THE FEEDING HABITS OF SOME LEAF HOPPERS OF THE GENUS EMPOASCA

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INTRODUCTION

From the collections of Empoasca made during 1929 and 1930, in the course of studies on leaf-hopper injury to legumes, several different species were isolated. The life histories and habits of these species are being studied, and the types of injury that they occasion on economic plants. This paper reports a study of the external symptoms produced on the plant, and of the particular tissues fed upon, by six species of Empoasca. The habits of these species as they may be correlated with their physiology, are discussed. Since this type of work involves a considerable knowledge of plant cytology and plant physiology, the writers have attempted to describe actual observations, and to discuss only in a limited way the theories and conclusions concerning the nature of the injury caused by Empoasca fabae which have been advanced by previous workers. Only those references to previous work which seem to have a direct bearing on the problem have been cited in this paper. The present study was intended primarily as a foundation for considerable future work which now seems necessary in order to solve satisfactorily the problem of determining the exact cause of the injury produced by these species of Empoasca.

TECHNIC

Individuals used in this work were taken from pure lines of each species. After it had been determined that individuals of the two sexes were similar in their feeding habits and in the symptoms produced, males were selected for producing injury. Their specific identity was later determined by examination of the internal genitalia. The work was carried on in the greenhouse at a temperature of 75° to 80° F. Individuals of each species, except maligna, which was studied only on leaves of apple (Medicago sativa) in small cages, potato (Solanum tuberosum), Ladino clover (Trifolium repens latum), red clover (T. pratense), goldenrod (Solidago sp.), cowpea (Vigna sinensis), garden beans (Phaseolus vulgaris), and Jerusalem artichoke (Helianthus tuberosus) were also used as hosts. The behavior of the leaf hoppers and the effect upon the plants were recorded. Except in a few instances where partially wilted tissue was restored to turgidity by soaking in distilled water, the external

1 Received for publication Feb. 11, 1931; issued August, 1931. This paper reports the results of a cooperative study of leaf-hopper injury to legumes made by the Division of Forage Crops and Diseases, Bureau of Plant Industry, and the Division of Cereal and Forage Insects, Bureau of Entomology, U. S. Department of Agriculture.
2 The authors are grateful to Dr. D. M. DeLong, Ohio State University, for verifying the identity of the species of Empoasca included in this study.
3 Order Homoptera, family Cicadellidae.
4 For a description of this cage see: SMITH, FLOYD F. A NEW TYPE OF INSECT CAGE. Jour. Econ. Ent. 24: 14-16, illus. 1931.
and internal injury produced by each species was studied before the breaking down of the plant tissues, a condition which is accompanied by the later appearing symptoms, such as hopperburn of potato, yellowing of alfalfa, etc.

The material for cytological study, after exposure to the individual leaf hopper, was killed and fixed in one of the following agents: Formalin-alcohol-acetic-acid solution, weaker Flemming's fluid, chromo-acetic solution, Carnoy's fluid, or 95 per cent alcohol. The paraffin method was used for sectioning. Delafield's haematoxylin with eosin or with safranin was used in the early part of the work but later Flemming's triple stain (safranin, gentian violet, orange G) or safranin and light green, were used almost entirely.

TYPES OF INJURY

The species of Empoasca studied may be divided into two groups according to the type of injury produced.

GROUP 1.—PRIMARILY MESOPHYLL FEEDERS

This group includes five species, bifurcata DeL., erigeron DeL., filamenta DeL., abrupta DeL., and maligna Walsh. These leaf hoppers in feeding produce a definite stippling on the upper surface of the leaves, which is generally characteristic for each species. The stippling of maligna is very finely peppered: erigeron normally produces a slightly coarser type of stippling: and bifurcata, filamenta, and abrupta normally produce increasingly coarser stippling in the order named. In the feeding tests on alfalfa with bifurcata, erigeron, filamenta, and abrupta the amount of stippling produced in a given time by one individual increased in the order of the species named. (Fig. 1.) Since alfalfa is not the preferred host of erigeron or bifurcata the smaller amount and variation in type of stippled area produced by these species on this plant as compared with that of filamenta is probably to be expected. The feeding of erigeron and bifurcata on Solidago (figs. 2, 3), one of the preferred hosts, was much more extensive, which would also indicate that alfalfa is not the preferred host of these species. However, the type of feeding was typical for each of these species on all hosts tested. Usually adults of group 1, when confined to the leaves of alfalfa, lived until the greater part of the available leaf area had become stippled. One adult of E. filamenta lived for five days on a leaf area 15 mm. in diameter, while adults of E. bifurcata and E. erigeron have lived three and four days, respectively, on leaf tissue of the same area without being transferred to a fresh leaf.

In normal feeding, the leaf hopper evidently punctures the lower epidermis of the leaf and then feeds on the mesophyll tissue in all directions from this point, thus producing whitish spots (stippling) on the upper surface. The species of this group when confined to the upper surface of the leaf cause slightly smaller stippled areas than when confined to the lower surface, but apparently they are able to live as well on one surface as on the other. Often the center of the spot where the leaf hopper has fed appears green and normal. (Fig. 3.) If feeding punctures are made close together the stippled areas coalesce. When confined on the stems, petioles, or midveins of leaflets, the species of this group fed only for a few hours and died, usually
within 24 hours. Adults of *filamenta* and *abrupta* were apparently able to live slightly longer than *bifurcata* and *erigeron* on these plant parts. No wilting of the plant occurred beyond the point at which these species fed.

A microscopic study of stained sections through the stippled areas on the leaves showed that the cell walls of the spongy mesophyll and of the palisade cells had been torn and the entire cell contents removed. In many instances large parts of the cell wall had disappeared. The
FIGURE 2.—Typical stippling produced by *E. cripson* on *Solidago sp.* one of its preferred hosts. Compare with Figure 3. The dark area near the tip of the leaf was produced by infection of mildew. × 4½
Figure 3.—Typical stippling produced by *E. bifurcata* on *Solidago* sp., one of its preferred hosts. Note the normal colored areas in the center of many spots; also the slightly coarser stippling than in Figure 2. The feeding on leaves in Figures 2 and 3 was produced by several adults during an undetermined interval of time. × 4½.
normal-appearing centers of the stippled spots showed uninjured palisade cells directly above the point of entrance of the beak in the lower epidermis. (Fig. 4.) The leaf hopper is apparently unable to puncture the plant at right angles to the long axis of its body and it cannot therefore reach the tissue directly above the point of puncture. *E. abrupta* reached an area from 10 to 15 palisade cells in diameter in the mesophyll from one puncture; the other species of this group reached an area of from 6 to 12 cells from one puncture. When punctures are made close together the areas of destroyed mesophyll become confluent. It appeared from the sections studied that *maligna*, *erigeron*, and *bifacata* tend to feed on the spongy mesophyll as well as on the palisade cells. (Figs. 4 and 5.) The palisade cells

![Figure 4](image1.png)

*Figure 4.*—Section of alfalfa leaf through center of stippled area produced by feeding of *E. bifacata* on the lower surface. Cells in the spongy mesophyll and in the palisade layer have been emptied of their contents. Observe group of uninjured palisade cells directly above the point of puncture. × 315

![Figure 5](image2.png)

*Figure 5.*—Section of alfalfa leaf through portion of stippled area produced by feeding of *E. erigeron*. Note the collapse of the upper epidermal cells. × 315
seem to be preferred by *filamenta* and *abrupta*. (Fig. 6.) In many stippled areas, however, exceptions may be found. Stained sections of the exposed stems and petioles showed punctures through the cortex and these cells were emptied of their contents. The phloem in the stems and petioles did not appear to attract these species, although the vascular bundles were penetrated in a few instances. In both the stems and the leaves sheath material that stained bright red with safranin was found in irregular accumulations in the middle lamella between the cells of the cortex or of the mesophyll. Only occasionally were cells observed that were either partially filled or surrounded with this material.

The stippled areas are located irregularly over the leaves, usually at some distance from the midvein or the lateral veins, but occasionally directly over them. Sections through the stippled areas about the veins, studied microscopically, showed the greatest accumulation of sheath material around the bundle. In some instances it was found that the stylets of *filamenta* had penetrated directly through the phloem and xylem intercellularly to the mesophyll above. The veins seem to interfere with the normal feeding of the leaf hoppers of this group, and no evidence was found that they were searching for the phloem as a source of food. (Fig. 7.)

Horne and Lefroy (5, p. 385) described the spotting of foliage by the leaf hoppers *Eupteryx atropunctata* Goze and *Chlorita viridula* Fall. They found that the assimilatory tissue was destroyed in the spotted areas but without killing the plant. Smith (10, p. 119–121), in his studies of the leaf hoppers *Eupteryx auratus* Liv. and *Zygina pallidifrons* Edw., found that the mesophyll tissue was attacked and that "spotting" of the foliage resulted. He stated that the spots enlarged after the leaf hoppers were removed, and he concluded that the salivary secretions gradually diffused through the cell walls.

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*Figure 6.* Section through portion of stippled area produced by *E. filamenta* on alfalfa leaflet. × 315
without injuring them but that they decolorized and destroyed the chlorophyll. In the present studies stippled areas on young leaves were found to enlarge slightly as the leaf expanded. With the binocular microscopic careful measurements were made of stippled spots on mature alfalfa leaves at 2-day intervals for 14 days after the leaf hoppers had been removed. These measurements failed to show any enlarging of the areas. Further, the green centers of the stippled areas and the small groups of cells forming salients into these areas did not disappear during the period of these observations. This seems to indicate that the injury caused by these species of Empoasca is largely mechanical and that a toxin, if injected, does not make itself apparent.

**GROUP 2.—PRIMARILY PHLOEM FEEDERS**

Group 2 includes *Empoasca fabae* (Harris) from Virginia and strains from other States widely separated, which resemble each other morphologically. All of these will be considered as one species in the present paper. Several workers have shown that *E. fabae* produces hopperburn of potato and a disease-like injury to alfalfa and many other plants. When this leaf hopper is confined on tender stems or petioles of apple, alfalfa or clover (fig. 8), wilting of the plant parts above the point of feeding occurs. When it is confined on the lower surface of the leaflet the midvein and lateral veins become lighter in color and wilting takes place in one or two days. When there is less feeding, wilting does not take place but the typical symptoms of tipburn, or of reddening or yellowing of leaves, according to the host plant, appear after a longer interval of time. Usually there is no evidence of stippling on the upper surface (see normal leaf, fig. 9), but occasionally very indistinct stippling, like small...
scratches, is apparent along the veins or in the mesophyll between the veins. (Fig. 10.)

A microscopic examination of sections through the leaves showed that the cells of the phloem are frequently punctured and are torn and distorted (reported as disorganized by Granovsky (4) or are filled, partially or completely, with the red-stained sheath material. The stylets of the insect pass intercellularly through the parenchyma of the midvein and the path is marked by an ill-defined sheath. Evidently the leaf hopper in search of fresh phloem tissue makes exploratory punctures in the neighborhood of the bundles of the main vein or its laterals and even reaches the epidermis on the opposite side of the leaf. (Fig. 11.) The cells of the spongy mesophyll and palisade layers in these areas are emptied of their contents and this produces the scratchlike stippling which is apparent on the upper surface. While the mesophyll cells are fed upon by *fabae* along the lateral veins, only one to three or four cells are fed upon about a single puncture (fig. 12), in contrast with the many cells fed upon by the species of Group 1. The sheath material observed between the cells and in the intercellular spaces was more abundant in the areas fed upon by *fabae* than in those fed upon by the members of the first group. (Fig. 11 and 12.) Stained sections through the petioles
Figure 9.—Normal leaflet of alfalfa.  × 5

Figure 10.—Alfalfa leaflet showing the fine scratch-like stippling produced by an adult *E. fabae* during 24 hours' feeding. Most of the scratches are near the veins and differ from the feeding areas in Figure 1.  × 4½

Figure 11.—Midrib of an alfalfa leaf which had been fed upon from the lower surface by an adult of *E. fabae*. The phloem is torn and intermixed with sheath material while the xylem vessels are not altered. The palisade cells above and to the left of the bundle have been fed upon and a considerable amount of sheath material is present. Note the shrinking of the tissue in the area of destroyed mesophyll.  × 210
and stems showed that the phloem is the tissue usually sought by the leaf hopper. Here again the phloem cells were disorganized by being torn and by having the sheath material located intercellularly and intracellularly. The cell walls of the cortex in these plant parts seem to collapse less readily and the well-defined cylindrical sheaths are obtained in sections. (Figs. 13 and 14.) In most of the sections from unwilted tissue the xylem had evidently not been penetrated in the bundles of the stem, petiole, or midvein. In a few of the lateral veins sheath material was found between the xylem tubes and
in close proximity to this group of cells. Because of the collapse of the cells, the early studies of the tissue which had wilted after exposure to adults of *fabae* resulted in a failure to determine which tissues they had fed upon. However, in later studies it was found possible to restore the flaccid or moderately wilted tissue to a condition approaching its original turgidity by submerging the small pieces desired for sectioning in distilled water for one or two hours before proceeding with the usual fixation, dehydration, and embedding. In exposed portions of midribs of leaves, and in slender, succulent young petioles and stems of alfalfa, Russian red clover, Ladino clover, and potato, which had wilted and were treated as above mentioned, positive evidence of plugging in the xylem tubes was found by sectioning and staining. (Figs. 15, 16, and 17.) The presence of this sheath material was also shown by microchemical tests to be present in the water-conducting cells.

Smith (10) found that the stylet sheath of the following insects was definite in outline and that it followed an intercellular path: White fly, *Asterochiton vaporariorum* Westw.; coccids, *Aspidiotus hederae* Vallot and *Dactylopius longispinus* Targ.-Tozz.; and aphids, *Myzus persicae* Sulz., *M. circumflexus* Buk., and * Macrosiphum solanifoli i* Ashm. All, except *A. hederae*, which reached only into the cortex, fed on the cells in the vascular bundle. Horsfall (6) found that the path of the proboscis of *Aphis rumicis* L. and of *Myzus persicae* followed as a rule the middle lamella through the epidermis and cortex or mesophyll. Apparently the objective of the beak of *M. persicae* is the vascular bundle, where usually the phloem cells, but
also occasionally the tracheal tubes, are pierced and plugged. Davidson (1) also found definite setal sheaths of the three species of aphids which he studied. Wardle (11) did not mention the presence of a feeding sheath in tissue which had been fed upon by Thrips tabaci. Woods (12, p. 14) described the setal sheath produced by Rhopalosiphum dianthi Schrank and noted the gradual enlarging of the spots about the feeding puncture in carnations.

Davidson (1, p. 45) found that the contents of the cells which were in contact with the saliva along the path of the stylets of Aphis rumicis were extensively plasmolyzed and exhibited a migration of the disorganized cytoplasm toward the source of irritation. With A. rumicis there was no spreading to surrounding tissue but with Myzus cerasi Fab. on peach and Macrosiphum rosarum Walk. on rose many cells were torn and destroyed. Horsfall (6, p. 10-11) found that in sections of leaves fed upon by Aphis rumicis cells contiguous to the setal sheath were normal, while in other sections plasmolysis, similar to that observed by Davidson, had taken place. Painter (8, p. 505), working with Psallus seriatus, found that marked plas-
molysis took place about its feeding punctures and that the entire cell contents became decidedly homogeneous.

The feeding puncture of *Empoasca fabae* generally follows an intercellular path and resembles the punctures of the insects studied by Smith, Horsfall, Davidson, and Woods. However, no evidence has so far been found that the cells surrounding the puncture made by *E. fabae* were plasmolyzed, nor was there any apparent thickening of cell walls such as was observed by Davidson with * Macrosiphum rosarum* on rose. As with the stippling caused by species of *Empoasca* in Group 1, the scratchlike stippling produced by *fabae* did not seem to enlarge after the leaf hopper had been removed.

![Figure 16](image)

The injury produced by *Empoasca fabae* is extremely localized, affecting only that part of the plant beyond the point of feeding, whether the injury is manifested as wilting or as yellowing or reddening. This fact when considered in relation to the feeding habits of this insect suggests that the disorganization of the phloem elements may result in a disturbance of the plant processes above the point of attack and that the production of substances by the plant itself may cause the partial (yellowing or reddening) or complete breakdown (potato hopperburn) of the tissues involved. This hypothesis is strengthened by the evidence shown in Figure 18. The sudden swell-
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ing at the upper end of the feeding area, the increased diameter and the development of the purplish pigmentation of the stem above, and the modification of the laterals, all point to the piling up of materials in these parts owing to interference with their normal downward movement in the phloem. Were a toxin being injected by the leaf hopper the symptoms would probably not have been manifested in this manner. The same individual that produced this abnormal condition caused wilting in a previous exposure of 24 hours on a young alfalfa tip. The wilting of the plant part beyond the point of feeding may be explained by the fact that many of the xylem vessels were plugged. The present studies indicate that this explanation is more
likely to be correct than the hypothesis of toxin injection advanced by other workers (2, 3). It is quite certain that the toxin, if one is introduced by *E. fabae*, is less positive in its reaction than that found in the feeding punctures of the capsids *Plesiocoris rugicollis* Fall. and *Lygus pabulans* L. (9).

The behavior of *Empoasca fabae* differed markedly from that of any of the other five species studied. Adults of species in Group 1 were able to live on slightly wilted foliage for some time, whereas *E. fabae*, when confined to this type of host material, died almost as quickly as if no food had been provided. When confined to the upper surface of the alfalfa leaf the adults of *E. fabae* usually lived only 4 to 10 hours. When confined to an area 15 mm. in diameter on the lower surface, the adults died unless they were transferred to a new leaflet at least once a day; if transferred regularly each day, they lived a maximum of 3 to 4 days. If confined in small cages 15 mm.

*Figure 18.—A shoot of potato showing an enlargement of the stem above the point of feeding by *E. fabae*. A single adult was confined for 9 days between the two black marks on the stem. Photographed 20 days after the first feeding of the leaf hopper. X 1.*

in diameter, upon tender stems or petioles, the adults usually lived 2 or 3 days without change to new stems or petioles, but if changed regularly every day they lived a maximum of 14 days. The longest records of adult life were obtained from individuals confined on the tender petioles of cowpeas. In a few tests adults died soon after being confined to large, but apparently succulent, stems of potato near the top of the plant; others confined upon the petioles and leaf veins lived longer. Sections of the stems showed feeding punctures into the cortex, but apparently the cortical layer was too thick for the adults to reach the phloem with their mouth parts and therefore death resulted. The phloem tissue was reached in the petioles and in the leaf veins.
DISCUSSION

The injury to the host plant produced by members of Group 1 is localized and, comparatively speaking, is not serious. The destruction of the mesophyll in the limited areas undoubtedly reduces the photosynthetic activity of the leaves in proportion to the size of the areas destroyed. However, the adjacent remaining uninjured areas retain their color and apparently their normal functions. The feeding by *Empoasca fabae* on the phloem or water-conducting tissue is much more serious in its results. One of the species in group 1 may make a dozen or more stippled areas in the mesophyll of a group of leaflets without seriously injuring them, but a single adult of *E. fabae* making approximately an equal number of feeding punctures in the petiole of a similar leaf will cause injury to the entire leaf.

A study of serial sections of a cowpea petiole on which a single adult of *E. fabae* had fed for 24 hours showed that 14 punctures into the phloem had been made and that 5 of the 7 bundles in the petiole had been fed upon. These results are in marked contrast with those obtained in feeding tests with *Gypona octolineata* (Say) and *Aphis rumicis*. An individual of *G. octolineata*, after feeding for three weeks on a tender apple stem apparently made only one puncture into the vascular tissue, as shown by studies of serial sections of this plant material. Davidson (1, p. 48) confined four apterous individuals of *A. rumicis* for 24 hours on localized areas of young bean plants and found only four stylet sheaths in the sections. In most feeding punctures of *E. fabae* whenever the phloem was reached all or nearly all of the phloem cells in that bundle were ruptured or otherwise disorganized. This disorganization of one of the tissues of translocation in the plant is much more serious than the disorganization of an equal amount of mesophyll tissue. The feeding in the xylem and the plugging of the tubes there evidently result in an equally serious injury, that is, wilting beyond the point of feeding, on certain hosts. Le Clerg and Durrell (7, p. 15) showed that the water flow in the vascular bundles of crowns of wilt-infected alfalfa plants was reduced 33 per cent as compared with that in crowns of healthy plants. The striking symptoms of wilting and dwarfing, occurring in wilt-infected plants which probably contained the same amount of plugging, are illustrated by these authors (7, p. 5). While accurate measurements of the proportionate amount of plugging of xylem vessels by *E. fabae* have not been made, in some instances more than one-third of the vessels seem to have been plugged. (Fig. 15.)

The feeding of the two groups of leaf hoppers, the one upon the mesophyll and the other upon the phloem, or xylem, is evidently not a matter of choice on the part of the insects. Instead it seems necessary, physiologically; for the life of the species that it procure its particular type of food from a definite region in the host plant. The phloem of rapidly growing plant parts is naturally rich in nutritive substances such as the albuminoids of the amino acid type, carbohydrates as sugars, and inorganic salts, as stated by Davidson (1, pp. 49, 50). These are all in soluble form and probably require little or no digestive changes before they are assimilated by the leaf hopper. The chloroplasts and other materials in the cytoplasm of the mesophyll cells present a very different type of food material. Whether *Empoasca fabae* has digestive enzymes unlike those of the other species
which would account for this difference in feeding habits, has not been determined.

SUMMARY

On the basis of the results obtained in a study of the feeding habits of six species of Empoasca, the species were divided into two groups. The first group included *maligna*, *abrupta*, *filamenta*, *bifurcata*, and *erigeron*. This group is characterized by a habit of feeding on the mesophyll tissue of the leaves and the regular production of definite spotting or stippling on the upper surface. The more mature foliage seems to be preferred to that of the more succulent, younger leaves. Strains of *E. fabae*, which constitute the second group, evidently feed by preference upon the phloem or water-conducting tissue, and the well-being of this species seems to depend upon the availability of fresh phloem tissue in succulent plant parts.

When *Empoasca fabae* is confined to mesophyll tissue, and the mesophyll-feeding species of Group 1 are confined to succulent phloem tissue on growing tips and petioles, all die within a short time. These differences in feeding habits seem to be correlated with the physiology of the species.

The feeding by *Empoasca fabae* in the phloem tissue or xylem vessels results in more serious injury to the host plant than does the feeding by an equal number of individuals of the other species of Empoasca on the mesophyll tissue.

No evidence was found that a toxin was introduced into the plant by any of the species. On the contrary, the present studies indicate that injury by *Empoasca fabae* is the result of interference with translocation of plant materials which produces either wilting when xylem vessels are plugged or yellowing or reddening when the phloem is disorganized and plugged.

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