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FURTHER EVALUATION OF ENTOMOGENOUS FUNGI AS A BIOLOGICAL AGENT OF APHID CONTROL IN NORTHEASTERN MAINE

**W. A. Shands, Geddes W. Simpson,
I. M. Hall, and Corinne C. Gordon**

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Further Evaluation of Entomogenous Fungi¹ as a Biological Agent of Aphid² Control on Potatoes in Northeastern Maine

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I. M. Hall⁵, and Corinne C. Gordon⁶

INTRODUCTION

Entomogenous fungi were recognized many years ago as being important biological agents for control of aphids on potatoes in northeastern Maine (5)⁷ From 1941 to 1963, epizootics among aphids on potatoes caused by fungi were observed in populations of the potato aphid, *Macrosiphum euphorbiae* (Thomas), and the green peach aphid, *Myzus persicae* (Sulzer) on potatoes; they were also observed in populations of these aphid species on their primary host plants, swamp rose, *Rosa palustris* Marsh., and Canada plum, *Prunus nigra* Aiton, respectively (17,10).

Diagnosis of dead, diseased aphids collected during those observations revealed the presence of at least five species of pathogenic fungi affecting potato-infesting aphids in northeastern Maine. These included *Entomophthora aphidis* Hoffman, *E. coronata*⁸ (Constantin), *E. planchoniana* Cornu, *E. sphaerosperma* Fresenius and *E. thaxteriana* Petch. There was much variability among years in the proportions of dead, diseased aphids affected by these species of fungi, but *E. thaxteriana* was the predominant species from 1955 through 1963 (9, 10).

An intensive survey and study were made each year from 1952 through 1962 to determine seasonal abundance of living and dead, diseased aphids by species on potatoes and to collect many of the infected specimens for exact diagnosis. Results of the study disclosed

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⁷ Figures in parentheses refer to papers with the same number in references cited following page 32.

⁸ This species has been placed in the genus *Conidiobolus* by recent authors.

that the action of entomogenous fungi was outstanding in reducing the size of aphid populations on potatoes, in particular the potato aphid, in northeastern Maine (10). The adverse effect upon population growth of the potato aphid became evident within a week after initial activity of the fungus. At that time dead, diseased aphids were very scarce. Furthermore, the abundance of dead, diseased specimens seldom comprised a large percentage of the potato aphid population. The evidence indicated that in some instances the action of the fungi may have been regulated by factors independent of host (aphid) density; also, populations of the potato aphid never became very large once the fungal activity was detected, especially when first noted early in July.

The study already reported through 1962 (10) was continued through 1969. However, the collection of dead, diseased aphids throughout the summer was done only from 1963 through 1966; thereafter, diagnosis was limited to dead, diseased specimens intensively collected from potatoes during a 1-week period when fungal activity was greatest. This was usually in mid-August, near the seasonal peak of aphid abundance on potatoes not being treated with insecticides. We report in this bulletin the results of the study from 1963 through 1969.

PROCEDURE

The more important procedures employed in the continuation of this study were the same as described earlier (10); they are summarized below.

Field studies

Records were made during all weekly counts of aphids on all of the sample units of potato plants⁹ used in making aphid counts. Records by species were made of the numbers of both living and dead, apterous and alate, aphids on each unit or subunit of plant sample. Other records on all sample units during all aphid counts included identity, abundance and stages of all arthropod predators and of parasitized aphids. Until the plants were about eight inches high, the whole plant was the unit of sample; thereafter it was three compound leaves per plant, or portions of these leaves, which were randomly located within the top, middle and bottom thirds of plant height or stem length (7, 12). All of the units and subunits of sample were examined *in situ*. Most counts were made in small replicated plots of potatoes on Aroostook Farm, near Presque Isle, which were separated in blocks and columns by strips of oats (18), but many counts were made in commercial plantings of potatoes there and elsewhere in northeastern Maine.

⁹ As used in this bulletin, a potato plant includes all of stems and foliage arising from one potato seed-piece.

Fungicides were applied to all of the plantings of potatoes at intervals of about one week from early July until early in September for the control of late blight, *Phytophthora infestans* (Mont.) de Bary. All of the commercial plantings and many of the small-plot plantings received from one to several applications of insecticide for control of aphids or other insects, but many of the small plots were not treated with an insecticide. The applications of fungicides and insecticides to potatoes in the small plots were made with a tractor-mounted power sprayer equipped with a spray boom especially designed to provide thorough spray coverage of upper and under surfaces of leaves (20). The fungicides, Maneb or tank-mix Zineb, were applied at rates recommended by the Maine Cooperative Extension Service for control of late blight.

From 1 to 10 dead aphids of the same species per plot or per field were dislodged from the sample leaves of potato plants during the aphid counts and allowed to fall or were placed into glass vials (10). When each collection was completed, the vial was closed with a cork stopper, then stored at 45°F until the end of the week, when all vials were airmailed to Riverside, California for diagnosis. Plugs of sterilized cotton were substituted for the cork stoppers as the vials were prepared for shipment.

Diagnosis of dead aphids

Diagnoses of the dead aphids in the vials were made soon after each week's collection was received in Riverside. The specimens were examined in wet-mount preparations by brightfield or phase-contrast microscopy to determine the cause of mortality. Examination of very dry individuals, into which water would not readily penetrate, was facilitated by the use of aceto-carmin stain, as advocated by Hall and Bell (3). Identification of the fungi was made from the characteristics of growth stages, particularly conidia, conidiophores and hyphal bodies, present on and/or within the body of each specimen. In most instances, it was possible to identify each pathogen to species level, but on occasion, the problem of the presence of only hyphal bodies or resting spores, as mentioned by Dean and Wilding (1), limited determination to genus. When no stages of a pathogen were detected, the cause of mortality was recorded as nonmicrobial.

Method of assessing relative importance of entomogenous fungi as a biological agent of aphid control

Attempts to recognize and distinguish among the effects of biological agents of aphid control upon aphid population trends and to assess

the relative importance of each agent have not been entirely satisfactory. This was, in part, because several factors of environmental resistance probably operated simultaneously at variable levels of intensity to effect the resulting changes in aphid abundance. These factors include parasitic and predatory insects, entomogenous fungi and physical factors. We concluded from earlier studies that (a) the naturally-occurring insect parasites, while of importance, did not exert an appreciable, lasting impact upon population trends of the potato aphid (11), (b) while arthropod predators were of considerable, variable importance during many years in reducing the potential size of the developing aphid population, they apparently were responsible for a striking degree of aphid control in only 2 out of the 20 instances considered; but, along with the pathogenic fungi, were largely responsible in the remaining instances (16), and (c) entomogenous fungi frequently were of outstanding importance in limiting the potential size of potato aphid populations (10). Physical factors seldom appeared to exert a substantial or lasting deleterious effect upon aphid population trends on untreated potatoes in the cool, humid climate of northeastern Maine during the years of study upon which these results were based (13, 14, 10).

Thus, the major problem in evaluating the biological agents of aphid control appears to be that of recognizing and separating the differences in effects of the fungi from those of predators. In earlier studies our attempts to assess the actions of entomogenous fungi were limited to the potato aphid (10), while those to assess the importance of predators concerned two groupings of the aphids on potatoes, viz., the potato aphid as one group and the other three potato-infesting species (the green peach aphid, the buckthorn aphid, *Aphis nasturtii* Kaltenschach, and the foxglove aphid, *Acyrtosiphon solani* (Kaltenschach)), as a second group.

The method we used for assessing the importance of entomogenous fungi against the potato aphid was based on the observation that, (a) without significant interference from adverse environmental factors, aphid population increase during the growth phase on potatoes in northeastern Maine approached a straight line when \log_{n+1} of the aphids per unit of plant sample was plotted against time (8, 10, 11, 15, 16), and (b) an increase in environmental resistance of sufficient magnitude from one or more of the biological agents, on untreated potatoes, most likely entomogenous fungi or predators, resulted in a downward departure from the expected rate of aphid increase. In the case of the potato aphid, which was especially susceptible to fungal attack, the initial downward departure from the expected rate of population growth in most instances was coincidental or closely associated with the initial finding of a dead,

diseased potato aphid during the weekly count of aphids on potatoes. To determine this degree of association, composite graphs were made to show the seasonal trends of potato aphid abundance and of the percentage of dead, diseased potato aphids (10).

The method of assessing the importance of predators involved an attempt to separate the effect of fungal attacks on the potato aphid from that of other causal agents, including predators. Simultaneous consideration was given to graphic comparisons of seasonal trends of predator abundance (percentage of plant samples infested by mobile stages of predators) in relation to the rates of population increase of two groupings of aphids, viz., the potato aphid, and the other three potato-infesting species, combined. In these comparisons consideration was also given to the time of first finding dead, diseased aphids in each species-grouping. The 3-species grouping of aphids was added because observations indicated that these species were less susceptible to fungal attack than was the potato aphid. The beginning of the downward departure from the expected rate of population growth of the aphids in that grouping, therefore may have differed from that of the potato aphid (15).

In the present study, an attempt was made to identify the action and assess more exactly the importance of fungi for controlling each of three species of aphids and to estimate the relative susceptibility of each of these three species to entomogenous fungi. The species were the potato, green peach and buckthorn aphids. More exact identification and exclusion of the role of predators in evaluating fungal action was made possible by finding that an index of the threshold level of suppressive effect from predators resulting in a downward departure from the expected rate of aphid increase, on average, was equivalent to that level of abundance occurring when about 2.3% of the 3-leaf plant-sample units were infested with mobile stages of predators (16). The following considerations of conditions in 1957 and in 1967 illustrate the method of studying the considerations employed in assessing the relative importance of entomogenous fungi as biological agents in suppressing aphid populations on untreated potatoes. During both years there was considerable variation in abundance of dead, diseased aphids and of predators; in each year, both agents provided substantial degrees of aphid population suppression.

Assessment of conditions in 1957

In 1957, the mid-week starting dates of downward departures from the expected rates of population increase were about July 31 for the green peach aphid, August 7 for the potato aphid, and probably sometime between August 7 and 14 for the buckthorn aphid; the first dead,

diseased specimens of these aphid species were found July 31, and August 14, respectively (Figure 1). Although not shown in Figure 1, our records revealed that the threshold level of predator abundance capable of causing a downward departure from the expected rate of aphid increase was exceeded during the period August 7 to September 4 and that the percentage of plants infested by mobile stages of predators constantly increased during the period, reaching a peak of 27.8% infestation of the plant sample units. From consideration of these conditions it appeared that (a) abundance levels of either fungi or predators were high enough to have initiated the downward departure from the expected rate of potato aphid increase, (b) entomogenous fungi were principally responsible for initiating the downward departure from the expected rates of increase of the green peach aphid, because predator abundance at the time was below the threshold level capable of causing a decline and because observations indicate that downward departures frequently can be detected when dead, diseased aphids are present (10). The very sharp downward departure in rate of increase probably resulted from both fungal attack and predators; and (c) the downward departure in the instance of the buckthorn aphid could have been initiated by either fungal attack or by predators. However, it would appear that the predators were of greater importance than fungal attack because of continuing suppression afforded by their increasing abundance from August 7 until September.

Assessment of conditions in 1967. In 1967, the mid-week starting dates of downward departures from the expected rates of population increase were approximately July 19 for the potato aphid, July 26 for the buckthorn aphid and August 9 for the green peach aphid. The first dead, diseased specimens of the potato aphid were found on July 19, while the corresponding date for the buckthorn and green peach aphids was July 26 (Figure 2). The starting dates of downward departures from the expected in rates of population increase of the potato and buckthorn aphids were the same as those for finding the first dead, diseased specimens, although only 0.2% or 0.1% of the populations of the two species consisted of dead, diseased specimens on these dates. On the other hand, a downward departure in the instance of the green peach aphid was not detected until one week after the relatively large 1.6% of its numbers were dead, diseased specimens during the week of initially finding them on the potato plants. The threshold level of predator abundance capable of initiating a downward departure from the expected in rate of aphid increase was exceeded throughout the period July 26 to September 5 (Table 2).

In view of these conditions, it would appear that downward departures of the potato and buckthorn aphids were initiated by entomo-

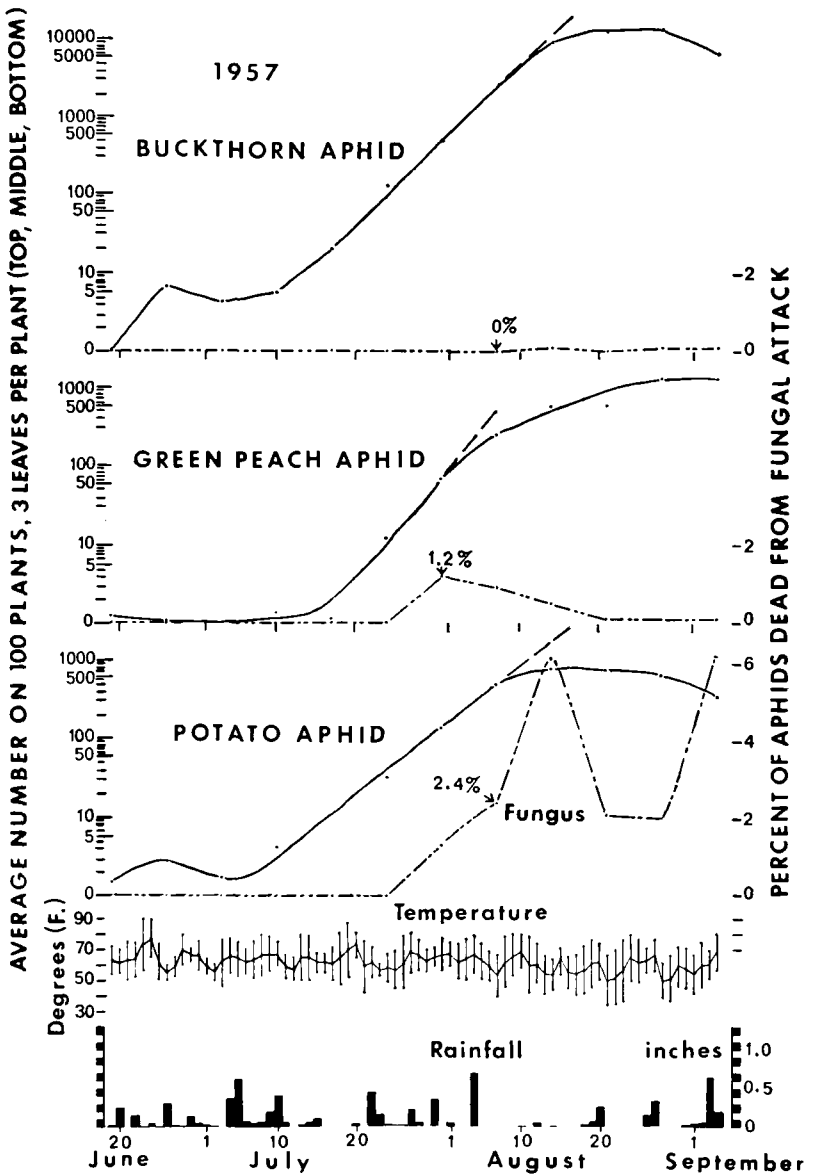


Figure 1. Population trends of the potato, green peach and buckthorn aphids and their downward departures from expected rates of increase in relation to prevalence of dead, diseased aphids of these species, respectively, on potatoes not treated with insecticides in 1957.

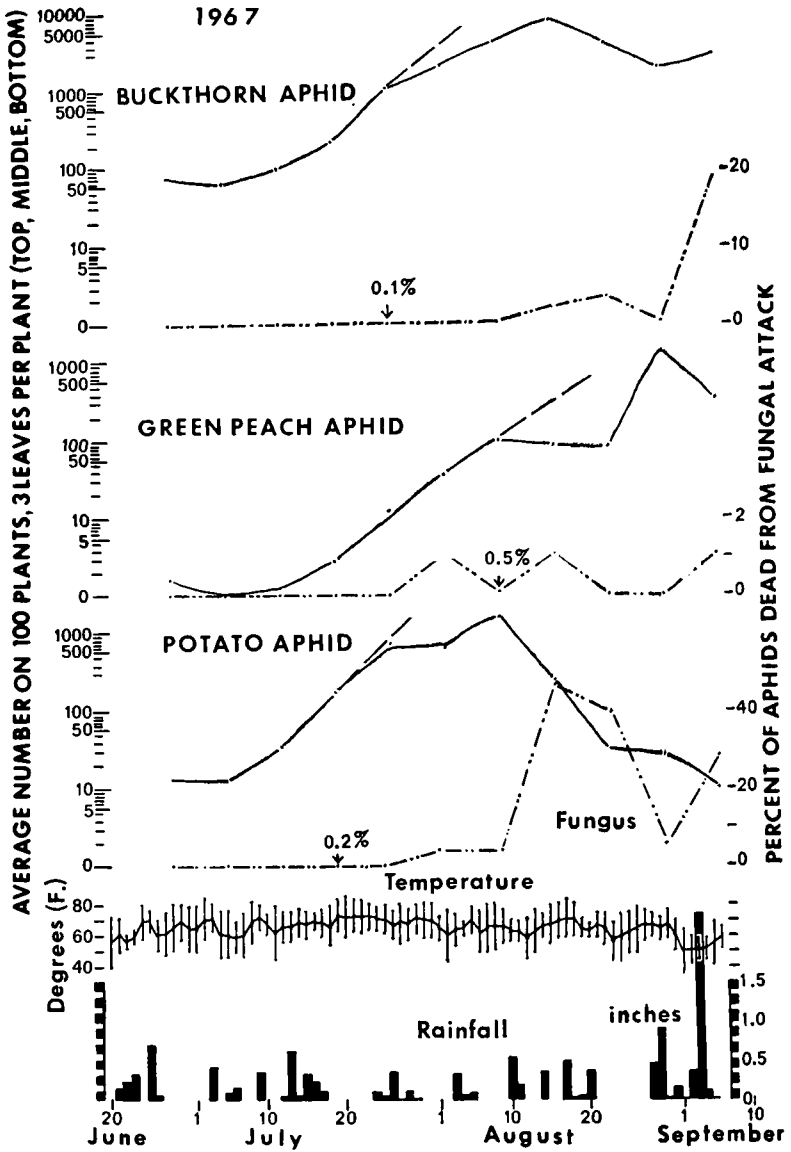


Figure 2. Population trends of the potato, green peach and buckthorn aphids and their downward departures from expected rates of increase in relation to prevalence of dead, diseased aphids of these species, respectively, on potatoes not treated with insecticides in 1967.

genous fungi; those of the green peach aphid may have been due largely to the action of predators, although fungal activity doubtless could have been responsible for this or was at least of some importance. From July 19 to the 26th, fungal attacks apparently were responsible for the rather sharp downward departure from the expected rate of potato aphid increase. After July 26, the effects of both agents, predators and fungi, contributed greatly to the rather sharp downward departures in the populations of all three species of aphids. Increased importance of fungi from August 9 to 21 was indicated both by increased abundance of the dead, diseased aphids and a sharper downward departure from the expected rate of aphid increase. Rapidly increasing abundance of dead, diseased aphids of all three species during the period August 30 to September 5 was associated with sharp decreases in abundance of the potato and green peach aphids but not in that of the buckthorn aphid. During that period in 1967 there was an increase in abundance of the buckthorn aphid even though fall migrants were maturing on potatoes and then leaving them for the primary host.

RESULTS AND DISCUSSION

Field counts of living and dead aphids and of arthropod predators on untreated potatoes during the period 1963 to 1969, inclusive, were made each year in three to six locations on Aroostook Farm; in most years there were five or six locations. The weekly averages of the counts on untreated potatoes were based on the examination of a total of 567 to 1620 plant-sample units when the unit was three leaves per plant, or 1700 to 4900 potato leaves; the weekly average for the seven year period consisted of 860 plant-sample units, or 2580 leaves. The weekly field counts on treated potatoes were made in about the same number of locations on Aroostook Farm as on untreated potatoes but the numbers of plant sample units examined weekly usually were substantially larger on treated than on untreated potatoes. From 10 to 13 weekly counts were made each year on both the treated and untreated potatoes.

Prevalence of dead, diseased aphids, 1963 through 1969

There were large differences among years in abundance of the living and of the dead, diseased aphids from 1963 to 1969, inclusive (Table 1). The potato aphid was consistently the most abundant species, followed by the buckthorn, green peach, and foxglove aphids. However, during two years the buckthorn aphid was the predominant species. The green peach aphid was more abundant than the buckthorn aphid in two years, but never the predominant species. The foxglove aphid was scarce throughout this seven-year period.

The yearly percentage of the all-season numbers of dead specimens of the potato aphid found on aphid-count leaves ranged from 0.7 in 1968 to 6.4 in 1967. Corresponding ranges were 0% to 0.7%, 0% to 0.1%, and 0% to 6.8% for the green peach, buckthorn and foxglove aphids, respectively. The percentages of dead, diseased aphids of each species were about the same as those found during the years 1952 through 1963 (8) except in the instances of the foxglove aphid, which was too scarce from 1963 through 1969 for percentages to be meaningful.

TABLE 1

All-season prevalence of dead, diseased aphids on foliage of potatoes on Aroostook Farm treated with insecticides, 1963 through 1969.

Year	Potato Aphid		Green Peach Aphid		Buckthorn Aphid		Foxglove Aphid	
	Number examined ^a	% dead diseased	Number examined ^a	% dead diseased	Number examined ^a	% dead diseased	Number examined ^a	% dead diseased
1963	139	4.1	91	0.7	811	0.1	1	6
1964	269	2.5	211	0.2	40	0.1	2	1
1965	128	1.6	35	0.2	14	0	T ^b 18	0
1966	140	1.7	9	0.2	24	T ^c	T ^b 20	0
1967	285	6.4	86	0.7	1783	2.1	T ^b 22	0
1968	118	0.7	5	0	21	0	T ^b 37	0
1969	354	3.4	55	0.7	51	0.1	T ^b 6	0

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

^b T = less than 0.5 hundred, or 50.

^c T = less than 0.05%

Seasonal abundance of living and of dead, diseased aphids and of mobile stages of arthropod predators

Table 2 contains weekly abundance records of living and of dead, diseased¹⁰ potato aphids and of mobile stages of arthropod predators on untreated potatoes located on Aroostook Farm from 1963 through 1969. Comparable data for living and for dead, diseased green peach and buckthorn aphids are in Table 3. The range in average number of potato aphids on three leaves per plant at the seasonal peak was from 1.2 in 1968 to 16.4 in 1967. The comparable range for the green peach aphid was 0.03 in 1968 to 14.4 in 1967, while for the buckthorn aphid it was from 0.07 in 1969 to 46.9 in 1966. The time of the seasonal peak ranged from July 31 in 1969 to August 19 in 1964 for the potato aphid, from August 7 in 1969 to August 30 in 1967 for the green peach aphid, and from August 7 in 1967 and 1968 to August 19 in 1964 for the buckthorn aphid. The peaks of all three species never occurred on the same date during the seven-year period, but that of two of the species

¹⁰A small proportion of these were doubtless nonfungus specimens, since not all of the dead aphids observed during field counts were subjected to diagnosis in the laboratory (see Table 3).

fell on the same date in six of the years. On average, the seasonal peaks were about August 8, 13, and 17 for the potato, buckthorn, and green peach aphids, respectively. Doubtless, the times of the peaks would have been later and aphid numbers at the peaks would have been larger in the absence of fungal activity.

The first date of finding dead, diseased specimens of the potato aphid varied from July 3 to August 3; for the buckthorn aphid the comparable range was from July 26 to August 17 and, for the green peach aphid it was August 2 to 17.

The range in dates of the largest percentages of dead, diseased aphids were August 14 to 26 for the potato aphid, August 7 to 24 for the buckthorn aphid, and August 7 to 28 for the green peach aphid.

During the seven years a maximum of 47.7% of the potato aphid population was comprised of dead, diseased specimens in 1967; the maximum was 2.4% for the green peach aphid. A maximum of 0.8% dead, diseased buckthorn aphids at any time during these years was exceeded only in 1967 when there was a late season peak of 18.9%. In most years the percentage of dead, diseased specimens on potato leaves was largest in the case of the potato aphid.

Assessment of importance of fungi in initiating downward departures from the expected rate of aphid population growth

Weekly averages shown on mid-week dates are inadequate for assessing with pinpoint accuracy the relative importance of biological agents in initiating downward departures from the expected rate of aphid population growth on untreated potatoes. For example, weekly averages for two consecutive work weeks when shown as being on the two mid-week dates may contain data from observations made within two days or as far apart as 12 or 13 days instead of being at the indicated interval of seven days. However, Table 4 contains some of the more pertinent data from Tables 2 and 3 which appear to separate the roles of entomogenous fungi and predators in initiating the downward departures from the expected rates of population growth of the potato, green peach, and buckthorn aphids.

The potato aphid. The initial detection of dead, diseased potato aphids was coincidental with the beginning of the downward departures from the expected rate of increase in three of the seven years from 1963 through 1969, viz., in 1966, 1967, and 1969. In one of these years (1965) dead, diseased specimens were found one week before that time; in two years (1963, 1964) one week after. In 1968, a year with two downward departures from the expected rate of increase, they were first found one week after the first departure date, and one week before that

TABLE 2

Population trends and prevalence of dead, diseased *M. euphorbiae*, and percent of plants^a infested by mobile stages of predators in untreated plantings of potatoes on Aroostook Farm, 1963 to 1969, inclusive.

Date ^b	Avg no. apterae per 100 plants ^a	% dead diseased	% plants ^a infested with predators	Date ^b	Avg no. apterae per 100 plants ^a	% dead diseased	% plants ^a infested with predators	Date ^b	Avg no. apterae per 100 plants ^a	% dead diseased	% plants ^a infested with predators
<u>1963</u>				<u>1964</u>				<u>1965</u>			
June 19	5.2	0	1.7	June 17	0.2	0	1.6	June 23	3.9	0	1.2
26	7.4	0	1.5	24	4.8	0	4.4	30	26.4	0	2.6
July 3	14.6	0	1.2	July 1	5.3	0	7.3	July 7	27.8	0	2.8
10	10.9	0	0.8	8	3.3	0	2.2	15	37.0	0	1.9
17	15.7	0	0.4	15	12.5	0	1.2	21	39.8	0	1.0
24	127.8	0 ^c	1.2	22	50.7	0 ^c	2.0	28	125.7	0	0.7
31	409.4	0.4	1.7	29	119.2	0.1	3.0	Aug. 3	264.1	0.3	1.6
Aug. 7	827.6	1.6	4.8	Aug. 5	149.2	0.7	2.7	11	1034.4	0.7 ^c	6.6
14	363.0	11.5	8.3	12	326.5	1.2	2.4	18	453.0	4.8	15.5
21	121.2	16.1	10.6	19	405.1	3.6	3.6	25	63.2	2.2	2.1
28	13.9	13.9	14.2	26	349.7	5.3	2.0	Sept. 1	3.7	0	0.3
Sept. 4	1.0	0	5.7	Sept. 2	154.3	0.8	1.4				
				9	18.8	0.7	1.1				
<u>1966</u>				<u>1967</u>				<u>1968</u>			
June 22	0.5	0	3.9	June 27	12.8	0	1.4	June 26	2.3	0	0
29	0.4	0	3.8	July 5	12.0	0	0.5	July 3	7.8	0.7	4.8
July 6	0.4	0	1.0	11	35.3	0	0.5	10	17.7	0 ^c	0.6
13	0.6	0	0.6	19	183.8	0.2 ^c	0.4	17	31.3	0	4.0
20	1.3	0	0.5	26	779.3	0.2	10.5	24	14.4	0	2.9
27	9.2	0	0.4	Aug. 2	690.7	4.1	8.2	31	40.1	0.6	0.3

Aug. 3	57.4	0.1 ^c	1.3	10	1641.8	4.0	4.7	Aug. 7	124.3	0.7 ^c	1.4
10	42.9	0.4	2.0	17	249.5	47.7	8.4	14	96.8	0.8	0
17	35.8	5.8	4.5	24	31.6	39.9	7.1	21	98.3	0.4	0.3
24	7.7	9.2	2.6	30	27.0	4.9	5.3	28	49.7	0.7	0
31	4.1	0	0.1	Sept. 5	9.2	28.3	3.6				
<u>1969</u>											
				June 27	10.5	0	1.3				
				July 3	13.3	0	3.3				
				10	10.7	0	0				
				17	8.7	0	0				
				24	223.3	0.2 ^c	0				
				31	740.1	0.1	0				
				Aug. 7	627.1	6.5	2.7				
				15	77.3	24.3	9.3				
				21	8.0	25.0	1.7				
				28	5.5	9.1	1.0				

^a 3 leaves per plant (top, middle, bottom).

^b Mid-week date.

^c Approximate beginning date of downward departure from the expected rate of aphid population increase.

TABLE 3

Population trends and prevalence of dead, diseased *Myzus persicae* and *Aphis nasturtii* in untreated plantings of potatoes on Aroostook Farm, 1963 to 1969, inclusive.

Date ^a	Avg no. apterae per 100 plants ^b	% dead diseased	Date ^a	Avg no. apterae per 100 plants ^b	% dead diseased	Date ^a	Avg no. apterae per 100 plants ^b	% dead diseased
<i>Myzus persicae</i>								
<u>1963</u>			<u>1964</u>			<u>1965</u>		
June 19	0	0	June 17	0	0	June 23	0.2	0
26	0.1	0	24	0.1	0	30	3.8	0
July 3	0	0	July 1	0.8	0	July 7	1.2	0
10	0	0	8	0.6	0	14	1.4	0
17	1.2	0	15	2.4	0	21	2.1	0
24	24.7	0	22	13.8	0	28	10.8	0
31	128.0	0 ^c	29	59.5	0 ^c	Aug. 3	41.5	0
Aug. 7	318.6	T ^d	Aug. 5	64.1	0	11	251.7	T ^{cd}
14	397.3	0.7	12	154.5	0.1	18	227.1	0.2
21	293.9	1.3	19	243.0	0.2	25	57.8	0.6
28	80.2	2.4	26	266.4	0.6	Sept. 1	2.3	0
Sept. 4	9.9	0	Sept. 2	247.3	0			
			9	220.3	T			
<u>1966</u>			<u>1967</u>			<u>1968</u>		
June 22	0	0	June 27	0.6	0	June 26	0.7	0
29	0	0	July 5	0	0	July 5	0	0
July 6	0	0	11	0.3	0	10	0.1	0
13	0	0	19	1.8	0	17	0.9	0 ^c
20	0	0	26	11.4	0	24	0.2	0
27	0.1	0	Aug. 2	36.3	1.6	31	0.4	0
Aug. 3	1.7	0 ^c	10	96.0	0.5 ^c	Aug. 7	3.4	0 ^c

10	4.5	0	17	86.6	1.7	14	0.9	0	
17	3.1	0.9	24	80.6	0	21	11.6	0	
24	1.1	0	30	1444.0	T	28	3.2	0	
31	0.5	0	Sept. 5	358.6	1.8				
			<u>1969</u>						
			June 27	0	0				
			July 3	0	0				
			10	0	0				
			17	0	0 ^c				
			24	15.3	0				
			31	11.8	0				
			Aug. 7	186.6	1.1				
			15	40.3	1.9				
			21	8.5	0				
			28	5.5	0				
			<i>Aphis nasturtii</i>						
			<u>1964</u>			<u>1965</u>			
<u>1963</u>			June 17	0	0	June 23	1.2	0	
June 19	7.9	0	24	1.1	0	30	2.1	0	
26	16.7	0	July 1	1.7	0	July 7	3.7	0	
July 3	27.4	0	8	1.1	0	14	0	0	
10	11.2	0	15	3.0	0	21	1.0	0	
17	48.6	0	22	12.5	0	28	11.1	0 ^c	
24	180.2	0	29	31.7	0 ^c	Aug. 3	15.8	0	
31	981.1	T ^d	Aug. 5	29.4	0	11	44.3	0	
Aug. 7	3293.7	T ^c	12	50.3	0.1	18	148.6	0	
14	3572.7	0.1	19	54.8	0.2	25	7.1	0	
21	2451.4	0.4	26	31.4	0	Sept. 1	0.2	0	
28	574.1	0.3	Sept. 2	8.9	0				
Sept. 4	12.9	0	9	13.4	0				

TABLE 3 (Cont.)

Date ^a	Avg. no. apterae per 100 plants ^b	% dead diseased	Date ^a	Avg. no. apterae per 100 plants ^b	% dead diseased	Date ^a	Avg. no. apterae per 100 plants ^b	% dead diseased
<u>1966</u>			<u>1967</u>			<u>1968</u>		
June 22	0.1	0	June 27	79.6	0	June 26	4.3	0
29	0.1	0	July 5	67.8	0	July 3	5.9	0
July 6	Te/	0	11	108.0	0	10	13.6	0 ^c
13	Te/	0	19	239.9	0	17	7.2	0
20	0.3	0	26	1182.1	0.1 ^c	24	2.2	0
27	1.1	0	Aug. 2	232.3	0.1	31	4.5	0
Aug. 3	5.6	0 ^c	10	4687.8	0.2	Aug. 7	18.3	0 ^c
10	8.7	0	17	8209.3	2.1	14	2.0	0
17	5.1	0.3	24	4282.8	3.5	21	6.1	0
24	5.6	0	30	2024.0	0.2	28	3.1	0
31	2.2	0	Sept. 5	3111.8	18.9			
			<u>1969</u>					
			June 27	1.2	0			
			July 3	0.8	0			
			10	0	0			
			17	1.0	0			
			24	10.5	0 ^c			
			31	33.8	0			
			Aug. 7	74.3	0.8			
			15	49.5	0.5			
			21	26.5	0			
			28	28.5	0			

a Mid-week date.

t 3 leaves per plant (top, middle, bottom).

c Approximate beginning date of downward departure from the expected rate of aphid population increase.

d Less than 0.05%.

e Less than 0.05/100 pl.

of the second date (Table 4). Thus, dead, diseased specimens of the potato aphid were first found from one week before to one week after the start of the downward departure from the expected rate of population growth of this aphid. As indicated in the preceding paragraph, the averages for these mid-week dates could have been made from observations within a period of 11 days. It would appear that predators alone could have been responsible for initiating the downward departures observed in possibly five of these seven years if we use 2.3% of the 3-leaf plant samples infested by mobile stages of predators as the threshold level of predator abundance capable of initiating a downward departure from the expected rate of aphid increase. The percentages of plant sample units having mobile stages were below that level at these times in five of the seven years (Table 2). Doubtless, the levels of predation shown in Table 2 were sufficiently high to enhance the degree of downward departure as shown by the duration of periods, each year, having more than 2.3% of the plant sample units infested by mobile stages (Table 4).

The green peach aphid. In only one of the seven years, 1965, was the date of first detection of dead, diseased green peach aphids on potatoes coincidental with the beginning of downward departures from the expected increase rate for that species (Table 4). Dead, diseased specimens were found one week before the start of the downward departure in one year (1967), one week afterward in one year (1963), two weeks afterward in two years (1964 and 1966) and three weeks afterward in one year (1969). No dead, diseased specimens were found in one year (1968).

Populations of predators on potato plants were in excess of the threshold level of 2.3% of the 3-leaf units of sample infested by mobile stages at the beginning of the downward departures in 1964 and 1967 and at the threshold of the first downward departure in 1968, but were below it at these times in 1966, 1963, 1965, 1968, and 1969 (Tables 2 and 3). It would thus appear that entomogenous fungi may have been largely responsible for initiating the downward departures from the expected rates of increase of the green peach aphid in three of the seven years; the levels of predation were adequate to initiate them in two years and to contribute to them in all but one (1969) of the remaining five.

The buckthorn aphid. The time of first detection of dead, diseased specimens of the buckthorn aphid was coincidental in two of the seven years (1963 and 1967) with the beginning of the downward departure from the expected rate of increase in population (Table 4). In one year (1963) diseased specimens were found one week before the

TABLE 4

Occurrence and prevalence of dead, diseased aphids and of periods during which predator abundance exceeded the threshold level for effecting demonstrable aphid control in relationship to the beginning of the downward departures from the expected rate of increase of aphid populations in plantings of untreated potatoes on Aroostook Farm, 1963 to 1969, inclusive.

Approximate beginning date of downward departures and prevalence of dead, diseased aphids on those dates							
	Potato aphid		Green peach aphid		Buckthorn aphid		Inclusive dates of predator abundance in excess of threshold ^a
	Date	% dd	Date	% dd	Date	% dd	
1963	July 24	0 ^c	July 31	0 ^c	Aug. 7	T ^b	Aug. 7 to Sept. 4
1964	July 22	0 ^c	July 29	0 ^e	July 29	0 ^e	June 24 to July 1, and July 29 to Aug. 19
1965	Aug. 11	0.7 ^d	Aug. 11	0 ^c	July 28	0 ^f	June 30 to July 7 and Aug. 11 to 18
1966	Aug. 3	0.1	Aug. 3	0 ^e	Aug. 3	0 ^e	June 22 to 29, and Aug. 17 to 24
1967	July 19	0.2	Aug. 10	0.5 ^d	July 26	0.1	July 26 to Sept. 5
1968	July 10	0 ^c	July 17		July 10	0 ^f	
	Aug. 7	0.7 ^d	Aug. 7	0 ^f	Aug. 7	0 ^f	July 3, and July 17 to 24
1969	July 24	0.2	July 17	0 ^g	July 24	0 ^e	July 3, and Aug. 7 to 15

^a A minimum of 2.3% of the plants populated by mobile stages of predators, using the 3-leaf method of count (top, middle, bottom leaves).

^b Less than 0.05%.

^c Dead, diseased specimens of this species were found during the aphid count made 1 week later.

^d Dead, diseased specimens of this species were found during the aphid count 1 week earlier.

^e Dead, diseased specimens of this species were found during the aphid count 2 weeks later.

^f No dead, diseased aphids of this species were found during any aphid count.

^g Dead, diseased aphids of this species were found during the aphid count made 3 weeks later.

beginning of the downward departure, and in three years (1964, 1966, 1969) they were not found until three weeks afterward. No dead, diseased buckthorn aphids were found in two years, 1965 and 1968. Populations of predators in two of the seven years (1964, 1967) and at the first departure in 1968 were in excess of the threshold level of 2.3% of the 3-leaf sample units populated by mobile stages at the beginning of the downward departure from the expected rate of buckthorn aphid increase on untreated potatoes and were below it at these times in the remaining four years, 1963, 1965, 1966, 1969 and at the time of the second departure in 1968 (Tables 2, 3). It would appear that in two years (1963 and 1967) fungal activity probably initiated the downward departures observed and may have contributed to them in two other years (1964 and 1966). Either fungi or predators could have been responsible for the situation observed in 1967. No fungal activity was observed in populations of the aphid in 1965 or in 1968.

Comparisons of responses to the fungi among aphid species

The data in Tables 2, 3 and 4 provide a basis for assessing the relative susceptibility of the potato, green peach, and buckthorn aphids to entomogenous fungi. The first dead, diseased potato aphid, on average, was found about 10 days before finding the first dead buckthorn aphid, and about 12 days before the first dead green peach aphid was found. The average beginning of the downward departures from the expected in rates of population-growth of the potato aphid occurred about two days earlier than that of the buckthorn aphid, and about five days earlier than that of the green peach aphid. The percentage of dead, diseased potato aphids each year was consistently much larger than that of green peach aphids which, in turn, was generally somewhat larger than that of buckthorn aphids. During the seven years, dead, diseased potato aphids were found in an average of 5.7 counts each year as compared to 2.7 counts for the green peach aphid and 2.4 counts for the buckthorn aphid. The responses of the buckthorn aphid to the presence of entomogenous fungi were more variable than those of the green peach aphid. The suppressive effect of fungal activity upon rate of increase was much greater in the instance of the potato aphid than was the case with either the green peach or buckthorn aphids; it was more variable upon population trends of the buckthorn than upon those of the green peach aphid. For these reasons, the potato aphid was by far more susceptible to the fungi than either the green peach or buckthorn aphids and, we believe, the buckthorn aphid may be slightly less susceptible than the green peach aphid to attacks by the species of entomogenous fungi encountered in these studies.

Environmental conditions affecting activity of fungi

The study from 1963 through 1969 provided little additional knowledge of factors favoring the initiation of fungal activity among aphids in fields of potatoes. Doubtless moisture or high relative humidity was important for germination of the resting spores (2, 4). However, we have only limited knowledge of the overwintering sites of the fungi of concern in northeastern Maine, the time and place of germination of their resting spores, whether or not their germination is initiated or influenced by factors other than moisture, and the means of dispersal of spores initiating the infection of the aphids under field conditions (10). Such knowledge would provide a better basis for understanding and study of the factors affecting abundance and effectiveness of fungi in controlling aphids on potatoes. Extended periods of dry weather with above-normal temperatures, and hot, dry winds were found to prevent inducement of an epizootic of green peach aphids from fungal activity on peach trees (6). Abundance at the seasonal peak and the all-season prevalence of dead, diseased aphids on potatoes were associated in a general way with above-normal rainfall in August and, to some extent, in July (Table 5).

TABLE 5

The relationship between rainfall and abundance of dead, diseased potato aphids (*Macrosiphum euphorbiae*) on foliage of field-growing potatoes, 1963 through 1969.

Year	Rainfall, inches ^a			Percent dead diseased		
	June	July	August	Untreated		Treated with Insecticide
				Peak ^b	Entire season	Entire season
1963	1.52	4.35	7.00	16.1	4.1	2.2
1964	1.18	5.58	3.57	5.3	2.5	1.8
1965	1.71	3.57	4.32	4.8	1.5	1.5
1966	1.70	4.25	1.39	9.2	1.7	2.7
1967	2.55	3.11	4.16	47.7	6.4	9.2
1968	1.62	3.37	2.38	0.8	0.5	0.9
1969	3.87	3.59	5.36	25.0	4.1	3.2

^a The average inches of rainfall during June, July, and August was 3.80, 3.81, and 3.31, respectively.

^b When dead, diseased aphids comprised the largest percentage of total aphid population.

There was no consistent relationship among years between the amount of rainfall in June, July, or August and the all-season prevalence or the time of peak and level of abundance of dead, diseased potato aphids at the peak. However, increasing percentages of dead, diseased aphids appeared to be associated with periods of frequent rainfall occurring during or for several days before the period of increase (Table 6; Figures 1, 2) (10). Neither were there consistent relationships among years

TABLE 6

Weather conditions associated with time of establishment and of perceptible effectiveness of fungal activity upon populations of aphids on untreated, field-growing potatoes 1963 through 1969.

Year	Date of first dead diseased aphids ^a	First perceptible reduction in rate of pop. growth ^b		Days before first finding dead, diseased aphids ^a											
				Rainfall (inches)			No. days Having rainfall			Daily mean temp. (F°)			Avg. daily range in temp. (F°)		
				15	10	5	15	10	5	15	10	5	15	10	5
				Days	Days	Days	Days	Days	Days	Days	Days	Days	Days	Days	Days
1963	7/29	7/24	0	.69	.58	0	5	2	0	71.3	72.9	77.6	21.7	23.4	20.8
1964	7/29	7/22	0	.78	.73	.04	8	5	1	68.1	65.2	67.5	22.7	22.0	21.4
1965	7/28	7/31	0.3	2.28	2.17	0.14	11	8	3	64.4	63.2	64.6	22.8	21.9	23.2
1966	8/ 2	8/ 3	0.1	2.22	1.18	.38	8	5	2	64.3	64.6	63.3	23.2	23.9	23.8
1967	7/17	7/19	0.2	2.37	1.67	1.29	9	6	5	66.8	67.6	68.1	21.1	20.0	16.6
1968	7/ 4	7/10	0.7	1.41	.88	.81	10	6	3	60.3	61.7	65.2	21.1	22.0	21.6
1969	7/24	7/24	0.2	1.25	.17	.13	7	3	2	64.2	66.6	62.0	21.9	23.7	25.2

^a In all instances, the potato aphid; however, in 1965 the diagnosed specimen came from plots not included in this phase of the study.

^b Except in 1965, these are beginning dates of the downward departure from the expected rate of potato aphid increase; the 1965 date is that for the same phenomenon of the buckthorn aphid.

between amount of rainfall, number of days with rainfall, daily mean temperature, or average daily range in temperature during periods of 5, 10, or 15 days before finding dead, diseased aphids on potatoes, the beginning date of downward departure from the expected rate of aphid increase, the date of the peak of abundance of the dead, diseased aphids, abundance at the peak, or the all-season abundance (Tables 1, 5, 6; Figures 1, 2).

Diagnoses of dead, diseased aphids

Diagnoses of dead, diseased aphids collected on potatoes from 1963 through 1969 revealed that *E. thaxteriana* was by far the predominant species of pathogenic fungus, except in the mid-August collections of 1968 when *E. planchoniana* was most commonly found (Table 7). Other species of fungi included *E. aphidis*, *E. coronata*, *E. sphaerosperma*, *E. lageniformis* Thaxter, and *E. obscura* Hall and Dunn. Representing new records for northeastern Maine, *E. lageniformis* was diagnosed from two dead specimens of the buckthorn aphid collected in mid-August 1963, and *E. obscura* was collected on August 12, 1965.

Yearly variation in seasonal abundance of the fungi in relation to weather. The more outstanding features of Figures 3, 4, 5, and 6 appear to be (a) size of populations of the potato aphid continued to increase for varying lengths of time after the presence of dead, diseased aphids were present in the population (as differentiated from the beginning and course of the downward departure from the expected rate of population growth, see Figures 1, 2 and Tables 2, 3); (b) once well established, the rate of increase in percentage of dead, diseased specimens was generally most rapid following a period of frequent rains; (c) the rapid collapse of the potato aphid population occurred shortly after the seasonal peak of abundance of dead, diseased aphids was reached, (d) the rapidity of this collapse was greater during periods of frequent rains than during relatively dry weather (Figure 6); and (e) no particular effect upon prevalence of dead, diseased specimens or upon population trends of living potato aphids were observed from differences in daily mean temperature or daily range in temperature.

Abundance and significance of dead aphids not infected with fungi. Substantial variability occurred among years and species of aphids in the numbers and relative abundance of dead specimens from which there was no evidence of infection with entomogenous fungi (Table 8). The phenomenon among grain-infesting species of aphids in England was discussed by Dean and Wilding (1). In our studies it

TABLE 7

All-season prevalence of entomophthoraceous fungi in dead, diseased aphids from potatoes on Aroostook Farm. Fungi subjected to microscopic diagnosis, 1963 through 1969.

Species of fungus	Percent of Diagnosed specimens			
	Potato aphid	Green peach aphid	Buckthorn aphid	Foxglove aphid
	<u>1963</u>			
	(784) ^a	(171) ^a	(121) ^a	(0) ^a
Entomophthora				
sp. ^b	4.0	3.5	13.2	
thaxteriana	94.0	95.9	85.1	
aphidis	0.5	0.6	0	
coronata	1.4	0	0	
sphaerosperma	0.1	0	0	
lageniformis	0.1	0	1.7	
	<u>1964</u>			
Entomophthora	(932)	(138)	(2)	(1)
sp. ^b	0.4	1.4	0	0
thaxteriana	98.3	98.6	100.0	100.0
aphidis	1.2	0	0	0
sphaerosperma	0.1	0	0	0
	<u>1965</u>			
Entomophthora	(983)	(62)	(1)	(2)
sp. ^b	0.5	0	0	0
thaxteriana	91.8	98.4	100.0	100.0
aphidis	6.1	1.6	0	0
planchoniana	1.4	0	0	0
obscura	0.1	0	0	0
thaxteriana & aphidis	0.1	0	0	0
	<u>1966</u>			
Entomophthora	(1065)	(18)	(1)	(0)
sp. ^b	0.1	5.6	100.0	
thaxteriana	94.2	88.9		
aphidis	2.9	0		
planchoniana	2.8	5.6		
	<u>1967^c</u>			
Entomophthora	(1116)	(87)	(277)	(0)
thaxteriana	75.1	98.9	86.3	
aphidis	21.3	1.1	8.7	
planchoniana	3.4	0	1.4	
sphaerosperma	0.2	0	3.6	
	<u>1968^c</u>			
Entomophthora	(122)	(0)	(0)	(0)
planchoniana	89.3			
aphidis	8.2			
thaxteriana	2.5			

TABLE 7 (Cont.)

Species of fungus	Percent of Diagnosed specimens			
	Potato aphid	Green peach aphid	Buckthorn aphid	Foxglove apt
	1969 ^c			
	(192)	(50)	(1)	(17)
<i>Entomophthora thaxteriana</i>	95.3	64.0	100.0	17.6
<i>sphaerosperma</i>	4.2	30.0		0
aphids	0.5	0		11.8
<i>planchoniana</i>	0	6.0		70.6

^a In parenthesis: total number diagnosed excluding those found not to be infected with pathogenic fungus.

^b Unidentifiable beyond genus because of the lack of identifiable characters, but in many instances very likely *Entomophthora thaxteriana*.

^c Sample specimens of dead, diseased aphids were collected during a 1-week period in n August; from 1963 through 1966, they were collected during all weekly counts of aphid on potatoes throughout the summer.

appeared to be more prevalent in the buckthorn aphid than in the green peach or potato aphids. That the condition was not due to action of insecticides is strongly indicated by the evidence in Table 9, which shows that the condition was, in general, as prevalent as or more so among dead aphids randomly collected for diagnosis from untreated potatoes as from those treated with aphidicides. These results are similar to those reported in 1961 and 1962 (10). In 1967, the following relationships were found for nonfungus, dead specimens collected at the peak of abundance of living and of dead aphids in mid-August.

Aphid species	Total No. Specimens	Percent nonfungus		Average Wt.
		Treated Potatoes	Untreated Potatoes	
Buckthorn	378	1.1	25.7	26.7
Green Peach	89	0	2.2	2.2
Potato	1138	0	1.9	1.9
<i>Foxglove</i>	0			
All species	1605	0.2	7.5	7.7

The buckthorn aphid nonfungus specimens were, in general, quite different in appearance from those of the same species that were diagnosed as fungus-killed. The latter, as were most of the other aphids found to be killed by fungi, were relatively soft-bodies and mashed rather easily in the wet mounts to reveal the presence of stages of the pathogens. In contrast, the buckthorn aphid specimens that were diagnosed as not having been killed by fungi were always blackened, shriveled, tough cadavers which resisted softening and mashing in either water or acetocarmine stain, and no evidence of stages of any pathogen was detected in any of them.

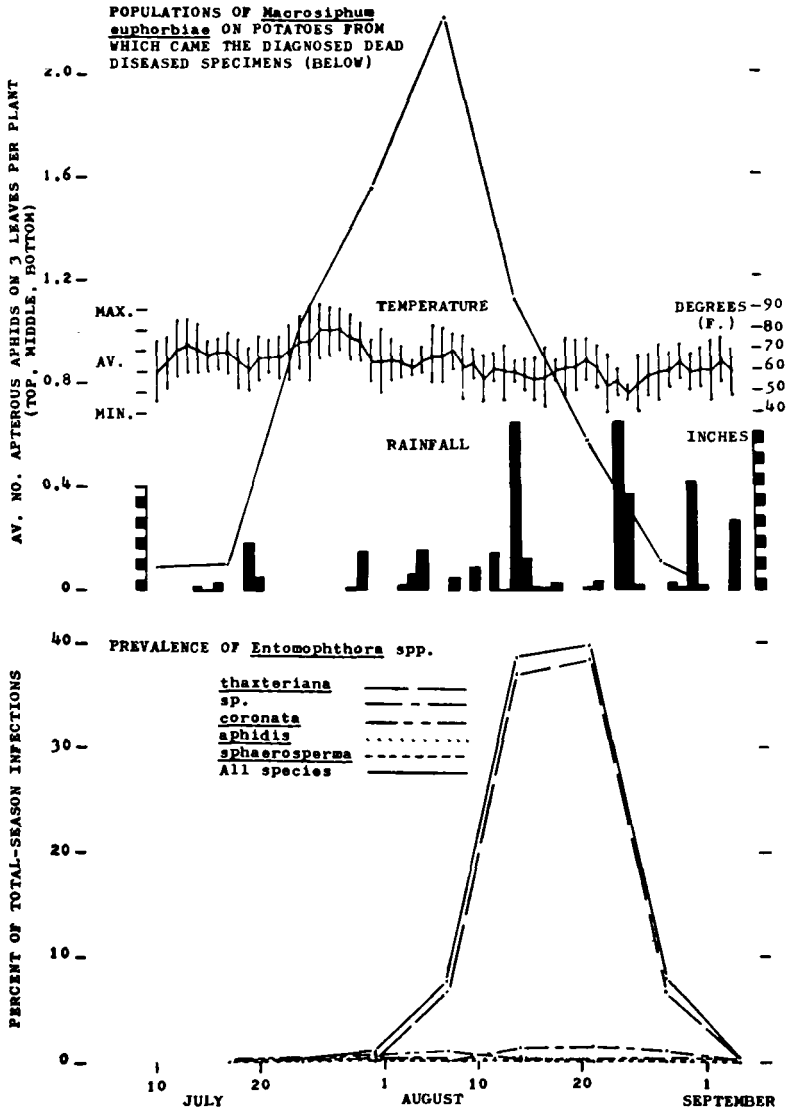


Figure 3. Seasonal occurrence in 1963 of entomogenous fungi affecting the potato aphid on field-growing potatoes in relation to temperature and rainfall.

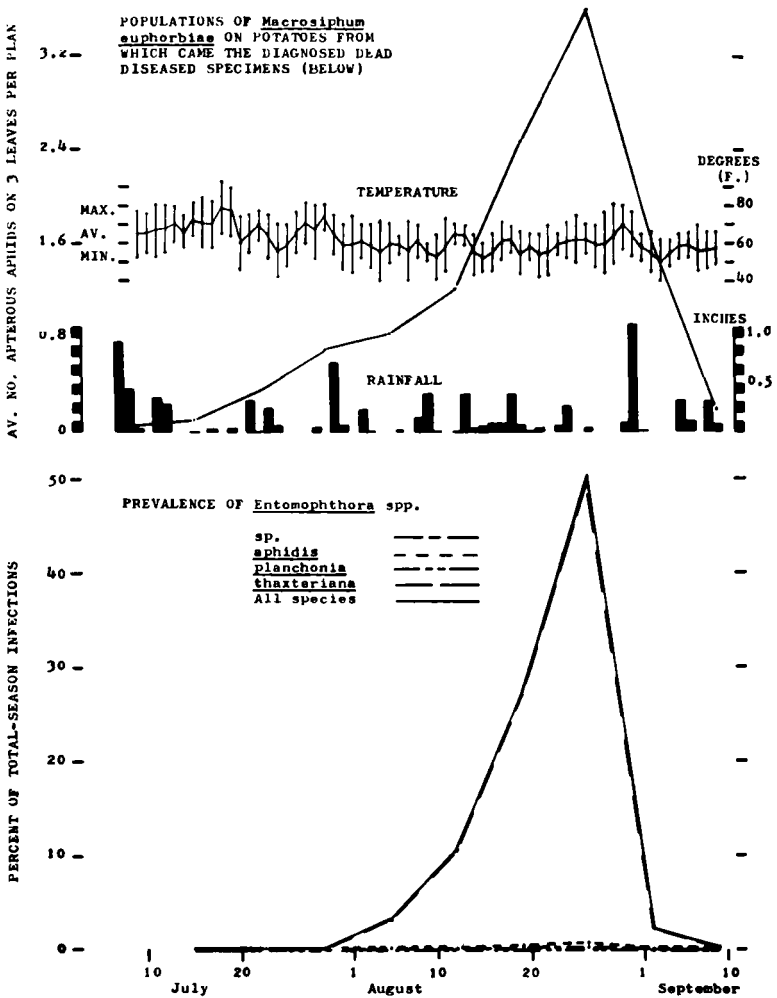


Figure 4. Seasonal occurrence in 1964 of entomogenous fungi affecting the potato aphid on field-growing potatoes in relation to temperature and rainfall.

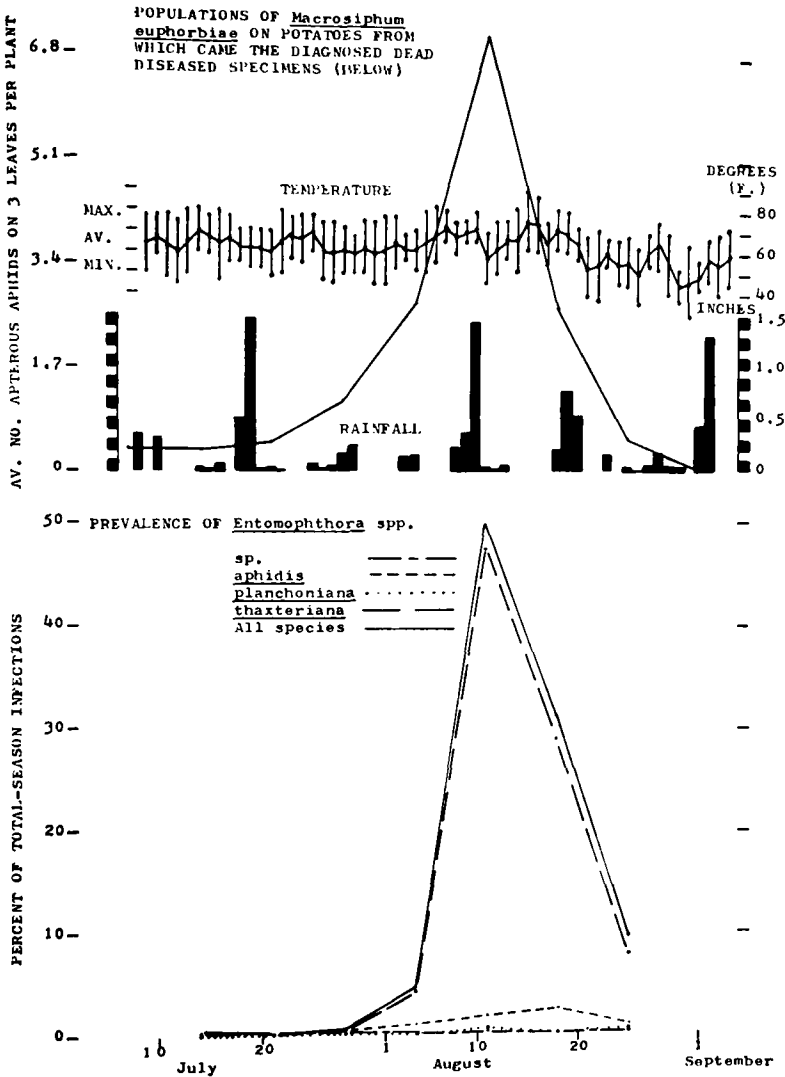


Figure 5. Seasonal occurrence in 1965 of entomogenous fungi affecting the potato aphid on field-growing potatoes in relation to temperature and rainfall.

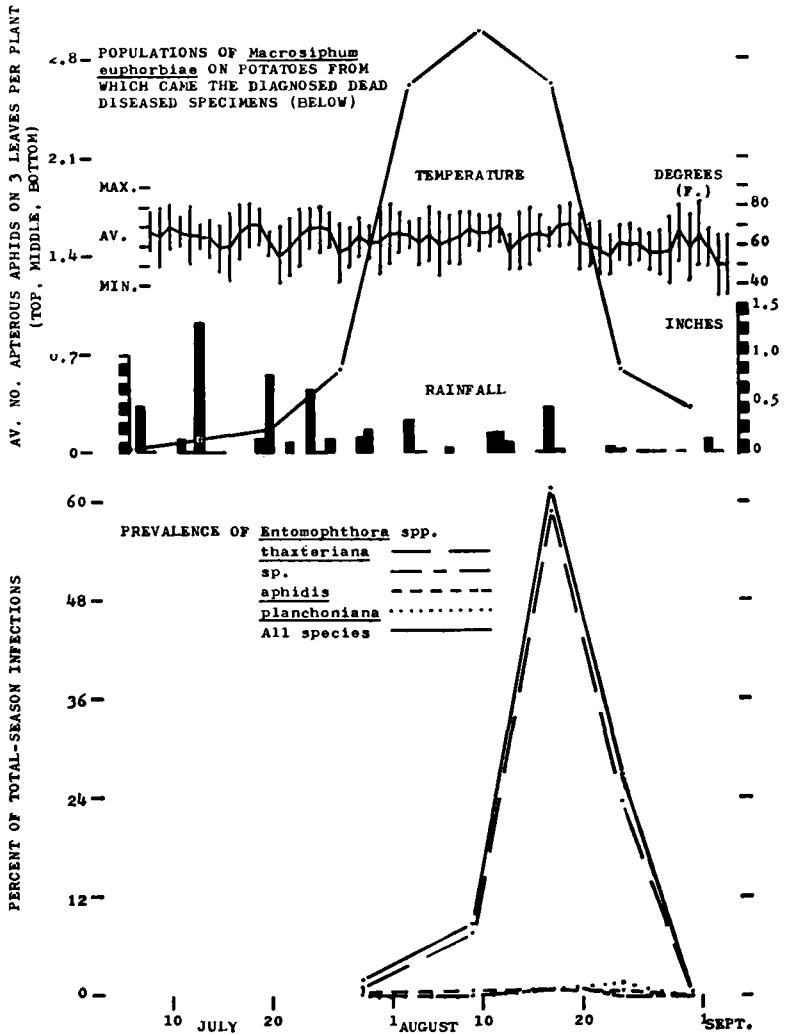


Figure 6. Seasonal occurrence in 1966 of entomogenous fungi affecting the potato aphid on field-growing potatoes in relation to temperature and rainfall.

TABLE 8

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) 1963 to 1969, inclusive.

Year	No. specimens diagnosed					Percent non-fungus				
	Buckthorn	Green peach	Potato	Fox-glove	All species	Buckthorn	Green peach	Potato	Fox-glove	All species
1963	260	183	909	0	1352	51.9	6.0	4.4	0	13.7
1964	8	201	1048	1	1258	62.5	5.5	5.5	0	5.9
1965	1	65	1044	2	1112	0	3.1	3.7	0	3.7
1966	4	172	1297	0	1473	75.0	4.1	1.9	0	3.5
1967	378	89	1138	0	1605	26.7	2.2	1.9	0	7.8
1968	3	0	125	0	128	100.0	0	2.4	0	4.7
1969	2	50	214	17	283	50.0	0	10.3	0	8.1

TABLE 9

The all-season prevalence of dead aphids not infected with fungus on field growing potatoes that were or were not being treated with insecticides 1963-1966.

Species	Number Diagnosed	% nonfungus		
		Untreated potatoes	Treated potatoes	Weighted Averages
		1963		
Buckthorn aphid	199	45.9	28.6	39.7
Green peach aphid	182	6.0	6.1	6.0
Potato aphid	822	5.0	4.3	4.6
Foxglove aphid	0	0	0	0
All Species	1203	13.6	7.6	10.6
		1966		
Buckthorn aphid	2	50.0	0	50
Green peach aphid	10	0	0	0
Potato aphid	1096	1.3	2.5	1.7
Foxglove aphid	0	0	0	0
All Species	1108	1.4	2.5	1.8

SUMMARY AND CONCLUSIONS

The intensive survey carried out from 1952 through 1962 (10) was continued from 1963 through 1969 to determine the importance of entomogenous fungi as a biological agent of aphid control on potatoes in northeastern Maine. Weekly records throughout a 12- or 13-week period of summer were made of living and of dead, diseased aphids by species on untreated and on insecticide-treated potatoes growing on Aroostook Farm near Presque Isle, Maine. Throughout the summers of 1963 through 1966, random samples of dead aphids on the aphid-count potato leaves were collected and sent to the University of California at Riverside where they were examined for pathogenic fungi. Samples of dead aphids for diagnosis during the remaining three years were collected intensively

over a period of one week in mid-August, near the seasonal peaks of both living and dead, diseased aphids on untreated potatoes.

An effort was made to assess the importance of entomogenous fungi in controlling each of the three species, the potato, green peach, and buckthorn aphids, during each of the seven years of the study. The method employed in the assessment involved chiefly a comparison of beginning dates of downward departures from the expected rates of aphid increase during the growth phase of the populations with (a) the dates of first finding dead, diseased specimens of the appropriate species of aphids, (b) the abundance of mobile stages of arthropod predators, or with (c) a combination of these two phenomena. Consideration was also given to the combined effects of the levels of abundance of fungal activity and of predators upon the duration and extent of the downward departures observed.

By these criteria, it appeared that fungal activity was chiefly responsible in initiating the downward departures from the expected rate of increase of the potato aphid in five of the seven years and it contributed to the extent and duration of the downward departure in the remaining years; predator abundance at the beginning of the downward departure in six of the seven years, and at the first one of two departures in 1968, probably was too low to have initiated the downward departures. However, in all years predators contributed to the duration and extent of all downward departures and to the ultimate collapse of the potato aphid population.

Fungal activity was considered to be the probable major, initiating cause of the downward departures from the expected rate of increase of the green peach aphid in three of the seven years, but of no importance in one year. Predators were abundant at the correct time to have initiated the downward departures observed in two of the seven years, and to have contributed substantially to the extent and duration of the departures in one year.

In the instance of the buckthorn aphid, fungal activity probably initiated the downward departures from the expected rate of population increase in two of the seven years and, possibly, aided substantially in two years. Predators were sufficiently abundant at appropriate times to have initiated the downward departures observed in two years and they probably contributed to it in two years, but were of no importance at the time of departure in 1969.

By the criteria used, the potato aphid was the most susceptible to fungal attack, followed by the green peach aphid. The buckthorn aphid appeared to be slightly less susceptible to fungus activity than was the green peach aphid.

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