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BIOLOGY OF THE FOXGLOVE APHID IN THE NORTHEASTERN UNITED STATES 1 OF 1

WAYE, H E; SHANDS, W A; SIMPSON, G W

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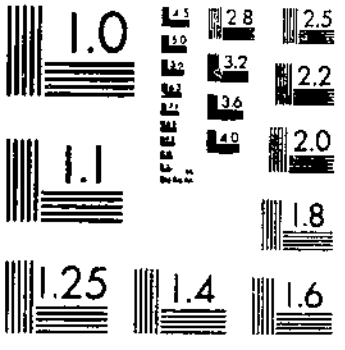

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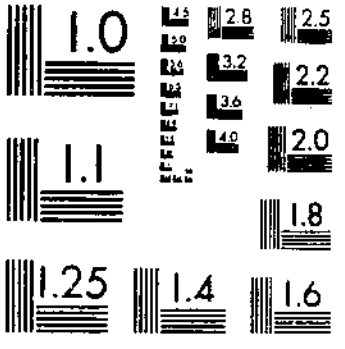

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Biology of the FOXGLOVE APHID in the Northeastern United States

TECHNICAL BULLETIN NO 1338

Agricultural Research Service
UNITED STATES DEPARTMENT OF AGRICULTURE
in cooperation with
Maine and New Jersey Agricultural Experiment Stations

Contents

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BIOLOGY OF THE FOXGLOVE APHID IN THE NORTHEASTERN UNITED STATES

By H. E. Wave[1] and W. A. Shands, *entomologists, Entomology Research Division, Agricultural Research Service,* and Gebbes W. Simpson, *professor of entomology, Maine Agricultural Experiment Station*[2]

The common name for the foxglove aphid (*Acyrthosiphon solani* (Kaltenbach)) was suggested by Patch (*43*),[3] who found foxglove (*Digitalis purpurea* L.) to be a primary host of this insect. Since this plant was not common in potato-growing districts of Maine, it seemed likely that other primary hosts existed in view of the large numbers of foxglove aphids that initially infested potatoes each year. Study of the biology of this aphid was intensified after the discovery by Wave et al. (*73*) of the common perennial hawkweed (*Hieracium* spp.) as a new primary host of the aphid. Previously the only intensive biologic study of this insect was that of Patch (*43*), who described its seasonal history on foxglove and listed numerous secondary hosts.

The purpose of this publication is to review the literature on the biology of the foxglove aphid and to present the results of research conducted on this subject in northeastern Maine from 1952 to 1961 and in New Jersey from 1959 to 1961.

Lacking information on the relationship of the foxglove aphid to the newly discovered primary host hawkweed, one objective of the study in Maine was to describe the aphid's seasonal history on this plant. Additional objectives were to determine the population dynamics of the aphid on hawkweed and on potatoes, the production of alatae in caged colonies on the primary host, the duration and magnitude of the spring migrant movement, and natural control agencies.

Principal objectives of the study in New Jersey were to ascertain the host plants of the aphid, its geographical distribution, and its mode of overwintering.

DISTRIBUTION

The distribution of the foxglove aphid is almost worldwide. An excellent world distribution map of this aphid has been published

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[1] Resigned September 1962; now with the University of Massachusetts. This bulletin includes the results of a thesis submitted by the senior author to the Faculty of the Graduate School of Rutgers University, the State University of New Jersey, in June 1961 in partial fulfillment of the requirements for the degree of doctor of philosophy.

[2] The authors gratefully acknowledge the assistance of L. M. Russell, Entomology Research Division, in identifying specimens of the foxglove aphid; C. F. W. Muesebeck and B. D. Burks, of this Division, in identifying hymenopterous parasites; C. G. Thompson, formerly of this Division, and I. M. Hall, Department of Biological Control, University of California Citrus Research Center and Agricultural Experiment Station, Riverside, in identifying entomogenous fungi; and E. L. Tuttle, formerly of this Division, for his observations.

[3] Italic numbers in parentheses refer to Literature Cited, p. 37.

by the Commonwealth Institute of Entomology (*6*). Distribution records of the foxglove aphid in the United States have been compiled, by States, from mounted and labeled collections in the U.S. National Museum, from the files of the Survey and Detection Operations of the U.S. Plant Pest Control Division (Agricultural Research Service), and from collections by the authors. The States included are Alabama, California, Colorado, Florida, Georgia, Louisiana, Maine, Maryland, Massachusetts, Nebraska, New Hampshire, New Jersey, New York, Ohio, Oregon, Pennsylvania, South Carolina, South Dakota, Tennessee, Utah, Virginia, and Washington. This aphid has also been reported from Montana (Knowlton *34*).

ECONOMIC IMPORTANCE

In most potato-growing areas the foxglove aphid is one of four economically important species infesting potatoes. The others include the potato aphid (*Macrosiphum euphorbiae* (Thomas)), the buckthorn aphid (*Aphis nasturtii* Kaltenbach), and the green peach aphid (*Myzus persicae* (Sulzer)). All four species cause injury either directly by their feeding punctures and toxic secretions or indirectly by spreading virus diseases. With the use of organic insecticides, direct feeding damage has become less serious. On the other hand, decreased maximum allowable virus infection in seed certification programs has increased the importance of aphids as virus vectors. A high degree of protection against the spread of potato viruses is paramount in potato seed certification programs, since a very small percentage of infection can lead to rejection of an entire field.

Elze (*13*) reported that several important virus diseases of potato, including leaf roll, mosaic, and crinkle, were transmitted by the foxglove aphid, the first disease readily. Dykstra and Whitaker (*10*) showed that the foxglove aphid, under certain conditions, serves as a vector of the viruses of leaf roll, rugose mosaic, crinkle mosaic, and mild mosaic. This virus vector's relationship to potato leaf roll has been mentioned by Smith (*66*), Simpson (*62*), and Simpson et al. (*64*). The foxglove aphid is also a vector of the nonpersistent potato veinbanding virus (PVY) (Bawden and Kassanis *3*) and potato aucuba mosaic (Heinze *23*).

Heinze (*24*) listed 27 plant disease viruses that are transmitted by the foxglove aphid, among which are some potato viruses. Day and Bennetts (*9*) in their review of arthropod vectors listed 14 such viruses that are transmitted by this aphid. The latest addition to the list of disease viruses transmitted by the foxglove aphid is tomato aspermy virus of tomato, tobacco, and chrysanthemum (Brierley et al. *5*. Govier *19*).

REVIEW OF LITERATURE

Taxonomy

The foxglove aphid was described by Kaltenbach (*32*) from potato as *Aphis solani*. Subsequently, this polyphagous species was described under numerous names by other workers. Hille Ris Lambers (*28*) comprehensively reviewed the synonymy, and he and MacGillivray

(*29*) clearly established the validity of *solani* as the correct name of the foxglove aphid.

Only two of the many names proposed for the aphid have been used extensively. Theobald (*70*) described the insect as *Myzus pseudosolani*. He (*71*) and others frequently used this name, which is now considered to be a synonym of *solani*. The name *convolvuli* Kaltenbach 1843 often has been applied to this species, but Hille Ris Lambers (*26*, *28*) and Palmer (*42*) showed that this name is a synonym of *persicae* (Sulzer).

Hille Ris Lambers and MacGillivray (*29*) stated that American and European aphidologists have disagreed considerably on the concept of the genus *Myzus*. Aphid specialists in North America have generally placed the foxglove aphid in the genus *Myzus* Passerini 1860 (Palmer *42*, Essig *14*, *15*, Mason *38*, Gillette and Palmer *18*). The foxglove aphid has been discussed or described under various specific names in the genus *Macrosiphum* Passerini in Europe (Schouteden *47*, *48*, Theobald *69*, Gaumont *17*, Börner and Schilder *4*) and in North America (Bartholomew *2*).

For several years most European workers have placed *solani* in *Aulacorthum* Mordvilko 1914, but recently Kennedy et al. (*33*), who listed *Aulacorthum* as a subgenus, and Russell (*45*) included it in *Acyrthosiphon* Mordvilko 1914.

Biology and Ecology

Although the taxonomic aspects of the foxglove aphid have been thoroughly explored, its biology and ecology have been neglected. MacGillivray and Anderson (*37*) obtained data on its maturation and reproductive period, longevity, and fecundity in the greenhouse.

Heinze and Profft (*25*) reported that in Germany the foxglove aphid overwinters as eggs on forget-me-not (*Myosotis alpina* La Pey.) and on shepherds-purse (*Capsella bursa-pastoris* (L.) Medic.). Hille Ris Lambers (*27*, *28*) stated that in Europe these aphids overwinter as eggs on various plants; i.e., they exhibit distinct polyphagy. He further stated that sexuales are produced on most of these host plants. Stroyan (*67*) recorded sexuales of the foxglove aphid from meadowsweet (*Filipendula ulmaria* (L.) Maxim) in England. Cottier (*7*) observed the aphid overwintering in the agamic form on *Rumex* sp. in New Zealand. Tambs-Lyche (*68*) found the foxglove aphid to be the commonest species on potato in Norway and stated that it may overwinter indoors. Heie (*21*) observed the aphid overwintering in beet clamps. The aphids have been observed to overwinter as adults and possibly as eggs in Scotland.

Jacob (*31*) recorded hibernation as adults on foxglove, and Fisken (*16*) observed apterae overwintering on perennial, greenhouse, and coldframe crops. Shaw (*61*) noted oviparae on buttercup (*Ranunculus repens* L.) and wild raspberry (*Rubus idaeus* L.) near potato fields. Eastop (*12*) stated that sexuales of the foxglove aphid are not known in Africa; however, Müller and Schöll (*40*) mentioned this aphid, among others, as coexisting in both holocyclic and anholocyclic strains.

Host Plants

Numerous noneconomic host plants for this aphid have been listed by various authors, notably Patch (*43*, *44*) in the United States, Cottier (*7*) in New Zealand, Eastop (*12*) in Africa, and Hille Ris Lambers (*27*, *28*) and Heinze and Profft (*25*) in Europe. Shands and Wave (*59*) recorded two new hosts for this aphid—yellow goatsbeard (*Tragopogon pratensis* L.) and alder buckthorn (*Rhamnus alnifolia* L'Her.). More recent observations have suggested that goatsbeard can serve as a primary host. F. F. Smith (unpublished data) found a heavy infestation of viviparous foxglove aphids on senescent leaves of a seedling tree, *Betula alba* L., in Maryland. The aphids were on the seedlings from October, when they were brought into an unheated greenhouse from outdoors, until late January.

The only recognized primary host of the foxglove aphid in the Northeastern United States prior to 1955 was foxglove. This host was not sufficiently widespread or abundant enough to account for the infestations that occurred each year (Simpson and Shands *63*). This discrepancy between low host-plant abundance and the relatively high initial infestations of potatoes stimulated research that led to the discovery (Wave et al. *73*) of the common perennial hawkweed as the primary host of importance.

Aphid Egg Surveys

Following the discovery of the primary host of importance, studies were started in an attempt to correlate overwintering aphid egg abundance on the primary host with subsequently developing populations of the aphid on secondary hosts. It was hoped that information gained from these studies (Wave *72*, Shands et al. *57*) could be used as a basis for forecasting population levels of the foxglove aphid that might develop in a given season. Data for these studies were obtained by making semiannual aphid egg surveys on the primary hosts in late fall and early spring, similar to those previously used in preparing forecasts for the other three potato-infesting species (Shands et al. *56*). Thus, growers could be warned in advance of the possible development of damaging numbers of potential vectors of potato virus diseases.

Traps

By means of wind-vane traps, considerable unpublished data have been accumulated from 1941 to 1959 on the duration and intensity of this aphid's annual spring influx to potato fields. The wind-vane type trap used in obtaining these data was described by Shands et al. (*54*). Davis et al. (*8*) collected the foxglove aphid in the Northwestern United States by means of yellow pan traps (Moericke *39*) and by wind traps. Eastop (*11*) and Lamb (*35*) also collected this aphid by means of yellow pan traps in Africa and New Zealand, respectively. It is not to be concluded, however, that this aphid is a migratory species, since the males are usually apterous, a situation that excludes true migration according to Hille Ris Lambers (*28*), and also because the aphid lives on the primary host the year round. Hille Ris Lambers (*28*) reported that both apterous and alate males occur in Europe, but

not in the same locale. The authors have observed an alate male only once.

Plant Injury

Light infestations of the foxglove aphid can severely injure potato foliage (fig. 1). Hoggan (*30*) noted that its feeding caused discolored

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FIGURE 1.—Typical injury to potato foliage caused by feeding of small numbers of foxglove aphids.

spots on tobacco, which, when the plant was heavily infested, coalesced to form large necrotic areas, sometimes killing the entire leaf. Elze (*13*) mentioned that the feeding of the foxglove aphid caused irregular curling of young potato leaflets and speculated that growth of the leaflet was hindered as a result of the feeding puncture. Smith and Brierley (*65*) reported that the simulation of lily rosette symptoms was induced in the young growth of Easter lily (*Lilium longiflorum*

Thunberg) by the feeding of fairly large numbers of the foxglove aphid.

Heinze (*22*) observed that the puncture injuries of this aphid on older potato plants produced symptoms similar to those of potato virus A. Little, if any, leaf deformity resulted from these punctures unless feeding occurred on very young unfolding leaflets. Severin and Tompkins (*49*) reported on the symptoms induced by the feeding of the foxglove aphid on two species of ferns. The injury consisted of beadlike chlorotic areas and was somewhat similar in both plants, but the intensity of the symptoms varied with the number of aphids.

PROCEDURE IN MAINE

Cage Study on Primary Host

The cage study was conducted on Aroostook Farm near Presque Isle, Maine, from 1956 to 1959. The procedure used was especially suitable for observing in the field the ontogenies of the different forms of the aphid as well as its population dynamics on hawkweed.

A single, immature, stem-mother foxglove aphid was caged in situ or introduced into each cage. Cages (fig. 2) were randomly located on naturally occurring stands of the plant. Two species of hawkweed—*Hieracium aurantiacum* L. and *H. floribundum* Wimm. & Grab.[4]—were used and either one or both were included in a cage de-

[4] Identified by C. D. Richards, Botany and Plant Pathology Department, University of Maine.

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FIGURE 2.—Cages used to enclose colonies of foxglove aphid on hawkweed.

pending on chance. Both are equally suitable as hosts. Foliage in each cage site was searched for natural infestations of stem-mother aphids before introductions were made. When more than one stem mother was found, all but one were removed before caging.

During the early part of the season the cages were removed every 2 to 4 days, and the foliage was examined to determine the number of aphids present, their form (apterous or alate), and their stage of development (instar). At each observation, records were also made of the developmental stage of the host plant and the feeding sites of the aphid. During the period of alate production the plants and cages were carefully searched at each observation and the alatae removed. Later in the season, after alate production had ceased, the interval between observations was lengthened to 1 week or more. Observations were continued into late October or early November to record the development of sexuales, mating, and beginning of egg deposition. Aphids probably survive considerably beyond that time before being killed by low temperatures. Nightly frosts could be expected any time after October 5 in northeastern Maine.

Although several types of cages are available for retaining aphids on small plants, parts of plants, or excised leaves, especially for greenhouse use (MacGillivray and Anderson *36*, Noble *41*, Anderson et al. *7*), the one constructed for this study was primarily for outdoor use. The cylindrical cage (fig. 3), 13 inches in diameter and 19 inches tall, was made of 6-gage "black" wire and covered with cotton scrim having 28 by 32 threads per square inch. The bottom edge of the cage (1–2

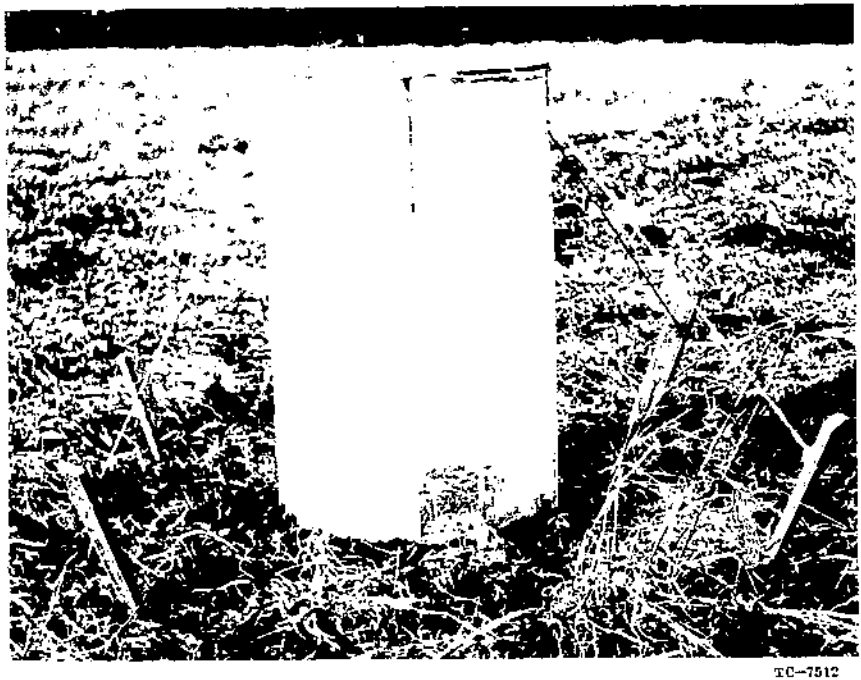

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FIGURE 3.—Aphid cage showing method of anchoring.

inches) was dipped in melted paraffin and allowed to harden to inhibit rotting of the scrim where it came into contact with the soil, which was banked along the outside edge to prevent escape of the aphids. Approximately 1 square foot of area was encompassed by a cage so that comparisons could be made between cages for the same year and for different years.

Cages were secured against movement from wind with jute twine anchored to four lath stakes driven into the ground (figs. 2 and 3). Cages remained in situ except for brief periods of removal to make observations and counts of aphids on the foliage.

Field Study on Primary Host

Aphid development and population growth were studied in the field on natural stands of hawkweed from 1956 to 1959. Beginning in early May and until late October weekly records were taken of the form and number of aphids on 50 randomly located plants at each of 10 locations, except during July and August, when observations were made at fewer stations.

To follow a given population for the entire season, sample locations were selected in undisturbed areas of grassland or weeds containing hawkweed. Sampling was done along lines arbitrarily drawn through the plant stand, and sample plants were randomly taken along these lines at predetermined intervals, generally two paces.

Since the unit of sampling was the whole plant (fig. 4), all the foliage, flower stalks, and flowers when present had to be examined for aphids. This was accomplished for each sample plant by examining in situ both the top and the bottom surfaces of the leaves with the aid of a camel's hair brush. The handle of the brush was used to turn the foliage with a minimum of disturbance to the aphids. Whenever a foxglove aphid was observed on a sample plant, it was examined with a hand lens to determine its approximate instar and form. As in the cage study, the feeding location of the aphid on the plant was also determined. Records were kept to show the number of aphids found on each plant.

Location of Sample Stations.—To obtain a representative sample of the foxglove aphid population in broad perspective, 10 sample stations were selected in central and southern Aroostook County (fig. 5). The total area in these population surveys exceeded 2,200 square miles. In addition to a wide distribution of sample stations, an effort was made to obtain as wide a range of habitat as possible. Descriptions of the habitat in which hawkweed grew at each station are as follows:

(1) Smyrna Mills—dense grass shaded by old apple trees and scattered woody shrubs.
(2) Sherman Station—open hayfield and along or under adjacent woody shrubs.
(3) Oxbow—open grassland along streambank.
(4) Masardis—dense grass and herbaceous weeds along ditchbank.
(5) Ashland—sparse to dense grass adjacent to and partially shaded by coniferous woods.

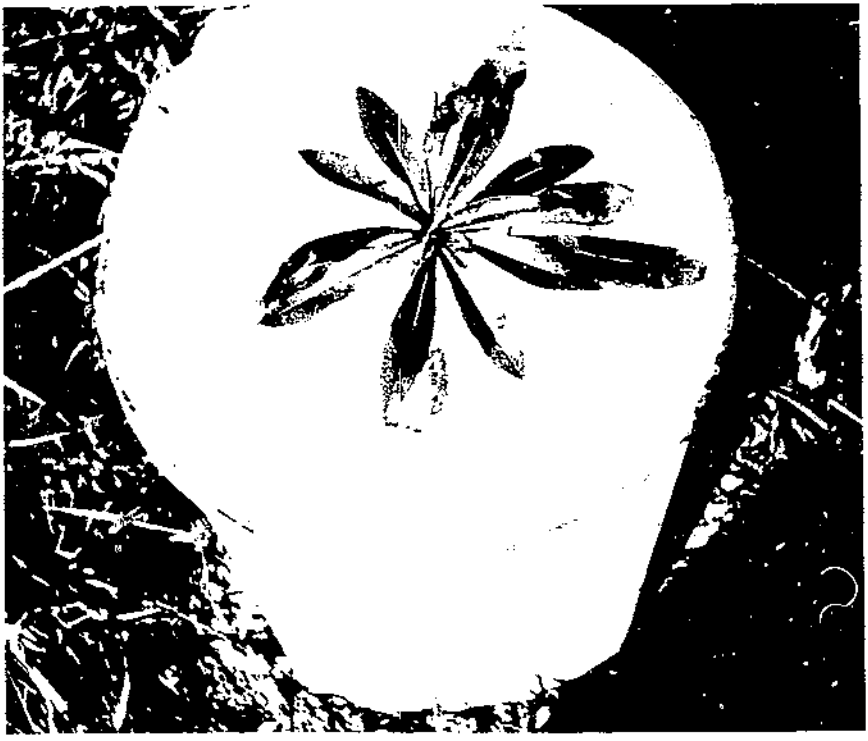

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FIGURE 4.—Hawkweed plant without flower stalk, illustrating sample unit employed in field study.

(6) State Road—sparse to dense grassland and in partial shade of adjacent mixed-growth woods (spruce-hardwood) or in shade of woody shrubs.
(7) Presque Isle—open sparse grass and along and under hedge of rose bushes.
(8) Fort Fairfield—dense grass and herbaceous weeds partially shaded by small apple trees.
(9) Mars Hill—very sparse grass totally shaded by willow thicket along edge of swamp.
(10) Bridgewater—dense grass along roadside, but partially shaded by adjacent deciduous woods.

Although the locations of four of the stations were changed slightly during the study, the data for the 3 years were comparable.

Aphid Egg Surveys.—Beginning in 1954, surveys of egg abundance on hawkweed were made at scattered locations in late fall. In 1958, they were also started at these locations in early spring. The survey was conducted by collecting 50 randomly located plants at each of 9 to 11 locations and examining the foliage for eggs in the laboratory. Records were made of the number of plants examined, the percentage of plants infested, and the number of eggs per plant at each location.

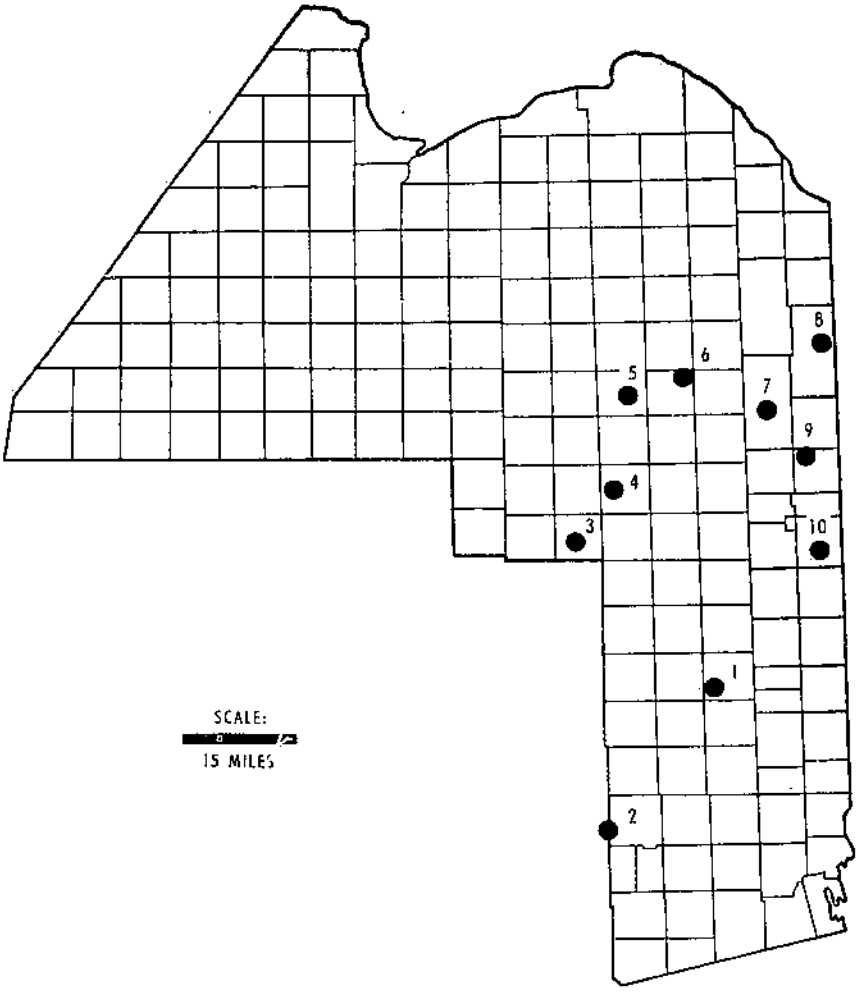

FIGURE 5.—Location of sample stations in Aroostook County, Maine.

Field Study on Potato

Yearly trends of the foxglove aphid populations on potatoes were followed from 1952 to 1961 by making counts in several fields not being treated with insecticides. The procedure (Shands and Simpson *51*) consisted essentially in recording at weekly intervals throughout the summer the number of aphids found on a leaf within the top, middle, and bottom third of each sample plant. In field plots, there were usually 25 sample plants per plot and 6 plot replications at each field location. Where entire fields of potatoes were used, there were 100 to 125 sample plants per field.

The sample plants were randomly located by a screen-grid method. Although potato fields varied in size, the sample portion was confined

to a square area of about 1 acre. Exceptions to this sampling procedure included counting aphids on (1) the entire plant until it became 8 inches tall and (2) only certain leaflets or half leaflets of each three-leaf sample when aphids became exceptionally abundant. Appropriate factors were used to convert counts on leaflets and half leaflets to the basis of three whole leaves (Shands et al. *55*). Except for the very early counts involving whole plants, aphid populations were expressed in terms of the numbers on three whole leaves per plant.

Trapping Study

A wind-vane trap operates by wind impingement against the trap. Aphids are simply filtered from a column of air passing through the trap. This method was considered a more accurate measure of the relative magnitude and duration of spring migrant flights of the foxglove aphid than the yellow pan trap (Moericke *39*), which may incite an alighting response. Shands et al. (*53*) pointed out some limitations in using the latter trap.

All the traps were located so as to be exposed to a clear sweep of wind; i.e., unobstructed by buildings, trees, or other impediments to wind movement.

The wind-vane trap developed by Shands et al. (*54*) was used from 1953 to 1959 to gather data on the movement of the spring migrants of the foxglove aphid, especially the duration and intensity of its annual influx into fields of potatoes.

The trap was made of welded ⅛-inch metal rods and covered with cotton scrim. It was shaped like a curved horn, with the plane of the large opening or base mounted in a vertical position (fig. 6). The vertical front opening was 19½ inches square and the small circular opening above was 3½ inches in diameter.

Attached at right angles to the base of the square opening was a metal shaft, which was an essential part of the swivel mounting that permitted the trap to function as a wind vane and thus keep the large opening oriented directly into the wind. The swivel effect was obtained by inserting the metal shaft into a short length of pipe of slightly larger diameter, which was securely fastened to the trap stand in a vertical position. The bottom end of the pipe was closed to retain a ball bearing on which the shaft rested, and the resulting tube was filled with grease.

In operation, the small circular upper opening of the trap was covered with a "baker's cap" (figs. 6 and 7) 6 to 8 inches in diameter, also of cotton scrim, which was held in place by elastic tape sewed into the hem. The top of the trap cap was held flat by four equally spaced gripper snaps that served to form large folds around the rim.

Wind currents striking the inside back of the trap funneled the entering aphids upward toward the opening of the trap cap. Wind currents likewise tended to "push" the aphids alighting on the back wall of the trap, causing them to walk or roll upward toward the cap. In addition, as a result of some stimulation, the aphids exhibited a distinct kinesis. This stimulus elicits a response to crawl upward after landing in the trap. Although this kinesis appears to be a natural orientation preparatory to subsequent flight, it is questionable

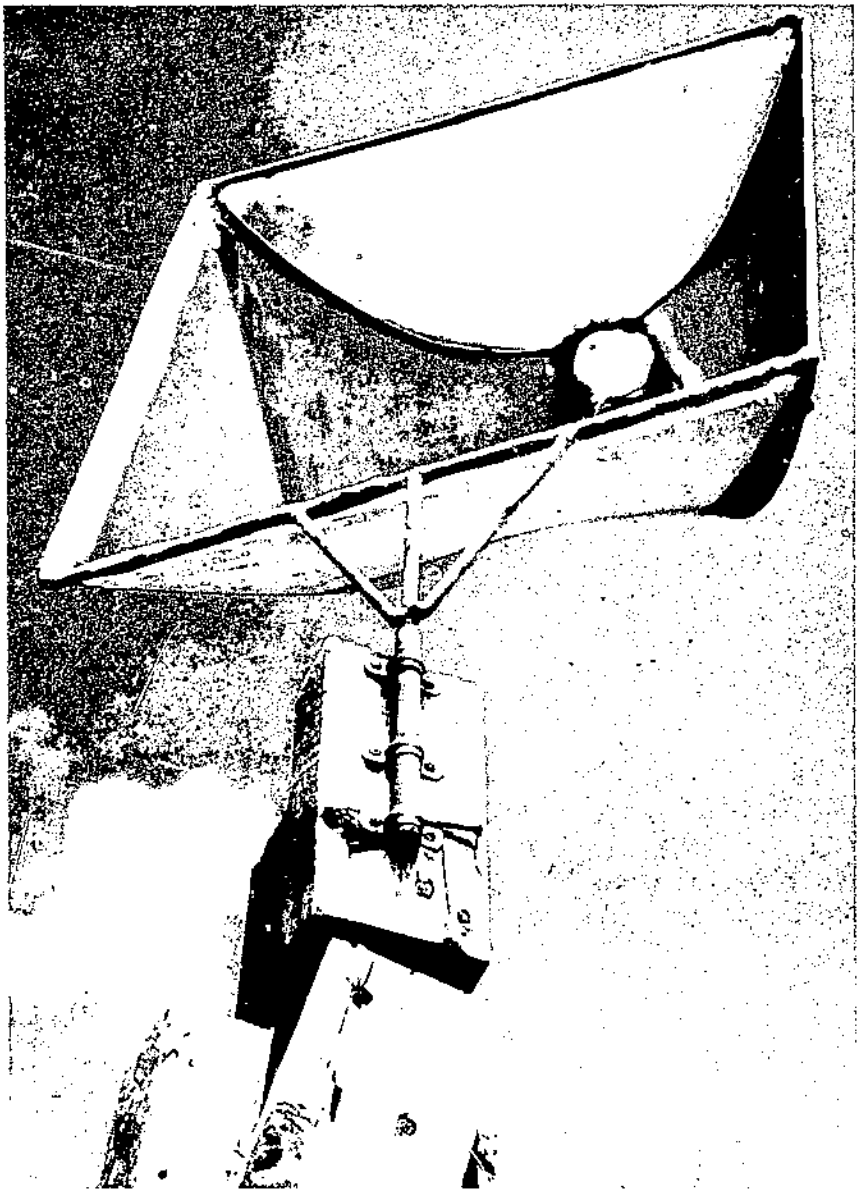

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FIGURE 6.—Wind-vane trap, showing method of mounting to trap stand.

whether it is due to a specific stimulus or to a combination of stimuli; for example, positive phototropism and negative geotropism. During periods when the air is calm, the cap tends to settle, and the aphids enclosed in the folds are effectively trapped.

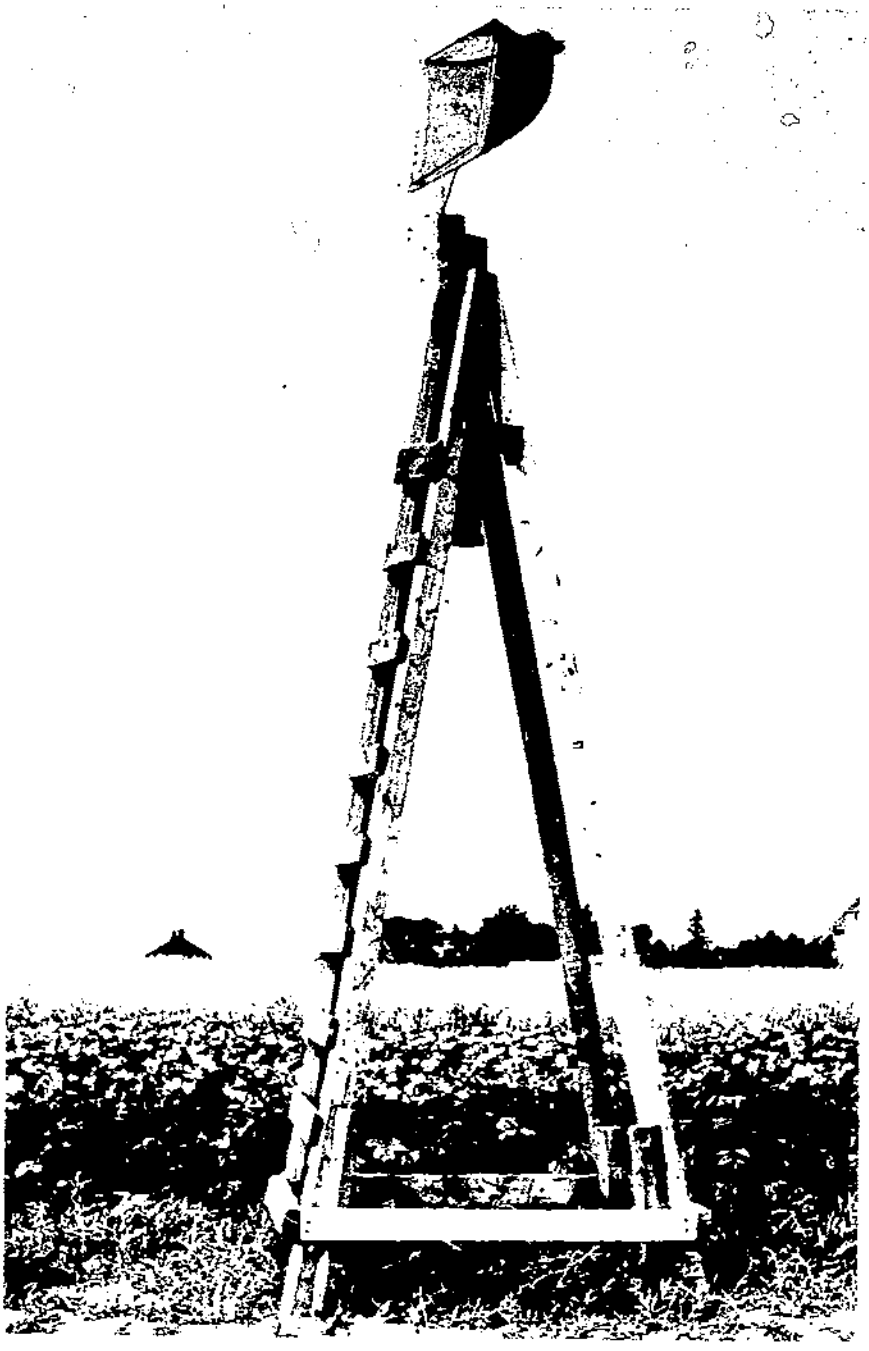

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FIGURE 7.—Complete trap assembly.

The number of airborne aphids caught at a given height depends on their density and the wind velocity. Several effective trap-operating heights have been demonstrated for some aphid species (Shands et al. *53*) ; however, the one used in this study was 12½ feet. Operating height was measured from the ground level to the bottom of the trap opening. Figure 7 shows a complete trap assembly, illustrating the construction of the trap stand and in particular the height of the trap above ground.

Seven traps were operated during June and July in the agricultural district around Presque Isle. Traps were emptied daily, except during inclement weather when beads of water retained on the trap covering precluded aphid removal. A mouth-suction aspirator was used to remove the aphids.

Natural Control Agencies

Parasitization of caged aphids was not a problem generally, but occasionally hymenopterous parasites appeared in the colonies. When parasitization occurred early in the season, the cages involved had to be discarded, since the numbers of developing aphids would have been adversely affected. Parasites were reared and identified from parasitized foxglove aphids collected on hawkweed from 1956 to 1959 and on potato from 1942 to 1960.

Fungus diseases occurred sporadically in the caged aphid colonies, but generally not until the production of alate forms had ceased. Whenever dead, diseased aphids were found in the cages, specimens were collected for determinations of the fungus. All diseased aphids were removed from the cages as far as possible to prevent or decrease further spread of the pathogen. Fungus-diseased specimens were also identified from collections made on potatoes from 1942 to 1962.

PROCEDURE IN NEW JERSEY

Aphid Survey

To delimit geographically the distribution of the aphid in New Jersey and to ascertain host plants of economic importance, hawkweed, the primary host, was examined from 1959 to 1961 in many rural areas. Secondarily, searches for the aphid were conducted on other possible host plants at each site. All examinations of plants were made in situ. Whenever foxglove aphids were found, they were identified with a hand lens or collections were taken for later verification. Where the plant material was unknown, specimens were collected for identification. Plants were examined for aphids in many and varied environments, including open grassland (fig. 8), roadside ditches, pastures, abandoned fields, and old orchards.

Cage Study on Primary Host

To determine the mode of overwintering of the foxglove aphid in New Jersey, cages were placed over natural stands of hawkweed in essentially the same manner as that described for Maine, except that

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FIGURE 8.—Open grassland with *Hieracium floribundum* in full flower intermixed with oxeye-daisy.

10 to 30 apterous, viviparous adults and nymphs instead of a single aphid were used to infest hawkweed in each cage. Caged colonies of the New Jersey strain of the aphid were maintained at Beemerville and New Brunswick in 1960–61. The former location is in the extreme northwestern corner of the State in Sussex County, and the latter is in Middlesex County in the central part of the State. During the winter there is a differential of 3.7° to 4.7° F. in the mean monthly temperatures between the two locations. Colonies of the aphid were established in early May at Beemerville but not until mid-September in New Brunswick. A strain of the aphid obtained from Presque Isle, Maine, was also established at New Brunswick on September 20 and 27 for comparison.

At Beemerville, each of 5 cages was initially infested on May 6 with 10 apterous, viviparous adults and nymphs of the foxglove aphid collected from various weed species. The cages were located at the dairy research farm of the New Jersey Agricultural Experiment Station and were placed on the hawkweed *H. floribundum* in a pasture overgrown with grass and herbaceous weeds and in partial shade of small deciduous trees. After establishment of the colonies, frequent observations and counts were made throughout the summer and fall to determine the form and number of aphids that developed. Of particular interest were observations to determine whether or not sexuales occurred.

At New Brunswick, eight cages were infested on September 13 with apterous, viviparous adults and nymphs obtained from collections of the aphid made in Beemerville. The caged colonies were located at

the vegetable farm of the New Jersey Agricultural Experiment Station in open grassland. Observations and counts of aphids in these cages were made periodically.

RESULTS IN MAINE

Population Trends

Population Growth on Hawkweed in Cages.—Two peaks occurred in the population growth curve of the aphid for 1956 (fig. 9)—one on July 27 and the other on August 20. A complex of factors may have operated to produce the dip in the population between August 2 and 13. First, the authors were unable to get an accurate count of the large numbers of aphids that developed in one cage. Second, fungus diseases appeared in some of the colonies about mid-July and resulted in a significant population loss.

Figure 9 also shows that the 1957 population crest was somewhat broader but lower than in 1956 and reached a maximum on August 16, or 8 days later than in 1956. In 1958, peak populations were of a shorter duration and considerably lower than in either of the 2 previous years. The highest 1958 peak was on July 25, 14 days earlier than in 1956 and 22 days earlier than in 1957. Both the time of occurrence and the number of aphids at the peak are determined largely by the temperatures and natural control agencies that occur during each annual cycle.

Population Growth in Natural Environments.—Population growth curves (fig. 10) were prepared by averaging consecutive observations into groups of three, with double weight given to the middle value. These values were then plotted as if they had been the observed ones.

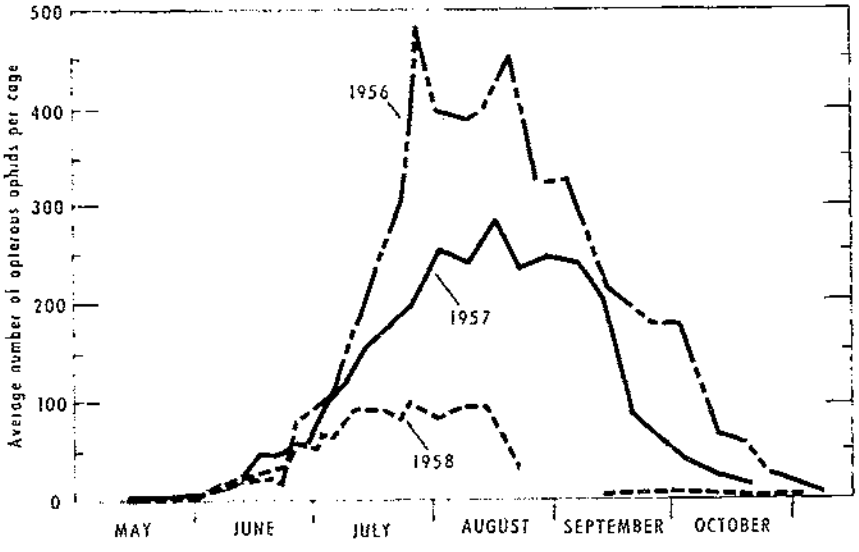

FIGURE 9. Average number of apterous foxglove aphids per cage on hawkweed in cage studies at Aroostook Farm, Maine.

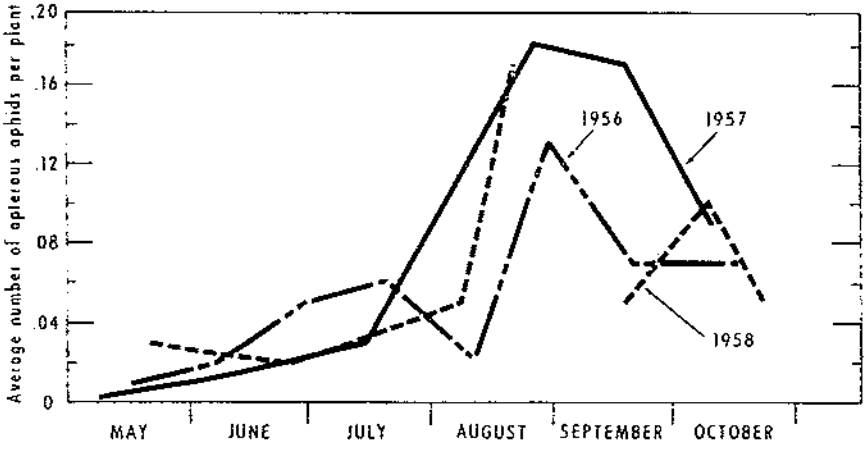

FIGURE 10.—Average number of apterous foxglove aphids per hawkweed plant in field studies in Aroostook County, Maine.

This procedure smoothed the curves and tended to avoid inconsistencies due to sampling where aphid populations were too low or too sparsely distributed to be detected.

The curve for 1956 describes an erratic picture of population growth, but it shows, nevertheless, that the population increased gradually from a low in mid-May, reached a peak in late August, and then declined. The population growth curve for 1957 shows a definite but stepwise population increase that culminated in late August and early September, then declined slowly until aphid counts were discontinued in October. The 1958 curve, although incomplete, shows a rather steady, slow population growth until early August, when the population began to increase appreciably. The peak probably occurred in late August or early September. A secondary peak occurred in early to mid-October, which was attributed to temperatures favorable for aphid development at that season.

The curves for the percentage of plants populated (fig. 11) were prepared by taking the weighted average of three consecutive observations as previously explained. These curves show the same general population growth trend as obtained for numbers of aphids (fig. 10).

When discrepancies occur, it is more meaningful to accept the curve described by percentage of plants populated than the curve described by number of aphids per plant. This becomes clear when one considers that a single viviparous adult aphid may deposit several nymphs on one plant, creating a large reading for the numbers of aphids per plant, whereas in actuality their distribution in space (percentage of plants populated) may be small. The percentage of plants infested provides a better index of the aphid production potential of the area sampled, especially during the early phase of aphid population growth. The productive potential of a given number of aphids early in the season is greater when they are evenly distributed. Nevertheless, by either method of comparison, the population growth curve of the aphid followed a similar trend. The population increased slowly until early

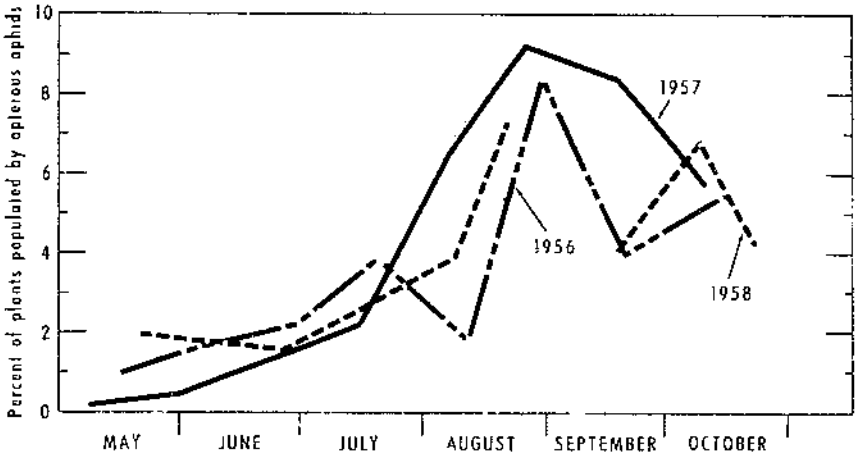

FIGURE 11.—Percentage of hawkweed plants populated by apterous foxglove aphids in field studies in Aroostook County, Maine.

August, increased rapidly to a peak in late August, and then declined, although at varying rates in the different years.

Population Growth on Potatoes.—Figure 12 shows the average seasonal population trend of the aphid on potato. The graph was pre-

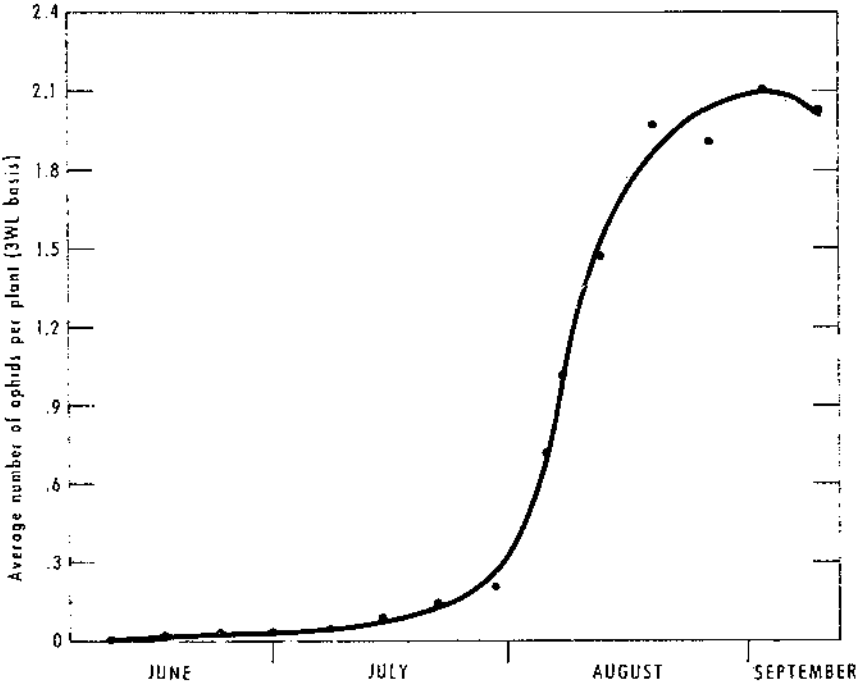

FIGURE 12.—Average number of foxglove aphids on three leaves per plant (top, middle, bottom) of untreated potatoes at Aroostook Farm, Maine.

pared by plotting at 5-day intervals the averages of the log n+1 of the population size on corresponding calendar dates each year. The population growth trend of the foxglove aphid on untreated potatoes begins to rise rapidly in late July and continues until the peak is reached in early September. This is about the same growth trend followed by the aphid on hawkweed in natural environments (fig. 10), but somewhat later than the peak of abundance on caged plants (fig. 9). It is apparent from figure 12 that this aphid is a low density species and that even at the peak of abundance there are, on the average, only about two aphids on three leaves per plant (top, middle, bottom).

The earliest date of infestation of potato (fig. 12), shortly after June 10, coincides with the average beginning date of spring migrant maturation on caged hawkweed (table 6). The last date in figure 12 is when observations were terminated because of harvesting operations or killing frosts.

Aphid Egg Surveys.—The results of the semiannual egg surveys on hawkweed are summarized in table 1.

TABLE 1.—*Foxglove aphid egg surveys on hawkweed in Aroostook County, Maine*

Season and year	Stations	Stations with eggs	Total plants	Plants infested	Eggs per 100 plants
Fall:	*Number*	*Number*	*Number*	*Percent*	*Number*
1954	11	6	110	10. 9	14. 0
1955	9	1	410	1. 0	2. 4
1956	10	2	500	. 4	. 4
1957	10	4	500	2. 0	2. 2
1958	10	7	500	3. 6	4. 0
1959 [1]	10	0	491	0	0
Spring:					
1958	10	4	500	1. 8	1. 8
1959	10	4	499	1. 4	1. 8

[1] Removal of snow from plants during sampling apparently dislodged all eggs.

With one possible exception, the egg surveys gave no clear-cut index to foxglove aphid populations that subsequently developed on hawkweed (fig. 10), other than that they were low. The exception was the large number of spring migrants that developed in 1955 (table 4) from the large number of eggs in the fall of 1954. Unfortunately the populations of foxglove aphids that developed on hawkweed in natural environments in 1955 were not followed.

Production of Alatae.—In 1956, alatae began maturing on June 19 (fig. 13), increased gradually to peak numbers on July 12, then rapidly declined; the last one matured on July 27. The total length of the maturation period was 38 days. The alatae developing from a single stem mother per cage (square foot) ranged from 5 to 58. Although a few of the alatae developed from progeny of the second generation in 1956, their distribution in time indicates that the greatest number matured from the third generation, and possibly some developed from the fourth as well.

In 1957, alatae began maturing on June 10, 9 days earlier than in 1956. Two peaks of abundance occurred in this year, one in mid-June

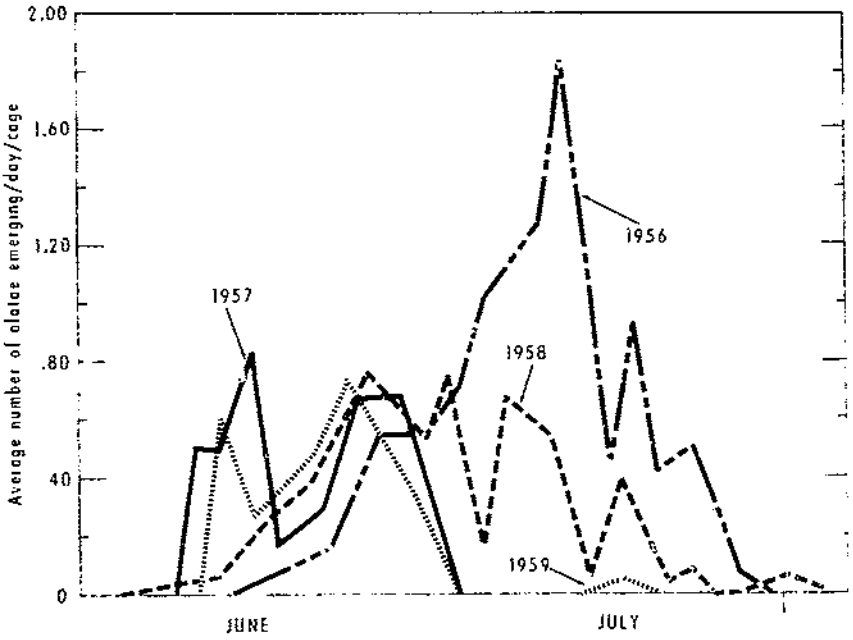

FIGURE 13.—Average number of winged foxglove aphids that matured on hawkweed per day per field cage, Presque Isle, Maine.

and the other in late June. After the late June peak, maturation abruptly ceased, the last alata maturing on July 3. The short maturation period (23 days) indicates that the bulk of the migrants that developed in 1957 were progeny of the second generation. Spring migrants developing per stem mother ranged from 0 to 32 in 1957, or less than one-half the total number that developed in 1956.

In 1958, alate maturation began on June 12, 2 days later than in 1957, but 7 days earlier than in 1956. The average number of alatae developing per day per cage increased gradually until a peak was reached on June 25, numbers then fluctuated somewhat but remained high until they declined after July 11. The last migrant matured on July 23, about the same time as in 1956. As in 1956, the long maturation period of 41 days suggested that migrants developed from progeny later than the second generation. Alatae developing per stem mother ranged from 2 to 29 in 1958. Although this range was about the same as that in 1957, the total number that developed was 71 percent greater in 1958.

In 1959, the number of spring migrants maturing per day per cage fluctuated greatly. This was due in part to the action of fungus diseases and predators, which decreased the number of cages that could be used for obtaining the average. Nevertheless, alatae began to mature on June 12, reached a peak on June 23, and then, with only an occasional one maturing, ceased maturation on July 31—about the same as in 1958. The alatae developing per stem mother ranged from

0 to 10, about one-third of those in 1958. The 49-day period over which alatae matured was the longest during the 4 years studied.

Productivity of Spring Migrants in Relation to Density of Hawkweed Stand.—Lack of uniformity in numbers of cages of each density of host and in some instances uncertainty as to the action of natural control agencies, especially fungus diseases, may have adversely affected the results of this study. The numbers of cages and plants per cage are shown in table 2.

TABLE 2.—*Cages and hawkweed plants per cage, Presque Isle, Maine*

Year	Cages with—		
	1 plant	2–10 plants	11–34 plants
	Number	*Number*	*Number*
1956	2	5	5
1957	5	5	6
1958	4	5	3
1959	1	1	3

Although not statistically significant, the data indicate a higher production of alatae with 1 plant or 11–34 plants per cage (per square foot) than with 2–10, as shown in table 3. This might have been due to crowding of the aphids in the single-plant group and poor plant nutrition from the crowded stands of the 11–34 plant group. Both of these factors have been shown to affect wing production in aphids (Shands and Simpson *50*).

TABLE 3.—*Winged foxglove aphids that matured per day per field cage with different numbers of hawkweed plants, Presque Isle, Maine*

Date	Aphids maturing per day per cage with—		
	1 plant per cage	2–10 plants per cage	11–34 plants per cage
1956	*Number*	*Number*	*Number*
June 13	0	0	0
22	.06	.04	.13
26	.25	.15	.45
30	.38	.15	.35
July 3	.17	.20	.60
5	.50	.60	.60
10	2.50	.36	.32
12	2.25	.80	.60
16	.88	.15	.05
18	.50	.70	.20
20	.25	0	.40
23	.67	.20	.13
25	.50	.20	0
27	0	.10	0
30	0	0	0

TABLE 3.—*Winged foxglove aphids that matured per day per field cage with different numbers of hawkweed plants, Presque Isle, Maine*—Continued

Date	Aphids maturing per day per cage with—		
	1 plant per cage	2–10 plants per cage	11–34 plants per cage
1957	*Number*	*Number*	*Number*
June 8	0	0	0
10	.50	0	.08
12	.40	0	.25
15	.47	.13	.72
17	0	.20	.25
21	.10	0	.33
24	.47	.07	.67
28	.45	.05	.38
July 1	.20	0	.17
3	0	.10	0
8	0	0	0
1958			
June 3	0	0	0
12	.03	.02	.07
16	.25	.20	.33
20	.69	.15	.02
23	.92	.07	.44
25	1.14	.10	.67
30	.45	.40	.33
July 2	.63	.50	.17
5	.17	.13	.11
7	.75	.10	.50
11	.25	.05	.92
14	.08	0	0
17	.25	0	.44
21	.06	0	0
23	0	0	.17
25	0	0	0
1959			
June 10	0	0	0
12	0	0	1.00
15	0	0	.44
20	.40	0	.67
23	0	0	1.22
29	.17	0	.50
July 3	0	0	0
6	0	0	0
10	0	0	0
13	0	0	0
17	0	0	.08
20	0	0	0
24	0	0	0
27	----------	0	0
31	----------	0	.08
Aug. 4	----------	0	0

Duration and Magnitude of Spring Migration.—Data from the aphid trapping study, as given in table 4, show in general that spring migrants began their annual influx to potatoes in early June, had vir-

tually completed their influx by late June, but in some instances continued into July, in one case as late as July 16. The magnitude of the aphid's spring migration varied considerably, from 2 aphids in 1959 to 37 in 1955.

TABLE 4.—*Spring migrants of foxglove aphid taken in 7 traps near Presque Isle, Maine, during springs of 1953–59*

Date	1953	1954	1955	1956	1957	1958	1959
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
June 5			2				
6							1
9			2				
10	1		3				
11					2		
12		1	2				
13		3	5				
14			3				
15			3		3		
16			3		2		
17			1				1
18	3		3				
19	2	2	2				
20		2	2				
21	1	1			1	1	
22		1					
23		1	2		1		
24			1				
25		1					
26		2	1	2			
July 2		1				1	
4			1	1			
6			1				
9						1	
16						1	
Total	7	15	37	3	9	4	2

Low numbers of alatae on the wing in 1956, 1958, and 1959 accounted for the sporadic recovery shown by the trap catches for those years. Data on alate maturation obtained from cage studies agreed well with those of trap catches in 1955 and 1957, the only years in which specific comparisons were valid. In 1955, the alate maturation period was June 6 to July 5 in the cage study and June 5 to July 6 in the trapping study. The comparison in 1957 was June 9 to July 3 for cages and June 11 to June 23 for traps. It appears, from these comparisons, that in years when the aphid is sufficiently abundant, trapping will give a reliable estimate of the duration and size of migration. As shown in table 5, there was a fair relationship between trap catches and foxglove aphid abundance on untreated potatoes up to the end of migration, when both the average number of aphids and the percentage of plants infested by them are considered.

TABLE 5.—*Relationship of foxglove aphid populations on untreated potatoes on Aroostook Farm to trap catches of aphids near Presque Isle, Maine*

Year and week	Unit of count [1]	Plants examined	Aphids per plant	Plants infested	Alatae per trap [2] to July 6
		Number	*Average number*	*Percent*	*Average number*
1953					
June 20–26	WP	825	0	0	
June 27–July 4	WP	825	.002	.24	1.0
July 5–11	3WL	825	.019	.70	
July 12–18	3WL	975	.013	.58	
1954					
June 19–25	WP	750	.006	.27	
June 26–July 3	3WL	1,050	.009	.57	
July 4–10	3WL	1,200	.004	.21	2.1
July 11–17	3WL	1,500	.018	1.04	
1955					
June 19–25	WP	1,150	.112	4.39	
June 26–July 2	WP	2,050	.104	4.83	5.3
July 3–9	3WL	2,050	.098	5.17	
July 10–16	3WL	2,050	.033	1.47	
1956					
June 24–30	WP	950	.004	.23	
July 1–7	WP+3WL	1,550	.004	.45	.4
July 8–14	3WL	1,725	.006	.43	
July 15–21	3WL	1,725	.012	.60	
1957					
June 23–29	WP	1,400	.008	.71	
June 30–July 6	3WL	1,550	.003	.28	1.3
July 7–13	3WL	1,550	.023	.86	
July 14–20	3WL	1,550	.030	1.35	
1958					
June 22–28	WP	1,150	.003	.09	
June 29–July 5	3WL	1,250	.004	.14	.6
July 6–12	3WL	1,800	.006	.32	
July 13–19	3WL	1,950	.040	1.39	
1959					
June 21–27	WP	900	.008	2.43	
June 28–July 4	3WL	900	.020	.67	.3
July 5–11	3WL	900	.022	.67	
July 12–18	3WL	900	.104	3.33	

[1] WP=whole plant; 3WL=three whole leaves, one from top, middle, and bottom third of plant.

[2] Total of 7 traps.

Plant Growth

New leaves, flower stalks, and stolons of overwintered hawkweed grow and develop rather rapidly early in the season. Hawkweed spreads quickly by this vegetative method of propagation. Observations on plant growth in northeastern Maine revealed that, on the average, flowering proceeds as follows: Elongation of flower stalk, early to mid-June; "early flower" stage, late June to early July; "full flower" stage, early to mid-July; and "late flower" stage, mid- to late July. By early August most plants are past flowering. (These phenomena occur 4 to 5 weeks earlier in New Jersey.) *H. aurantiacum* blooms somewhat earlier than *H. floribundum*. After blooming, the flower stalk gradually dies from the top down, and the plant loses its general succulence. Later, some of the older leaves lose their green color, turn yellow or red, and die.

Feeding Sites of Aphids

During the period of growth and development of hawkweed, the foxglove aphid feeds principally at the succulent growing tips of the leaves, flower stalks, and stolons. The stem mother is most frequently found on the newly expanding center leaves. As the plant matures and loses its succulence, the aphid changes its feeding site and is then found largely on the underside of older leaves, especially those that have lost their green color and are adjacent to the ground. Whether this is due to increased sugar content or other nutrients in the leaves was not determined.

Seasonal History

Several phenomena in the seasonal history of the foxglove aphid make convenient reference points in observing its development. In table 6, data are given on the time when these phenomena occur, based on observations in the cage and in the field studies.

Hatching.—In northeastern Maine the aphid overwinters in the egg stage and hatching generally begins in early May soon after the snow cover has melted; however, hatching may begin in late April in some years; e.g., 1956. Depending on prevailing conditions, hatching continues for 2 to 4 weeks.

Development of Stem Mother.—The first-generation aphids, which hatch from the overwintered eggs, are apterous, viviparous forms called stem mothers (fundatrices). A variable period of development ensues, depending again on prevailing temperatures, before the stem mother becomes adult. This variable period of maturation ranged from about 2 to 4 weeks or longer. The beginning of the period ranged from mid- to late May (table 6). Shands et al. (*58*) reported that low temperatures lengthened the developmental time of the potato aphid from about 3 weeks to 6 weeks. The developmental period of foxglove aphid stem mothers also was increased by about 2 weeks during 1956 as compared with other years. Progeny of the stem mother, or the second generation, develop into either apterous viviparae (fun-

TABLE 6.—*Dates of occurrence of some phenomena in seasonal history of foxglove aphid on caged hawkweed in northeastern Maine*

Phenomenon	1955	1956	1957	1958	1959	1960	1961
Hatching	May 1	Apr. 27	May 5	May 5	----------	----------	----------
Beginning of stem-mother maturation	May 16	May 28	May 20	May 19	May 24	May 18	----------
Beginning of spring migrant maturation	June 6	June 18	June 9	June 11	June 5	----------	[1] June 14
End of spring migrant maturation	July 5	July 27	July 3	July 23	July 31	----------	----------
Beginning of sexuale maturation	----------	Sept. 28	Oct. 2	Oct. 3	Oct. 2	----------	Sept. 27
Beginning of egg deposition	----------	Oct. 19	Oct. 11	Oct. 20	Oct. 14 [2]	----------	[2] Oct. 10

[1] Approximate. [2] In greenhouse.

datrigeniae), which remain on the primary host, or alate viviparae (spring migrants), which fly to secondary hosts.

Development of Spring Migrant.—Spring migrant maturation generally begins about June 10 (table 6) and is of rather long duration. The length of the maturation period can likely be attributed to the fact that both the second and third and possibly later generation fundatrigeniae produce alate individuals (migrants). Patch (*43*) reported that migrants matured largely from the third generation on foxglove. On hawkweed, migrants developing in the second generation took about 3 weeks to mature. The developmental period of the migrants in the third generation was not determined. but it probably began 2 to 3 weeks after maturation of the second generation. The end of migrant maturation in the 5 years reported ranged from early to late July and the later maturation dates in 1956, 1958, and 1959 probably resulted from these migrants developing from later generations of fundatrigeniae.

Viviparae.—After spring migrant maturation ceases, the apterous, viviparous form (primary viviparae) of the aphid continues to live on the primary host until fall, maintaining the colony parthenogenetically.

Viviparae produced by the spring migrants or their progeny on potato or other secondary hosts are called secondary viviparae. Progeny of the secondary viviparae are largely apterous, but in some years alatae (vagrantes) develop and disperse to other plants. These vagrantes generally go from potato to potato, but they may also reinfest the primary host or other secondary hosts.

Abnormalities in some progeny of the secondary viviparae of the foxglove aphid (Wave et al. *74*) occurred in the late summer and fall of 1956 and 1957, when unprecedented numbers of alatae developed at Presque Isle, Maine, on potato plants not treated with insecticides. Many of the alatae exhibited abnormalities in both the number and position of the wings. Some abnormal alatae had only two fully developed wings, but several had no wings or had only rudimentary wings. A few abnormal alatae were also observed among the spring migrants on hawkweed.

Late Summer Production of Alatae.—Caged potato plants (four per cage) grown in the field were artificially infested during August with a few foxglove aphids. The colonies were allowed to develop until mid-September or early October, when the numbers of alatae were determined. A total of 10 cages was used in 1957 and 1958, but only 5 in 1959.

The late summer production of alatae in the cage studies is shown in table 7.

TABLE 7.—*Late summer production of alatae on potato plants in cage studies in northeastern Maine*

Year	Apterae	Alatae	Abnormal alatae
	Number	*Number*	*Number*
1957	Large	6	1
1958	Large	1, 287	157
1959	8,500	15	6

Alatae were recorded during counts made in experimental plots of potatoes in the late summer of 1956, 1957, and 1958, but none were recorded in 1959. Seldom had alate foxglove aphids been observed to mature on potato plants prior to 1956, and then only in trace numbers.

Development of Sexuales.—Fall migrants (remigrantes) apparently do not develop in this species, since the "sexuparae" are produced by the primary viviparae and the males are apterous. The sexuales generally begin to mature on hawkweed in early October (table 6), and the oviparae appear somewhat earlier than the males.

At this season of the year diurnal temperatures fluctuate widely and frequently go below freezing. Under these conditions the maturation period of the sexuales is considerably longer than that of the summer forms of the aphid. The first sexuales undoubtedly begin to appear by mid-September, but they do not mature until October.

In greenhouse cultures the proportion of males to oviparae is always very small; however, they become much more abundant on bristlestem hemp nettle (*Galeopsis tetrahit* L.) and on chickweed (*Stellaria media* (L.) Cyrillo) than on potato.

Mating and Egg Deposition.—Mating begins soon after the males mature and continues until late October. Frequently several males attempt to copulate with a single female, even though the males are much less numerous than the oviparae. Egg deposition begins a few days after mating, generally about mid-October (table 6), and continues until the oviparae are killed by low temperatures, usually in late November. In 1959 no eggs were observed on November 20, but living oviparae were still present.

Eggs are laid singly, generally on the undersurface of the hawkweed leaves. Occasionally eggs are laid on leaf hairs on both the upper and lower leaf surfaces. The eggs when freshly laid are a pale, watery green. Upon development they turn darker green and after a few days an intense, shiny black. Development is then arrested and the egg overwinters in this state.

Shands et al. (*60*) observed that oviparae of the foxglove aphid under some field conditions were capable of depositing up to an average of five eggs. Under some greenhouse conditions they were capable of depositing an average of 15 eggs. All the determinations on egg production were made by dissecting the aphids and counting the number of eggs in each specimen.

The study indicated that the foxglove aphid, in contrast to some of the other potato-infesting species, tended to retain mature eggs until the abdomen became distended. Dissections of oviparae in subsequent years (unpublished data) corroborated our previous findings. Regardless of the potential egg-laying capacity of the oviparae, the number of eggs deposited is governed largely by the effective oviposition period. Factors affecting this period are the rate of development and time of maturation of the oviparae and males, the temperature during the oviposition period, and the onset of cold weather. Therefore, it is apparent that egg production may be higher when mild weather prevails late into the fall.

Natural Control Agencies

Parasites.—The following primary and secondary hymenopterous parasites were reared from foxglove aphids that were collected on potato and hawkweed:

Primary Parasites:
- Braconidae, Aphidiinae:
  - *Praon aguti* Smith
  - *Praon pequodorum* Viereck
  - *Praon* sp.
  - *Monoctonus* sp.
  - *Aphidius avenaphis* (Fitch)
  - *Aphidius nigripes* Ashmead
  - *Aphidius* sp.
- Eulophidae, Aphelininae, *Aphelinus semiflavus* Howard

Secondary Parasites:
- Pteromalidae, Sphegigasterinae:
  - Asaphini:
    - *Asaphes lucens* (Provancher)
    - *Asaphes* sp.
  - Pachyneurini:
    - *Pachyneuron virginicum* Girault
    - *Coruna clavata* Walker
- Cynipidae, Charipinae, *Charips* sp.
- Ceraphronidae, *Lygocerus* sp.

Praon spp. were the most abundant primary parasites and *Asaphes lucens* was the most abundant secondary parasite. *Aphelinus semiflavus* was the most troublesome in caged colonies of the aphid. It was so small it entered through the fine mesh of the screen-covered cage.

Entomogenous Fungi.—The fungi identified from dead, diseased foxglove aphids collected in northeastern Maine from 1942 to 1962 were as follows:

Entomophthoraceae:
- *Entomophthora aphidis* Hoffm. ex Fres.
- *Entomophthora sphaerosperma* Fres.
- *Entomophthora planchoniana* Cornu
- *Entomophthora thaxteriana* Petch
- *Entomophthora* sp.

Delacroixia coronata (Cost.) Sacc. & Syd. has also been collected and identified from the foxglove aphid (Harris *20*).

RESULTS IN NEW JERSEY

Host Plants of Economic Importance

Host plants of economic importance were found to be various species of hawkweed, chickweed (*Stellaria media* (L.) Cyrillo), and burdock (*Arctium minus* (Hill) Bernhardi). In table 8 are 16 species of plants on which collections were made. The following five species apparently are new records for the foxglove aphid: Burdock, celandine (*Cheli-*

donium majus L.), common chicory (*Cichorium intybus* L.), white campion (*Lychnis alba* Miller), and pokeweed (*Phytolacca americana* L.).

TABLE 8.—*Date, geographical location, and host of foxglove aphids observed or collected in New Jersey in 1960*

Date	Location	Host
April 15	New Brunswick	*Stellaria media* (L.) Cyrillo.
May 6	do	*Convolvulus* sp.
Do	do	*Lychnis alba* Miller.
Do	do	*Cerastium vulgatum* L.
Do	Beemerville	*Hieracium* sp.
June 2	Clarksville [1]	*Solanum tuberosum* L.
June 7	New Brunswick	*S. media.*
June 8	do	*S. media.*
June 21	Beemerville	*H. floribundum* Wimm. & Grab.
Do	do	*S. media.*
June 28	New Brunswick	*Plantago major* L.
Do	do	*Phytolacca americana* L.
Do	Springfield	*Viola tricolor* L. var. *hortensis* DC.
July 11	Beemerville	*P. major.*
Do	do	*Cichorium intybus* L.
Do	do	*Capsella bursa-pastoris* (L.) Medic.
July 18	Swartswood	*Hieracium* sp.
July 25	Buttzville	*Arctium minus* (Hill) Bernhardi.
Do	Branchville	*Hieracium* sp.
Aug. 8	Beemerville	*C. intybus.*
Do	do	*Hieracium* sp.
Do	Andover	*A. minus.*
Do	Oldwick	*A. minus.*
Aug. 15	Baleville	*A. minus.*
Sept. 13	Beemerville	*Plantago* sp.
Do	do	*Lactuca* sp.
Do	do	*A. minus.*
Oct. 3	Princeton	*Oenothera* sp.[2]
Oct. 7	Cokesbury	*A. minus.*
Do	Mountainville	*A. minus.*
Oct. 8	Pine Brook	*A. minus.*
Nov. 4	Beemerville	*A. minus.*
Do	Mountainville	*A. minus.*
Dec. 8	Beemerville	*Chelidonium majus* L.

[1] Alate form, probably a migrant.
[2] Ornamental variety.

With few exceptions, the aphid was generally found on the older bottom leaves of mature plants, especially those in contact with the soil where the humidity was high. Furthermore, the plants on which aphids were found were in habitats containing abundant soil moisture; e.g., in shaded places or along ditchbanks. Since the foxglove aphid was never found on these plants in dry areas, it appears to survive best in environments with high humidity.

Although no differences were observed between the two hawkweed species as to host preference of the foxglove aphid, there were differences in species abundance. In New Jersey, *H. floribundum* was much more abundant than *H. aurantiacum*, whereas the reverse was true in northeastern Maine.

Distribution

Figure 14 shows that the foxglove aphid is generally distributed in the northern half of New Jersey. The concentration of collection sites in the northwestern sector resulted from more intensive searching in that area. Nevertheless, because of cooler temperatures in the higher elevations, populations of the aphid probably are larger there than elsewhere. On the other hand, the apparent absence of the aphid in the southern half of the State does not imply it is not present there, since sampling was not so intensive. However, somewhat higher temperatures in the southern half than those in the northern half may tend to restrict development of this aphid. Furthermore, the well-drained sandy soils that constitute the agricultural lands of southern New Jersey do not provide suitable environments for maintaining the high humidity that the foxglove aphid apparently requires.

Mode of Overwintering

In this study no attempt was made to obtain data for the plotting of population trends, since the primary objective was to ascertain which forms of the aphid developed on hawkweed. However, populations of the aphid were generally larger late in the season rather than earlier, as shown in table 9. Alate forms were produced throughout the season. Furthermore, the table shows that viviparous forms of the aphid did not survive on the plants until the observation of March 21 or 28, indicating that the adult aphids did not overwinter in Beemerville. In addition, intensive searching on hawkweed outside the cages on March 21 and 28 revealed no aphids.

TABLE 9.—*Populations of foxglove aphids (New Jersey strain) developing on hawkweed in caged colonies in Beemerville, N.J., 1960–61*

Date	Cage 1	Cage 2	Cage 3	Cage 4	Cage 5
	Number	*Number*	*Number*	*Number*	*Number*
June 21 [1]	15	15	20	10	[2] 9+1
July 11	3	8	25+1	8	15
July 18			20+1		
July 25		38	15		
Aug. 1			9		
Aug. 8		14	60+1		
Aug. 15			>60		
Sept. 5		>20			
Sept. 13	21	110	75	([3])	2
Oct. 7	45	55	95+1		30
Nov. 4	9+3	8	32+9		14
Dec. 8	12+1	20+1	60+1		32+2
Mar. 11 [4]					
Mar. 21	0	0	0	0	0
Mar. 28	0	0	0	0	0

[1] 10 apterous viviparae introduced into each cage May 6.
[2] 9 apterae plus 1 alata.
[3] Aphids present but no count made.
[4] Ground covered with 4 inches of snow.

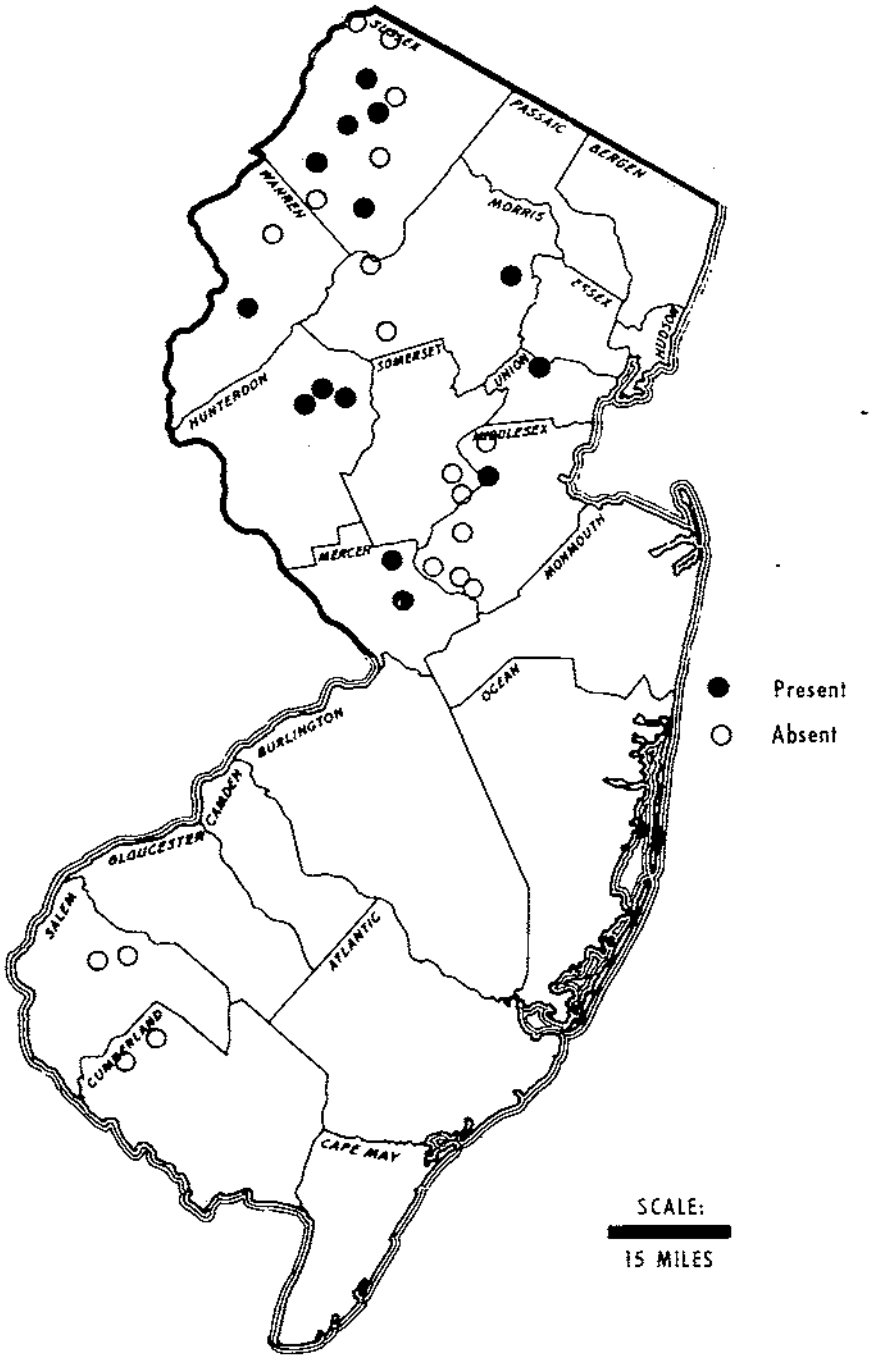

FIGURE 14.—Distribution of foxglove aphids at collection sites in New Jersey in 1960.

Similarly, observations were made periodically throughout the winter on populations of the New Jersey strain of the aphid caged in New Brunswick. Table 10 shows that viviparae were present on hawkweed throughout the winter and that deposition of nymphs was resumed in one instance by February 27. Moreover, another overwintered viviparous adult was observed on hawkweed just outside the cages on the same date. The cage site was covered with several feet of snow from December 11 to about January 5, and the snow cover undoubtedly aided the aphids' survival during that period. At no time during the investigation with the New Jersey strain were sexuales or eggs observed at either New Brunswick or Beemerville.

TABLE 10.—*Populations of foxglove aphids (New Jersey strain) developing on hawkweed in caged colonies in New Brunswick, N.J., 1960–61*

Date	Cage 1	Cage 2	Cage 3	Cage 4	Cage 5	Cage 6	Cage 7	Cage 8
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Sept. 27 [1]	20	15	45	1	3	15	10	30
Oct. 18	[2] 165+8	18+1	10+1	20	2	30+3	80	48+8
Oct. 29	200+12	+3	+0	+0	+0	60+4	+3	------
Nov. 11	80+2	35+7	------	30	-----	175+9	100+21	60+7
Nov. 22	35+1	95+4	6	22+2	[3] 0	125+9	135+11	60+1
Dec. 2	18	90+1	------	------	-----	120+3	50+1	------
Jan. 5	4	------	------	------	------	------	1	------
Feb. 27	[4] 2	0	0	0	-----	0	0	0
Mar. 2	0	0	------	0	-----	0	0	0
Mar. 7	0	------	------	------	-----	------	------	------

[1] 13 to 33 apterous viviparae and nymphs were introduced into each cage Sept. 13.
[2] 165 apterae plus 8 alatae.
[3] Cage discontinued.
[4] Overwintered primary vivipara and recently deposited first-instar nymph.

Although no quantitative data were gathered on the Maine strain, 11 cages were infested with from 100 to 300 apterous viviparae or oviparae and males on September 20 and 27 to obtain the occurrence time of various phenomena for comparison with the New Jersey strain. The data showed that mature oviparae and males were present by September 27 and that egg deposition began by October 9. Oviparae were present and still depositing eggs in some of the cages on December 2. Further observations were not possible after December 11 because of the snowfall, which buried the cages to a depth of about 4 feet. Subsequent observations, beginning on February 27, revealed only eggs in the cages. Hatching began in the cages on March 7, 8 days after the observation of an overwintered vivipara in cages of the New Jersey strain (table 10).

Similarly, a Maine strain of the aphid, obtained in three air-express shipments on September 4, 10, and 17 in 1959, developed sexuales, which began to mature by October 16. The deposition of overwintering eggs by these forms began about October 28. However, because of the paucity of males, the eggs were nonviable and no data on hatch-

ing were obtained. Since the Maine strain of aphids was obtained in September, it is possible that they had already received the necessary stimulus to produce sexual forms before shipment to New Jersey.

DISCUSSION

Shands and Simpson (*52*) have shown that the growth of an aphid population may be represented by a sigmoid curve. The peak of the curve shows considerable annual variation in aphid numbers but relatively little in the time of occurrence. These authors showed that the time of peak populations of the four potato-infesting species on potato was about August 20; however, this varied during a period of 16 years from mid- to late August. Further, they contended that natural factors retarding the rate of population growth increased in severity as the time of peak numbers was neared. The precise date of the peak was affected largely by biological control agents, weather, and the time of the maturation and egress of fall migrants.

The peaks of foxglove aphid population on hawkweed in Maine during the investigations in both field and cage studies closely approximated the sigmoid curve described, in that the peaks occurred about August 20. However, the differences in numbers of aphids per plant between natural and caged environments were considerable. Perhaps the most important factor causing these differences was the effect of caging itself, which not only protected the aphids from most predators and parasites but also prevented their normal dispersal. Since the innate tendency of the aphid to move to less populated plants was restricted, populations in the cages increased considerably above those in the field. Nevertheless, the time of occurrence of peak numbers did not appear to be affected by the large populations in the cages.

The length of the spring migrant maturation period and the generation in which the migrant appeared were determined from cage studies, but no clear-cut reason can be assigned for the variability in the number of alatae to develop per stem mother. It appears that the reason for the variability between stem mothers may be inherent in the genetic constitution, since individuals in identical habitats and under the same population pressures exhibit such differences.

Observations on the seasonal history of the foxglove aphid indicate that it is not a true migratory species, since the aphid can live and reproduce on the primary host throughout its annual cycle, the males are apterous, and this species apparently lacks fall migrants (remigrantes). However, hawkweed may be repopulated by vagrantes in late summer and early fall and thus serve to reinfest the plants or supplement the existing population.

Although careful search on hawkweed in the cage sites at Beemerville on March 21 and 28 (table 9) failed to disclose a single living aphid, the fact that an apterous vivipara survived in the vicinity of New Brunswick (table 10) lends support to the belief that the aphid can overwinter in the adult stage in New Jersey. The finding of a vivipara on February 27 precludes its possible development from egg to adulthood at such an early date. Furthermore, no sexuales or eggs of the New Jersey strain were observed.

Since the aphid overwintered as an adult in New Brunswick, its occurrence in Beemerville may be explained on the basis that it remigrates into areas where it is unable to survive through the winter. During mild winters foxglove aphids indubitably overwinter as adults even as far north as Beemerville, but the winter of 1960–61 was too severe for them to survive as adults.

Possibly genetic differences, rather than differences due to physical factors such as temperature and photoperiod, exist between the New Jersey and the Maine strains of the foxglove aphid. This deduction is based on the fact that the Maine strain developed sexuales and deposited eggs in 1959 and 1960, whereas the New Jersey strain, under identical conditions, did not. Schöll and Daiber (*46*) reported that the occurrence of the holocyclic and anholocyclic populations of the green peach aphid in South Africa are due to different races. They indicated that these races differed not only in physiological behavior but in morphological characteristics and food-plant preferences. Müller and Schöll (*40*) mentioned that the foxglove aphid coexists in both holocyclic and anholocyclic strains in South Africa. Perhaps the Maine strain of the foxglove aphid is the holocyclic and the New Jersey strain the anholocyclic strain of this aphid.

SUMMARY

The foxglove aphid (*Acyrthosiphon solani* (Kaltenbach)) is one of four potato-infesting species that injure the potato plant by their feeding punctures and toxic secretions and by spreading virus diseases. Study of the biology of this aphid species was intensified after the discovery of a new primary host, the common perennial hawkweed (*Hieracium* spp.). Previous to this the only intensive biologic study was that describing its seasonal history on foxglove (*Digitalis purpurea* L.).

Studies on the ontogeny of the aphid and its population dynamics on hawkweed, a primary host, were conducted in northeastern Maine from 1954 until 1961, both in caged colonies and in the field. In caged colonies, frequent observations and counts of aphid numbers were made on all the foliage in the cages. The cylindrical cage used in the study was constructed of 6-gage "black" wire covered with cotton scrim. Aphids were examined on the foliage in situ, and the cages were removed only during periods of observation. In the field, weekly examinations for aphids were made on 50 randomly located hawkweed plants at each of 10 widely scattered locations. Data collected from both sources were used to plot population trends and to determine some seasonal phenomena in the ontogeny of the aphid.

Population trends of the aphid on hawkweed were determined from the average number per plant and the percentage of plants populated. By either method of comparison, the population growth curve was similar. In general, populations of the aphid increased slowly until early August, increased rapidly to a peak in late August, and then declined, but at varying rates in different years.

The cage study showed that alatae maturing from progeny of a single stem mother ranged from 0 to 58; duration of maturation ranged from early June to early or late July (23–49 days); and alatae

appeared in the second, third, and possibly later generations, and this varied annually.

The duration and intensity of the aphids' annual influx to potatoes were determined by means of wind-vane traps. The study showed that during years when the aphid was sufficiently abundant, trapping would give a reliable estimate of the duration and size of the migration.

The following phenomena in the aphids' seasonal history were obtained: Hatching of the stem mother generally began in early May; the stem-mother maturation period ranged from 2 weeks to a month or more, depending on weather conditions; spring migrants began to mature about 3 weeks after stem-mother maturation; the period of migrant maturation extended from early June to late July; sexuales began to mature by early October; and egg deposition began about mid-October. Semiannual aphid egg surveys were conducted on hawkweed in an attempt to forecast subsequently developing populations.

In addition to population trends, notes were made on the ontogeny of the primary host plant, the feeding sites of the aphids on the plant, and observations on egg production. Records were also made of the parasites and entomogenous fungi that attack the aphid.

Population growth trends, late summer production of alatae, and natural control agencies were also studied on potato, both in the field and in caged colonies.

Studies on the host plants, distribution, and mode of overwintering of the foxglove aphid were conducted in New Jersey from 1959 to 1961. The foxglove aphid was collected from 16 species of plants; 3 of these are rather common hosts and 5 are apparently new records for this aphid. Observations and collections of the aphid from hawkweed and other hosts throughout the more rural areas of New Jersey revealed that its distribution was restricted largely to the northern half of the State.

Cage studies indicate that the New Jersey strain of the aphid overwinters as apterous viviparae. At no time were sexuales or eggs observed. The aphid probably remigrates into areas where it is unable to survive through the winter. In Maine the aphids overwinter as eggs. Observations on a Maine strain of the aphid at New Brunswick showed that sexual forms developed and deposited eggs and these eggs overwintered and began to hatch in early March.

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