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TB51: Seasonal History of the Buckthorn Aphid and Suitability of Alder-Leaved Buckthorn as a Primary Host in Northeastern Maine

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Cover Photo: A patch of alder-leaved buckthorn, *Rhamnus alnifolia* L'Her. This wild plant is the most important primary (overwintering) breeding host of the buckthorn aphid, *Aphis nasturtii* Kaltenbach, in Maine; it occurs most commonly in wet soils of calcarious origin and is frequently found growing along the edges of streams, in poorly drained parts of pastures or in swampy sections of woods. Many buckthorn aphids feed and develop in the twisted or cupped leaves seen here on the upper parts of the plants. The spring migrant forms of the aphid fly from alder-leaved buckthorn to potato fields and to other secondary, summer host plants soon after reaching maturity, chiefly in June.

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W. A. Shands[4] and Geddes W. Simpson[5]

INTRODUCTION

The buckthorn aphid, *Aphis nasturtii* Kaltenbach, is one of four species of aphids commonly infesting potatoes, *Solanum tuberosum* L., in Maine. It is widely distributed over the northeastern part of the United States and is a pest of potatoes elsewhere in the world, including parts of England and Europe. The other three species of potato-infesting aphids in Maine are the green peach aphid, *Myzus persicae* (Sulzer), the potato aphid, *Macrosiphum euphorbiae* (Thomas) and the foxglove aphid, *Acyrthosiphon solani* (Kaltenbach).

These four species of aphids are potentially injurious to potatoes from either or both of two standpoints, viz. when sufficiently abundant their feeding damage will reduce yield of tubers (Shands *et al.* 1950, Simpson and Shands 1954), and they may transmit several plant viruses from diseased to healthy potato plants when feeding and moving from plant to plant. The resulting virus diseases reduce yield and quality of tubers to varying degrees depending upon variety of potato, the virus or combination of viruses, the time of infection and other factors.

The buckthorn aphid is an important vector of two viruses that affect potatoes, viz. *Marmor cucumeris var. upsilon* Holmes (potato virus Y) and *Marmor solani* Holmes (potato virus A). Infections of these viruses result in the potato diseases known as potato vein-banding mosaic and potato mild mosaic (Holmes 1939); when the potato plants are also infected with the virus *Marmor dubium* var. *vulgare* (Holmes) (potato virus X), the resulting mosaic diseases (rugose mosaic or mild mosaic, respectively) are much more severe and injurious than when it is not present. In our large-cage tests, the buckthorn aphid was a poor vector of the potato leaf roll virus, *Corium solani* Holmes.

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[1] *Aphis nasturtii* Kaltenbach (Hemiptera:Aphididae).
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The buckthorn aphid has been a pest of potatoes in northeastern Maine for many years. Patch (1912) first recorded its presence in Maine, but did not indicate it was then a pest of potatoes. Later (Patch, 1924), she discovered the basic features of its life cycle, seasonal history, habits and many of its food plants including potatoes and the primary or overwintering host "buckthorn—, Rhamnus" Still later (Patch 1925, 1938), she said that the buckthorn aphid was the third most abundant species of aphid infesting potatoes (the two most abundant were the green peach and potato aphids) and she listed many host plants of the aphid, including *Rhamnus alnifolia* L'Her. and *Rhamnus cathartica* L., as primary hosts of the aphid in Maine. Simpson (1940) reported much variation in actual and relative abundance of these four species of aphids on potatoes at several places in Aroostook County during the period 1931 to 1938, inclusive. The buckthorn aphid was the predominant species in some fields during six of the eight years.

In our studies on Aroostook Farm, near Presque Isle, the buckthorn aphid was the most abundant of the four species on potatoes not treated with insecticides during 18 out of 29 years from 1941 to 1969, inclusive. The potato aphid was the dominant species in seven years during the period 1962 to 1969; the green peach aphid was the most abundant during 3 years, while the buckthorn and green peach aphids were about equally abundant in 1943.

The results of surveys in 1941 and 1942 showed that alder-leaved buckthorn, *R. alnifolia,* was by far the most widespread, abundant and important primary host of the buckthorn aphid in northeastern Maine. Investigations were then begun to determine the importance of the plant as a source of buckthorn aphids infesting potatoes each year in that section, and to assess the probable utility of seasonal surveys of aphids or aphid eggs on alder-leaved buckthorn for making advanced estimates of abundance of the buckthorn aphid on potatoes. This bulletin contains results of these investigations.

SEASONAL HISTORY AND DEVELOPMENT OF THE BUCKTHORN APHID

In northeastern Maine, eggs of the buckthorn aphid overwinter on alder-leaved buckthorn. They usually begin hatching during the latter part of April as the buds of this plant begin to swell. The time of hatching is influenced greatly by the time the snow melts and exposes the eggs not only to air temperature and direct sunlight, but also to the increasing radiant heat from the dark soil beneath the plants after the snow melts.

The dark green nymphs of the buckthorn aphid hatching from the over-wintered eggs mature to apterous stem mothers (fundatrices). The stem mothers and their descendents for one or more generations feed

on the tender, succulent, rapidly expanding new growth from the buds at any place on the plant; however, in early spring the colonies tend to be larger and more numerous on bud growth near the soil surface than on the upper periphery of the plants.

Until early August, all descendents of the stem mothers mature as viviparous asexuales, or agamic females which reproduce parthenogenetically by depositing their nymphs on plant foliage. On alder-leaved buckthorn a small percentage of the stem mother's progeny (2nd generation) may mature as alate spring migrants. Spring migrants comprise a very large proportion of the third generation; however, some alatae may develop in succeeding generations for as long as colonies of the aphid persist on alder-leaved buckthorn.

The maturing spring migrant buckthorn aphids soon fly from alder-leaved buckthorn to secondary or summer host plants, including potatoes. There they move from plant to plant as they feed and deposit nymphs. After these nymphs mature as apterous adults, colonies are established which tend to remain on the plants where started. (Both nymphs and adults of this aphid are much less mobile than are some of the other potato-infesting species.) While most of the descendents of the spring migrants on secondary hosts for several generations become apterous adults, some mature as alate summer dispersal forms which move about freely. These begin to appear in July, usually earlier on certain of the weed hosts than on potatoes, and become more numerous and widespread until about mid August or later.

Early in August, two new kinds of alatae of the buckthorn aphid begin to mature on potatoes and on some other secondary hosts. These are fall migrant females and males. As described by Patch (1924), even while still in the abdomen of the wingless mother aphid, one can recognize two color phases in the developing nymphs, dark green ones which become alate males and lighter green ones which will mature as fall migrant asexuales. The fall migrant females and males begin maturing about the same time, and both fly to and infest the primary host at the same time. Trapping studies have shown that at Presque Isle the fall migration occurs as long as fall migrant females and males mature on secondary hosts; it may continue until the end of October.

The asexual fall migrants of the buckthorn aphid deposit nymphs on alder-leaved buckthorn, most of which mature as yellowish apterous, oviparous females. The darker, smaller alate males—already present on the plants—fertilize the oviparae, which deposit the eggs principally by the buds of alder-leaved buckthorn (Figure 1). These are the overwintering eggs; they are green in color when first deposited but, after undergoing partial development, soon turn black (Patch, 1924).

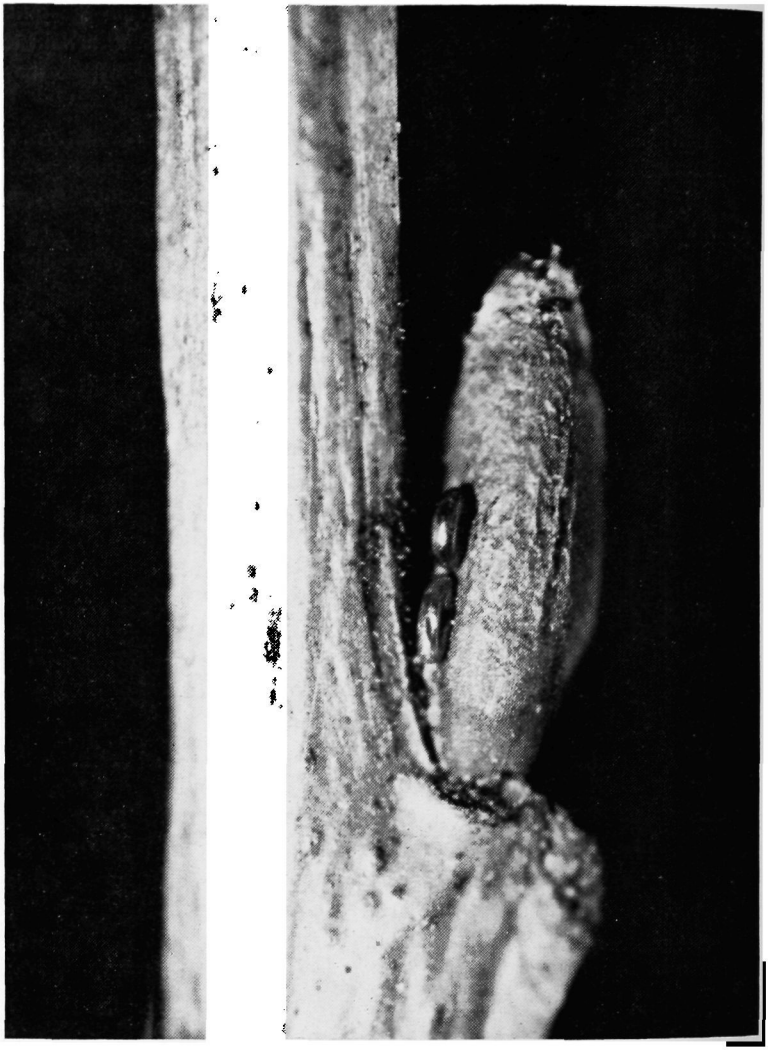

FIGURE 1. Aphid eggs beside a bud on a twig of alder-leaved buckthorn

Variation among years in the beginning of the spring migration of the buckthorn aphid was greater than that of its fall migration (Table 1). Over the period 1942 to 1969, inclusive, except for three years when observations were inadequate to establish the date, the date of the beginning of the spring migration in central Aroostook County varied from as early as June 2 in 1942 to as late as June 27 in 1947. During the same 28-year period the comparable range for the start of the fall migration

was August 7 in 1955 to about August 20 in 1948. Variability in the beginning of the spring migration was due chiefly to weather conditions as they affected the time of hatching of the eggs and the rates of development of the first two generations.

Table 1

Approximate beginning times of the spring and fall migrations of the buckthorn aphid in Central Aroostook County, 1942 to 1969, inclusive.

Year	Spring migration	Fall migration
1942	June 2	August 13
1943	Before June 24	Before August 20
1944	[1]	About August 15[2]
1945	[1]	Before August 15[2]
1946	June 10	Before August 12
1947	June 27	Before August 20
1948	Before June 7	August 15 to 16
1949	June 6	August 14
1950	Before June 2	August 15
1952	June 12	August 15
1953	June 5	August 14
1954	June 17	August 14
1955	June 6	August 7
1956	June 17	August 15
1957	June 4	August 13
1958	June 12	August 15
1959	June 4	August 13
1960	[1]	August 12
1961	June 14 to 15	August 13
1962	June 10	August 15
1963	June 5	August 13
1964	June 8	August 14
1965	June 12 to 15	August 17
1966	June 4 to 5	About August 15
1967	About June 15	[1]
1968	June 10	[1]
1969	June 13	[1]

[1] Observations were inadequate for establishing a definite date. No observations of this nature were made in 1951.

[2] Alate male buckthorn aphids were first caught in windvane traps near Presque Isle on August 16 in 1944 and on August 10 in 1945.

On potatoes in the greenhouse, MacGillivray and Anderson (1958) found that the nymphal stages of the buckthorn aphid had a mean developmental time of 6.9 days at an average temperature of 67.4°F as compared to 8.3 days at an average of 68.2°F for the green peach aphid, 8.6 days at 71.2°F for the potato aphid, and 9.3 days at 72.6°F for the foxglove aphid. Under these conditions they found the average total number of offspring per adult of the buckthorn, green peach, potato, or foxglove aphids to be 63.9, 75.5, 65.7, or 60.3, respectively.

PRODUCTIVENESS OF SPRING MIGRANTS OF THE BUCKTHORN APHID ON ALDER-LEAVED BUCKTHORN

PROCEDURE

A study was conducted from 1946 to 1958, inclusive, to determine the importance of alder-leaved buckthorn as a breeding host for spring migrants of the buckthorn aphid. Naturally occurring single specimens or, in a few instances, small colonies of the aphids were caged in spring each year on new growth of alder-leaved buckthorn in naturally occurring patches of the plant near Presque Isle. Rarely, a recently matured adult stem mother alone or with a few newly deposited progeny near her was caged on the branch where found. Some specimens were transferred to another branch of the same plant or to a nearby plant more accessible for caging or for making observations of aphid colony development without injury to the caged branch or to nearby branches. Experience showed that injury to a caged branch, or to a nearby non-caged branch which at first appeared to be of minor importance, occasionally proved to have severely damaging consequences to that branch or to others.

When the young stem-mother nymph was transferred to another branch for caging, she was allowed to crawl from the infested bud to the uninfested one. Drawstring cages, 6 inches in diameter and 12 to 16 inches long and made of scrim (26 strands per inch) enclosed all new growth on the terminal 6 to 9 inches of the infested branch. Each cage or colony contained the progeny or descendents of a single stem mother.

The caged colonies were observed at infrequent intervals until adults of the second generation began to mature. Thereafter, the colonies were examined three times each week, at intervals of two or three days, until they ceased to exist. At each examination all alate forms were removed with an aspirator and preserved for subsequent identification and counts. Notes were made at the time of each observation describing the size and vigor of the aphid colony and the branch in each cage.

RESULTS

Figures 2 and 3 show the seasonal production of spring migrants of the buckthorn aphid on new growth of caged branches of alder-leaved buckthorn for the years 1946 to 1958, inclusive, and the average for the period 1947 to 1958, inclusive. The basic data used in constructing the freehand curves in these figures are summarized in Table 2. The averages in Table 2 were derived by giving equal weight to all yearly averages, or dates, irrespective of the numbers of cages examined each year.

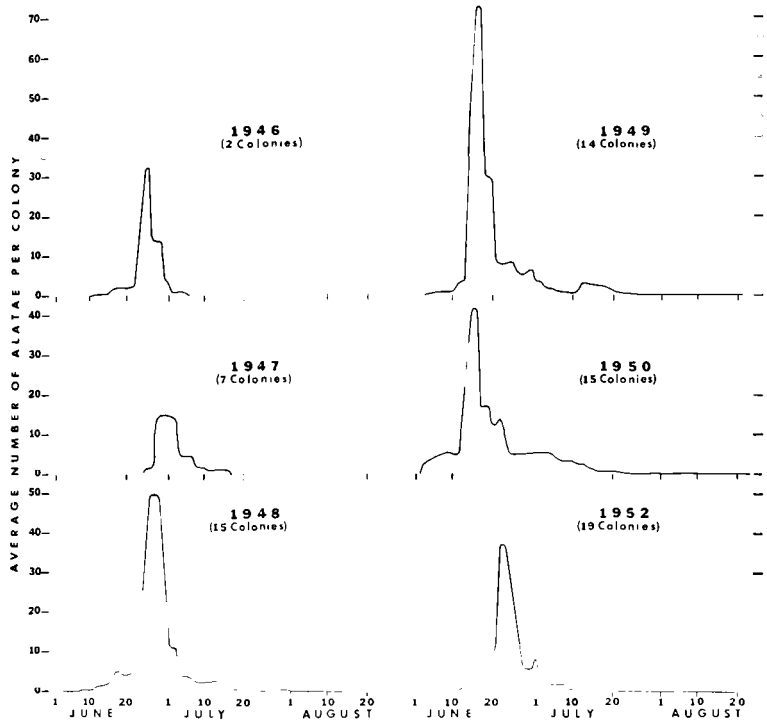

FIGURE 2. Productiveness of alate buckthorn aphid spring migrants at Presque Isle on caged branch terminals of alder-leaved buckthorn, 1947 to 1953, inclusive. The colony in each cage was initiated by one stem mother.

The date of first maturation of stem mother aphids varied from May 10 in 1948 to June 5 in 1947; the average date for the 11 years was May 24 (Table 2).

The starting date of maturation of the spring migrants varied from as early as June 2 in 1950 to as late as June 27 in 1947. The approximate date of the peak of maturation of spring migrants varied from June 16 in 1950 to July 3 in 1956 and in 1958. The maturation date of the last alate specimen varied from July 12 in 1946 to as late as August 25 in 1949. The average maturation dates of the first, peak and last of the spring migrants were June 10, June 25 and August 6, respectively.

Maturation of spring migrant forms in the cages extended from as few as 21 days in 1947 to as many as 80 days in 1949; the average for the 11 years was 57 days. The comparable range in number of days during which an average of two alatae or more per colony per day

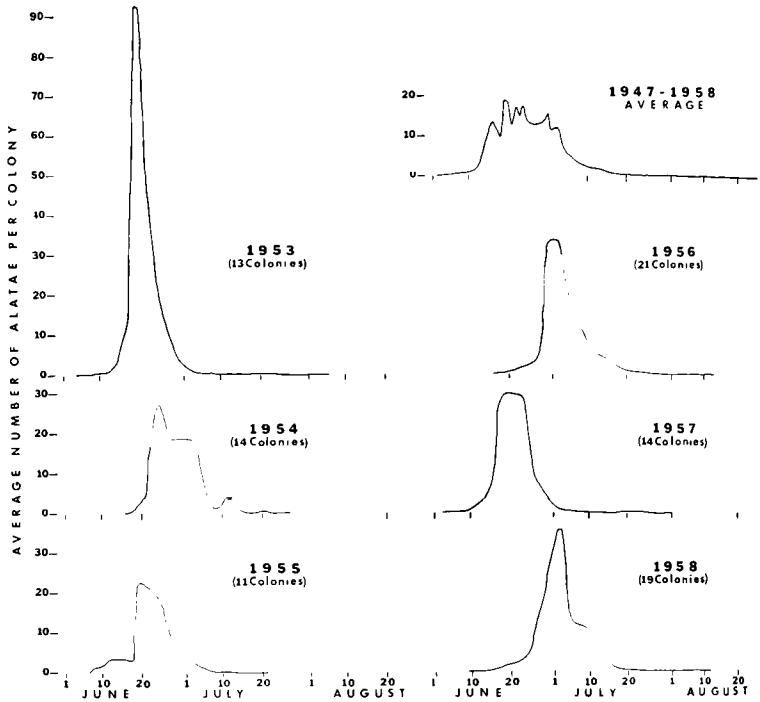

FIGURE 3. Productiveness of alate buckthorn aphid spring migrants at Presque Isle on caged branch terminals of alder-leaved buckthorn, 1954 to 1958, inclusive, and the average for the period 1947 to 1958, inclusive.

matured varied from nine days in 1946 to 40 days in 1950; the average was 24 days.

The range in number of alatae to mature in single colonies was from 3 to 1605; both extremes occurred in 1949 (Table 2). The averages of the minimum or maximum number of alatae per colony in each of the 11 years were 55 and 872, respectively. The yearly average number of spring migrants per colony varied from as few as 106 in 1947 to as many as 480 in 1953; the average for all 11 years was 323 per stem mother.

DISCUSSION OF RESULTS

Several factors may have influenced colony productiveness of spring migrants of buckthorn aphids on alder-leaved buckthorn. These include the amount and condition of new growth per cage, the proportion of the stem mother progeny maturing as alatae and thus removed

Table 2

Productiveness of spring migrants of the buckthorn aphid on new growth of singly caged terminals of twigs of alder-leaved buckthorn near Presque Isle, Maine, 1946 to 1958, inclusive.

Year	Number of caged colonies	Approximate times of maturation: Stem mothers First	Spring migrants First[1]	Spring migrants Peak	Spring migrants Last[1]	Number days of maturation: Total	Number days of maturation: Appreciable[2]	Number of alatae maturing per colony: Maximum	Minimum	Average
1946	2	May 25	June 10-15	June 26	July 12	31	9	181	103	142.0
1947	7	June 5	June 24-27	July 1	July 16	21	10	348	17	106.0
1948	15	May 10	June 3- 7	June 28	August 14	70	29	819	119	417.5
1949	14	May 19	June 3- 6	June 17	August 22-25	80	25	1,620	3	453.7
1950	15	May 20	June 2- 5	June 16	August 18-22	78	40	1,605	46	383.8
1952	19	May 27	June 10-13	June 23	August 16-18	66	24	771	61	270.3
1953	13	May 17	June 4- 6	June 20	July 31-Aug. 6	59	17	791	63	479.9
1954	14	May 28	June 16-18	June 25	July 26-28	40	20	683	15	291.4
1955	11	May 24	June 5- 7	June 19	July 18-20	43	22	502	38	219.0
1956	21	June 4	June 16-18	July 3	August 10-13	56	25	671	24	277.9
1957	14	May 22-23	June 3- 5	June 24	July 29-31	56	21	970	107	305.5
1958	19	May 26	June 9-13	July 3	August 8-11	60	26	815	110	345.1
Average (1947-1958)		May 24	June 10	June 25	August 6	57	24	872	55	322.7

[1] Last observation before or after alatae were found, respectively.

[2] The number of days during which 2 alatae per day per colony matured in the cages.

from the cages, and soil moisture, as well as the skills and techniques of the observers. Some of these factors had interrelated effects.

In many instances there were variations among cages in the length of branch caged, the number of buds on the caged portion of the branch, the number of buds which grew, the length of new growth per bud, and the total amount of new growth per cage. Based on determinations made at the end of caging, in 1958—a year of above average colony productiveness (Table 2)—new growth developed on from two to six buds per cage and the length of new growth from these buds varied from 5½ to 29 inches per cage; on average there was new growth from 3.0 buds per cage having a total length of 10.0 inches.

The total length of new growth per cage and its suitability for breeding of the aphid probably were influenced largely by the size of the aphid colony and by precipitation. Usually, about 20% of the progeny of the stem mother aphid (second generation) matured as spring migrants and were removed from the cages soon after maturing. The alatae do not appear to deposit nymphs on the caged foliage of the buckthorn plant; ordinarily, they begin depositing nymphs after reaching the secondary host.

In some years none of the second-generation aphids was destined to be a spring migrant, while in others possibly as high as 40% matured as alatae. The numbers of third-generation aphids were much larger when none or a small percentage of the second generation became spring migrants than when the percentage was above average. Feeding of large populations of third-generation aphids severely damaged the condition of the new growth. In some cages the damage was severe enough to stunt the new growth and to cause early defoliation, thus shortening the period that the host plant was suitable for breeding of the aphid.

On the other hand, the aphid population size developing in the cages in the third generation—when most spring migrants matured—was small when a relatively large percentage of the second-generation aphids became spring migrants. Under these conditions the season's growth of foliage had occurred and its prime condition for aphid breeding had passed before large populations of the buckthorn aphid could have developed.

Observations indicated that above normal amounts of precipitation during spring and summer lessened the severity of aphid feeding damage to the foliage of alder-leaved buckthorn and extended the length of time that the new growth in cages remained suitable for aphid breeding. Below normal soil moisture resulted in converse effects.

Ample amounts of soil moisture and moderately severe aphid feeding damage appeared to extend the time during which foliage conditions

remained suitable for aphid breeding in the cages. Apparently that amount of feeding damage stimulated some new growth from leaf axils as well as at the distal ends of the new growth.

Colony productiveness in the cages during this study was not affected by arthropod predators, parasites or entomogenous fungi. In some years, predators substantially reduced the potential number of spring migrants that might have developed on this plant at some places. Larvae of syrphids (Diptera:Syrphidae) and, occasionally, *Scymnus* sp. (Coleoptera:Coccinellidae) were the most common predators. Dead aphids affected by internal parasites seldom were found on the alder-leaved buckthorn plant. The external mite parasites *Erythraeus* sp. or *Leptus* sp. (Acarina:Erythraeidae) in some years were commonly found infesting stem-mother buckthorn aphids and their progeny on alder-leaved buckthorn in some places but were of no importance in these cage studies.

Based on our general observations, the average numbers of spring migrants of the buckthorn aphid per stem mother on caged branches may be fairly representative of their productiveness under natural conditions when predators or the ecto parasites *Erythraeus* or *Leptus* are of minor importance. In cages, the average number of spring migrants per stem mother of the buckthorn aphid on alder-leaved buckthorn (323) was much more than that of the green peach aphid, *Myzus persicae* (Sulzer) on Canada plum *Prunus nigra* Ait. (203), or the potato aphid, *Macrosiphum euphorbiae* (Thomas), on swamp rose, *Rosa palustris* Marsh. (117) (Shands *et al.* 1969, 1972).

FALL POPULATION TRENDS OF THE BUCKTHORN APHID ON ALDER-LEAVED BUCKTHORN

PROCEDURE

Counts of buckthorn aphids were made in autumn on Aroostook Farm, near Presque Isle, Maine, at two places for several years during the period 1949 to 1955, inclusive, and at three places from 1958 to 1964, inclusive. Other species of aphids seldom were found on the alder-leaved buckthorn plants at that or at any other time of the year; when present, they were in trace numbers only.

The fall counts of the buckthorn aphid usually were started soon after the beginning of the aphids' fall migration to primary hosts from potatoes and other secondary, summer hosts. The counts were repeated at intervals of 7 to 10 days until about or soon after the fall peak of abundance of the aphid on alder-leaved buckthorn. The time of the final count usually was about or soon after mid September, or about the time oviparae became abundant on the plant.

The counts of aphids on alder-leaved buckthorn ceased to be an adequate index of abundance of the buckthorn aphid after the oviparae began to mature, or when the population of immature aphids on the foliage was extraordinarily large. In either of these events, many of the aphids spent much of the time crawling over the woody parts of the plants and were not on the foliage for sampling. Oviparous adults seldom were found on the leaves; frequently they were seen near or beside the buds in oviposition activities or were crawling over the branches or trunks of the plants.

The leaf was the unit of sample for measuring abundance of the aphid on alder-leaved buckthorn. The sample leaves were randomly located over the patch and the counts were made on the leaves *in situ* with the aid of a 14 x hand lens when needed. A sample consisted of 100 leaves. Abundance of the buckthorn aphid was expressed as the average number of apterae and alatae per leaf and percent of leaves infested.

RESULTS AND DISCUSSION

The average time of the fall peak of apterous buckthorn aphids on alder-leaved buckthorn occurred in late August and in early September (Figure 4). The range in time of the peak was from August 29 in 1963 to September 12 in 1952, 1958 and in 1962.

The average number of apterous buckthorn aphids per leaf at the peak varied from as few as three in 1958 to as many as 119 in 1963. The average number during the 11 years was 47 (Figure 4).

In some years, both green and black aphid eggs were commonly observed on the alder-leaved buckthorn as early as September 5. When this occurred, the oviparae likely matured in late August or early September since several days are required for the newly-laid green eggs to turn black.

The number of generations of the buckthorn aphid developing in autumn on alder-leaved buckthorn was not determined; however, there may have been several. Probably, most of the progeny of the fall migrants became oviparae, but some may have become parthenogenetic adults. Nymphs in all stages were occasionally seen on the leaves in late October and, a few times, in early November. Usually, however, most of the plants were devoid of leaves by early November.

The size of the buckthorn aphid population at the fall peak on alder-leaved buckthorn doubtless was influenced by the number of fall migrants reaching the plants, as well as by the time of plant defoliation. The numbers of fall migrants of the buckthorn aphid reaching the alder-leaved buckthorn were influenced largely by the level of infestation of that aphid on potatoes. Our data and observations strongly indicate

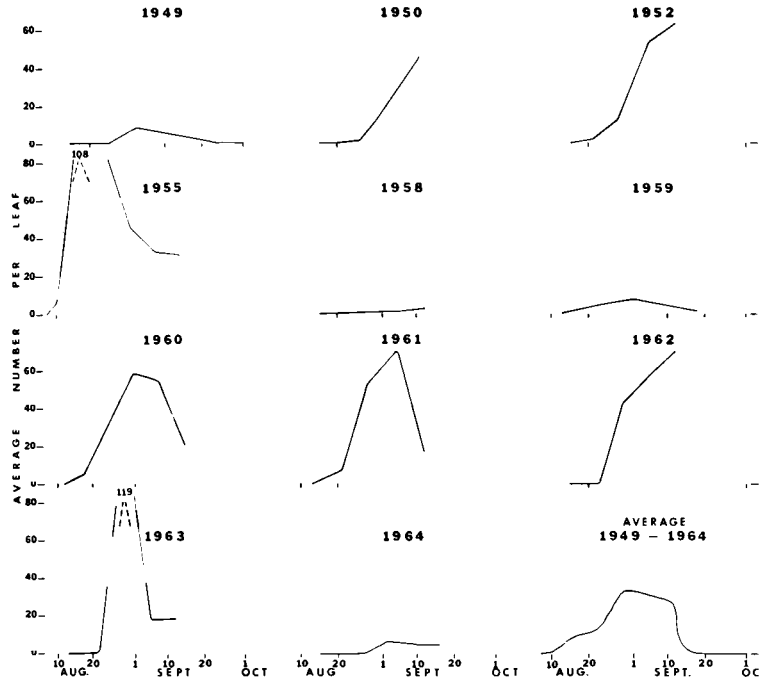

FIGURE 4. Fall population trends of the buckthorn aphid at 3 stations of alder-leaved buckthorn on Aroostook Farm, Presque Isle, Maine, 1949 to 1964.

that, since the advent of the general use of herbicides in the mid 1940's, weed hosts of the aphid in cropland or in wasteland have been unimportant sources of summer dispersal forms for supplementing aphid populations on potatoes or of fall migrants reaching alder-leaved buckthorn. The rate and time of defoliation of alder-leaved buckthorn probably was affected both by the size of the aphid population and by weather conditions. Defoliation occurred more rapidly and was completed sooner in warm, dry autumns or when aphid populations on the leaves were large than in cool, wet weather or when aphid numbers were small.

Arthropod parasites and predators appeared to be of no appreciable importance in limiting fall abundance of the buckthorn aphid on alder-leaved buckthorn. Entomogenous fungus, as well, probably had little direct effect; its greatest effect in most years was that of reducing the number of fall migrants maturing on potatoes and on other secondary host plants which, potentially, could have infested the primary host.

ABUNDANCE OF APHID EGGS ON ALDER-LEAVED BUCKTHORN

Sampling to determine abundance of aphid eggs on alder-leaved buckthorn (Shands and Simpson 1954) was conducted at six to nine locations in central and southern Aroostook County (Table 3). The sampling was done in early November of each year and again about mid April at all stations. These times were chosen because they represented the latest reliable dates before the onset of winter and the possibility of deep snow cover, and before hatching of the eggs might start in spring.

PROCEDURE

Sampling at each station consisted of cutting nine bunches of 10 twigs of alder-leaved buckthorn randomly located as to position on the plants but spread to include the entire area of plants at the locale. The twigs were examined for eggs soon thereafter in the laboratory with the aid of binocular microscopes. Records were made to show, by bud position, the numbers of fully distended or shriveled aphid eggs beside approximately 810 buds; typically, these were the nine distal buds on each twig (Shands and Simpson 1954). Abundance of eggs at each station was expressed as the average numbers per 100 buds of fully distended and shriveled ones. A shriveled egg was one that was not perfectly distended. Shriveled eggs were not viable.

RESULTS AND DISCUSSION

The abundance of aphid eggs on alder-leaved buckthorn varied greatly among years both at the onset of winter and in spring before hatching began (Table 3). In most years, there was substantial variation among stations as well.

The average number of eggs per 100 buds in early November varied from 2.5 in 1965 to 300.4 in 1946; the average for the 24-year period 1945 to 1969, inclusive, was 104.2 (Table 3). The comparable averages in mid April of the following year ranged from 2.9 in 1960 to 204.1 in 1959; the average was 71.6 for the period 1946 to 1960, inclusive.

There was also much variablity among years in prevalence of shriveled aphid eggs at the onset and end of winter (Table 3). In November the percentages of shriveled eggs varied from as high as 81.9% in 1951 to a low of 14.8% in 1965; the average for the 24-year period 1946 to 1969, inclusive, was 56.5%. The comparable range for mid April of the years following was 96.9% in 1952 to 53.5% in 1960; the average was 81.2% for the 15-year period 1946 to 1960, inclusive.

The over-winter loss of fully distended eggs varied from a low of 50.8% found in mid April, 1957, to a high of 97.0% at that time in

1943 (Table 3). The average winter loss of fully distended eggs was 73.1% for the 18-year period 1942 to 1960, inclusive. The comparable winter loss of shriveled eggs for the 15-year period 1946 to 1959, inclusive, was only 32.2%.

The reasons for greater over-winter loss of fully distended eggs than that of shriveled eggs are not clear; it may have been more apparent than real. Most of the apparent loss was due to shriveling between the November and April count dates of eggs that were still fully distended at the time of the count in November. Likely, the winter loss of 41% in total population of eggs was due to or represented largely by shriveled eggs. Probably, only a small part of the loss in total population of eggs was that of fully distended eggs. Also, the small loss of fully distended eggs was probably due largely to the predatory action of birds and to washing rains in late fall before snow cover was deep and in early spring after the snow had melted. Ordinarily the plants were totally or almost covered by snow during most of the winter.

PROBABLE USEFULNESS OF SEASONAL SURVEYS OF ABUNDANCE OF APHIDS OR APHID EGGS ON ALDER-LEAVED BUCKTHORN

Regression analyses were made to assess the probable value of data on abundance of the buckthorn aphid or aphid eggs on alder-leaved buckthorn for predicting buckthorn aphid abundance on potatoes. The method used was correlation of abundance data for two variables at a time. These data included average numbers of apterous buckthorn aphids at the fall peak on alder-leaved buckthorn, aphid eggs per 100 buds on this plant in late fall and again in early spring of the year following, and buckthorn aphids on potatoes not being treated with an insecticide using the 3-leaf method of count (Shands and Simpson 1953; Shands *et al.* 1954) (Table 3). The determinations for potatoes were made on two occasions during the summer: about July 10-15 and, again in the same places, August 10-20. These two dates corresponded to the end of the aphids' spring migration—before supplemental infestation of the potato plants occurred from flights of summer dispersal forms of the aphid maturing on potatoes or on other secondary hosts—and to the summer peak of aphid abundance on potatoes, respectively.

From 1943 to 1945, inclusive, the counts of buckthorn aphids were made on untreated potatoes in an average of 16 fields well distributed over central and southern Aroostook County. In 1946 and 1947, after the advent of the general use of insecticides on most commercial plantings of potatoes, they were made in an average of 10 fields on Aroostook Farm and in the vicinity of Presque Isle. Beginning in 1948, the counts in July and August each year were made in an average of more than

seven locations within a 300-acre square section of Aroostook Farm. The combined expression for aphid abundance from each of the counts on potato plants was average number of apterous buckthorn aphids on three leaves per plant (top, middle, bottom); it was derived by dividing the sum of the averages for all fields, or count locations by the number of fields or locations. In most instances, the average for each field on Aroostook Farm was based upon examination of these subunits on 150 plants or 450 leaves; usually, those for fields elsewhere than on Aroostook Farm were derived from similar counts on 100 plants or 300 leaves at each location. Although not included in this bulletin, the aphid abundance data for potatoes used in this study are available from the Life Sciences and Agriculture Experiment Station, University of Maine at Orono.

RELATIONSHIPS BETWEEN ABUNDANCE OF BUCKTHORN APHIDS OR OF APHID EGGS ON ALDER-LEAVED BUCKTHORN AND THAT OF BUCKTHORN APHIDS ON POTATOES

There was considerable variation in the number of years for which data were available for use in studying these relationships. The correlations of buckthorn aphid abundance at the fall peak on alder-leaved buckthorn were limited to 11 years during the period 1949 to 1964, inclusive (Fgure 4); those for fully distended eggs or for all aphid eggs on the plant in mid April were limited to 18 years from 1942 to 1959, inclusive, or 15 years from 1945 to 1959, inclusive, respectively (Table 3); and those for fully distended eggs or for all eggs on the plant in early November to the 28 years from 1942 to 1969, inclusive, or to 24 years from 1946 to 1969, inclusive, respectively (Table 3). Buckthorn aphid abundance data on untreated potatoes were available for 27 years from 1943 to 1969, inclusive, excluding 1951. The numbers of paired values in each correlation varied in accordance with these limitations for the two variables being compared.

DISCUSSION OF RESULTS

No correlation, at the 5% level of statistical significance, was observed between abundance of the buckthorn aphid on potatoes and the abundance of this aphid on alder-leaved buckthorn at the fall peak or in the preceding year. Nor was the abundance of buckthorn aphids on potatoes correlated with that of fully distended aphid eggs or all aphid eggs on alder-leaved buckthorn in early November, soon after the eggs were deposited, or in mid April before the potatoes were planted (Table 4). Neither was abundance of aphid eggs at either of these times dependent at the 5% level upon that of the buckthorn aphid on

Table 3

oundance of aphid eggs in late fall and in the following early spring by buckthorn buds, 1942 1969, inclusive.

ear	No. sampling Stations	In late fall		In early spring		Percent winter loss of fully distended eggs
		Avg no.eggs per 100 buds	Percent shriveled	Avg no.eggs per 100 buds	Percent shriveled	
42	6	13.3[1]	—	0.4[1]	—	97.0
43	6	31.6[1]	—	11.3[1]	—	64.2
44	7	4.9[1]	—	1.7[1]	—	65.3
45	8	25.9[1]	—	47.0	87.5	77.2
46	7	300.4	79.1	156.0	95.7	89.3
47	7	22.6	52.2	11.8	64.8	61.6
48	7	48.5	55.7	23.1	72.0	70.0
49	8	37.9	54.8	23.6	65.8	52.8
50	8	209.6	52.6	123.3	82.5	78.3
51	8	41.8	81.9	23.0	96.9	90.5
52	8	182.1	52.5	122.6	77.9	68.7
53	8	169.2	64.2	94.0	87.3	80.2
54	8	143.8	62.9	81.9	91.8	87.4
55	8	82.0	73.2	38.3	87.4	78.0
56	8	271.9	72.1	201.4	81.5	50.8
57	8	165.2	77.1	96.4	93.5	83.4
58	8	37.3	60.4	29.1	80.4	54.3
59	8	7.0	23.6	2.9	53.5	74.7
60	8	247.4	60.3	—	—	—
61	8	12.4	67.6	—	—	—
62	8	184.7	59.7	—	—	—
63	8	61.0	60.6	—	—	—
64	8	32.9	34.2	—	—	—
65	8	2.5	14.8	—	—	—
66	9	165.1	49.4	—	—	—
67	9	12.8	34.6	—	—	—
68	9	59.2	71.6	—	—	—
69	8	4.0	40.6	—	—	—
erage	—	104.2[2]	56.5[2]	71.6[3]	81.2[3]	73.1[4]

Fully distended eggs, only; shriveled eggs not counted until spring, 1946.
24-yr. avg.
15-yr. avg.
18-yr. avg.

alder-leaved buckthorn at the fall peak of the preceding year, before the eggs were laid. This was not surprising since the sampling stations which determined fall abundance of the aphid on this primary host were only on Aroostook Farm, while those for aphid eggs on the plant and for buckthorn aphids on potatoes were more widely distributed. Possibly a higher order and level of significance may have occurred had the distribution of sample stations been the same for the buckthorn aphid or aphid eggs on alder-leaved buckthorn and for the aphid on potatoes.

Table 4

Correlations (r values) of average abundance of apterous buckthorn aphids on alder-leave buckthorn in falla, aphid eggs on the plant in late fall and in spring of the year following, at of apterous buckthorn aphid on untreated potatoes at two times in summer, 1942 to 1969.

	Factorb					
Factorb	X_2	X_3	X_4	X_5	X_6	X_7
	In central and southern Aroostook Countya					
X_1	0.321(11)c	0.167(11)	0.041(6)	0.275(6)	-0.124(9)	0.036(9)
			**	*		
X_2			0.809(14)	0.650(14)	0.233(12)	0.259(15)
			**			
X_3			0.867(14)	0.541(14)	0.537(12)	0.486(15)
X_4					0.036(12)	0.065(15)
X_5					0.425(12)	0.423(15)
	In a 300-acre square area near Presque Isle					
X_1	-0.042(11)	0.009(11)	0.386(4)	0.408(4)	-0.124(10)	-0.131(10)
X_2			0.297(12)	0.450(12)	-0.377(22)	-0.052(22)
X_3			0.253(12)	0.525(12)	-0.209(22)	-0.105(22)
X_4					0.277(11)	0.094(11)
X_5					0.244(11)	0.052(11)

a The aphid counts on alder-leaved buckthorn were limited to the same 300-acre area as tha in the lower half of this table.

b Description of factors, below.

c In parenthesis, no. years of paired comparisons used in computing the correlation coefficient

*P=0.05

**P=0.01

Factor	Description
X_1	No. apterous buckthorn aphids at fall peak/100 leaves.
X_2	Total no. aphid eggs/100 buds in early November.
X_3	No. fully distended aphid eggs/100 buds in early November.
X_4	Total no. aphid eggs/100 buds in April of year following.
X_5	No. fully distended aphid eggs/100 buds in April of year following.
X_6	No. apterous buckthorn aphids on 3 leaves (top, middle, bottom)/ potato plant soon after aphid spring migration.
X_7	No. apterous buckthorn aphids on 3 leaves (top, middle, bottom)/ potato plant near summer peak.

The size of the population of all aphid eggs or only the fully distended ones on alder-leaved buckthorn over central and southern Aroostook County in mid April was significantly ($P=0.01$ or $P=0.05$) related in a positive manner to those on the plant at the same stations in early November of the preceding year (Table 4).

Likewise, populations of the buckthorn aphid on untreated potatoes at the end of the aphids' spring migration or near the summer peak tended to be dependent, but not at the 5% level, upon abundance of fully distended aphid eggs on alder-leaved buckthorn in early November of the preceding year (Table 4). The order and level of this significance at both of these times likely would have been higher had the distribution of sampling stations for potatoes and alder-leaved buckthorn been the same in all years.

RELATION OF BUCKTHORN APHID ABUNDANCE ON POTATOES TO THAT OF APHIDS OR APHID EGGS ON ALDER-LEAVED BUCKTHORN IN A RESTRICTED LOCALITY

Comparisons like those in the upper part of Table 4 were made when all sampling stations for determining abundance of apterous buckthorn aphids or aphid eggs on alder-leaved buckthorn and buckthorn aphids on potatoes were situated within a 300-acre square area of Aroostook Farm. The results of these correlations are in the lower part of Table 4.

DISCUSSION OF RESULTS

Neither abundance of buckthorn aphids on potatoes in summer nor that of aphid eggs on alder-leaved buckthorn in mid April or in November of the preceding year was significantly ($P<0.05$) correlated with that of buckthorn aphids on alder-leaved buckthorn at the fall peak of the preceding year.

There was some tendency for abundance of fully distended eggs on alder-leaved buckthorn in mid April to be related to that of all eggs or only fully distended ones on the plant in November of the preceding year; however, the r-values, 0.450 and 0.525, respectively, had a statistical significance of $P>0.1$ but <0.05. Possibly the order and level of significance would have been higher with a larger number of sampling stations of alder-leaved buckthorn on Aroostook Farm.

In this 300-acre area, abundance of the buckthorn aphid on potatoes was not correlated at the 5% level with that of aphid eggs on alder-leaved buckthorn in mid April, before the potatoes were planted, or in early November of the preceding year.

These results indicate that potatoes on Aroostook Farm were infested initially by spring migrants from alder-leaved buckthorn growing in places away from as well as on the farm, since there was a tendency for buckthorn aphid abundance on potatoes to be associated positively with that of fully distended aphid eggs on alder-leaved buckthorn when the egg-sampling stations were widely spread (upper part of Table 4). The results of trapping studies at Presque Isle strongly indicated that the buckthorn aphid flew or moved in air currents for considerable distances.

SUMMARY AND CONCLUSIONS

Studies were conducted to quantify several aspects of the seasonal history of the buckthorn aphid and the importance of alder-leaved buckthorn as a breeding source of those infesting potatoes in northeastern Maine. The results presented and discussed concern chiefly chronological and phenological aspects of the utilization of alder-leaved buckthorn as a primary host of the aphid; the productiveness of spring migrants of the buckthorn aphid on alder-leaved buckthorn; fall population trends of the buckthorn aphid on alder-leaved buckthorn; abundance of aphid eggs on alder-leaved buckthorn in late fall and in early spring of the year following; and the probable utility of surveys of abundance of the buckthorn aphid in autumn and of aphid eggs in late fall and in early spring for formulating advanced estimates of buckthorn aphid abundance on potatoes.

Overwintered eggs of the buckthorn aphid on alder-leaved buckthorn began hatching after mid April. Some of the second generation aphids from these eggs and a high percentage of third generation adults of the aphid on alder-leaved buckthorn matured as spring migrants and moved to secondary hosts, including potatoes. On potatoes, in July some of the descendents of the spring migrants matured as summer dispersal forms, and in early August others matured as fall migrants—males and asexuales—and flew to and reinfested the primary host, following which the maturing, apterous, oviparae were fertilized and eggs were deposited.

The beginning time of the spring migration during the period 1942 to 1969, inclusive, ranged from June 2 to June 27, while that of the fall migration was August 7 to August 20.

On caged twigs of alder-leaved buckthorn, during a study period of 11 years, May 24 was the average date of first maturation of stem mothers of the buckthorn aphid; June 10, June 25, and August 6 were the average dates of first maturation, peak of maturation, and last maturation of the spring migrants. The average number of spring migrants per colony in cages infested by one stem mother ranged by

years from 106 to 480; the average for all 11 years was 323. Several factors had interrelated effects upon colony productiveness, the most important of which appeared to be soil moisture and the proportion of stem-mother progeny maturing as alatae.

The time of the fall peak of abundance of the buckthorn aphid on alder-leaved buckthorn ranged from August 29 to September 12; the average number of apterae per leaf, by years, ranged from 3 to 119, while that for the 11-year period was 47. The first eggs were deposited usually by September 7.

The abundance of aphid eggs on alder-leaved buckthorn varied greatly among years, among locations at either time of year, and between the sampling times of early November and mid April of the following year. The average numbers per 100 buds at all sampling stations were 104 in November and 72 in mid April. An average of 57% of the eggs in November were shriveled, while in mid April it was 81%. The over-winter loss of shriveled eggs averaged 32%, that of fully distended ones was 73%, and that of the total population of eggs was 41%. Indications were that only a small part of the winter loss in total egg population was fully distended eggs; also, that most of the 73% loss of fully distended eggs was due chiefly to shriveling which occurred among eggs fully distended at the time of sampling in early November of the preceding year.

A statistical assessment was made of the relation of abundance of buckthorn aphids on potatoes to that of aphid eggs or of the aphid on alder-leaved buckthorn at three times before the potatoes were planted. The abundance in mid April of all aphid eggs or only the fully distended ones on alder-leaved buckthorn was correlated in a positive manner at the 1% or 5% probability levels with those in November of the preceding year. However, at neither time was abundance of eggs related to buckthorn aphid abundance on the plant in autumn. The sampling stations for buckthorn aphids on alder-leaved buckthorn were fewer and encompassed much smaller areas than those for sampling aphid eggs on the same plant.

There was some tendency, although not significant at the 5% level, for abundance of buckthorn aphids on potatoes to be related in a positive manner to that of fully distended aphid eggs on alder-leaved buckthorn in November and in April but not to that at the fall peak of the aphid on this plant before the eggs were desposited.

Lack of significant relationships from similar comparisons of data from sampling stations restricted to the small area of the experimental farm probably was due to having too few stations available on the farm, and to spring migrants initially colonizing the potatoes coming from alder-leaved buckthorn located away from as well as on that farm.

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