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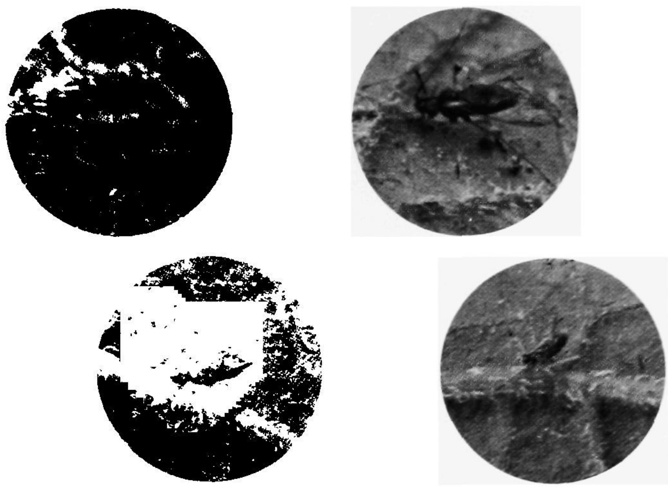

The large aphid in the upper left hand circle is a nymphal form of the potato aphid recently killed by a parasitic fungus that attacks plant life, likely **Entomophthora thaxteriana** (Petch). This particular fungus does not produce rhizoids which would tend to fasten the dead aphid to the potato leaf, so it is being held to the leaf only by its rather fragile proboscis which is still inserted into the leaf. The abdomen of the dead aphid appears in the photograph to be tilted upward. When the leaf is turned over in its normal position, the abdomen of the aphid is tilted downward at an angle.

The smaller, yellowish aphid which appears to be beneath the dead, diseased potato aphid is a healthy buckthorn aphid. For some reason, not now understood, living potato and buckthorn aphids appear to be attracted to dead, diseased aphids. The living aphids may walk up and over a dead, diseased aphid along its longitudinal axis or, as in this case, walk beneath and "nuzzle" it. Such habits suggest two important ways in which healthy aphids may become infected by fungi. Spores produced by the fungus growing within the body of the dead, diseased aphid are violently discharged from near the surface of the aphid's body The discharged spores adhere to the leaf around the body of the dead aphid. Spores may also stick to other leaves in the vicinity or fall to the soil beneath the plant. Some spores may also float through the air Infection of healthy aphids occurs when spores germinate after adhering to the bodies of such aphids.

The dead, diseased potato aphids in the other three circles are in varying stages of decomposition following infection by a fungus. Another important means for spreading entomogenous fungi is illustrated in the upper right hand circle where a dead, diseased, winged potato aphid is shown. Winged aphids infected by a fungus can spread the disease to aphids found on plants on which the winged, diseased aphids alight whether these plants are potatoes, other secondary hosts of the aphids, or the overwintering, primary host plants.

IMPORTANCE OF ENTOMOGENOUS FUNGI IN CONTROLLING APHIDS ON POTATOES IN NORTHEASTERN MAINE

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INTRODUCTION

Aphids often seriously limit the production of the Irish or white potato grown for seed or food in Maine and elsewhere. The economic importance of the potato industry in Maine is considerable because currently it ranks second in value of all the state's agricultural industries. Maine produces approximately 15 percent of the nation's annual crop of white potatoes. The potato-growing area in Maine is located very largely in the northeastern part of the state.

When aphid populations are large, feeding damage is reflected as reduced yield of tubers. Aphids are also vectors of some virus diseases which can seriously limit both yield and quality of the crop not only for table stock but also for seed purposes. Four species of importance infest potatoes in Maine — the buckthorn aphid (*Aphis nasturtii* Kaltenbach), the potato aphid (*Macrosiphum euphorbiae* [Thomas]), the green peach aphid (*Myzus persicae* [Sulzer]), and the foxglove aphid (*Acyrthosiphon solani* [Kaltenbach]).

During the period 1941 to 1951, a part of the joint studies by the U. S. Department of Agriculture and the University of Maine at Presque Isle included observations and collection of data to allow preliminary appraisal of the role of several natural agents in controlling aphids that infest field-growing potato plants. Results of these studies showed that natural agents caused wide yearly variations in populations of these aphids, not only on potatoes and other annual host plants but also on their overwintering, primary host plants. Among these agents were unfavorable weather, parasites, predators and fungus diseases of the aphids. Long ago Patch (1907)° observed the tremendously important role of fungi in controlling

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° See page 41 for references cited.

aphids on potatoes in northeastern Maine; more recently Shands et al. (1955) also pointed this out.

Although natural agents yearly reduce aphid populations much below their biotic potential, observations showed that they varied greatly in importance from year to year. This variation was particularly important for entomogenous fungi. The named species of fungi recovered from naturally infected dead, diseased aphids collected from potatoes in northeastern Maine during the period 1941 to 1962 included *Entomophthora thaxeriana* Petch (=*E. ignobilis* Hall and Dunn), *Entomophthora aphidis* (Hoffman), *Entomophthora sphaerosperma* (Fresenius), *Entomophthora planchoniana* Cornu, and *Entomophthora coronata* (Costantin).

In some years epizootics of disease among the aphids on field-grown potatoes virtually obliterated the infestation within a few days. Similar epizootics were observed in the spring among caged, naturally occurring populations of the potato aphid on its primary host, swamp rose (*Rosa palustris* Marshall). Occasionally such epizootics were seen in the fall in natural infestations of the potato aphid on swamp rose and of the green peach aphid on the primary host, Canada plum (*Prunus nigra* Aiton) However, the fungi ordinarily were not so spectacular in their action against the aphids, either on potatoes or on the primary hosts. Preliminary observations indicated that although fungus diseases fluctuated greatly from year to year, in most years they played an important role.

In continuing the jointly conducted investigations of potato-infesting aphids in northeastern Maine, greater emphasis was placed, during the period from 1952 through 1962, on study of the natural agents of aphid control, including fungus diseases. A large number of experimental plots and some commercial fields were sampled each week. A record was made of each dead aphid observed on the sample leaves, including field diagnosis as to the agent apparently responsible for mortality. Many of the dead specimens were collected for further study. During the period 1952-58 some of those aphids appearing to be infected with pathogenic fungi were submitted to laboratory diagnosis and high percentages of those collected from 1959 through 1962 were diagnosed and studied at the University of California. In this bulletin we present, discuss and evaluate some of the data from these investigations. We also suggest approaches that might be used to stabilize, at a high level, the role of entomogenous fungi in the control of aphids on field-growing potatoes in northeastern Maine and possibly in some other areas.

PROCEDURE

The more important procedures employed in this study are presented below. Records were made during all counts of aphids on all sample units of potatoes to show by species the numbers of living and dead aphids appearing to be infected with entomogenous fungi. The method of sampling, outlined by Shands and Simpson (1953), consisted of examining, *in situ*, all of the foliage of each sample plant until the plants reached a height of 8 inches, and thereafter of examining only three compound leaves or parts of three leaves per plant, located at random within the top, middle and bottom thirds of foliage height or stalk length. Most counts were made at Aroostook Farm, near Presque Isle, on replicated small plots separated in blocks and columns by strips of oats (Shands et al., 1950); but many counts were made in commercial plantings there and elsewhere in northeastern Maine.

Most of the fields, and many of the plots of potatoes used in this study were treated with insecticides. A field or series of plots was considered as being "treated" if regular or specifically scheduled applications of insecticides were made throughout most or all of the season, and as being "untreated" if no insecticide was applied or if an application was made only as the plants were emerging. Where one or more applications of insecticide were made starting in August, the records prior to that time were considered as being of untreated potatoes and those after as being of treated plots.

The potato plants in all fields or plots on Aroostook Farm received weekly applications of a fungicide at recommended rates for the control of late blight, *Phytophthora infestans* (Montagne) DeBary. The fungicide was yellow cuprous oxide during the early 1950's, but in later years zineb or maneb was used. The insecticides were incorporated and applied with the fungicide mixtures, nearly all of which were sprays. Most sprays were applied with a tractor-mounted machine equipped with a spray boom. The boom was especially designed to provide superior spray coverage of upper and under surfaces of leaves (Slosser, 1945), at 125 gallons per acre and under a line-gauge pressure of 150 to 200 psi. Some sprays were applied at lower rates or under greater pressure. Dusts were applied with a 6-row power duster equipped with a 10- to 12-foot trailing apron. The rate and frequency of application of insecticides in treated plots varied depending on objectives of each experiment, but they were seldom made more often than weekly.

The collection, preservation, shipment and diagnosis of the dead, diseased aphids underwent some changes as we became more familiar with this aspect of the investigations, especially as advances were made in taxonomy of the entomophthoraceous fungi. The general procedure adopted in 1960 (Shands et al. 1962) was also followed in 1961 and 1962. From 1 to 10 dead aphids of the same species per plot or field were dislodged from the leaves of sample potato plants. Dislodging was accomplished by holding the infested leaves at an angle and nudging the aphid with the open end of a glass vial until it fell inside. The dead aphid was sometimes transferred to the vial with a camel's-hair brush. When a collection was completed — most often there was only one aphid — the vial was closed with a cork stopper. Each day's collections were stored at 45° F. until the end of the week, when they were airmailed for diagnosis. Plugs of sterilized cotton were substituted for the cork stoppers when the vials were prepared for shipment.

Diagnoses of the dead aphids collected from 1959 to 1962 were made at Riverside, California, while those from 1954 to 1958, inclusive, were made by C. G. Thompson, formerly in charge, Pioneering Insect Pathology Laboratory, Entomology Research Division, Agricultural Research Service, U. S. Department of Agriculture, at Beltsville, Maryland. The dead aphids were examined in wet-mount preparations with a brightfield or phase-contrast microscope to determine the cause of mortality. The dried collections taken in 1954 and 1959 were not examined until 1955 and 1961, respectively. Diagnoses of collections for the remaining years were made on receipt or soon afterward.

Prior to 1960 dead, diseased aphids were not collected as extensively or intensively as during and after that year. In 1960, 80 percent of all dead, diseased potato aphids found on sample units were diagnosed as compared with 81 per cent in 1961 and 56 percent in 1962. Virtually all dead, diseased buckthorn, green peach and foxglove aphids found were diagnosed. Although increasing emphasis was placed on collecting for diagnosis beginning in 1955, records to show field abundance of the dead, diseased aphids were made during all aphid counts on potatoes throughout the period 1952 through 1962.

FIELD STUDIES OF BIOLOGICAL FACTORS AS NATURAL CONTROL AGENTS FOR APHID POPULATIONS ON POTATOES

The exact assessment of the roles of different biological agents in controlling aphid populations on potatoes is considered to be almost impossible because of the complexity of the ecological factors involved. However, our study of aphid population dynamics provided the basis for detecting and measuring in a general way the importance of the biological agents as a whole. For over 20 years we have continued to investigate the biotic potential and population growth patterns of natural infestations of aphids on untreated, field-growing potatoes in northeastern Maine, especially as influenced by certain biological agents. This period of study included years of high and low aphid abundance. This background provides some basis for assessing the roles of biological agents of aphid control on potatoes in this area, including parasites, predators and entomogenous fungi. The assessments are based on quantitative data for seasonal abundance of the aphids and of these biological agents, obtained concurrently in each environment.

In northeastern Maine the typical seasonal population trend of aphids on potatoes not treated with an insecticide is a sigmoid curve (Shands and Simpson, 1959). These aphids reproduce parthenogenetically and have a short developmental time and a relatively long reproductive period. Thus, most of the growth phase of this curve approximates a straight line when the common logs $_{n\,+\,1}$ of aphid numbers found on the plants are plotted against time. The slope of this line expresses the rate of population growth. The slope may differ from year to year, depending on seasonal differences in many factors of the enviroment. But once the angle of this line becomes apparent, any appreciable decrease in its slope indicates that the rate of aphid population growth has declined.

The correlation of appropriate data for one or more factors suspected as important in changing the slope of the line permits us to conclude whether each factor is associated with the population decrease observed. If the correlation is sufficiently clear cut, we may even form some opinion as to the extent to which a factor is responsible for the decrease.

The overall effect from the operation of one or more of such adverse factors can be approximated by comparing the area beneath the curve of actual aphid population trend with that of the expected trend had the population growth rate not been reduced.

The feasibility of this determination depends on the time of the seasonal peak in relation to whether the plants can support such numbers of the aphids until that time. Assuming that the plants can furnish such support, and barring the intervention of unusually adverse physical or biological factors, we can predict that aphid populations will continue to increase until at least the start of the fall migrations. The size of an aphid population at its peak on potatoes in northeastern Maine seldom, if ever, is limited by density-dependent factors. In the absence of adverse factors, very likely the potato plants could not support numbers as large as those that might be present shortly before the peak. An estimate such as that being considered here has definite limitations for determining the effectiveness of one or of a complex of environmental factors in controlling aphids on potatoes, but it is a concrete approach.

We have prepared curves to represent the actual seasonal population trends of the aphids on field-growing potatoes, together with the relative seasonal abundance of dead, diseased aphids found on the same units or subunits of sample at each count. We have also tried to include approximations of the aphid population trends had there been no interference of adverse factors. These graphs will be referred to at appropriate places.

Importance of Arthropod Parasites and Predators

The arthropod parasites and predators of the potato-infesting aphids in northeastern Maine include insects and spiders. At least one species of spider mite, *Erythaeus* sp., is an external parasite of the aphids; however, it is more abundant and effective against the aphids on the primary hosts in spring than on the potato plants in summer. Over 40 species of insects have been reared from the aphids in northeastern Maine, somewhat less than half of which are hyperparasites. Other than spiders, the insect predators of the aphids have been found to be chiefly coccinellids, syrphids, and chrysopids.

The results of the studies of the parasites and predators of potato-infesting aphids in northeastern Maine will be presented in separate publications. Suffice it to say here that, by employing the method of evaluation described above, we have been unable to detect any perceptible effect of parasites upon population trends of the most heavily parasitized species — the potato aphid — during the period from 1952 to 1962. On the other hand, predators exerted an appreciable degree of aphid control during 2 of these 11 years, 1957 and 1959. In fact, in 1959 very substantial aphid control resulted from the action of predators. In that year the first detectable effect of predators in retarding the rate of aphid population growth was separate from that of fungus diseases and it started one week later. In 1957, when this effect was not clear cut, the beginning of the effect of predators coincided with that of the entomogenous fungi and thus could not be entirely separated from it.

The lack of a detectable effect from the action of parasites is not particularly surprising; neither is the finding that predators exerted a substantial degree of control of aphids on potatoes during 2 out of 11 years. To be very effective against the aphids in summer, a continuing pressure from factors adverse to population increase must be exerted, or a catastrophic pressure of short duration is required. Naturally occurring, primary parasites of the aphids have met neither of these requirements since 1941. On the other hand, some predators exert continuing adverse pressure upon the aphids for a considerable period of time. Coccinellids consume appreciable numbers of aphids throughout their larval and adult stages and many aphids are killed by both immature and adult spiders.

We do not imply that among the biological agents affecting aphid population control on potatoes, parasites are of no appreciable value, or that only in some years are predators of substantial importance. Both of these agents are of importance every year, and their combined depressive effects doubtless are appreciable. Nevertheless, by our criteria the effect from parasites was not great enough to exert a detectable reduction in rate of population growth of the potato aphid — the species attacked most abundantly. However, pressure from predators was sufficiently adverse to be detected but only in 2 out of 11 years for which data are presented.

Importance of Entomogenous Fungi

Table 1 shows differences of considerable magnitude in the relative and actual abundance of dead, diseased aphids during the period 1952 through 1962, on field-growing potato plants not treated with insecticides. Except in 1953 and 1954, when the foxglove aphid was affected about the same or to a slightly greater extent, mortality of the potato aphid from attack by fungi generally was substantially greater than that of the other three species. The buckthorn aphid was least affected; during most years there were only trace numbers of this species killed by fungi. Mortality of the foxglove aphid from fungal attack during 5 of the 11 years was greater than that of the green peach aphid. During 3 of the remaining 6 years the green peach aphid was affected to a greater extent, while during the other 3 years there was little difference

Table 1. The all-season prevalence of dead, diseased aphids on foliage of potatoes not treated with insecticides, 1952 through 1962.

	Potato aphid		Green peach aphid		Buckthorn aphid		Foxglove aphid	
Year	Number*	Percent dead	Number*	Percent dead	Number*	Percent dead	Number*	Percent dead
1952	148	2.03	25	0	2085	0.01	73	0.12
1953	302	1.78	268	.01	5512	.02	189	2.38
1954	668	3.93	511	.42	2400	.28	229	3.40
1955	209	.31	230	0	4862	0	43	0
1956	416	12.91	523	.83	2959	.42	465	.32
1957	541	3.45	634	.22	7531	.05	792	.20
1958	269	3.32	289	.40	645	.04	102	.39
1959	169	.23	101	.10	152	.03	16	.13
1960	183	.87	41	.02	99	0	2	0
1961	141	2.82	505	.56	2066	.13	3	0
1962	131	6.06	56	.71	33	.06	9	2.40

*In hundreds. Only the sum of the weekly counts has been rounded to the nearest hundred.

between these two species. Dead, diseased specimens found during all of the weekly aphid population counts on potatoes ranged each year from 0.23 to 12.91 percent for the potato aphid during the 11-year period, 0 to 3.40 percent for the foxglove aphid, 0 to 0.83 percent for the green peach aphid, and 0 to 0.42 percent for the buckthorn aphid. Major emphasis throughout the remainder of this bulletin is devoted to a consideration of fungi attacking the potato aphid because of the relatively low order of abundance of fungus-killed buckthorn, green peach, and foxglove aphids. Also, the foxglove aphid ordinarily is not very abundant on potatoes in northeastern Maine.

The year-to-year differences in total-season numbers of aphids of the same species shown in table 1 have no particular significance since there was some variation among years in the number of fields or plots included in the study, as well as in the number of count dates and of sample units. For any one year, however, the data show the correct relationship of each species of aphid to the other three species for the entire season.

Role of Entomogenous Fungi in Controlling the Potato Aphid

Figures 1 to 6 show for field-growing potatoes at Presque Isle, not treated with an insecticide, the yearly population trends of the potato aphid in relation to prevalence of dead, diseased individuals on the same plants for the years 1952 through 1962. The average numbers of potato aphids per 100 three-leaf samples, for all counts each week, are plotted on a semi-logarithmic basis at

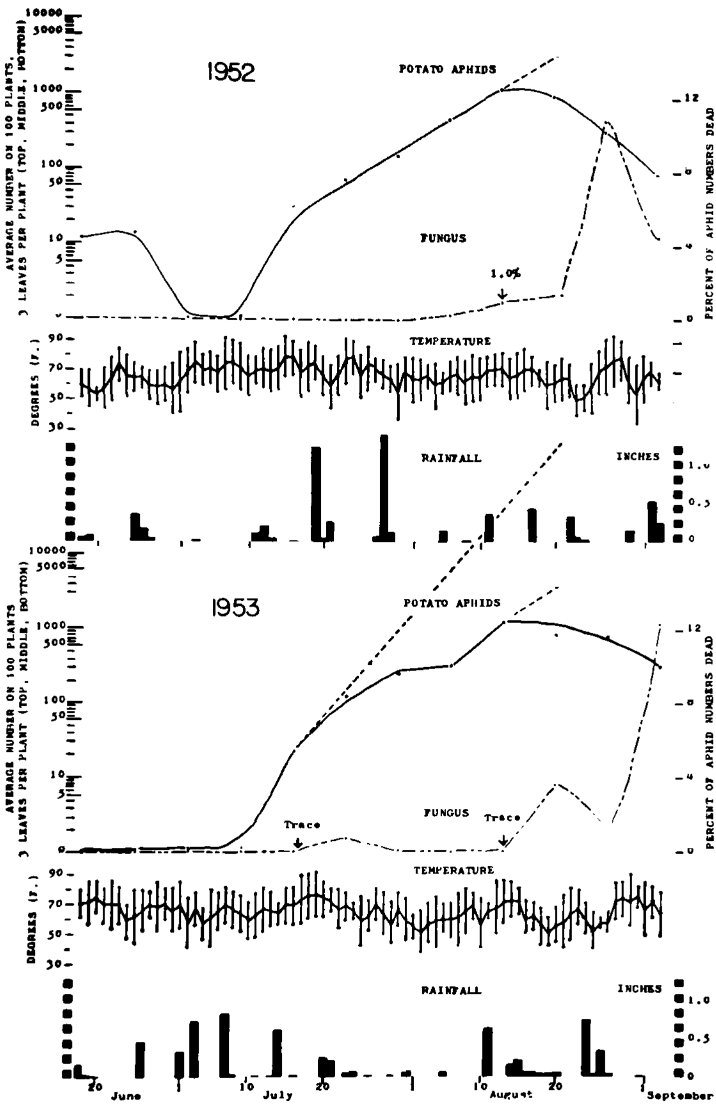

Figure 1.—Influence upon population trends of the potato aphid on potatoes of the abundance of fungus-killed potato aphids in relation to temperature and rainfall at Presque Isle, Maine. 1952, 1953.

midweek points. The percentages of those that were dead from fungus disease are also plotted at midweek points. The freehand lines drawn among these points indicate the seasonal abundance of the aphid and the relative seasonal abundance of fungus-killed specimens. Each point is based on an average figure representing field counts involving from 400 to 1700 sample plants (1200 to

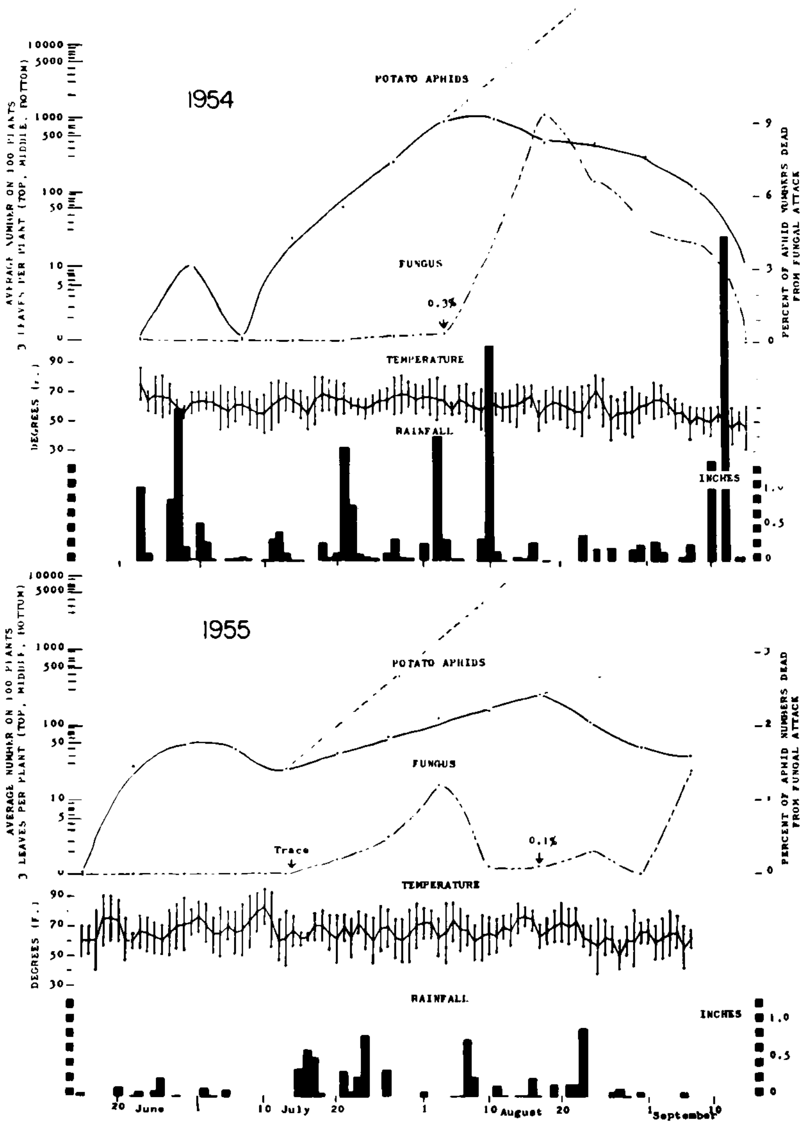

Figure 2.—Influence upon population trends of the potato aphid on potatoes of the abundance of fungus-killed potato aphids in relation to temperature and rainfall at Presque Isle, Maine, 1954, 1955.

5100 compound leaves) in 4 to 14 fields or plot locations. The average weekly count involved over 1100 sample plants (3300 compound leaves) located in more than 8 fields or replicated-plot locations. Also shown immediately beneath the yearly curves are the standard U.S. Weather Bureau daily records at Presque Isle for maximum, minimum and average temperature and for rainfall.

Substantial parts of the growth phases of population trends in figures 1 to 6 approximate a straight line[4] because the increases in aphid numbers on a time basis are exponential. Downward departures from this straight-line relationship indicate that one or more factors adverse to the aphid caused reductions in rate of population growth. Thus the trend and probable size of the population at the peak each year, had there been no adverse factors, were approximated by extending the straight-line growth phase as a dotted line to the time of the beginning of the fall migration, except in figure 2 for 1955, where the lower dotted line does extend to that time.

In 1953 (figure 1) and 1955 (figure 2) there appeared to be early-season decreases in rate of aphid increase, followed by a second such decrease later in the season. This pattern necessitated for each of these years two dotted-line extensions of population growth phases, the second of which was at a lower rate of increase than the first. The first reduction in 1955 came so early there was little basis for estimating the slope of a line that would show an unimpeded rate of aphid population growth. However, assuming that the rate of population increase would have been at least equal to that in 1954 (figure 2), the slope of the line for estimated growth rate in 1955 was made the same as that for 1954. In figure 2 for 1955, the point at which the estimated line departs from the actual population trend indicates that factors adverse to aphid increase became operative earlier than in most other years included in the study. The second or lower dotted line, which began to separate from the real population trend on August 13 in 1953 and on August 17 in 1955, indicates recurrence or increased intensity of operation of one or more factors unfavorable to aphid increase.

[4] Little significance need be attached to the drop in population indicated immediately preceding the beginning of the straight-line relationship since it is due chiefly to sampling a smaller fraction of the foliage as the plants undergo very rapid proliferation. In addition there is an added complex of increasing population from incoming spring migrants during a part of the time, followed by cessation of the migration and decreasing populations from the action of predators, parasites and other natural factors while the actual number of aphids per plant is small.

Table 2. Weather conditions associated with time of establishment and of perceptible effectiveness of fungus diseases on populations of aphids on untreated, field-growing potatoes, 1952 through 1962.

Year	Dates of initial detection[1]	Perceptible reductions in rates of population growth: Date	Perceptible reductions in rates of population growth: Percent of dead diseased aphids	Rainfall (inches): 15 days	Rainfall (inches): 10 days	Rainfall (inches): 5 days	Days with rainfall (number): 15 days	Days with rainfall (number): 10 days	Days with rainfall (number): 5 days	Daily mean temperature (F°): 15 days	Daily mean temperature (F°): 10 days	Daily mean temperature (F°): 5 days	Average daily range in temperature (F°): 15 days	Average daily range in temperature (F°): 10 days	Average daily range in temperature (F°): 5 days
1952	Aug. 6	Aug. 13	1.0	1.78	1.78	0.18	5	4	1	68.3	65.5	64.4	24.3	23.1	23.8
1953	July 17	July 17	Trace	2.18	1.45	.61	7	6	3	64.5	65.8	67.2	24.5	23.4	22.2
	Aug. 13	Aug. 13	Trace	.75	.67	.62	4	2	1	61.1	62.4	65.0	25.7	26.3	25.4
1954	July 27	Aug. 4	.3	3.68	2.88	2.48	13	8	5	63.8	64.2	61.8	18.8	17.7	11.6
955	July 14	July 14	Trace	.17	.08	0	3	1	0	71.0	70.6	72.4	28.1	29.9	30.0
	[2]	Aug. 17	.1	1.46	1.46	.27	9	7	4	67.9	67.9	72.6	22.8	20.3	16.4
956	Aug. 8	Aug. 15	2.2	1.74	.53	.02	8	4	1	61.5	59.8	61.2	23.9	25.6	28.4
957	July 31	Aug. 7	2.4	1.25	1.24	.62	9	8	4	63.8	62.4	65.4	22.0	21.0	21.2
958	July 2		6.7	1.81	1.78	.31	9	6	3	58.7	60.8	63.6	22.2	21.0	20.6
	July 30	Aug. 6	.4	2.54	1.90	1.70	8	5	3	64.9	64.4	62.6	19.5	18.9	15.4
959	July 8	July 22	.1	1.07	1.07	.16	4	4	1	62.5	63.3	66.4	22.4	22.4	24.8
960	July 6		2.6	1.20	.54	.54	8	4	3	64.1	65.1	61.8	24.5	25.6	23.0
	July 27	Aug. 3	.3	2.18	.99	.34	10	7	4	64.1	63.9	64.2	23.3	23.3	26.8
961	Aug. 9	Aug. 9	.2	2.88	.95	.47	9	5	2	65.9	64.8	68.2	24.2	26.2	25.6
962	July 18	July 18	Trace	5.08	4.97	2.89	11	7	4	59.3	62.0	58.8	18.5	18.8	16.6

Weather conditions for intervals of differing durations prior to first detection of dead diseased aphids.

First detection of the season or first detection after a subsequent interval during which no dead, diseased aphids were found for a period of at least 2 weeks.

After the initial detection on July 14 there was never a count of aphids during which no dead, diseased ones were found. The weather conditions shown in this line are those preceding August 17, when the population growth rate was reduced a second time in 1957.

A striking feature of figures 1 to 6 is the relation of fungus disease to a decrease in rate of aphid population growth. This phenomenon has been shown by an arrow beneath the point where the curve of estimated growth trend separates from the established trend, together with the percentage of dead, diseased potato aphids at that time. The start of this departure ranged from about July 14 to August 17 in 1955 (figure 2) which dates were the extremes for all 11 years included in this study.

Table 2 shows for each year the percentage of dead, diseased aphids when each reduction in rate of aphid increase became evident, together with the corresponding dates of first detection of the dead, diseased aphids. In most instances there was only a small percentage of dead, diseased aphids when a decrease in rate of population growth first became apparent. In fact, in 10 out of the 13 instances shown this value was 0.4 percent or less. It was 1.0, 2.2, and 2.4 percent in the other three instances.

Table 2 also shows, with two notable exceptions, that retardation in rate of aphid increase first became evident in a week or less after the presence of fungus-killed aphids first was detected. No apparent reduction in rate resulted from the rather high percentages of dead, diseased aphids found July 2, 1958, and July 6, 1960. These were fictitiously high percentages, caused by very low aphid populations, for in each instance only a single dead, diseased specimen was found. Also, we cannot be certain that field diagnoses were correct, since microscopic examinations of the dead specimens were not made.

Further comparison reveals that even a low incidence of disease was associated with a profound effect upon the population trend. Populations of the potato aphid increased relatively little after fungus diseases gained even a minute foothold (figures 1 to 6); in fact, the aphid peak usually came about, or soon after, the time of the first perceptible reduction in rate of aphid increase, when the percentage of dead, diseased aphids was very small (table 2).

Dead, diseased specimens of the potato aphid usually were not particularly abundant in any season during this 11-year period. Even when most abundant, they comprised only 6 to 12 percent of the total number at a given time, except on one occasion in 1956 when 36 percent of those found were dead, diseased specimens (figure 3.)

The deceleration in rate of population growth after the appearance of dead, diseased aphids strongly indicates that fungus disease was a potent factor adverse to aphid increase. This deterrent effect

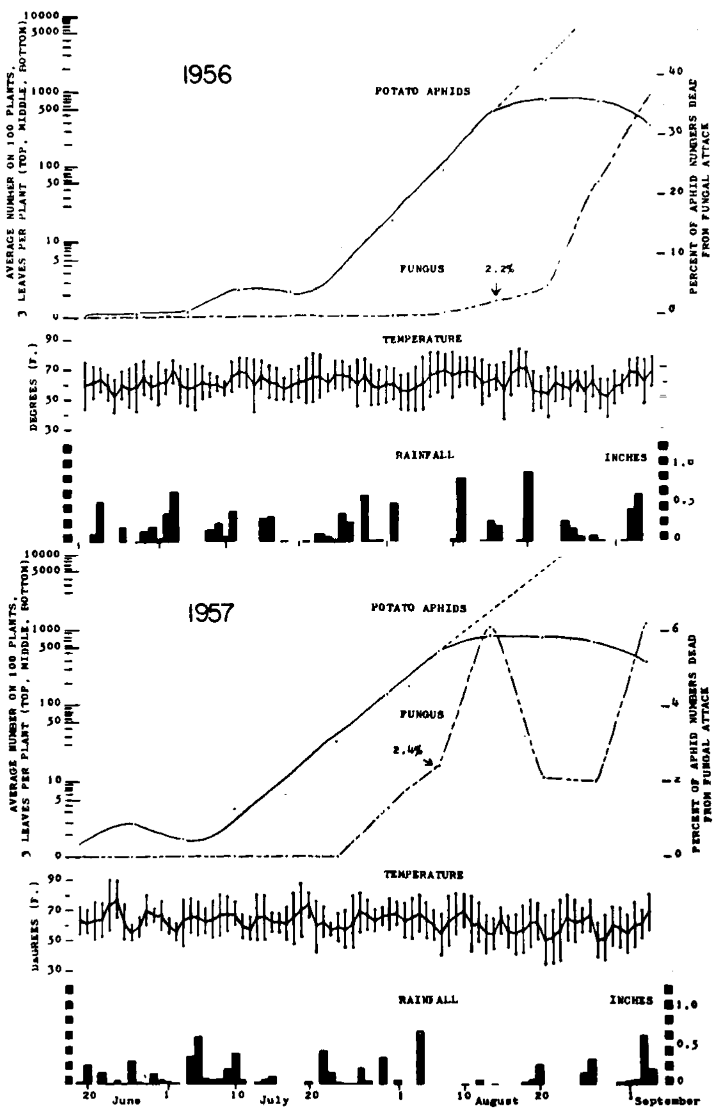

Figure 3—Influence upon population trends of the potato aphid on potatoes of the abundance of fungus-killed potato aphids in relation to temperature and rainfall at Presque Isle, Maine, 1956, 1957.

was so great that we questioned whether sublethal infections of fungus occurred which reduced the biotic potential of the potato aphid, possibly through reduced fecundity of the adults, or whether there was an increased mortality of the newly deposited nymphs, which could not be observed in the field counts. Dustan (1923) found bloodstream infections of the fungus *Entomophthora sphaerosperma* in 15 percent of the alate specimens of the apple sucker, (*Psylla mali* [Schmidberger]), collected from an infested orchard in Nova Scotia. Gilliatt (1925) found that 80 percent of the apple suckers which dropped to the ground at the time of watering the caged breeding hosts were actually infected with *E. sphaerosperma*. Contrary to their first opinions, the method of applying moisture was not the reason for the difficulty experienced in maintaining a continuing supply of the insect from the caged host plants. Rather, the waterings created environmental conditions favoring activity of the fungus pathogen.

Possibly a full measure of the pathogenicity to aphids of the commonest fungus during most of the 11 years—*E. thaxteriana*—may not be indicated by the data. Since this fungus does not produce rhizoids that fasten the dead host to the potato plant, many of the affected aphids, each held to a leaf only by its fragile proboscis, may have been jarred from the potato plants by wind and rain. The other identified species of fungus which were common during the period develop rhizoids, and the collection counts may present a more accurate level of prevalence of each such fungus. After only a very few days, however, the developing rhizoids and decomposition of the mummified individuals make almost impossible the removal or identification of the dead host aphids.

We derived the amount of control of the potato aphid provided by fungus diseases and other natural agents by comparing actual population peaks with peaks estimated on the basis of a lack of adverse factors. Shands and Simpson (1959) found that in northeastern Maine the peak of aphid populations on potatoes seldom, if ever, was limited by density-dependent factors. However, in some or even many years, the potato plants most likely could not support peak numbers of a population not checked by natural factors. Even though limitations must be placed upon interpretation of estimates computed in this way, such estimates do serve to show that natural factors provide a high degree of control of the potato aphid on untreated potatoes. This control ranged from 68 percent in 1952 (figure 1) to more than 99 percent in 1953 (figure 1) and 1955 (figure 2). While the actions of arthropod parasites and predators were among the natural factors responsible, entomogenous fungi appear to have been the one agent of outstanding importance, except in 1957 and 1959 when predators were exceptionally abun-

Environmental Conditions Affecting Fungus Activity

Heavy or frequent precipitation favors the development of species of fungi that attack plants or phytophagous insects under field conditions. Our observations (Shands et al., 1962) strongly indicate that epizootics of entomophthoraceous fungi attacking aphids on potatoes in northeastern Maine usually follow an extended period of frequent, rather heavy precipitation, with a microclimate having a high relative humidity during a considerable part of each day, and moderate temperatures. These conditions were especially present when the predominating species was *E. sphaerosperma*, less so when it was *E. aphidis*.

Knowledge of weather conditions favoring initial establishment of entomophthoraceous fungi in the potato field is important, since a marked reduction in rate of potato-aphid population growth occurs within a week after fungus-killed specimens are first found on potatoes. Table 2 shows, for periods of 5, 10, and 15 days immediately preceding the first detection of dead, diseased potato aphids each year, the amount of rainfall, the number of days with precipitation, the daily mean temperature and the average daily range in temperature. Similar data for a second "date of initial detection" are included for 1953 and 1958 when dead, diseased aphids again were found after a lapse of at least two weeks during which none were found. Similar data are included for 5-, 10-, and 15-day intervals in 1955 preceding the time when a second perceptible reduction in rate of population growth was observed. Although very scarce during these 2-week intervals (figure 2), dead, diseased aphids were always found.

Lack of information on biology and epizootiology of entomophthoraceous fungi severely limits an evaluation of weather conditions as to degree of favorableness or of unfavorableness for the establishment of fungi. Such evaluation is especially difficult during the required period preceding the first appearance of dead, diseased aphids. The length of this period could vary at different times of year. It also could vary with increasing size of the potato plants and density of foliage, as the stalks begin to spread apart and approach the recumbent or 'vine' condition. These changes likely reduce the amount and frequency of rainfall required to provide a microclimate favoring development of the fungi. Gilliatt (1925) found a period of 16 days was required for germination of resting spores of *E. sphaerosperma* held in hanging drops of tapwater in the laboratory. Less time may be required for germination of the resting spores of some other species, as indicated by Hall and Halfhill (1959), who found that from 2.3 to 5.8 percent of the resting spores of *E. virulenta* Hall and Dunn germinated within 2 days. Possibly, then, we can assume that the annual establishment of fungus activity follows germination of resting spores already present in the area and that the time required for germination of spores and subsequent infection of aphids is up to 15 days. The data in table 2 show that abundant, frequent rainfall preceded initial detection of dead, diseased potato aphids, except in two or three instances. In these exceptions, the daily mean temperature was fairly low or the average daily range in temperature was rather wide. Either condition would indicate that the dewpoint was reached sometime every day. Thus, a microclimate of high humidity was present beneath the potato leaves for a considerable time each day, even in the excepted instances.

Unfavorable effects from the surprisingly low rainfall and relatively high average daily temperatures preceding initial establishment of fungus infection on July 14, 1955, doubtless were compensated for in part by the low minimum temperatures, indicated by the wide daily range in temperature. Successful establishment of fungus infection under those conditions is considered unusual. While we are uncertain of the species predominating at that time, it appears likely to have been the one described by Hall and Dunn (1957) as *E. ignobilis*, and since placed by Hall and Bell (1963) in synonomy with *E. thaxteriana*. This fungus appears capable of developing under drier conditions than *E. sphaerosperma* or *E. aphidis*. Also, while Hall and Dietrick (1955) found *E. thaxteriana* (= *E. ignobilis*) to be only mildly pathogenic for the spotted alfalfa aphid (*Therioaphis maculata* [Buckton]) on alfalfa in California, Hall and Bell (1960, 1961) found it would develop at lower temperatures than the other four species of entomophthoraceous fungi with which they worked.

In this study we considered that the place of first appearance of dead, diseased aphids and spread of the fungi to the potato-infesting aphids was important. Often dead, diseased specimens of the apple-grain aphid (*Rhopalosiphum fitchii* [Sanderson]), or of the English grain aphid (*Macrosiphum avenae* [Fabricius]), were found on young oat plants in the strips separating and surrounding each experimental plot of potatoes on Aroostook Farm several days before dead, diseased potato aphids were found on the potatoes. The fungus likely first became established on the aphids infesting the oats, then spread to the aphids on potatoes in the adjacent plots. During early summer the dense, short, succulent growth of the oats appeared to provide a microclimate favoring establishment of entomophthoraceous fungi as well as reproduction of the grain-infesting aphids. This particular microclimate should be carefully evaluated, especially if critical studies are made of the possibility of inducing epizootics of entomophthoraceous fungi in aphid populations on potatoes.

Table 3. The relation between rainfall and abundance of dead, diseased potato aphids (*Macrosiphum euphorbiae*) on foliage of field-growing potatoes, 1952 through 1962.

	Rainfall, inches			Percent dead diseased		
				Untreated		Treated with insecticide
Year	June	July	August	Peak[1]	Entire season	Entire season
1952	3.69	3.85	3.12	10.8	2.0	4.0
1953	2.40	3.08	2.24	12.3	1.8	1.6
1954	6.16	5.42	6.69	9.3	3.9	3.7
1955	2.87	3.57	3.06	1.4	.3	.4
1956	2.55	3.85	3.17	36.4	12.9	5.2
1957	2.51	3.27	1.65	6.2	3.5	1.7
1958	3.69	3.43	7.30	7.8	3.3	3.8
1959	4.11	1.95	5.43	8.3	.2	1.4
1960	3.46	3.65	1.25	1.6	.9	1.1
1961	3.22	4.92	4.11	6.4	2.8	2.1
1962	3.01	7.11	3.87	12.1	6.1	5.7

[1] When dead, diseased aphids comprised the largest percentage of total aphid population. This peak occurred in late August or early September, except in 1954 and 1960 when it was reached during the period August 14-20.

No appreciable or consistent relationship has been established between amount of rainfall in June, July or August and peak abundance of dead, diseased potato aphids. Nor has such a relationship been established for rainfall during these months and the all-season prevalence of dead, diseased aphids on untreated or on insecticide-treated potatoes (table 3). Although not so in all years, fungus diseases generally were more prevalent and provided better control of the potato aphid during seasons with heavier rainfall. The frequency and distribution of the rainfall with respect to time of season, stage of crop growth and stage of seasonal aphid population trend are likely more important than monthly totals. More critical assessment of these factors can be made as we learn more about the biology and epizootiology of these fungi.

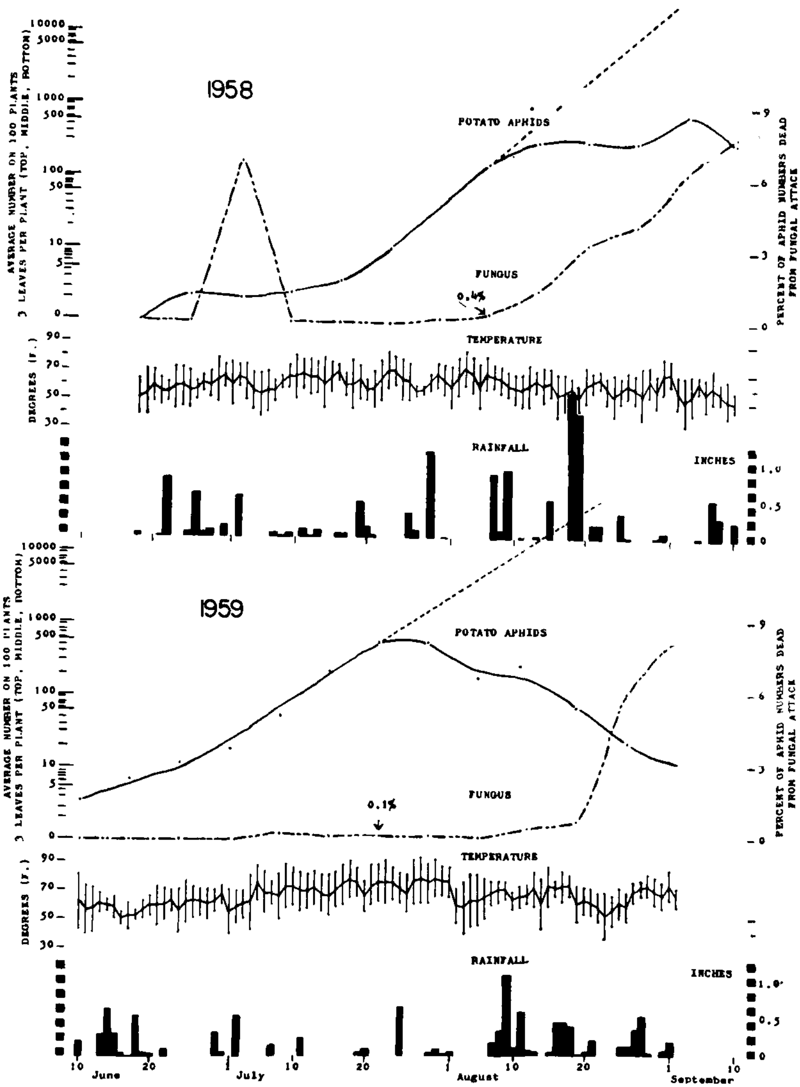

Figure 4—Influence upon population trends of the potato aphid on potatoes of the abundance of fungus-killed potato aphids in relation to temperature and rainfall at Presque Isle, Maine, 1958, 1959.

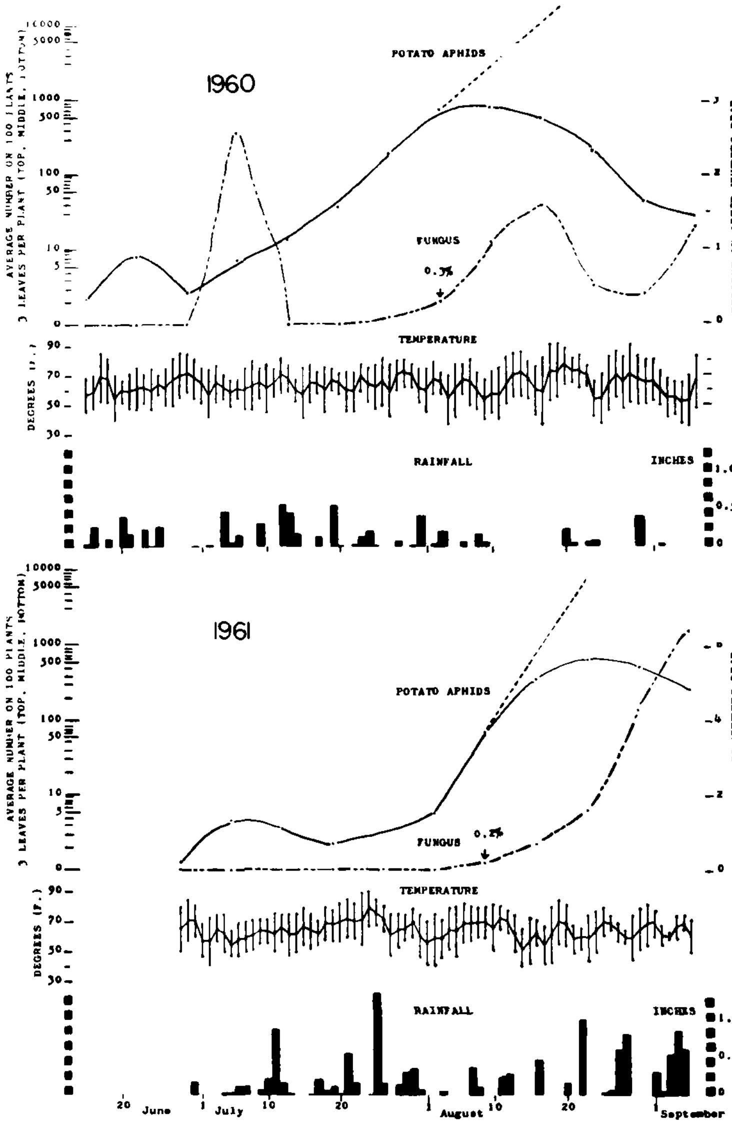

Figure 5—Influence upon population trends of the potato aphid on potatoes of the abundance of fungus-killed potato aphids in relation to temperature and rainfall at Presque Isle, Maine, 1960, 1961.

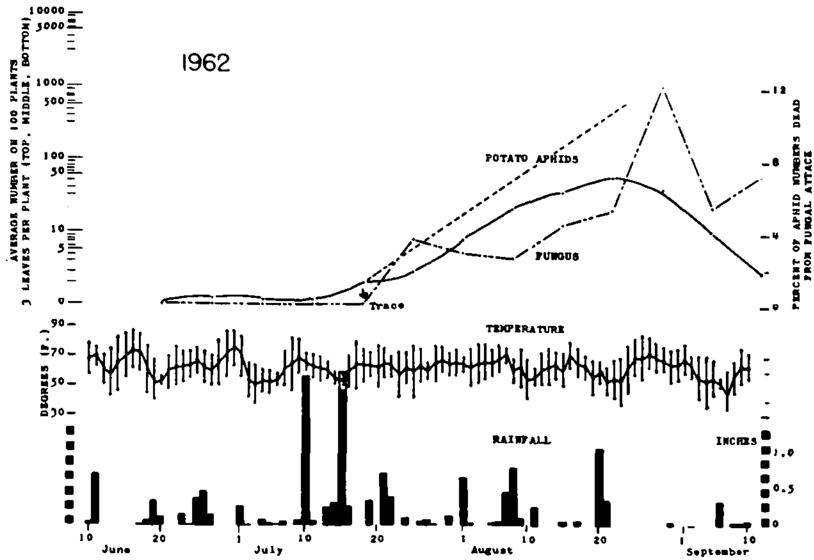

Figure 6—Influence upon population trends of the potato aphid on potatoes of the abundance of fungus-killed potato aphids in relation to temperature and rainfall at Presque Isle, Maine, 1962.

DIAGNOSES OF DEAD, DISEASED APHIDS

Identity of the Pathogenic Fungi

Diagnoses of samples of dead, diseased aphids collected during the period 1941 through 1953 from field-growing potatoes were made at Beltsville, Maryland, by Vera K. Charles, Flora G. Pollock and John A. Stevenson, Division of Mycology, Bureau of Plant Industry, U. S. Department of Agriculture. They found the most abundant species to be *Entomophthora aphidis* and *E. sphaerosperma* (Shands et al., 1958). *Entomophthora coronata* was identified from one collection (Harris, 1948).

The diagnoses from 1954 through 1958 were made by C. G. Thompson. In 1954 and 1955 he found a species of *Entomophthora* which he recognized as being closer to *E. coronata* than to *E. aphidis*. Although *E. aphidis* and *E. sphaerosperma* also occurred commonly, the predominant pathogen was this species of *Entomophthora*. This fungus with its *coronata*-like conidium is now thought to be *E. thaxteriana*.

In 1957, following a year of reduced emphasis on diagnoses of aphids from Maine, Thompson tentatively identified the fungus

Table 4. All-season prevalence of entomophthoraceous fungi in dead, diseased aphids from potatoes on Aroostook Farm. Fungi subjected to microscopic diagnosis, 1955 through 1962.

Species of fungus	Potato aphid	Green peach aphid	Foxglove aphid	Buckthorn aphid
	Percent of diagnosed specimens[1]			
	1955			
	(40)[2]	(0)[2]	(11)[2]	(3)[2]
Entomophthora				
sp.[3]	65	—	91	33
aphidis	20	—	9	33
sphaerosperma	15	—	0	33
	1957			
	(153)	(16)	(0)	(20)
Entomophthora				
sp[3]	1	0	—	5
thaxteriana	99	100	—	95
	1958			
	(53)	(9)	(12)	(2)
Entomophthora				
sp.[3]	13	89	50	100
thaxteriana	60	11	8	0
aphidis	8	0	17	0
sphaerosperma	19	0	25	0
	1959			
	(77)	(20)	(4)	(9)
Entomophthora				
sp.[3]	1	0	0	11
thaxteriana	86	70	100	78
aphidis	13	30	0	11
	1960			
	(581)	(18)	(0)	(0)
Entomophthora				
sp.[3]	1	0	—	—
thaxteriana	87	89	—	—
planchoniana	10	11	—	—
aphidis	2	0	—	—
	1961			
	(725)	(396)	(0)	(151)
Entomophthora				
sp.[3]	2	1	—	15
thaxteriana	98	98	—	85
aphidis	1	1	—	1
	1962			
Entomophthora				
	(1682)	(225)	(46)	(3)
sp.[3]	Trace	0	0	0
thaxteriana	99	99	100	100
planchoniana	Trace	Trace	0	0
aphidis	1	Trace	0	0
sphaerosperma	Trace	Trace	0	0

[1] Rounded to the nearest percent.

[2] In parentheses: total number diagnosed excluding those found not to be infected with a pathogenic fungus.

[3] Unidentifiable beyond genus because of the lack of identifiable characters, but very likely *Entomophthora thaxteriana*.

that was so abundant in 1954 and 1955, and again was predominant in 1957, as *Entomophthora planchoniana*. In 1958 he made some diagnoses as *Entomophthora* sp., but most were considered to be *E. planchoniana*. Apparently he thought one or more species in addition to *planchoniana* were also present. However, the findings of Hall and Bell (1963) indicate that the fungus identified by Thompson as *E. planchoniana* actually was *E. thaxteriana*. The presence of *E. thaxteriana* as the predominant species during the period 1959 to 1962 suggests that it may have been present in 1954 and 1955 as well as in 1957 and 1958.

Yearly Variation in Prevalence of the Species of Fungi

Because of the poor condition of the dead, diseased aphids in the 1954 collections diagnosed in 1955, few identifications of the fungi beyond genus could be made. Although the fungus was first thought to be *E. aphidis*, the most common diagnosis was *Entomophthora* sp. The predominant fungus in 1955 again was not identifed to species, but substantial proportions of the diagnoses of dead, diseased potato and buckthorn aphids were reported as *E. aphidis* and *E. sphaerosperma* (table 4). One specimen of the foxglove aphid was infected with *E. aphidis*. In 1957, what is now considered to be *E. thaxteriana* was predominant for the potato, buckthorn and green peach aphids, although trace infections of an unidentified *Entomophthora* also were recorded for the potato and buckthorn aphids. In 1958 an *Entomophthora* was most common on the buckthorn, foxglove and green peach aphids, while *E. thaxteriana* was prevalent in the potato aphid. Smaller but substantial percentages of infections in the potato and foxglove aphids proved to be *E. sphaerosperma* or *E. aphidis*. As stated earlier those species of *Entomophthora*, which were not further identified, are suspected of being the most common species for the period, *E. thaxteriana*.

During the period 1959 through 1962, by far the predominant species of fungus was *E. thaxteriana* for all four species of aphids. Except in 1959 when 13 percent of the infections in the potato aphid proved to be *E. aphidis*, only 1 or 2 percent of those diagnosed during the other three years were caused by *E. aphidis*. Rather comparable relationships were found for relative abundance of *E. thaxteriana* and *E. aphidis* in the green peach and buckthorn aphids. No infections of *E. aphidis* were recorded for the foxglove aphid during the 4-year period. Although it was not found during 1959, 1960, or 1961, trace infections of *E. sphaerosperma* in the potato and green peach aphids in 1962 could portend increasing abundance of this very potent fungus pathogenic for potato-infesting aphids in northeastern Maine, if environmental conditions favor its development.

Yearly Variation in Seasonal Abundance of the Fungi in Relation to Weather

A consideration of some of the ecological factors affecting seasonal prevalence of the entomophthoraceous fungi during the period 1959 through 1962, is confined to the potato aphid since this species usually is much more subject to fungus attack than the other potato-infesting species of aphids in northeastern Maine (table 1).

Figures 7, 8, 9, and 10 show for these four years the seasonal prevalence of the several species of pathogenic fungi that were found to be affecting the potato aphid in relation to seasonal trends of abundance of this aphid on field-growing potatoes, and in relation to temperature and rainfall. The populations shown for the potato aphid are weighted averages of the weekly counts in all fields or plots from which the diagnosed specimens came, including both insecticide-treated and untreated potatoes. The gaps in the curves showing relative seasonal abundance of the three species of fungi in 1959 (figure 7) resulted from a loss of a week's collections of dead, diseased aphids which did not affect the curve showing seasonal distribution of all species of the fungi combined.

The time of first appearance of dead, diseased potato aphids on untreated, field-growing potatoes during the 4-year period was July 8 in 1959, July 6 in 1960, August 9 in 1961, and July 18 in 1962 (table 2; figures 4, 5, 6). Except in 1961, the first specimen each year was found during the early part of the initial period of rapid increase in numbers of the aphid. Apparently the exceptionally wet weather during early summer in 1961 favored field establishment of fungus disease well before the beginning of the rapid rise in aphid numbers (figure 9).

Differences between years occurred in the period of rapid increase and the time when the peak of fungus activity was reached. This was also true of the potato aphid. In 1959, both phenomena for the aphid preceded by substantial intervals those for fungus disease; in fact the aphid peak came when the percentage of dead, diseased aphids was still very small (figure 7). Owing possibly to the frequent, heavy precipitation during the latter part of the summer, more than one-third of the dead, diseased potato aphids found all season were taken during the last week of August (figure 7) when

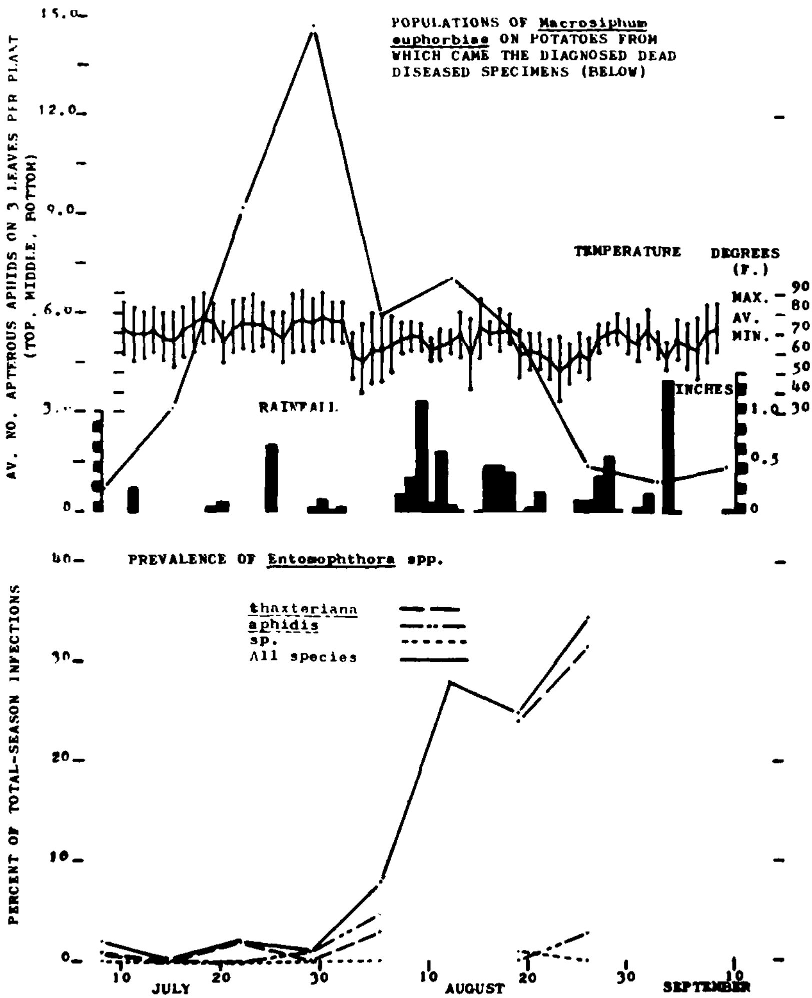

Figure 7—Seasonal occurrence in 1959 of entomogenous fungi affecting the potato aphid on field-growing potatoes in relation to temperature and rainfall.

8.3 percent of the population was dead from fungus attack (table 3).

Although the period of rapid increase and time of peak for the fungus diseases followed rather closely behind those for the potato aphid both in 1960 and in 1961, both of these phenomena for diseases and aphids, in 1960, were about three weeks ahead of

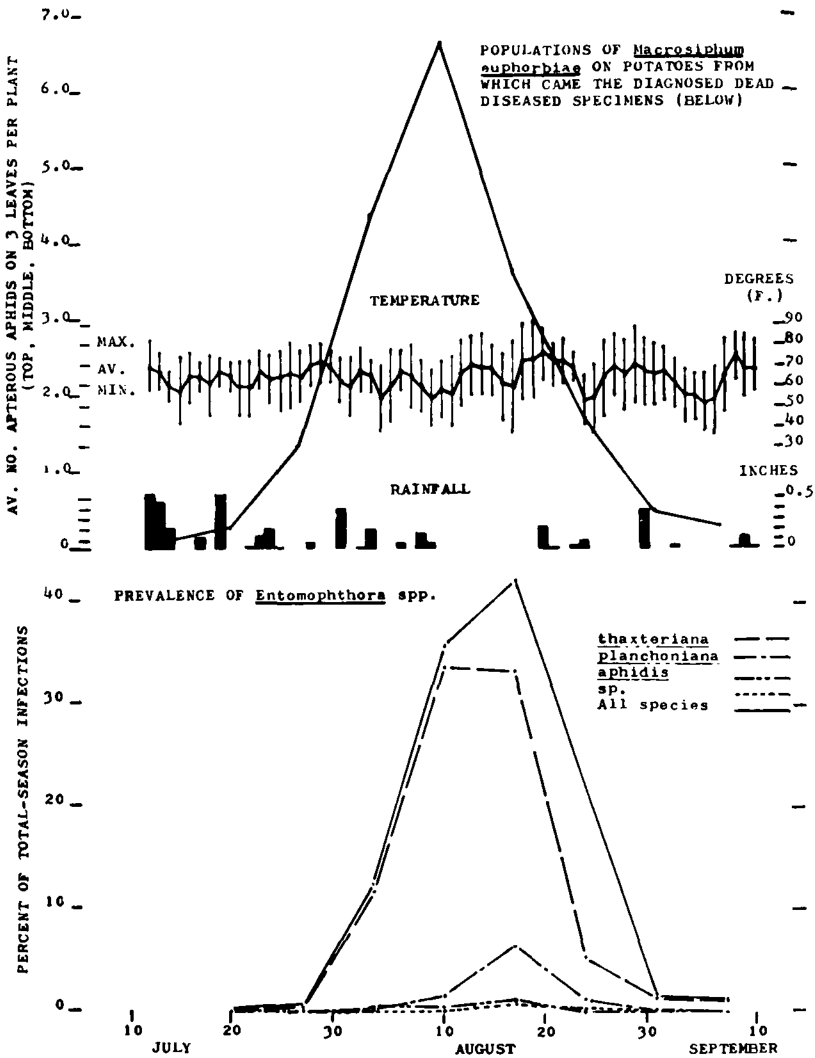

Figure 8—Seasonal occurrence in 1960 of entomogenous fungi affecting the potato aphid on field-growing potatoes in relation to temperature and rainfall.

those in 1961 (figures 8, 9). Except for this general difference, the similarities of several relationships between aphids and disease during the two years are rather striking. The differences between years in amounts and distribution of rainfall, together with pre-

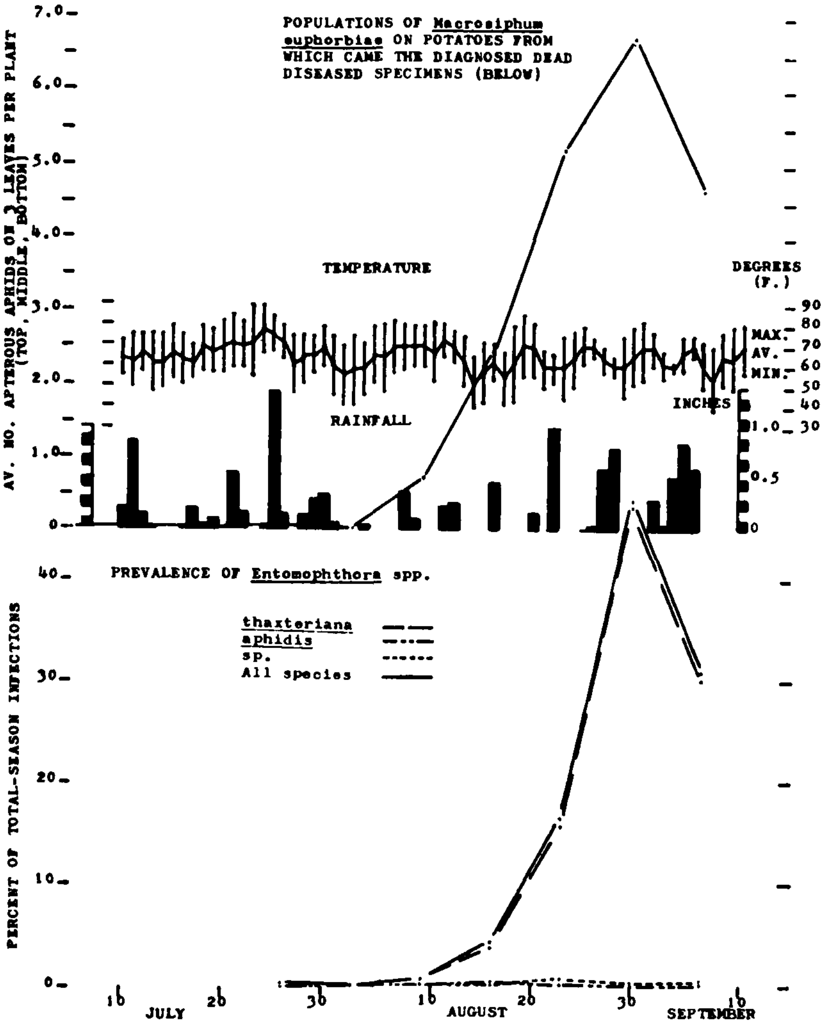

Figure 9—Seasonal occurrence in 1961 of entomogenous fungi affecting the potato aphid on field-growing potatoes in relation to temperature and rainfall.

dominance of the same species of fungus both years, *E. thaxteriana*, make these similarities particularly striking. Surprisingly, in both years a high degree of potato-aphid control occurred, despite the dry summer of 1960 and the late start of fungus activity in 1961 (figures 5, 8, 9). The early, effective fungus activity during relatively

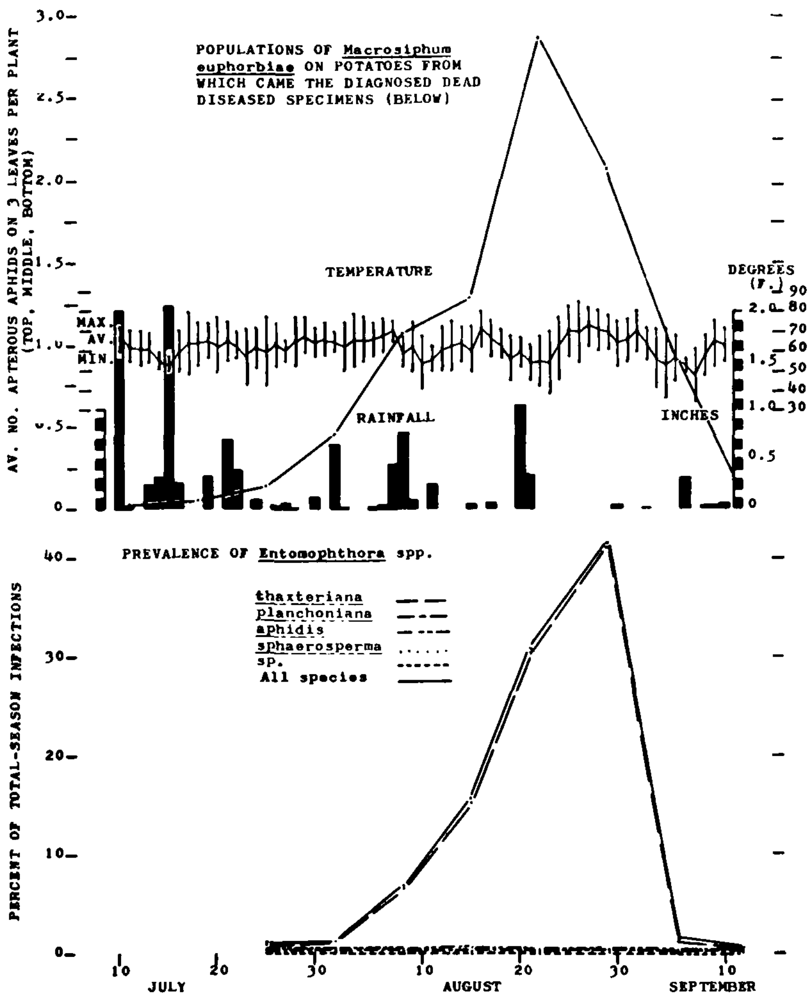

Figure 10—Seasonal occurrence in 1962 of entomogenous fungi affecting the potato aphid on field-growing potatoes in relation to temperature and rainfall.

dry weather in 1960 apparently was made possible by the rainfall of late June and early July, coupled with below-average range in daily temperatures in critical periods. These environmental conditions most likely permitted the fungi to multiply and spread. The retarded beginning of fungus activity in 1961 was due in part, if not largely, to retarded development of the potato aphid population; in other words, very few potato aphids were present for infection by fungi on potatoes until rather late in the season. Potato aphids were equally abundant at the peak in 1960 and in 1961.

Both fungus activity and populations of the potato aphid on potatoes declined sharply in early September, 1961 (figure 9). However, the evidence strongly indicated that during the wet, warm weather of September, fungus activity spread to and continued to affect populations of the buckthorn aphid on the primary host, alder-leaved buckthorn, *Rhamnus alnifolia* L'Heritier de Brutelle.

In 1962 fairly early initial establishment and activity of the fungi were made possible by frequent, heavy rainfall and moderate temperatures coupled with a below-average range in daily temperatures during July. These conditions prevailed until well past the time of the exceptionally low seasonal peak of the potato aphid (figures 6, 10). Apparently with the below-average daily range in temperature during midsummer, rainfall was adequate to permit a microclimate favoring fungus activity until late August.

A striking difference among years was the continuing increase in percentage of dead, diseased specimens in a rapidly decreasing population of the potato aphid in 1959, as compared with sharp, rapid decreases in prevalence of diseased aphids following the aphid peaks in 1960, 1961, and 1962 (figures 7, 8, 9, 10). Although the reasons for this difference are not clear, it would appear that action of the fungi in some of these years may have been regulated by factors independent of the density of the host, even though density-dependence in the sense contended by Steinhaus (1954) is recognized for many insects.

Table 5. The prevalence of dead aphids not infected with entomogenous fungi on insecticide-treated and untreated, field-growing potato plants in northeastern Maine (mostly at Presque Isle), 1952 through 1962.

	Number of specimens diagnosed				Percent nonfungus				
Year	Buckthorn aphid	Green peach aphid	Potato aphid	Foxglove aphid	Buckthorn aphid	Green peach aphid	Potato aphid	Foxglove aphid	All Species
1955	17	2	146	4	35	0	9	0	11.2
1957	55	45	248	49	36	13	8	22	14.4
1958	10	16	93	21	80	25	15	19	21.4
1959	23	35	132	9	54	21	8	11	15.8
1960	0	18	752	0		5	1		1.0
1961	218	413	748	2	31	4	3	50	7.8
1962	6	235	1725	48	50	5	3	4	2.9

Table 6. The prevalence of dead aphids not infected with fungus on field-growing potatoes that were or were not being treated with insecticides, 1961 and 1962.

Species	Number diagnosed[1]	Percent nonfungus: Untreated potatoes	Treated potatoes	Weighted average
		1961		
Buckthorn aphid	218	31.9	29.3	30.7
Green peach aphid	413	4.0	4.3	4.1
Potato aphid	748	4.6	1.7	3.1
Foxglove aphid	2	0	100.0	50.0
All species	1381	9.8	6.1	7.8
		1962		
Buckthorn aphid	6	0	100.0	50.0
Green peach aphid	235	4.8	4.6	4.7
Potato aphid	1725	1.8	2.8	2.5
Foxglove aphid	48	0	6.9	4.2
All species	2014	2.0	3.3	2.9

[1] Excluding those diagnosed as nonfungus.

Abundance and Significance of Dead Aphids not Infected with Fungi

Occasionally, dead aphids appearing to be diseased when collected were found upon diagnosis not to be infected with pathogenic fungi or with any other recognized pathogens. They are referred to here as "nonfungus." During the 7-year period for which data are available, from 1 to 21 percent of the diagnosed aphids each year were nonfungus (table 5). The condition has been most prevalent in the buckthorn aphid, with 32 to 80 percent each year in this category and least common in the potato aphid with 1 to 15 percent. The corresponding degree of prevalence in the green peach and foxglove aphids ranged from 0 to 25 percent and 0 to 22 percent, respectively. The phenomenon is not understood. The data in table 6 do not suggest that the nonfungus condition was associated in any way with the application of insecticides, either in 1961 or in 1962. In California, however, Hall and Dunn (1959) found that germination of the resting spores of five species of entomophthoraceous fungi, including *E. thaxteriana,* was somewhat retarded by some insecticides.

DISCUSSION AND CONCLUSIONS

The naturally occurring epizootics of fungus diseases of the potato aphid on potatoes followed in this study differed substantially in several ways from those of fungus diseases of some other insects. They occurred annually but varied from year to year in degree of aphid control. In some years before the period included in this study, epizootics of fungus disease virtually eliminated aphid infestations on potatoes within a few days, but none of those since 1952 was so catastrophic. Most of these fungus-caused epizootics in aphid populations on potatoes have been milder and slower in reaching a peak than those of *E. sphaerosperma* against the apple sucker in Nova Scotia. Jacques and Patterson (1962) considered that the apple sucker infection was not typically catastrophic for populations of that insect. Nevertheless our studies showed that a high degree of control of the potato aphid occurred, except in 1952 when the fungi were late in becoming established. This remarkable degree of control appeared to be associated with one or more factors in addition to aphid mortality from fungus attack. Of significance was a marked reduction in rate of increase in numbers of the potato aphid coinciding with the first detection of initial establishment of fungus infection among the aphids in the potato plantings.

Year to year differences in effectiveness of the fungi against the potato aphid probably were influenced by several factors in addition to weather, although the latter most likely was directly or indirectly of greatest importance. Our knowledge of yearly variation in the relative abundance of each species of fungus in the complex has increased in recent years, but it was very limited before 1955. The generally low mortality of the spotted alfalfa aphid from *E. thaxteriana* (= *E. ignobilis*) (Hall and Dietrick, 1955), and that of the potato-infesting species recorded throughout our study, plus the taxonomic findings of Hall and Bell (1963), lead us to think that this species may have predominated in northeastern Maine each year during the period 1952 through 1962. The diagnoses indicate that *E. sphaerosperma* and *E. aphidis* predominated in earlier years when the epizootics of fungi among aphids on potatoes were occasionally catastrophic in their action. Possibly yearly variation in overall effectiveness of the less drastic epizootics since 1952 has been due in part to the proportion that the fungus species-complex was comprised by fungi other than *E. thaxteriana*, together with possible variations in susceptibility of each of the four species of aphid to attack by each species of fungus. Some of the yearly variation in effectiveness of fungi against the potato aphid was due to variations in the initial occurrence of diseases in the field. In practically all instances, the estimated total-season degree of control increased with earlier initial establishment of fungus activity.

We were unable to determine whether applications of fungicides to the plants decreased or delayed the overall control action of fungi against the potato-infesting species of aphids. Such a delay was observed when some fungicides were tested in the laboratory against five species of entomophthoraceous fungi affecting the spotted alfalfa aphid in California (Hall and Dunn, 1959) or against *E. sphaerosperma* affecting the apple sucker in Nova Scotia (Jacques and Patterson, 1962). Possibly greater control of the potato-infesting species by entomophthoraceous fungi could be obtained without fungicide on the potato plants, but frequent application of fungicidal sprays is a basic necessity for control of late blight in all commercial acreages of this crop in the northeast.

Large differences occur among species of insects in the density of populations required for the development of epizootics of fungi. For example, Steinhaus (1954) stated that disease-producing microorganisms are density-dependent mortality factors, affecting a great proportion of the insect population as the density of the insect population increases. In the instance of the apple sucker in Nova Scotia, Jacques and Patterson (1962) found that while development of *E. sphaerosperma* was dependent on density of the host population, the threshold density of the insect population for disease activity was relatively low. Ullyett and Schonken (1940) concluded that against larvae of the diamondback moth, (*Plutella maculipennis* [Curtis]), *E. sphaerosperma* is neither wholly density-independent or wholly density-dependent. They found that initial establishment of the disease was dependent upon the weather, but its spread was largely dependent upon density of insect population. They therefore concluded the disease was a density-independent mortality factor.

Ullyett (1953) further reported that disease factors are neither wholly density dependent or density independent but pass through phases which include both characteristics. In review, Tanada (1963) stated that the density dependence of pathogens is generally accepted by ecologists. He contended that workers such as Ullyett and Schonken failed to realize that even though the appearance or the initiation of fungus infections is dependent largely on weather and climatic conditions, dependency on such conditions has no bearing on the density dependence of disease. These physical factors merely act as conditional factors of natural control by permitting or not permitting a pathogen to act.

It was observed that the entomophthoraceous fungi studied in Maine became established when populations of the aphids on potatoes were very small. This establishment would suggest a relatively high level of distribution of the more commonly diagnosed species of fungi throughout the potato fields, as a result of fungus activity during previous seasons. Neither was prevalence of dead, diseased potato aphids consistently associated with or dependent upon population density of the insect host. The percentage of dead, diseased specimens increased as population density decreased in 1952, 1953, 1954, 1959, and in 1960; the percentage increased during both increasing and decreasing host density in 1955, 1957, 1958, 1961, and in 1962 (figures 1 to 6 inclusive).

The importance of entomophthoraceous fungi as a cause of mortality in potato-infesting aphids in northeastern Maine appears to be largely governed by the relative motility of the several species of aphids. Of the four species, the potato aphid is by far the most motile and most subject to attack from fungi. The buckthorn aphid is the least motile and least affected by fungus disease. The green peach and foxglove aphids are intermediate in both respects. Aphid motility doubtless increases the chances for the aphid to encounter and to pick up the sticky conidia or resting spores of entomophthoraceous fungi adhering to the potato foliage or on the soil over which it crawls, or to come in contact with the ejected conidia floating through the air. Although no data are available, we cannot exclude the possibility of variation among these four species of aphids in susceptibility to infection by entomophthoraceous fungi.

Two examples illustrate the degree of motility of two species of aphids. Davies (1932) found that 84 percent of potato aphids and 75 percent of green peach aphids on potato plants changed feeding sites daily, while 52 percent or more of them moved to different leaves within one day. When Davies placed green peach aphids on potato plants, he found that over 99 percent of them moved to other plants within one day; several moved as far as 21 feet.

Shands and Simpson (1959) showed that under average conditions all potato plants are infested with at least one aphid when for the first time approximately 39 percent of the 3-leaf samples become infested. This percentage may range from about 25 percent when the more motile potato and foxglove aphids are abundant, to as high as 60 percent when the relatively sedentary buckthorn aphid is by far the most abundant species. When one considers the spotty initial infestation in potato plantings their data show that three of the four species are rather motile.

The feasibility of using entomogenous fungi to control aphids on potatoes in Maine is worthy of consideration. Appropriate entomophthoraceous species could be used to establish field infections each year about July 1, at the end of the spring migrations when aphid populations are very small. Such a manipulation could hold aphid populations at very low levels throughout the remainder of the field-season, except possibly when July and August are exceptionally dry. To control all four species of aphids, however, we must first find species of fungi as effective against the green peach, foxglove and buckthorn aphids as any of the locally occurring species of entomophthoraceous fungi are against the potato aphid. Effective use of any or all of the species of fungi occurring locally would provide worthwhile control of all of the potato-infesting species of aphids, especially of the potato aphid.

We suggest two approaches to determine whether early-season establishment of entomogenous fungi in potato fields can be accomplished, as follows: (1) The spores can be cultured on artificial media or on confined aphids and spread by natural or artificial means, or (2) a constant nearby source for artificial or for continuous natural multiplication and spread of disease can be accomplished by culturing the pathogens on a plentiful supply of other species of host aphids on a crop interplanted with potatoes. Dustan (1924, 1925, 1927) and Gilliatt (1925) experienced considerable success by making as many as three successive early-season orchard plantings of apple suckers infected with *E. sphaerosperma*. The fungus was collected on apple suckers taken from infested trees or from caged colonies of the insect maintained for propagation of the disease. The results of Hall and Dunn (1958) suggest that *Entomophthora exitialis* Hall and Dunn and *E. virulenta* may have been successfully established in parts of California by placing cultures of the fungi at various release sites in fields of alfalfa infested with the spotted alfalfa aphid. Shands et al. (1958) recovered *Acrostalagmus aphidum* Oudemans from dead, diseased specimens of the potato aphid collected three weeks after water suspensions of the spores had been sprayed on potato plants in small plots on August 5. On August 26, 56 percent of the dead, diseased specimens of the potato aphid collected were infected with *A. aphidum*, and they were found in one of three check plots as well as in all four of the plots sprayed with the spore suspension. This fungus may not be suited to the year-round conditions in northeastern Maine because only one dead, diseased aphid taken from potatoes since the initial recovery in August, 1955 has been diagnosed as being infected with *A. aphidum*. That single specimen was a potato aphid, collected on August 20, 1958, in a field of potatoes less than ½ mile from the one sprayed with the spore suspension of *A. aphidum* on August 5, 1955.

Strip-crop plantings of oats in Maine have been infested very early in the season with substantial numbers of the grain-infesting aphids, the apple-grain aphid, *R. fitchii* and the English grain aphid *M. avenae*. These aphids have been subject to infection with *E. thaxteriana* and possibly other species of entomophthoraceous fungi that affect the potato-infesting species of aphids. Dead, diseased specimens of the grain-infesting aphids usually have been found on the oats about a week before those of the potato-infesting species have been observed on potatoes in the contiguous plots. Some possibilities for propagation and natural or manual spread of entomogenous fungi from interplantings of host crops to the potatoes can be given. These possibilities include supplementing the infestations of auxiliary, host aphids on the interplanted crop; developing means for insuring early-season epizootics of the fungi in the populations of host aphids infesting the interplanted crop; and causing or aiding the spread of the fungi from the host aphids on the interplanted crop to the potato-infesting aphids on the potatoes.

Other, possibly better, methods of insuring epizootics of fungus disease in aphid populations on potatoes likely will become apparent as we increase our understanding of the biology and epizootiology of the entomogenous fungi. In addition, attempts should be made to find fungicides that will have little inhibitory effect on the entomogenous fungi.

SUMMARY

Prior to 1952, more than ten years of exploratory observations of the natural agents of aphid control in fields of potatoes in northeastern Maine were carried on in the course of the investigations of four species of potato-infesting aphids conducted jointly by the U. S. Department of Agriculture and the Maine Agricultural Experiment Station. These observations showed that there was much variation from year to year in the abundance and importance of parasites, predators and fungi in controlling aphids on the potato plants. In particular, the entomogenous fungi played an important role in limiting the size of aphid populations on potatoes in that area. The named species of pathogenic fungi diagnosed in dead, diseased aphids collected from potatoes in northeastern Maine included *Entomophthora thaxteriana* Petch (=*Entomophthora ignobilis* Hall and Dunn), *Entomophthora aphidis* (Hoffman), *Entomophthora sphaerosperma* (Fresenius), *Entomophthora planchoniana* Cornu, and *Entomophthora coronata* (Constantin).

From 1952 through 1962, intensive field studies of the fungus diseases were conducted by these two institutions as a part of their

continuing joint program of research on potato-infesting aphids. By use of established procedures, a large number of fields and experimental plots were quantitatively sampled for aphids, including those dead from attack by fungi. Microscopic diagnoses of the pathogenic fungi in many of the dead, diseased aphids were made by personnel of the California Agricultural Experiment Station at Riverside. Assessment of the importance of entomogenous fungi in controlling the populations of aphids on untreated potatoes was made by comparing the actual trends with the approximated trends had there been no interference by adverse factors. Comparisons among years were made of the relative seasonal abundance of the species complex of entomophthoraceous fungi determined by the laboratory diagnosis.

Field studies of aphid biology and of associated ecological factors were made near Presque Isle, Maine. Results showed that, among the biological agents affecting aphid population trends from 1952 through 1962, entomogenous fungi were outstanding in reducing the size of populations of the potato aphid developing on potatoes treated with fungicides but not with insecticides. The potato aphid was most affected by fungi and the buckthorn aphid least affected by them. The green peach and foxglove aphids were intermediate. Predators exerted a noticeably adverse effect upon aphid population trends in two of the 11 years. Employing the method of evaluation used in determining the effects of the fungi on aphid populations, we were unable to detect any perceptible effect of parasites upon population trends of the potato aphid. We do not imply that parasites are without effect on aphid populations; but merely indicate that another method of detection and evaluation may need to be developed.

The adverse effect of the fungi upon population trends of the potato aphid appeared to be manifested chiefly as a reduction in rate of aphid population growth. The reduction first became evident within a week after initial establishment of the fungus. At this time dead, diseased aphids were still very scarce, usually less than 0.4 percent of the total number of potato aphids found during the counts on the potato plants. The yearly variation in total-season mortality from fungus disease ranged from 0.23 to 12.93 percent; in most years mortality ranged from 6 to 12 percent at the seasonal peak. Ordinarily there was little, if any, increase in numbers of the aphid once the fungi became established. Generally the overall effectiveness of the entomogenous fungi increased as the time of field establishment came earlier in the summer.

Weather factors doubtless are of major importance in determining the time of initial establishment and subsequent seasonal effectiveness of the fungi. However, duration and quality of weather conditions that favor fungus activity appear to change as the season advances and alterations occur in the physical environment of the potato plants, including increased size, density, and tendency toward proneness. The evidence available indicates that a longer period of favorable environmental conditions may be required for initial establishment than for subsequent multiplication of the fungi. Evidence also indicates that conditions which result in a moderately warm microenvironment having a high relative humidity for a considerable time favor both establishment and multiplication of fungi.

Laboratory diagnoses disclosed that *E. thaxteriana* was by far the predominant species of pathogenic fungus from 1959 to 1962, and it likely was present in at least some of the earlier years. While the wide-spectrum, highly pathogenic *E. sphaerosperma* and *E. aphidis* predominated during spectacular fungus epizootics among aphids on potatoes in the 1940s, they were not particularly abundant during the period 1952 through 1962. *E. sphaerosperma* was not recorded in 1959, 1960, or 1961, but traces of this fungus occurred in the potato and green peach aphids in 1962. Dead aphids infected with *E. planchoniana* were present in small numbers in 1960 and 1962, but not in 1959 or 1961.

From 1959 through 1962, intensively collected, sequential samples of dead, diseased aphids from potatoes were subjected to diagnosis in the laboratory. The first dead, diseased potato aphid each year was found during or before the period of rapid increase in numbers of that species. The period of rapid increase, time of peak abundance, and subsequent decline in abundance of dead, diseased specimens closely followed that of the potato aphid population during three of these four years, but in 1959 these phenomena for fungus diseases lagged much behind those for the potato aphid. In 1959 the peak of aphid abundance came when the percentage of dead, diseased specimens was very small. The abundance of the dead, diseased specimens increased sharply toward the end of the season, as and after the aphid population declined to rather a low level. The phenomenon of increasing abundance of dead, diseased potato aphids during or after substantial declines in population of the insect occurred in several of the 11 years included in this study.

Although the reasons are not clear, evidence indicates that in some instances action of the fungi may have been regulated largely [illegible] ty of the host. Evidence also indicates that the activity of fungi in causing mortality of potato-infesting aphids in northeastern Maine appears to be largely governed by the relative motility of the several species of aphids or by variation among these species in susceptibility to fungus infection.

The abundance of dead aphids not infected with pathogenic fungi was not influenced by application of insecticides to the foliage of potatoes. No determination was made of possible effects of fungicides applied to the foliage of field-growing potatoes upon the activity of the entomogenous fungi because of the need to control late blight.

Two general approaches are suggested to determine whether early season establishment, multiplication and spread of entomogenous fungi can be beneficially accomplished in fields of potatoes. These include (1) mass culturing of the pathogenic fungi on artificial media or on confined aphids followed by artificial or natural spread of the spores early in July, and (2) enhancing the chances of early-season establishment, propagation and spread of the fungi in naturally occurring or supplemented populations of host aphids other than the potato-infesting species on a crop adjacent to or interplanted with the potatoes.

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