has a latent period in the insect of at least 8 days, although the average period is considerably longer and may extend to 20 days. Infective insects remain so for long periods, probably for the duration of their lives. At least one species can retain the virus for as long as 144 days during semihibernation. Nymphs can acquire the virus, and once they successfully inoculated a test tree. As few as two insects can effect transmission, but attempts to transmit with single insects have failed.

Despite the equal ability of all five vectors to transmit phony peach under experimental conditions, only *coagulata* and *undata* are primary natural vectors. They are the only species among the group that feed regularly on peach. *G. versuta*, an occasional visitor to peach trees, is a weak second. *C. costalis* and *H. insolita*, confining their feeding to grasses and herbaceous plants, seldom transmit the disease naturally.

The period when natural spread takes place is not definitely delimited. Spread may occur between May 1 and August 31. Circumstantial evidence suggests that most natural transmission occurs in June and July.

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