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THE BIOLOGY OF APPLE APHIDS.*

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INTRODUCTION.

Few groups of insects are of greater biological interest than are the aphids. The occurrence of long series of parthenogenetic individuals, interspersed at more or less regular intervals with true sexual forms; the rapidity of reproduction; the presence of both winged and wingless individuals; the precise selection of host plants by the various species, and the remarkable periodic migrations from one host plant to another; together with the evident ecological basis for all of this complexity of behavior, present many interesting problems in the field of insect biology.

The studies upon which this paper is based were first undertaken at the New York Agricultural Experiment Station during the seasons of 1915 and 1916. During the fall and winter of 1916, and the spring of 1917 the project was further developed at Ohio State University. The investagitions were later continued at the Oregon Agricultural Experiment Station. While it has been attempted throughout to investigate the more fundamental phases of the problem, the ultimate aim of the work has been to broaden our knowledge of a group of troublesome and destructive pests. For this reason, and to avoid scattering our efforts over too large a field, the studies have been practically limited to the three most commonly injurious species, the Rosy Apple Aphis, *Anuraphis roseus* Baker; the Apple-Grain Aphis, *Rhopalosiphum prunifoliæ* Fitch; and the Green Apple Aphis, *Aphis pomi* DeGeer.

The writer takes this opportunity to express his indebtedness to Doctor Herbert Osborn, Professor P. J. Parrott, and the late

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Importance and Distribution of the Species.

Aphids occupy a prominent place among the insect pests of our cultivated plants. This is no less true of apple than of other crops. In fact, next to the codling moth, aphids probably present a more generally serious problem to apple growers than does any other insect pest.

Owing to the variety of forms in which these insects occur, the complexity of host relationships, and to the inadequacy of many of the earlier descriptions, much confusion has arisen in the technical names applied to the species. Baker and Turner have made careful studies of the synonomy. The writer has not made a sufficient study of the taxonomy of the group to form an opinion of the value of their conclusions. However, as they have covered the field more thoroughly than any other workers, their conclusions have been accepted in this paper. It is to be hoped that their work will stand, and that further changes and confusion in nomenclature will be avoided.

Of the three species under consideration, the Rosy Apple Aphis is the most serious offender in bearing orchards, because of its characteristic attacks upon the developing fruit clusters, with the resulting deformation of the fruit. A severe infestation of young trees frequently results in a contortion of the shape of the entire tree.

The Green Apple Aphis, while capable of deforming the fruits in a manner similar to the preceding species, tends to confine its attacks to the more rapidly growing portions of the tree, and hence is primarily a pest of young plantings.

The Apple-Grain Aphis is primarily a pest of small grains, and has attracted more attention in that role than it has as a fruit pest. However, in some fruit growing sections it produces extreme infestation of the blossom clusters. Even in this case, however, the lack of toxicity to the apple tissues renders this species of rather minor economic importance.

In their excellent publication on *Aphis pomi*, Baker and Turner (2, p. 957-958) give an interesting review of the history and distribution of this species. It is evident that this aphid has been present in this country from the earliest days of apple growing. The species was undoubtedly introduced from Europe

on nursery stock, and it has spread throughout America coincidentally with the establishment of orchards in new sections.

The species is widely distributed throughout the world. Baker and Turner list it from Japan and Orange Free State, and further state that "it is rather remarkable that this species has not become even more widely spread, since it is typically a nursery species and in the egg state is easily transported on nursery stock." It seems probable to the writer that its distribution is more widespread than published records may indicate, and that close investigation would show it to be present in practically all apple growing sections of the world where the trees are of European origin.

The Apple-Grain Aphis seems to have been introduced coincidentally with the Green Aphis, and, as shown by Davis (5, p. 2), it seems to be equally widespread in North America.

The Rosy Apple Aphis was also introduced into this country early in the history of apple growing. Its spread has evidently been retarded to some extent by its dependence upon the alternate host plant, *Plantago lanceolata*, upon which the continued existence of the species is dependent. The correlation between the spread of this species and of *Plantago lanceolata* has been presented in an interesting way by Matheson (10, p. 721-724).

General Life Histories and Habits of the Species.

The life histories of the three species considered in this study have many points of similarity. All spend the winter as eggs on apple. These eggs hatch as the buds burst in the spring, and the aphids which emerge are apterous, agamic, viviparous females, termed stem mothers.

From these stem mothers there arise the later generations. The generations which follow contain both winged and wingless individuals. Throughout the summer, only viviparous agamic females are produced.

With the approach of fall, males and oviparous females are produced, and the over wintering eggs are deposited.

These characteristics are common to the life histories of the three species, but there are variations in the seasonal activities which will be taken up in the discussions of the several species.

KEY FOR DISTINGUISHING THE SPECIES.

I. Newly hatched nymphs of stem mothers, appearing on the bursting buds in early spring.
   - A. Dark green, more or less covered with whitish pulverulence; several rows of tuberculate spots lengthwise of body; antennæ reaching nearly to bases of cornicles; cornicles relatively long, prominent; scattered infestation on fruit and leaf buds..... *Rosy Aphis*
   - B. Dark green. Antennæ short, reaching to the middle pair of legs; cornicles extremely short, disc-like; scattered infestation on leaf and fruit buds..... *Apple-Grain Aphis*
   - C. Dark green, some individuals varying to lemon yellow; antennæ of intermediate length, not reaching bases of cornicles; cornicles short, conical in shape; typically occurs in dense colonies on water-sprouts and other terminal growths..... *Green Aphis*

II. Mature viviparous females on apple during spring and summer.
   - A. Dark bluish slate color, varying to yellowish brown, usually more or less pulverulent; antennæ reaching to about the middle of the abdomen; cornicles long, somewhat curved, blackish; usually found in tightly curled leaves of fruit or leaf clusters..... *Rosy Aphis*
   - B. Pale yellowish green in color with a series of transverse darker green spots, which together form a broad, deeply serrated, green band extending the full length of the abdomen; antennæ and cornicles relatively short; cornicles green or dusky in color; infesting fruit and leaf clusters, causing little or no curling of the foliage.. *Apple-Grain Aphis*
   - C. Bright green in color, varying to lemon yellow in some individuals; cornicles and cauda black in striking contrast with the bright green body; usually found in dense colonies on the more succulent tissues; moderate to severe curling of the foliage..... *Green Aphis*

III. Female migrants appearing on apple in early summer and in the fall; throughout the summer in the case of the green aphis.
   - A. Antennæ reaching the bases of the cornicles; cornicles long, slender, slightly curved; lateral margins of the abdomen brownish, marked by three large black spots anterior to the cornicles; middorsum of abdomen black. The black markings are intensified in the fall migrants..... *Rosy Aphis*
   - B. Antennæ shorter, not reaching the bases of the cornicles; cornicles short and straight; abdomen soft green, a row of spots on lateral margins anterior to the cornicles; dorsum of abdomen without distinct black markings (or marked with rather indistinct black or dusky transverse bands on the dorsum of the abdomen in the fall migrants)..... *Apple-Grain Aphis*
   - C. Antennæ and cornicles intermediate in length, abdomen unmarked rich green varying to yellow in striking contrast to the black cornicles, cauda, and thorax..... *Green Aphis*

IV. Males first appearing on apple foliage about the time the fruit matures in the fall.
   - A. Winged; abdomen small, somewhat recurved under body, usually entirely black; otherwise resembling female migrant with its long antennæ and cornicles..... *Rosy Aphis*
   - B. Winged; abdomen small, usually entirely black, somewhat recurved under body; otherwise resembling female migrant with its relatively short antennæ and cornicles..... *Apple-Grain Aphis*
   - C. Wingless, much smaller than the female of the species, antennæ reaching the bases of the cornicles; general color brownish, varying to olive; cauda and genitalia black..... *Green Aphis*

V. Oviparous females, appearing on apple from the time the fruit matures until the leaves have dropped; wingless in all species and distinctly more elongate in form than the viviparous females.
   - A. Antennæ reaching nearly to bases of cornicles; color nearly uniform pale yellowish, varying to greenish..... *Rosy Aphis*

B. Antennæ shorter, scarcely reaching beyond middle pair of legs; cornicles somewhat shorter than in preceding species; antennæ, legs and cornicles more dusky.....*Apple-Grain Aphis*
C. Antennæ intermediate in length; color rich green varying to yellow with striking black cornicles and cauda.....*Green Aphis*

The Apple-Grain Aphis.

The eggs of this species are the first to hatch in the spring. The exact date varied with climatic conditions, but generally occurs as the apple buds begin to show green at the tips. Baker and Turner (2, p. 966; 4, p. 312) have found that the eggs of this species may hatch at any time after early January, providing climatic conditions are suitable. Such hatching frequently occurs in the vicinity of Washington, according to these authors. This premature hatching is, of course, ordinarily fatal to the nymphs that emerge. In western New York hatching ordinarily occurs during mid April, and in western Oregon observations show that hatching occurs in early March.

The tiny nymphs migrate to the developing buds where they proceed to suck their nourishment from the developing tissues. These stem mothers mature just as the blossoms begin to show pink. Rapid reproduction immediately after this period greatly increases the numbers of individuals in the colonies, and in Eastern fruit sections extreme infestation may occur. The tendency of this species to attack the blossom clusters, and the conspicuous infestation that frequently results gives this species one of its common names—The Apple-bud Aphis.

With the dropping of the petals, the winged forms begin their migration to the summer host plants. By the time the apples reach the size of marbles the apple is entirely deserted.

During the summer months reproduction is continued by agamic viviparous females on grains and grasses of various kinds, but the species seems to prefer oats when this is available.

With the approach of fall, female migrants fly back to the apple where they give birth to the oviparous females. Following this the winged males are produced, and these also migrate to the apple. As the oviparous females mature they are fertilized by the winged males.

After fertilization, the oviparous females become restless, leave the leaves where they were produced, and crawling down the stems seek places for oviposition. Oviposition takes place

as the leaves are dropping, and continues until the females are destroyed by frosts.

This species has a tendency to secrete the eggs about the buds, or in cracks, crevices, or irregularities of the bark, so that ordinarily they are not readily observed. When infestation is unusually severe however, the eggs may be plastered promiscuously over the stems and twigs of the infested tree in a manner more typical of *Aphis pomi*. The writer observed such colonies of eggs of the Apple-Grain Aphis at Columbus, Ohio, during the winter of 1915-16.

Not all of the aphids of this species migrate to the apple in the fall, and even in the colder sections of the country infestation may continue on grain throughout the winter months.

The Rosy Apple Aphis.

The eggs of this species hatch somewhat later than those of the preceding species, and the apple buds are in a slightly more advanced stage of development. The time between the hatching of these two species varies from one or two days to ten or fifteen days, depending upon climatic conditions.

As with the preceding species, the newly emerged nymphs at once seek the developing buds, where they are to spend their lives. The stem mothers mature as the blossoms are in the pink stage, at which time many of the aphids of this species will be found protected by the curling of the infested foliage.

The dropping of the petals marks the period of maturing of the second generation, and there is a great increase in the numbers of this species. These aphids tend to remain within the curled leaves of the parent colony until forced out by over crowding. When this occurs there is a marked increase in the centers of infestation in the tree.

With the development of the third generation winged forms appear. During mid June this species reaches its maximum abundance on apple, and after July first the decrease is rapid. The apple is practically deserted by the end of July, although isolated colonies may be found after this date.

During the summer months reproduction is continued by agamic viviparous females on the narrow leaf plantain.

With the approach of fall, migrants are produced which renew the infestation of the apple. As with the preceding species, these migrants are first mostly females which produce the oviparous females on apple, later the males predominate on

plantain. These fly back to the apple and fertilize the oviparous females.

This species secretes its eggs in crevices of the bark of the branches or even the trunk of the tree. Hence they are difficult to observe in any numbers. Oviposition takes place as the leaves are dropping from the trees, and continues until frost destroys the females.

In the colder sections of the country this species has not been observed to overwinter on plantain, but in the mild climate of western Oregon, overwintering on plantain as well as apple is the rule.

The Green Apple Aphis.

This species is the last to hatch. The exact date of hatching varies in different localities, but the buds are usually well advanced at the time of hatching.

As with the other species the newly hatched nymphs crawl to the developing buds, where they obtain their nourishment. The eggs of this species are clustered in immense numbers on the terminal growths of the infested trees. Accordingly, the initial infestation occurs in dense isolated colonies on the terminals. With the development of the winged forms the infestation is scattered, and colonies arise throughout the orchards.

This species spends the entire summer upon apple. With the approach of fall, males and oviparous females are produced. Oviposition begins with this species much earlier than in the case of the other two species, and in early September, about the time the fruit matures, the first eggs may be found. Egg laying continues until the females are killed by cold weather.

Seasonal Successions of the Species.

Observations at Geneva, New York, (12, p. 37–39) showed that the relative abundance of the three species of aphids concerned in these studies passes through a seasonal cycle or succession that seems to be fundamentally constant in all of the sections in which these studies have been continued.

Activities begin with the hatching of the Apple-Grain Aphis just as the first green shows at the tips of the developing apple buds. This is followed by the hatching of the Rosy Aphis. The Green Aphis is the last to hatch, and the apple buds are usually well advanced by this time.

The "stem-mothers" of the Apple-Grain Aphis begin to give birth to living young just as the apple blossoms are showing pink. Rapid reproduction immediately after this period soon greatly increases the numbers of this species, and in regions where it commonly infests apple it rapidly becomes by far the most abundant species.

Very shortly after the maturing of the stem-mothers of the Apple-Grain Aphis, those of the Rosy Aphis and the Green Aphis mature. The dropping of the petals marks the time of maturing of the second generation of the Rosy Aphis, and about this time the Apple-Grain Aphis begins its migration to its summer host plants. While the Apple-Grain Aphis is becoming less abundant because of migration to the summer food plants, reproduction by the second generation of the Rosy Aphis greatly increases the numbers of this species, so that during the interval extending from about the middle to the last of June the Rosy Aphis is the more abundant of the two species.

After July first, migration of the Rosy Aphis is rapid and by the latter part of the month this species has practically deserted the apple. While the Rosy Aphis is decreasing in numbers, the Green Aphis is establishing new centers of infestation in the orchard and, under favorable conditions, the species increases rapidly. By the end of July, the Green Aphis is the only one of the three species remaining on apple, and this condition continues throughout the rest of the summer.

With the approach of fall, the males and oviparous females of the Green Aphis are produced and eggs usually appear as the winter apples ripen. About the time the fruit matures, winged female migrants of the Rosy Aphis and the Apple-Grain Aphis return to apple where they produce the oviparous forms. Later the winged males of these two species migrate to apple, where they fertilize the oviparous females. Eggs are deposited as the leaves are dropping.

Regional Variations in Behavior.

These studies, made in districts so widely separated and so distinctly different in climate, have brought out several interesting facts relative to the regional variations in the behavior of apple aphides. A report (6) on this phase of the work has been published in the *Journal of Economic Entomology*.

Relative Abundance of the Species.

Probably the first difference to be noted is the relative abundance of the several species in the two regions.

In western New York the Apple-Grain Aphis is normally the most abundant of the three species. Although the actual injury from this species is slight because of its low toxicity upon apple, the species, nevertheless, produces a heavy and conspicuous infestation, especially upon the blossom clusters, where it occurs in enormous numbers.

In the fruit districts of the Willamette Valley, Oregon, this species is rare upon apple, and each spring a thorough search has been necessary in order to find even a single colony in any of the orchards in which examinations were made. Apparently this same condition applies in California (17, p. 94). However, the species occurs more or less commonly on grains and grasses in both Oregon and California. This seems to indicate that the species is not conspicuous as an apple pest in regions where the climate permits wintering on grains and grasses. This accords with observations by Davis (5, p. 10), who finds that in the southern part of the United States this species may winter entirely upon grains and grasses, no eggs being deposited upon apple.

Next to the Apple-Grain Aphis, the Green Aphis is the most abundant in apple orchards of western New York. This species increases in abundance during midsummer and young plantings as well as the more succulent portions of mature trees frequently suffer severe injury.

In western Oregon, the Green Aphis is by no means uncommon, but severe injury from this species is not of frequent occurrence. The greatest abundance occurs in early summer; later in the season, infestation usually subsides to a minimum.

The Rosy Aphis is by far the most common species in western Oregon, while in western New York, it is ordinarily the least numerous of the three. Because of the high toxicity of this species upon apple, and because of its habit of malforming the fruit, this is a serious pest wherever it occurs. The great abundance of this species under normal conditions in western Oregon ranks this insect with the codling moth as one of the major pests of the apple.

Hatching.

Spring advances rapidly in western New York with a proportionally rapid hatching of the eggs of the aphids under consideration. The gradual approach of spring in western Oregon is accompanied by a long hatching period. There is a corresponding and even more striking prolongation of the intervals between the hatching periods of the several species.

During the spring of 1916, the Apple-Grain Aphis began hatching in the locality of Geneva, N. Y., on April 22; the Green Aphis on April 26, a difference of four days. The Rosy Aphis was intermediate between the two, but there was so little difference in time that the hatching of the first two species appeared to occur almost simultaneously. Baker and Turner (2, p. 966), working at Vienna, Virginia in 1915, observed a difference of eleven days between the beginning of the hatching period of the Apple-Grain Aphis and that of the Green Aphis Peterson (13, p. 366), studying these species in New Jersey in 1919 observed a difference of fifteen days between the beginning of the hatching periods.

In western Oregon, the hatching of the Green Aphis begins from nine to fifteen days later than the Rosy Aphis. The extreme scarcity of the Apple-Grain Aphis in the orchards under observation here has made it impossible to determine the exact date of hatching; however, it occurs certainly from ten to fifteen days prior to the hatching of the Rosy Aphis. This makes an interval of from nineteen to thirty days between the hatching of the Apple-Grain Aphis and the Green Aphis.

The length of the hatching period shows a similar regional variation. Baker and Turner record a period of seventeen days between the hatching of the first and last eggs of the Green Aphis in Virginia. At Geneva, N. Y., (12, p. 37) in 1916, hatching began on April 26 and was completed by May 2, a period of six days. At Corvallis, Oregon, in 1921, the eggs upon one tree under observation began hatching March 20, and continued to hatch until April 18, a period of twenty-nine days.

Summer Activities.

The most pronounced regional difference noted in the behavior of these aphids during the summer months occurred in the time of appearance of the winged forms.

At Geneva, N. Y., in 1916, the second generation of the Apple-Grain Aphis consisted entirely of winged individuals, and the species quickly disappeared from the apple. Baker and Turner (4, p. 314) reported 89.1 per cent of the second generation winged at Vienna, Virginia in 1915. At Corvallis, Oregon, in 1919 the winged forms were very few in the second generation. They became predominant in the fourth generation.

The Rosy Aphis also shows a tendency to delay the production of winged forms, which accounts to some extent for the more serious nature of the pest under western Oregon conditions.

The Green Aphis shows a tendency in this same direction under Oregon conditions. Baker and Turner (2, p. 977) found that "in the second generation, the winged form outnumbers the wingless" in Virginia. During the spring of 1916, the writer observed colonies at Geneva, N. Y. in which at least ninety per cent of the second generation developed wings. This high percentage of winged forms in the second generation seems characteristic of the Green Aphis under Eastern climatic conditions. The scarcity of winged forms in the later generations is equally characteristic.

Observations in western Oregon show that there is much less tendency to thus segregate the development of winged forms. In this section, winged forms are usually not numerous in the second generation, but are much more common in the later generations than is the case in the East.

Winter Activities.

The hibernation of *Aphis pomi* as observed in Oregon shows no conspicuous variation from the behavior of the species elsewhere.

The Apple-Grain Aphis in western Oregon winters principally as viviparous females on grains and grasses, where growth and reproduction take place during the winter months when the temperature permits. Comparatively few migrants appear on apple in the fall, and hibernation in the egg stage on apple is uncommon.

The Rosy Aphis in western Oregon produces numerous migrants which return to the apple in the fall, and are normally sufficient to produce a severe infestation. However, in this section, only a portion of the plantain forms become winged in the fall. A considerable percentage remain on plantain through-

out the winter months. Reproduction and growth continue during the winter, although reduced to a very low rate. Specimens born in the insectary at Corvallis, November 27, matured February 10—a developmental period of seventy-four days.

Wintering on plantain is apparently normal with this species in the climate of the Willamette Valley, for infestation has been observed in the field throughout every winter from 1917 to 1921. During the winter of 1919–20, the Rosy Aphis on plantain in the field, where protected by snow, withstood a temperature of thirteen degrees below zero. Where there is no protection the species succumbs to a much less rigorous temperature.

With the approach of spring, the overwintering forms on plantain become more active, and winged forms are produced to spread the infestation.

Economic Aspects of Regional Variations.

The effects of regional variations in the behavior of apple aphids are of direct significance to the commercial fruit grower. The more severe injury to apple orchards normally resulting from attacks of the Rosy Aphis in western Oregon, makes the control of this pest in this section even more imperative than in regions where injury is less pronounced.

As a rule, the Green Aphis is less injurious in orchards of western Oregon than in New York fruit districts, and in normal seasons causes the western Oregon orchardist little concern.

The Apple-Grain Aphis is of no importance as an apple pest in western Oregon.

By wintering on plantain, the Rosy Aphis becomes independent of apple in western Oregon. The continuous breeding on plantain produces a source of supply of these insects, which serve as a reservoir for the species, and which accounts in part for the greater infestation of apples in this region. Any campaign which might be undertaken for the actual eradication of the species from western Oregon would have to be waged against the plantain forms as well as the infestation on apple.

In western Oregon the greater capacity of the Green Aphis for dispersal in the later generations would probably greatly interfere with the control of this species during seasons of unusual abundance.

The most unfortunate effect, however, of the regional variations noted is the failure of the standard "delayed dormant" treatment to successfully control the rosy aphis in western

Oregon in spite of the success with which this treatment is applied in the East. The unsatisfactory results which are attending the use of the "delayed dormant" spray of nicotine suffate for the control of this species in the Willamette Valley are probably due to the long-drawn-out hatching period more than to any other factor.

Feeding Habits.

As soon as the young aphids emerge from the eggs, they migrate to the developing buds. Ordinarily the nymphs may be found on the buds within twenty-four hours after hatching, but occasionally during inclement weather, young nymphs may be found secreted about the bases of the buds, apparently in a more or less inactive condition until weather conditions become more favorable.

With the separation of the leaves in the developing buds, the tiny aphids creep downward about the bases of the out-pushing foliage. Here these creatures are very well sheltered from wind and rain, as well as from sprays that may be applied to the trees.

As the developing leaves take form, the aphids assume positions on the under surfaces. As the numbers of aphids increase it may be noted that the tendency is to feed upon the midrib and main tracheal branches of the leaves, and the aphids will be found arranged along the main veins of the leaves. This is especially true of the rosy aphis and the oat aphis, both of which tend to remain upon mature leaves, where the colonies were originally established. In the case of the green aphis the tendency is to follow the growing tips of the plant, and thus feed upon the more succulent tissues. The tender, elongating stem as well as the foliage often becomes coated with the insects.

The young nymphs of all of the species have more or less tendency to migrate, especially when the parent colonies are overcrowded. These migrating nymphs usually seek the young, tender, more succulent leaves, where they establish new colonies.

Ecological Studies.

The evident suspectibility of aphids to climatic influence, and the unusual degree to which the behavior of these insects is directly regulated by environmental conditions, make ecological studies of this group of especial interest and value.

General Influence of Environment.

The activities of aphids seem to an unusual extent to be directly regulated by environmental influence. The number of generations occurring during the season seems to be entirely dependent upon whether or not conditions are favorable for the rapid development of the insects. The time of production of winged forms seems to be dependent upon conditions of climate and the stage of development of the host plants. The development of gamogenetic forms seems to be dependent upon ecological conditions, and when coditions are suitable for the continued parthenogenetic reproduction, their production may be reduced or entirely omitted.

Undoubtedly, the response of these aphids to the varying conditions of environment is directed by the inherent tendencies of the species. The extent to which the seasonal cycles of aphides are hereditary, and the degree to which they are influenced by environmental factors has not been determined. Some workers, Uichanco (19), Tannreuther (18), place great emphasis on the hereditary influence. Our observations upon the species under consideration indicate that the inherent tendencies of the species directs the nature of the response, but the stimulus is supplied by environmental phenomena. Thus the gamogenetic forms are produced in all generations which survive until fall and which are influenced by appropriate environmental conditions. In the East the second generation of *Rhopalosiphum prunifoliæ* usually consists predominantly of winged migrants. Under the different environmental conditions of western Oregon, winged forms do not predominate until the fourth generation. This same tendency was shown in this species grown under greenhouse conditions at Geneva, New York; indicating that the time of production of winged forms is a reaction to environmental influence rather than an incident in a definitely inherited seasonal cycle.

Besides the effects of the physical environment, aphids are profoundly influenced by their associates and enemies. These have chiefly to do with the protection or destruction of the forms present. Attacks of natural enemies during early summer materially hastens the vacation of apple by the migratory species. These relations of the aphids to their organic environment are probably no less complex, and are equally as interesting as the reactions to the physical environment.

Analysis of the Environment of Apple Aphides.

In studying the environmental influences affecting plants, Livingston (9, p. 421) emphasizes the fact that while environmental conditions may be separated into groups, the different kinds of conditions do not influence the organism separately, but the entire complex of conditions acts as a unit in its influence upon the organism. While this is undoubtedly true, it is nevertheless possible and profitable to analyze the environmental complex, and to study the component factors, much as a chemist studies the elements which unite to form a chemical compound.

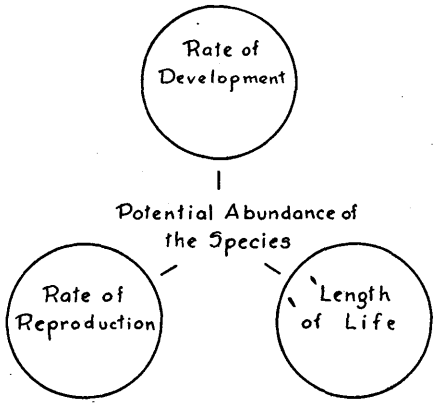

Fig. a.

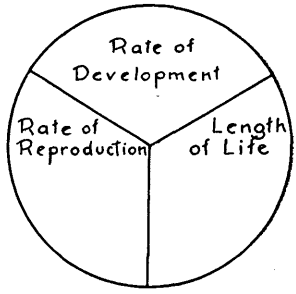

Fig. b.

In order to make such an analysis of the environmental complex, it seems desirable first of all to consider the life processes of the organism which are influenced by the environmental factors considered. In the case of our three species of apple aphids, the potential abundance of the organisms may be regarded as depending upon three major phenomena: length of life, rate of reproduction, and rate of development. This may be represented diagramatically as in Fig. a, and may be condensed into Fig. b.

In studying the environment, it will be found that there are many interrelations between the several environmental factors themselves as well as the direct influences of the various factors upon the organisms. These interrelations between the environmental factors result in many indirect influences upon the organism, which may be less obvious, but are often of even greater importance than the direct influence of any given factor.

Thus if we consider the factor of Temperature, we find that the temperature of the atmosphere at any time is influenced by a number of other factors. This may be represented diagramatically:

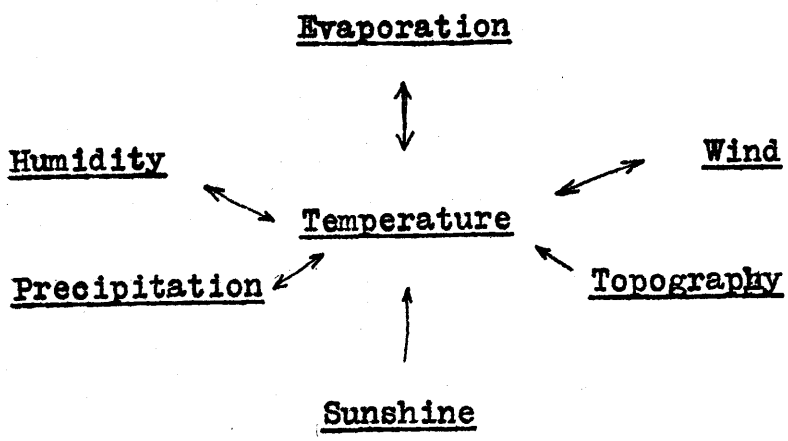

Fig. c.

It will be noted—as indicated by the arrows in the diagram—that in several instances the influence is reversable, the factors having reciprocal effects upon each other. It is readily realized that a complete grouping of the physical factors of the environment would show an almost endless number of such interfactoral influences. It has been attempted to show such an arrangement diagramatically in Fig. d.

It will be noted that a number of factors which are important in their influence upon the environment, have little or no direct influence upon the activities of the organism.

The nature and degree of the response to any influence of the environment is determined and directed by the inherent tendencies of the organism. Hence, the influences of the environmental factors may be regarded as acting through the inherent tendencies of the organism as shown in the diagram.

The diagram is not to be considered as attempting to show exhaustively all the interrelations of the factors of the environment. Other factors may be added and changes will suggest themselves to the reader. The diagram does, however, indicate in a graphic and interesting way the extreme complexity and the great delicacy of the environmental relations.

Studies of Certain Environmental Factors.

It was attempted to study in detail the influence of some of the more important environmental factors. While these studies are not exhaustive, data have been collected which are interesting. In order to concentrate the study, most of these investigations have been centered upon *Aphis pomi.*

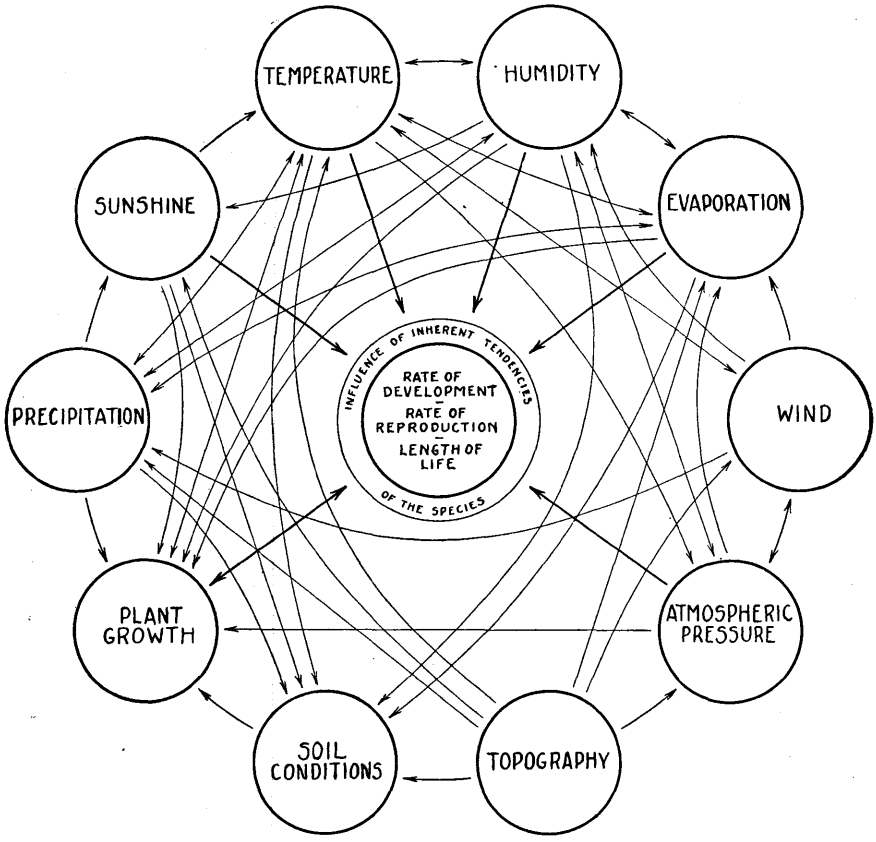

Fig. d.

A. Evaporation.

During the summer of 1919 and again in 1920, experiments were conducted in the hope that the measurement of atmospheric evaporation—combining, as it does, effects of both temperature and humidity—might, under normal outdoor conditions, give a fairly accurate index to the rate of metabolism of our apple aphides.

This work has been entirely in the nature of a field study and no attempt was made to modify or control the conditions of temperature or moisture.

The experimental plot was located on the college farm at Corvallis, Oregon, about one mile from the Agricultural Building, and had an elevation of approximately 225 feet above sea level. This plot consisted of one and two-year-old Greening apple trees planted in two rows about four feet apart with the trees about three feet apart in the rows. To the westward about sixty to seventy-five feet distant there was a dense growth of alders along the banks of Oak Creek. These trees, being some thirty-five feet in height, served to break the force of the strong, westerly "sea-breezes" prevalent during the summer months.

As the aphid eggs hatched, numbers of the nymphs were transferred to suitable buds on the experimental trees, and here allowed to mature. To obtain nymphs of the later generations, a number of adults would be placed on a suitable aphid-free leaf cluster. The following day these adults were removed, and the nymphs born during the twenty-four-hour-period were allowed to remain. These nymphs were permitted to mature in order to obtain the length of the developmental period. The developmental period was reckoned from the day after birth till the day of the appearance of the first young, inclusive.

The trees upon which the experiments were being conducted were protected by a special type of cage. This consisted of a cylinder of galvanized wire cloth, open at one end. To the open end of this cage was attached a cheesecloth skirt. The cage was inverted over the tree, and held in position at the proper height by means of a stake set nearby. The cheesecloth skirt was gathered about the trunk of the tree and tied with a cord. A band of cotton batting placed at the proper height on the tree rendered a perfect fit between the cloth skirt and the tree, and prevented binding of the trunk from the tie-cord. This type of cage is easily removed for examination of the aphids; is as readily replaced, and has proved quite satisfactory for this work.

The evaporation records were obtained by means of a "non-absorbing" evaporimeter or atmometer similar to instruments used in many evaporation studies by various workers during recent years. Standardized, spherical, porous, porcelain cups were obtained from the "Plant World," and results

as here given should be comparable with results obtained elsewhere by means of similar instruments.

Observations were made daily at 9:30 A. M. The amount of evaporation was determined by filling the evaporimeter at this time. A graduated pipette was used and readings were made to tenths of c.c's.

TABLE I.

Relation of Evaporation to Rate of Development of *Aphis Pomi* DeGeer. Summary of Data for 1919 and 1920.

Length of Developmental Period Days.	Average Total Evaporation for Period, c. c.	Average Daily Evaporation c. c.	Number of Records.
36	453.9	12.6	1
29	342.5	11.8	1
24	392.5	16.4	1
22	406.6	18.5	1
19	412.6	21.7	1
18	408.0	22.7	2
16	294.0	18.4	1
15	265.3	17.7	6
14	236.5	16.9	10
13	256.9	19.7	10
12	265.8	22.1	8
11	266.2	24.2	15
10	305.2	30.5	14
9	284.2	31.6	14
8	252.4	31.5	5
7	262.3	37.5	2

A study of the data presented in Table I shows that there is a general correlation between the rate of evaporation and the rate of development of *Aphis pomi*. On the whole, a high rate of evaporation was accompanied by a rapid development of the aphids; and a low rate of evaporation, by a comparatively slow development of the insects. While this correlation seems to be true in a general way, there is considerable variation from the mean.

These results show that under the condition of this investigation, evaporation, as registered by the standard evaporimeter used, is not a satisfactory measure of aphis metabolism. This condition apparently results from the fact that the combination of factors—humidity, temperature, wind, etc.—which influence evaporation, affect evaporation from the standard porous cup in a manner which is not closely comparable to its effect upon the metabolism of *Aphis pomi.*

As pointed out by Livingston (8, p. 127) the rates of evaporation from different types of evaporimeters under any given complex of atmospheric conditions are not comparable. It is, therefore, not surprising that evaporation from an instrument as used in these experiments would not give an accurate index of the effects of the atmospheric conditions upon aphis metabolism. It is possible that an evaporimeter more closely simulating the conditions of the aphid body might give a closer correlation between atmospheric evaporation and insect metabolism.

B. Temperature.

During the summers of 1920 and 1921 experiments with *Aphis pomi* were continued, and accurate records of temperature were kept in an attempt to learn the influence of this factor in the development of the species.

In general the procedure was similar to that described under the study of Evaporation. The temperature records were obtained by means of a Tycos Dial Type Mercury Recording Thermometer, manufactured by Taylor Instrument Companies, Rochester, New York. The daily mean temperature was determined by reading the temperature on the charts for each half hour, and averaging these forty-eight readings. The mean temperature for any given period of days was obtained by averaging the daily mean temperatures.

The actual mean temperature of the developmental periods of the several series were first plotted on a graph. It was found that those points lie approximately along a hyperbolic curve having the formula* $x = \frac{a}{y-b}$. This formula may be expressed: length of developmental period in days $= \frac{180}{\text{Temperature in degrees F} - 41}$

*The writer is indebted to Professor E. B. Beaty of the Department of Mathematics, Oregon Agricultural College, for the computation of the formula for this curve.

If the curve thus plotted be extended it will be found that as the temperature is lowered, the development of the aphids becomes less rapid, until, at a temperature of 41°F or less, development ceases entirely. In other words, only temperatures above 41°F are "effective" (16, p. 114, 116) in the development of *Aphis pomi*. By subtracting all temperatures of 41° or less, and by computing the mean of the remaining temperature readings, the mean effective temperatures were obtained.

TABLE II.

Relation of Temperature and Evaporation to Rate of Development of *Aphis Pomi* DeGeer, 1920.

Aphid Series Number	Date of Birth	Date First Young Produced	Developmental Period, Days	Total Evaporation, c. c.	Average Daily Evaporation, c.c.	Mean Temperature, ° F.	Duration Effective Temperature, Days	Mean Effective Temperature, ° F.
1	Mar. 28	May 3	36	453.9	12.6	45.1	23.3	49.7
2	May 3	May 16	13	312.4	24.0	52.6	10.4	57.4
3	May 13	June 1	19	412.6	21.7	51.3	14.5	56.5
4	May 16	June 3	18	406.0	22.6	51.6	13.9	56.5
5	May 31	June 12	12	249.1	20.8	56.8	11.6	57.3
6	June 2	June 16	14	231.5	16.5	55.9	13.3	56.2
7	June 9	June 21	12	216.8	18.1	57.5	11.4	58.1
8	June 14	June 27	13	324.0	24.9	57.5	12.2	59.6
9	June 17	June 27	10	274.7	27.5	58.2	9.5	60.0
10	June 21	June 30	9	238.1	26.5	59.5	8.6	61.8
11	June 27	July 6	9	265.3	29.5	64.5	8.7	65.7
12	June 30	July 9	9	302.7	33.6	63.8	8.7	63.9
13	July 7	July 18	11	218.8	19.9	61.1	10.9	61.3
14	July 9	July 18	9	166.7	18.5	61.0	9.0	61.1
15	July 18	July 28	10	273.6	27.4	62.5	9.8	62.7
16	July 28	Aug. 6	9	226.1	25.1	64.5	8.0	66.1
17	Aug. 12	Aug. 23	11	368.7	33.5	63.8	10.7	64.5
18	Aug. 20	Sept. 2	13	298.6	22.9	59.3	12.0	60.2
19	Aug. 20	Sept. 11	22	406.6	18.5	57.6	20.5	58.6
20	Aug. 23	Sept. 2	10	212.9	21.3	57.5	9.0	59.8

By subtracting from the developmental period, the time during which the temperature was 41° or less, the duration of effective temperature was determined.

In general, the records as plotted on the graph do not coincide exactly with the theoretical curve of development. This is no doubt due largely to the fact that observations of the aphids were made only once daily, which would tend to cause a lagging in the recorded rate of development of the insects. Toward the end of the growing season, the development of the aphids in some of the series was retarded to some extent by the

lack of succulence of the plant tissues, in spite of the fact that the most succulent growing tips were selected for rearing the aphids. The extent to which development may be retarded by such a limiting factor is shown by series 19 (Table II), which was reared upon mature foliage. For its development this series required a period of effective temperature of 20.5 days although accompanied by a mean effective temperature (58.6°) high enough to permit development in half the time consumed. This effect of the growth of the plant upon the development of *Aphis pomi* was also noted by Baker and Turner (2, p. 982-984) who regard it as a food relationship. It is evident that the condition of the foliage of the food plant frequently constitutes a limiting factor of considerable importance to the activities of *Aphis pomi*.

The Reproduction of Aphis pomi.

Influence of Age upon the Number of Nymphs Produced.

During the studies of these aphides it has been noticed that for a period immediately after maturity, the number of nymphs produced each day was usually considerably larger than was the case later in the life of the adult. Toward the end of the life of the aphid, the number of nymphs produced was still further reduced, and finally, immediately preceding death, several days would frequently elapse with no reproduction.

In Table III is shown the reproduction records of a number of lots of Aphis pomi during the summer of 1921. These lots were selected because of the fact that at least some individuals in each lot completed their normal period of life. The periods covered by these lots extended through most of the summer, thus obviating the effects of temperature and other factors.

It will be noted that the daily reproduction continued at quite an uniform rate for a period of sixteen days. During this period the average number of nymphs produced per adult per day was 3.23. The highest average for the series for any day was 3.87; the lowest 2.76. This was followed by a period of four days during which an average of 2.29 nymphs per day. The highest average for this period was 2.51; the lowest 2.13. During the next period of three days a daily average of 1.55 nymphs per adult was produced. In this period the highest average was 1.66; the lowest 1.47. Following this, beyond the twenty-third day of adult life, a daily average of less than one

TABLE III.

The Effect of Age upon the Number of Nymphs Produced by *Aphis pomi*.

Age after Maturity Days	1		2		3		4		5		6		7		8		9		10		11	
	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A
Lot No. 4	24	12	30	10	27	8	34	7	22	7	7	7	17	6	21	6	21	6	17	6	17	6
5	11	6	22	6	5	5	11	5	21	5	21	5	15	5	15	5	24	5	19	5	33	5
6	1	3	4	3	9	2	9	2	2	2	5	2	6	2	5	2	11	2	10	3	19	3
10	40	10	44	10	20	10	33	9	22	8	29	8	27	8	26	8	28	8	30	8	30	8
11	72	15	57	15	29	10	21	8	55	8	28	8	29	8	25	7	21	7	15	7	25	6
12	46	7	30	7	30	7	48	7	27	7	18	7	26	7	26	7	23	7	22	7	24	7
15	25	10	40	10	40	10	44	10	46	10	37	9	37	9	41	9	38	9	38	9	36	9
16	30	10	45	10	43	10	50	10	28	10	29	10	33	10	33	10	38	10	27	10	36	10
18	66	10	37	11	36	11	34	11	43	11	47	11	37	11	36	11	35	11	34	11	52	11
31	40	12	37	12	38	12	41	12	42	12	19	12	32	12	25	12	38	12	39	12	32	11
32	16	13	36	14	36	14	56	14	31	10	20	10	26	10	13	10	26	10	26	10	30	10
33	30	10	60	10	41	11	19	11	36	11	17	11	26	11	26	11	33	11	28	11	51	11
36	12	10	33	10	34	10	10	8	21	8	21	8	20	8	19	8	27	8	23	8	21	8
Totals.....	413	128	475	128	388	120	410	114	396	109	298	108	331	107	311	106	363	106	328	107	406	105
Av. per Adult.....	3.23		3.71		3.23		3.60		3.63		2.76		3.09		2.93		3.42		3.07		3.87	

TABLE III—Continued.

Age after Maturity Days	12		13		14		15		16		17		18		19		20		21		22	
	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A
Lot No. 4	25	6	17	6	26	6	30	6	38	6	26	6	16	6	15	6	6	5	7	5	6	5
5	25	5	36	5	21	5	17	4	18	4	8	4	4	3	5	3	5	3	5	3	5	3
6	10	3	11	3	14	3	13	3	7	3	3	3	3	3	3	3	7	3	2	3	1	3
10	16	8	20	8	20	8	35	8	29	8	26	8	24	8	15	7	17	7	17	7	14	7
11	25	6	26	6	30	6	18	6	21	5	16	5	18	5	18	5	16	5	10	5	14	5
12	18	7	24	7	27	7	27	7	22	7	14	7	31	7	17	7	24	7	7	7	6	6
15	34	9	13	9	14	9	28	9	18	8	9	6	18	6	9	6	0	1	0	1		
16	13	10	12	10	11	10	20	8	19	9	28	9	20	9	30	7	30	7	13	7	14	7
18	45	11	23	10	30	7	39	7	35	7	34	7	12	7	13	7	18	7	2	7	6	7
31	32	11	35	9	15	8	21	8	18	8	18	8	8	8	11	8	14	8	17	8	5	7
32	25	10	46	10	34	10	31	10	19	10	19	10	17	10	19	10	19	10	21	10	20	10
33	34	11	40	11	26	11	27	11	19	11	21	11	21	11	23	11	22	11	20	11	19	11
36	27	8	28	8	13	8	18	8	23	8	9	8	13	8	9	8	9	8	15	8	11	8
Totals.....	329	105	331	102	281	98	324	95	286	94	231	92	205	91	187	88	187	82	136	82	121	79
Av. per Adult.....	3.13		3.25		2.87		3.41		3.04		2.51		2.25		2.13		2.28		1.66		1.53	

In Table III, "A" indicates the number of adults present in each lot; "N" indicates number of nymphs produced.

TABLE III—Continued.

Age after Maturity Days	23		24		25		26		27		28		29		30		31		32		33	
	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A
Lot No. 4	5	5	5	5	0	5	0	4	1	4	0	3	0	1	0	1						
5	2	3	0	3	1	3	2	3	0	3	1	3	0	3	0	2	0	2	0	1	0	1
6	9	3	3	3	3	3	5	3	3	3	2	3	2	3	4	3	0	2	0	2	0	2
10	16	7	6	7	2	7	2	7	6	7	6	7	2	7	1	7	1	7	0	7	0	6
11	7	5	8	5	5	5	5	5	2	5	2	5	6	5	6	5	6	5	0	5	0	5
12	3	6	1	6	0	6	0	4	1	4	0	4	0	4	0	4	0	3	0	2		
15																						
16	14	7	4	7	7	7	7	7	7	7	16	7	2	7	0	7	0	7	0	7	0	7
18	2	7	3	7	2	7	1	7	0	7	2	7	0	7	0	7	0	4	0	4	0	3
31	5	7	3	7	8	7	5	7	3	7	3	7	2	7	2	7	1	7	5	7	3	7
32	17	10	17	10	18	10	16	10	19	10	15	10	7	10	9	10	9	10	8	10	3	10
33	19	11	14	11	15	11	8	11	11	10	9	10	8	10	3	8	4	8	2	6	2	5
36	17	8	7	8	9	8	8	8	9	8	4	8	6	8	2	8	2	8	2	7		
Totals.....	116	79	71	79	70	79	59	76	62	75	60	74	35	72	27	69	23	63	17	58	8	46
Av. per Adult.....	1.47		0.90		0.89		0.77		0.83		0.81		0.49		0.39		0.37		0.29		0.17	

TABLE III—Continued.

Age after Maturity Days	34		35		36		37		38		39		40		41		42		43		44	
	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A
Lot No. 4																						
5																						
6	0	1	0	1	0	1	0	1	0	1	0	1										
10	0	6	0	4	1	4	0	4	0	4	0	4										
11	4	5	0	3	1	3	1	3	0	2	0	1	0	1	0	1	0	1	0	1		
12																						
15																						
16	0	7	0	6	0	6	0	3	0	1												
18	0	1	0	1																		
31	1	7	0	7																		
32	0	10	0	10	0	10																
33	2	5																				
36																						
Totals.....	7	42	0	32	2	24	1	11	0	8	0	6	0	1	0	1	0	1	0	1		
Av. per Adult.....	0.17		0		0.08		0.09		0		0		0		0		0		0			

In Table III, "A" indicates the number of adults present in each lot; "N" indicates number of nymphs produced.

nymph per adult was produced. After this time the number of nymphs grew steadily less until reproduction ceased entirely.

The longest reproduction period occurred in the case of Lot. No. 11, which extended over a period of 37 days. Incidentally the record for longevity also occurred in this lot—one individual living for a period of 43 days after maturity.

The Influence of Environmental Factors upon the Rate of Reproduction.

The number of nymphs which can be produced in a day by one female is distinctly limited by her inherent capacity for reproduction. Thirty-six nymphs produced by five adults, an average of 7.2 per adult is the highest record for these studies.

Matheson (10, p. 700) found the greatest number of nymphs to be produced by one female to be thirteen, and this occurred in only one instance throughout his studies. Baker and Turner (2, p. 973) give 16+ as the largest number of nymphs produced by one female in one day. However, such cases are exceptional and the capacity of the average female is much less. Because of this inherent limitation of the number of nymphs produced, there is considerably less possibility for the rate of reproduction to be influenced by environmental factors.

The results of these investigations indicate that temperature is influential in determining the number of nymphs produced, but it is evident that other factors such as humidity, evaporation, and sunshine are of direct importance. It has been noted that a bright warm day, following a period of cool cloudy weather, would be accompanied by a considerable increase in the number of nymphs produced. However, to determine the exact relation of environmental influence upon the rate of reproduction, will require further study with observation of as many factors of the environment as possible.

Effects of Environment upon Longevity.

The environment had an important effect upon the length of life of the apple aphids. Periods of cold, rainy weather in early spring destroys many of the young nymphs before they reach maturity. On the other hand, unusually high temperatures during late summer, apparently hastened the metabolism of the insects excessively, shortening the lives of the individuals affected. Individuals feeding upon very hard, mature foliage do not live as long after maturity as do those on more succulent foliage.

Effects of Aphids upon Growth of Apples.

The most serious injury resulting from aphid infestation is the destruction of fruits by the direct attack of these insects. The several species show important differences in their power of injury to the fruit and foliage. The Rosy Aphis is the chief offender. Its attack produces a marked and characteristic contortion of the tissues attacked. It has frequently been observed that a single stem mother is sufficient to produce the characteristic curling of an apple leaf upon which it is feeding. Frequency with which this species attacks the developing fruit clusters, and its marked toxicity to the tissues combine to make the Rosy Aphis a serious orchard pest.

The Green Aphis seems to be quite as capable as the preceding species in producing injury to the infested fruit clusters. However the Green Aphis tends to feed upon the more succulent tissues of the plant, and hence attacks the fruit clusters much less frequently than does the Rosy Aphis.

The Apple-Grain Aphis very frequently infests the fruit clusters, but it seems to lack toxicity, and its attacks produce little or no visible effect upon the foliage or fruit.

At Geneva, N. Y. (12, p. 41-59) during the summer of 1916 a careful study was made of the comparative effects of the three species upon the growth of the fruit. The greatest inhibition in growth occurred in fruits attacked by Rosy Aphis.

The apples infested by the Apple-Grain Aphis showed little reduction in size. The effects of the Green Aphis upon the infested fruits were quite similar to the injury produced by the Rosy Aphis. In measuring the apples it was found that early in the season, the axial diameters were greater than the transverse diameters. The latter increased more rapidly, however, and soon became greater than the axial diameters. In the uninfested series the two diameters were approximately equal on June 30, whereas the infested series were equal about July 12. This indicates that the aphis attack inhibited the growth of the transverse diameter of the infested fruits to a greater extent than that of the axial diameter. This was found to be true in the case of each species, and varied directly with the severity of the injury produced.

Summary.

Aphids are a group of insects of great biological interest and are among the most destructive of the orchard pests.

The species reported upon in this paper probably are world-wide in their distribution. They have infested apples in this country since the beginnings of our fruit growing industry.

All three species winter in the egg stage upon apple. The Green Apple Aphis spends the entire summer upon apple. The Apple-Grain Aphis spends the summer upon various grains and grasses. The Rosy Apple Aphis spends the summer upon plantain. The two latter species may continue to live upon their secondary food plants throughout the winter in mild climates. The three species pass through a seasonal succession that seems fundamentally constant in every section in which these studies have been conducted. These insects show variations in behavior as a result of climatic influences in different regions, which are of considerable significance from an economic standpoint.

Aphids seem unusually susceptible to the influence of environmental conditions. The number of generations produced during the season, the production of winged forms, and the production of gamogenetic forms, all seem to be regulated to a considerable extent by environmental conditions. An attempt has been made to illustrate, diagrammatically, the complex interrelations of the various factors of the environment. Detailed studies were made of the influence of evaporation and of temperature upon the development of *Aphis pomi*. It was found that evaporation, as registered by the instrument used, does not give a satisfactory index to the rate of development of this insect. When no other factor limits the development of the insect, temperature is a satisfactory index to the development of *Aphis pomi*, and the relationship may be expressed mathematically.

A study was made of the influence of age upon the rate of reproduction of *Aphis pomi*. This involved 128 adults, and covered a maximum reproductive period of 37 days. The average rate of reproduction for the first sixteen days was 3.23 nymphs per adult. After this time, the average rate of reproduction declined rapidly.

Studies of the effects of aphids upon the growth of apples showed an inhibition of the growth in direct proportion to the severity of the attack. The inhibition of the growth of the transverse diameter of the fruit was more pronounced than that of the axial dimension. The Rosy Apple Aphis produced the greatest effect upon the fruit, while the Green Aphis was scarcely less injurious. The Apple-Grain Aphid had comparatively little effect upon the growth of the infested fruit.

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