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W.A. Shands

Geddes W. Simpson

H.E.Wave

C.C.Gordon

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Importance of Arthropod Predators in Controlling Aphids on Potatoes in Northeastern Maine

> W. A. Shands Geddes W. Simpson H. E. Wave C. C. Gordon





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The imported 7-spotted lady beetle, Coccinella septempunctata L. is an effective predator of potato-infesting aphids. Some of the newly hatched larvae, A, greatly enlarged, are attacking green peach aphids on this potato leaf. Tests showed that a mature larva, B, ready to pupate, during its development would consume from 600 to 750 green peach aphids of all sizes when given as food nothing but this species of aphid. Other tests showed that adult beetles. C, ate about 100 green peach aphids per day when offered only aphids of that species as food.

Acknowledgment

The authors are especially grateful to the many Temporary Field Assistants of the Maine Agricultural Experiment Station and Entomology Research Division, ARS, USDA, who assisted in making the counts of predators and aphids on the field-growing potatoes during the period of this study, (they are too numerous to include here); also, to the several specialists in the insect taxonomy unit of Entomology Research Division, ARS, USDA, who identified samples of the predators collected during the early years of the study.

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IMPORTANCE OF ARTHROPOD PREDATORS IN CONTROLLING APHIDS ON POTATOES IN NORTHEASTERN MAINE

W. A. Shands¹, Geddes W. Simpson², H. E. Wave³, and C. C. Gordon⁴

INTRODUCTION

Aphids⁵ are currently the most important insect pests of potatoes in Maine. They transmit several pathogenic viruses from diseased to healthy potato plants. They may reduce yield and quality of tubers. When sufficiently abundant, aphids also inflict on the growing plants, feeding damage that will be reflected as reduced yield at harvest.

When soil moisture is adequate, healthy potato plants can withstand, without appreciable loss of yield, the feeding injury from substantial numbers of aphids not infected with a virus. However, a single viruliferous aphid is capable of infecting many healthy potato plants, depending upon the kind of virus and the amount of interfield and interplant aphid movement. Because of this situation, the successful commercial production of potatoes is dependent upon reasonably good control of the aphids on potatoes grown for culinary purposes and a high degree of control of those in the seed-potato crop.

Natural control agents, including climatic conditions and several biological agents, directly and indirectly exert an important influence on the potential size of aphid populations on potatoes each year. The important biological control agents of aphids include several species of pathogenic fungi (Shands et al. 1963), many species of parasites (Shands et al. 1955, 1965), and arthropod predators. Our studies showed that entomogenous fungi frequently exert a high degree of control of potato aphid on potatoes, while parasites were somewhat less effective. The application of some insecticides to potatoes reduced the effectiveness of the aphid parasites in the treated crop. Other observations indicated that several of the aphidicides, and other insecticides applied to potato plants, were highly toxic to and markedly reduced the effectiveness of some aphid predators infesting the potatoes.

 ¹ Visiting Professor of Entomology, University of Maine, Orono, Maine 04473; formerly Research Entomologist, Entomology Research Division, ARS, USDA.
 ² Professor of Entomology, University of Maine, Orono.
 ³ Associate Professor, Plant and Soil Sciences, Highmoor Farm, Monmouth, Maine 04259; formerly Entomologist, Entomology Research Division, ARS, USDA.
 ⁴ Biological Technician, Entomology Research Division, ARS, USDA, Orono.
 ⁵ The buckthorn aphid, Aphis nasturtii Kaltenbach; the green peach aphid, Myzus persicae (Sulzer); the potato aphid, Macrosiphum euphorbiae (Thomas); and the foxglove aphid, Acyrthosiphon solani (Kaltenbach) (Hemiptera:Aphididae).

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From 1942 to 1969, concurrent studies were made to identify and assess the importance of biological agents affecting abundance of the potato-infesting species of aphids in northeastern Maine. We report here the results of studies relating to arthropod predators of aphids on the potato crop, principally from 1952 through 1969.

Table 1

The more common arthropod predators of potato-infesting aphids in northeastern Maine

ARACHNIDA Many species of spiders
COLEOPTERA: COCCINELLIDAE Adalia bipunctata (L.) Anatis ocellata (L.) Coccinella transversoguttata Faldermann Coccinella trifasciata perplexa Mulsant Hippodamia convergens Guerin-Meneville Hippodamia parenthesis (Say) Hippodamia tredecimpunctata tibialis (Say) Mulsantina hudsonica (Casey) Psyllobora virgintimaculata (Say) Scymnus sp.
DIPTERA:SYRPHIDAE ¹ Melanostoma mellinum (L.) Metasyrphus sp. Sphaerophoria sp. Sphaerophoria cylindrica (Say) Sphaerophoria menthastri (L.) Syritta pipiens (L.)
NEUROPTERA:CHRYSOPIDAE Chrysopa chi var. upsilon Fitch Chrysopa oculata var. chlorophona Burmeister
HEMIPTERA: ANTHOCORIDAE
¹ The only parasite observed was <i>Promethes</i> sp. (Hymenoptera:Ichneumonidae); it was reared from pupae of <i>Sphaerophoria</i> sp., probably cylindrica.
THE ARTHROPOD PREDATORS OF POTATO-INFESTING APHIDS IN NORTHEASTERN MAINE

Collecting predators for identification was limited to the more commonly occurring species on potatoes (Table 1). Altogether, spiders and 18 species of insects belonging to three families were considered as being the most abundant, viz., 10 species of coccinellids, six of syrphids, and two of chrysopids. We did not consider the anthocorids here sufficiently abundant to be considered important as predators of aphids on potatoes.

Over a period of several years, spiders were systematically collected from potato plants during weekly aphid counts. These specimens were submitted for identification but, to date, no identifications have been reported to us. Spiders were especially abundant on potato plants early in the season and appeared to be represented by many species. At this time of year, many forms may have been immature, thus adding to difficulties in recognizing individual species.

Our list of predators of aphids in potato fields is much less extensive than the one of predators found in cotton fields of Arkansas (Whitcomb and Bell 1960), which contained predators of pests in addition to aphids. Their list contained about 600 species of predators in 45 families of insects and 23 families of spiders and mites. Metcalf (1916, 1917) recorded 19 species of syrphids in Maine, only two of which were specifically mentioned as feeding on potato-infesting species of aphids. Tamaki (1967) reported that six species of syrphids were the only predators that effectively suppressed fall populations of the green peach aphid on peach trees in the potato area around Yakima, Washington.

SEASONAL DISTRIBUTION OF LIFE STAGES OF THE ARTHROPOD PREDATORS ON POTATOES

The seasonal distribution of the life stages of the more abundant arthropod predators was determined on untreated potatoes at Presque Isle. The potatoes, bordered by strip plantings of oats, were grown mostly in replicated small plots or small fields. The counts of predators were made on the leaves examined for aphids as the aphid counts were made; the number of predators on each subunit of sample was for the whole compound leaf, irrespective of the size of the subunit used for the aphid count (Shands and Simpson 1953, Shands *et al.* 1954).

The seasonal distribution of some of the life stages of coccinellids, syrphids, chrysopids and spiders is shown in Table 2 for two years, viz., 1953 and 1967 when the abundance of insect predators was below average and above average, respectively. The numbers of each predaceous stage and the percentages of total-season numbers found during each weekly count were based on examination of three leaves per plant (top, middle, bottom) on an average of 1,850 plants in 1953 and 980 plants in 1967. Based on these data, in each of these years there were two generations of coccinellids, or one complete generation and a partial second one. While there probably was but one generation of syrphids or of chrysopids on the potatoes, other observations showed that some species in both of these groups of predators completed one generation earlier in the season on the primary host plants of three of the potato-infesting species of aphids, viz., swamp rose, *Rosa palustris* Marsh., alder-leaved buckthorn, *Rhamnus alnifolia* L'Her., and Canada plum, *Prunus nigra* Aiton.

The spiders were rather well distributed throughout the season on

		Coccinellids			Syrphids				Chrysopids	
Date	Eggs ^b	Larvae	Pupae	Adults	Eggs	Larvae	Pupae	Eggs	Larvae	Spidersc
					1953					
Total numbers:	49	46	39	45	5	3	0	9	1	đ
Percent of total i	numbers b	y dates for	each stag	e						
June 30	20.4	0	0	0	0	0		0	0	
July 8	61.2	21.7	0	0	0	0		0	0	
17	0	2.2	0	2.2	0	0		0	0	
22-24	6.1	6.5	0	4.4	80.0	0		22.2	0	
28-31	2.0	6.5	0	4.4	0	33.3		22.2	0	
August 5-8	6.1	4.3	0	2.2	0	33.3		0	0	
13-14	4.1	4.3	2.6	0	0	33.3		11.1	0	
20-22	0	13.0	7.7	2.2	0	0		0	100	
28	0	4.3	0	20.0	0	0		22.2	0	
September 3	0	32.6	30.8	42.2	20.0	0		22.2	0	
14	0	4.3	59.0	22.2	0	0		0	0	

 Table 2

 Seasonal distribution of some of the life stages of arthropod predators during two years at Presque Isle, Maine, on aphid-count leaves of field-growing potatoes not treated with insecticides.^a

					1907					
Total numbers:	58	473	257	275	5	36	65	47	14	27
Percent of total n	umbers by	dates for	each stage	?						
June 27-30	70.7	0	0	2.9	0	0	0	0	0	22.2
July 5-7	3.4	0	0	.7	0	0	0	0	0	0
11-13	5.2	.2	0	.4	0	0	0	0	0	7.4
18-20	1.7	.6	0	0	0	0	0	0	0	0
26-27	5.2	75.1	.8	2.5	0	2.8	0	63.8	0	11.1
August 2	1.7	18 .0	49.8	5.5	0	8.3	0	25.5	0	11.1
9-10	0	.8	23.3	20.0	0	19.4	1.5	6.4	14.3	18.5
16-17	1.7	2.5	16.7	32.7	20.0	25.0	3.1	4.3	42.9	11.1
23-24	5.2	2.1	3.5	15.6	0	13.9	2 0.0	0	7.1	14.8
30	0	0	4.3	14.2	0	30.6	60.0	0	28.6	0
September 5	5.2	.6	1.6	5.5	80.0	0	15.4	0	7.1	3.7

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* The numbers of each predaceous stage and the percentages of total-season numbers found during each weekly count period were based on examination of 3 leaves per plant (top, middle, bottom) on an average of 1,850 plants in 1953 and 980 in 1967.

^b Numbers of egg masses.

• All stages.

^d Complete abundance records of spiders were not made in 1953.

potatocs (Table 2); however, in 1967 and in most other years, they appeared to be most abundant during and for a short time after the aphids' spring migrations, while the potato plants were still small. Because of their mobility and effectiveness as predators of aphids on potatoes, this pattern of seasonal distribution of spiders results in an all-season suppressive pressure against aphid population growth, with the greatest pressure occurring when the potential size of aphid population is influenced most. Our observations indicate that spiders as a group probably are the most important predators of the potato-infesting aphids in northeastern Maine, in view of their seasonal distribution, abundance, and effectiveness as predators of the aphids on their primary hosts as well as on potatoes and other secondary hosts. Further detailed study of this group of predators seems desirable when the opportunity arises.

COMPOSITION OF COCCINELLID POPULATIONS ON POTATOES

To determine the relative abundance of the most common species of the coccinellid predators in the potato crop, records were made during many years to show, by species insofar as possible, the numbers of each developmental stage on each unit or subunit of sample potato plant in all aphid counts throughout the summer. The counts were made on potatoes grown on Aroostook Farm, near Presque Isle, for use in studies of aphid biology or in experiments designed to control aphids with insecticides. The counts of predators and aphids were made weekly in all untreated plantings as well as in those being treated with insecticides. Altogether, the yearly total number of potato plants sampled, three leaves per plant (top, middle, bottom), in the predator counts varied from about 35,000 to 60,000. The numbers of sample potato plants in treated and in untreated plantings were approximately equal in most years.

YEARLY VARIABILITY IN RELATIVE ABUNDANCE OF THE MORE COMMON SPECIES

Coccinella transversoguttata Faldermann and Hippodamia tredecimpunctata tibialis (Say) were by far the most common species of coccinellids on field growing-potatoes during the period 1955 to 1969, inclusive (Table 3); in fact, they were also the most common species present during the period 1942 to 1954, inclusive. Depending upon the year, observations on the potato plants showed that the range in percent of the total adult population of coccinellids comprised by C. transversoguttata or by H. tredecimpunctata tibialis varied from 5.7 to 66.0 or 24.1 to 92.9, respectively.

Miscellaneous or undetermined species comprised a relatively small proportion of the populations of adult coccinellids except in 1956 and

again in 1965. In 1956, indications were that miscellaneous species of coccinellids comprised a larger than usual proportion of the beetle population. However, the placement of some of the 16.1% of beetles in the miscellaneous category was due to hesitancy of inexperienced summer assistants to make identifications as to species during the early part of the summer. In 1965, most of the beetles in the miscellaneous grouping were the convergent lady beetle, Hippodamia convergens Guerin-Meneville. Some of the miscellaneous beetles from 1965 to 1969, inclusive, were the imported species, C. septempunctata, L, which was introduced during each of these years into some of the plots or small fields. The yearly proportions of larval populations of coccinellids on potatoes during the period 1955 to 1969 were essentially similar to those shown for the adults in Table 3.

Table 1	3
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Yearly percentages of all-season composition of adult populations of coccinellids on potatoes growing on Aroostook Farm, 1955 to 1969, inclusive.ª

	Percent of total	Percent of total numbers observed in all count						
Year	C. transversoguttata	H. tredecimpunctata tibialis	Undetermined or miscellaneous ^b					
1955	58.5	32.5	9.0					
19 56	34.5	49.4	16.1					
1957	8.2	90.5	1.3					
1958	12.3	83.1	4.6					
1959	13.9	85.5	0.5					
1960	18.6	79.7	1.7					
1961	32.7	62.4	5.0					
1962	59.3	40.7	0					
1963	48.5	50.0	1.5					
1964	5.7	92.9	1.4					
1965	18.1	61.7	20.1					
1966	12.4	87.1	0.5					
1967	9.2	85.1	5.7					
1968	66.0	24.1	9.9					
1969	49.0	48.1	2.7					

^a The range in numbers of adult coccinellids observed yearly for determining these

percentages was 54 to 2,138; the average yearly number was 524. ^b Most of those in 1965 and traces of those in 1966 and 1967, respectively, were H. convergens. The percentages of the total adult coccinellid population com-prised by C. septempunctata from 1964 to 1969, inclusive, were 0.4, 4.0, 0.5, 3.5, 8.6, and 2.0, respectively; in each of these years introductions of this imported beetle were made in some of the plots or small fields.

ABUNDANCE OF MOBILE STAGES OF PREDATORS ON FIELD-GROWING POTATOES TREATED OR NOT TREATED WITH INSECTICIDES

Analysis and study of the data for predator abundance on potatoes were carried out (1) to examine three possible methods of expressing predator abundance, (2) to determine the variability among years in abundance of predators. Observations were made to record any effects

upon predator abundance from applying insecticides to some of the potatoes. The data employed in the study were obtained from replicated small plots or small fields of potatoes treated or not treated with an insecticide; all of the plantings received customary applications of a fungicide for control of the late blight fungus, *Phytophthora infestans* (Mont.) de Bary.

MATERIALS AND METHODS

The procedures used in obtaining the data were described in the preceding sections of this bulletin. The data for predator abundance on insecticide-treated potatoes came from all plots in which insecticides of any kind were applied at any time during the summer, including granular systemic and nonsystemic foliar formulations. Most of the granular systemic insecticides were applied at one or two rates in the planting furrow. The nonsystemic, and some of the systemic, insecticides were applied as foliar sprays at differing frequencies and rates per acre. Every year, some of the insecticide treatments consisted of single applications of each insecticide at one or more rates of active ingredients per acre. All materials tested as foliar sprays were applied at 1170 1/hectare under a line pressure of 14,060 g/cm² by a machine specially designed to provide thorough spray coverage of the potato foliage (Slosser 1945).

The counts of aphids and predators were, in most instances, made weekly for 12 or 13 weeks throughout the summer in all plots or fields. Usually, about equal numbers of sample potato plants were examined weekly in insecticide-treated and in untreated plantings.

RESULTS AND DISCUSSION

None of the three expressions for predator abundance (Table 4) is entirely adequate when used alone or under all conditions. Probably either the percent of plants infested by mobile stages of predators or the average number of mobile stages per 100 plants by the 3-leaf method of count is adequately expressive for small aphid populations. However, when aphid numbers are moderate-to-large, the average number of predators per 100 aphids appears to be a better measure of predator abundance in relation to the potential suppression of aphid population growth. The large differences among years is due to variability of both predators and aphids. For example, on untreated potatoes, aphids were less abundant in 1959, 1964, 1966, 1968 and 1969 than in most of the other years, while the numbers of predators per plant were substantially larger than average in 1957, 1959, 1963 and 1967.

The relationship between the percent of plants (3 leaves per plant: top, middle, bottom) infested by mobile stages of predators and the average number of mobile stages per 100 plants is of interest and importance since it permits a more concrete expression of predator abundance than either of the other two methods. During the period 1959 to 1969, inclusive, the average number of predators on 100 3-leaf-per-plant sample units was 1.11 times the percentage of the sample units infested (Table 4). If the percentage figure is used as an index number, the number of predators per plant can be approximated by multiplying this percentage for a given field count by 1.11, then multiplying this by the number of 3-leaf groups of leaves per plant at the time of the count. Thus,

Avg no. mobile stages of predators per/plant = $\left[\binom{\% \text{ plants infested}}{\text{by mobile stages}}\binom{\text{Avg no. 3-leaf}}{\text{groups / plant}}\right] \left[1.11\right]$

Mobile stages of arthropod predators were consistently much less abundant on potato plants treated with insecticides than on untreated plants (Table 4). During the period 1959 to 1969, inclusive, they were found on only about 56% as many plant-sample units in treated as in

All-season abundance of mobile stages of growing on Aroostook Farm.	of arthropod predators ^a on potatoes, 1953 to 1969, inclusive.
Predators on potatoes	Predators on potatoes not

Table 4

	Pre	edators on pot	atoes	Predators on potatoes not				
	trea	ted with insec	ticides	treated with insecticides				
Year	% plants	Ave. no/100	Ave. no/100	% plants	Ave. no/100	Ave. no/100		
	infested ^b	plants ^b	aphids	infested ^b	plants ^b	aphids		
1953 1954 1955 1956 1957 1958 1959 1960 1961 1962 1963 1964 1965	5.75 1.52 0.44 0.34 1.00 1.33 2.37	0.72 0.50 2.09 0.69 3.06 2.55 5.91 1.54 0.52 0.44 1.06 1.63 2.51	0.01 0.06 0.05 0.08 0.04 0.25 0.59 0.45 0.05 0.21 0.27 0.40 0.86	6.29 2.74 2.41 0.76 4.28 2.86 2.08	1.60 1.13 3.20 2.62 10.41 3.41 6.52 2.93 2.46 0.78 4.79 3.15 2.21	0.01 0.06 0.15 0.09 0.15 0.44 2.31 0.77 0.09 0.34 0.40 1.19 0.99		
1966	1.32	1.42	1.00	1.56	1.62	1.10		
1967	2.22	2.36	1.01	7.25	9.13	0.74		
1968	1.51	1.58	3.34	0.96	1.05	2.23		
1969	1.29	1.50	1.44	2.67	3.12	2.10		
Avg.	1.74	1.77 (1.86)° 0.59 (0.87)	° 3.08	3.54 (3.4	3)° 0.77(1.11)°		

^a From 1959 to 1969, inclusive, the averages were based on all larvae and adults of coccinellids, larvae of syrphids and chrysopids, and spiders. Prior to 1959, spiders were not included.

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

e Figures in parentheses are corresponding averages for the period 1959 to 1969, inclusive.

untreated plantings. Furthermore, for the period 1953 to 1969, inclusive, the numbers of the predaceous stages on the sample units were only 50% as abundant on treated as on untreated plants; during the period 1959 to 1969 the comparable figure was 54%. In addition, the numbers of pre-

daceous stages per 100 aphids were about one-third more abundant on untreated plants than on treated plants. While some insecticides affected populations of predators to a greater degree than others, all of the insecticides reduced the number and effectiveness of the aphid predators.

EFFECT OF STRIP PLANTINGS OF OATS BORDERING SMALL PLOTS OF POTATOES UPON ABUNDANCE OF PREDATORS ON THE POTATOES.

Several methods have been used successfully for increasing the numbers and effectiveness of insect predators for controlling aphids (Smith 1969). Included among these is the use of "trap plants" which cause aggregations of the desired predators which later move to and supplement the naturally occurring populations of predators on the crop plant needing protection from aphids. Banks (1955) found that populations of the bean aphid, *Aphis fabae* (Scopoli), were greatly affected by coccinellids which moved to the beans from nearby nettles, *Urtica dioica* L., infested with the aphid *Microlophium evansi* (Theobald).

Observations in connection with our use of border plantings of oats for inhibiting interplot movement of aphids on potatoes (Shands et al. 1950) suggested that strips of oats interplanted with potatoes might result in increased populations of predators and control of aphids on the potatoes. Oats planted early, when the potatoes were planted, frequently became heavily infested with the English grain aphid, Macrosiphum avenae (Fabricius), and the apple grain aphid, Rhopalosiphum fitchii (Sanderson). Large populations of adult coccinellids and, at times, adult syrphids were attracted to the aphid-infested oats. In some years, this resulted in an overabundance of predators on the oats which subsequently caused a collapse of the aphid population on the oats. When this occurred, the predators, especially immature larvae and later-emerging adults of the coccinellids, moved to the potatoes and, at times, noticeably increased predator abundance and aphid control on the potatoes. Indications were that fourth-instar larvae of C. transversoguttata moved considerable distances to potatoes, possibly as much as 12.2m.

From 1956 to 1965, varying degrees of control were imposed upon aphids on oats in strip plantings of the crop bordering replicated small plots of potatoes which were not treated with insecticides; during this period a study was conducted to assess the effects of these controls upon predator abundance and control of aphids on potatoes.

MATERIALS AND METHODS

In all years, there were two parallel columns of six potato plots each bordered by strip plantings of oats. The six plots of potatoes in both columns were separated on the ends by 10m strips of oats. The strips of oats on both sides and between the plots in one column were sprayed two or three times with an insecticide during the latter part of and after the influx of spring migrants of the oat-infesting species of aphids (footnote a, Table 5); those beside and between the potato plots in the other column were not treated. The distance between the two oat-potato columns varied from 30m to 90m, depending upon the year.

	Avg all-season no. on 3 leave	es/plant (top, middle, bo	ttom) of 100 pc	tato plants
			Cocci	nellids
Year	Treatment of Oatsa	Apterous aphids	Larvae	Adults
1956	Sprayed	4,667	0.93	1.20
	Not sprayed	1,419	1.20	0.40
1957	Sprayed	29,224	1.40	3.13
	Not sprayed	1,763	3.33	10.33
1958	Sprayed	625	0.07	1.48
	Not sprayed	673	0.27	1.07
1959	Sprayed	274	2.41	4.00
	Not sprayed	206	0.71	2.41
1960	Sprayed	439	1.18	0. 92
	Not sprayed	181	2.15	1.64
1961	Sprayed	6,715	0.55	1.21
	Not sprayed	5,531	0.61	1.45
1962 ^b	Sprayed	378	0.05	0.21
	Not sprayed	413	0.92	0.46
1963	Sprayel	1,905	2.17	3.17
	Not sprayed	2,921	2.11	3.83
1965	Sprayed	713	1.64	0.30
	Not sprayed	602	1.15	1.03

 Table 5

 Effect upon populations of aphids and coccinellids on untreated potatoes of applying or not applying aphidicides to plantings of oats bordering the potatoes.

^a Two applications of rotenone at 0.25 to 0.3 lb/a/a were made in 1956 and in 1959; while in 1967 and 1968 3 were made at the 0.3-lb rate. From 1960 to 1965, inclusive, 3 applications of endosulfan were made each year at 0.5 lb/a/a. The applications were about 7 to 10 days apart beginning June 13 to 27 depending upon the season. Application of the aphidicide was begun not long after the start of the influx of spring migrant aphids in the oats; the plants usually were well infested with alatae and small nymphs at the time of first application.

^b Some drift of endosulfan spray mist applied to the oats penetrated the potato plants and may have affected early season populations of the aphids and coccinellids on the potato plants.

The untreated strips of oats on both sides of the column of potato plots were 24m wide in 1956 and 10m wide in 1967; in the remaining years they were only 1.4m wide. The treated strips of oats were 1.4m wide in all years. The specially designed sprayer (Slosser 1945) used to apply the aphidicides to the oats was fitted with large metal shields on each side to prevent spray drift into the plots of potatoes. The spray mixtures were applied at 1170 1/hectare under a line pressure of 14,060 g/cm².

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Each plot of potatoes consisted of four rows $15.5 \text{ m} \log \text{ and } 0.9 \text{ m}$ apart. The seed-pieces were planted 0.3 m apart in the row. In most years the Katahdin variety of potato was planted. Fertilization and other cultural practices for these small-plot plantings were those recommended by the Maine Extension Service, except that no insecticide was applied to the potatoes in any of the plots.

Weekly counts of aphids on potatoes (Shands and Simpson 1953, Shands *et al.* 1954) were made for a period of 12 or 13 weeks throughout the summer on 25 plants per plot, located in a screen grid on the two middle rows in all 12 plots of untreated potatoes. Weekly records were also made of the number and developmental stage of each species of predator observed on the aphid-count leaves.

Weekly counts were made of aphids by species and of aphid predators by species and developmental stage on all oat plants in 50 randomly located drill lengths of 90 cm each in treated and untreated strips bordering the sides of the plots of potatoes. These counts were started before the first application of insecticide was made and they were continued until the untreated oats in the strips were infested with few, if any, aphids.

RESULTS AND DISCUSSION

The counts showed that the aphidicides provided generally good-toexcellent control of the aphids on the oats; the counts also indicated that all stages of the arthropod predators were, generally, much more abundant on oats not treated with insecticides than on those in the treated strips, especially in years when the predators or the oat-infesting aphids were abundant.

Aphid populations on the untreated potatoes were large during four of the nine years, but were small during the remaining five years (Table 5). During three of the four years of large populations, the yearly average all-season abundance of aphids on potatoes bordered by untreated oats was 62% of that on potatoes bordered by oats treated with an aphidicide; the range was 18 to 94%. In the other one of these four years, the all-season abundance of aphids was 53% greater on potatoes by treated oats than by untreated oats.

In three of the five years of small aphid populations on potatoes, the yearly average all-season abundance of aphids on potatoes was 32%less in plots bordered by untreated oats than on those bordered by treated oats; the range was 16% to 54%. In the remaining two years, the average all-season numbers of aphids on potatoes by treated oats were 10% larger and 9% larger, respectively, than on potatoes bordered by untreated oats. Larvae of coccinellids on untreated potatoes in six of the nine years ranged from 1.1 to 18.4 (mean, 4.8) times as abundant in plots bordered by untreated oats as in those bordered by treated oats. The larvae were about equally abundant during one of the remaining three years in plots bordered by treated oats or by untreated oats, while in the remaining two years they were only 29% or 70% as abundant, respectively, on potatoes bordered by treated oats as on those by untreated oats.

In six of the nine years, the all-season abundance of coccinellid adults on potatoes in plots bordered by untreated strips of oats was greater than on those bordered by the insecticide-treated strips. On average, the yearly differences between the two kinds of environments in abundance of the adults were not as large as they were for the larvae. This was probably due to relatively greater mobility of the adults; they appeared to move more readily in and out of the plots than did the larvae, especially when aphids were not abundant on the potato plants.

Although not entirely consistent among years, the results indicate that all-season aphid abundance was smaller on untreated potatoes bordered by untreated oats than on those bordered by treated oats. They indicate, also, that this probably resulted from the generally greater abundance of the mobile stages of coccinellids in the plots of potatoes, many of which moved to the potatoes from the untreated oats when the aphids there were scarce or became scarce, or which emerged as adults on the untreated oats after the aphid populations on oats had collapsed.

The width of the untreated oat strips bordering the 4-row plots of potatoes appeared to have less influence upon predator abundance or aphid abundance on the potatoes than did the general level of predator abundance on the oats (Table 5). In two of the three years of large aphid populations, the greatest differences in sizes of aphid populations on potatoes in the two environments occurred in 1957 and 1956 when the width of the strips was 9 m and 22 m, respectively. However, the differences in abundance of the mobile stages of coccinellids were not markedly different in 1957 and in 1961 when the width of the oat strips was 9 m and 1.4 m, respectively. Possibly the 1.4 m strips on each side were wide enough to provide a maximum of potential movement of predators from the oats to the potatoes.

From these results, there is little question that strip plantings of untreated oats in fields of untreated potatoes will result in better control of aphids on the potatoes than if the oats are not used. However, the minimum width and optimum spacing of the oat strips for maximum aphid control from predator movement from oats to potatoes are not known. This would be an important consideration for the commercial potato grower. Furthermore, in four years of the nine-year test, the degree of aphid control was much below that required to prevent loss in yield from aphid feeding damage.

DELINEATION OF EFFECTS OF THREE BIOLOGICAL AGENTS OF CONTROL UPON POPULATIONS OF APHIDS ON POTATOES

Separation of the effects of parasites, predators, or entomogenous fungi upon aphid population trends on potatoes is an important undertaking. It is a prerequisite for assessing the overall importance of these biological agents of aphid control on that crop. In efforts to do this, Shands *et al.* (1963, 1965) found that separation and assessment of the roles of the entomogenous fungi or of the parasites were difficult and frequently uncertain. The cause of this was the simultaneous operation at variable levels of two or even all three of these biological agents of aphid control. They concluded that entomogenous fungi were outstandingly important in reducing the size of aphid populations, especially those of the potato aphid, and that parasites had no clear-cut impact on population trends of that aphid. While not without some effect, the evidence indicated that parasites were less important than predators in year-to-year suppression of aphid population potentials on potatoes in northeastern Maine.

METHODS FOR ASSESSING THE IMPORTANCE OF ENTOMOGENOUS FUNGI AND INSECT PARASITES

The attempts to delineate the effects of entomogenous fungi and of internal insect parasites upon aphid populations on field-growing potatoes in northeastern Maine formerly were confined to the potato aphid since it is usually the species first and most affected by these agents (Shands et al. 1963, 1965). Detection of the time of initial impact and assessment of the overall effect of these agents upon the aphid population trend was based on the time and ultimate degree of departure of the actual population trend of the aphid below that theoretically expected with no increase in environmental resistance. It was based on the observation that, in northeastern Maine, where aphids are the primary insect problem on potatoes, without the interference of adverse environmental factors, aphid population increase during the growth phase approximates a straight line when plotting against time the common $\log n + 1$ of aphid numbers per unit of sample. Quantitative data, concurrently obtained, for prevalence of dead, diseased or parasitized potato aphids were plotted on the same graphs. On the graphs for potatoes not treated with aphidicides, any appreciable downward departure in population trend from the expected one was considered as probably resulting from an increase in

importance of one or more of the natural agents of aphid control. Consideration was given to whether the abundance of dead, diseased or parasitized aphids in the population may have coincided sufficiently well and been adequate in numbers to cause the observed departure in population trend from the expected one.

It is important to remember in reading what follows that the downward departures mentioned occur during the growth phase or in some cases during a resurgence of the population following an initial setback. These departures do *not* represent "natural" reductions in a population already past its peak whether due to out migration or to changes in the physiology of the plant.

METHODS FOR ASSESSING THE IMPORTANCE OF ARTHROPOD PREDATORS

This same general method was used at the outset of the present study to assess the importance of naturally occurring arthropod predators in controlling aphids on potatoes in northeastern Maine. However, the method for evaluating the role of predators differed somewhat from those used in assessing the roles of entomogenous fungi and parasites, in that population trends of two groupings of aphids were used, rather than one. Also, a different expression of predator abundance was shown between the two aphid population trends on the graphs. The latter expression was the percent of plants (3 leaves per plant: top, middle, bottom) infested by mobile stages of arthropod predators. The two groupings of aphids were the potato aphid, only, and the other three species of aphids, combined. This was done since naturally occurring predators appeared to be rather non-species-specific in attacks upon the aphids while entomogenous fungi or parasites affect the potato aphid much more than they affect the other three species. Thus, coincidental departures in population trends of both groupings of aphids from the expected may result from the action of one or more of the three biological agents; however, when the date of a departure for the 3-species grouping differs from that for the potato aphid, there is a strong likelihood that predators were the agent chiefly responsible, especially if abundant.

EFFECT OF NATURALLY OCCURRING INUNDATIVE POPULATIONS OF PREDATORS UPON APHID POPULATIONS ON POTATOES

Two examples of application of the method described in the immediately preceding section of this bulletin should clarify recognition and assessment of the impact of arthropod predators upon aphid population trends on potatoes. These examples were chosen from studies conducted in 1959 and in 1967 because of the exceptionally large populations of mobile stages of arthropod predators on the potato plants, the relative clarity and lack of complexity as to the causal agents involved, and their effect upon aphid population trends. The data came from a series of replicated plots on a restricted part of Aroostook Farm. In 1959, the counts were confined to six plots in one location; in 1967 they were made in 30 plots in one field.

MATERIALS AND METHODS

In 1959 and in 1967, the potatoes in 86 cm rows were grown in replicated 4-row plots 15.5 m long, separated on the sides by strips of oats 1.4 m wide and, on the ends, by 9 m plantings of oats. No insecticide was applied to the potato plants; otherwise, the cultural practices custom-arily employed in commercial potato production were used in growing the potatoes.

Weekly counts of aphids by species were made on 25 sample units per plot throughout the summer, located in a screen grid on the two middle rows of each plot. The unit of sample was three leaves per plant or parts of these three leaves (Shands and Simpson 1953, Shands *et al.* 1954). At each aphid count, records were made of the number of specimens of each developmental stage of each species of predator on each compound leaf observed, irrespective of the size of the subunit of sample for aphid numbers, i. e. leaflets or half-leaflets of top, middle, and bottom leaves. The expression for aphid abundance was adjusted to the avg. no. of three leaves per plant and that for predators was percent of plants (three leaves per plant) infested by mobile stages of arthropod predators, including spiders, larvae and adults of coccinellids, and larvae of syrphids and of chrysopids. The predator complex both in 1959 and 1967 consisted largely of larvae and adults of coccinellids.

RESULTS AND DISCUSSION

In each of these years, on two occasions there were downward departures from the expected rates of aphid increase. In Fig. 1 these departures are indicated by short extensions (dashes) of the lines showing the expected aphid population trends. In 1959, these downward departures began at the same time for both groupings of aphids, i. e. the potato aphid and the other three species of aphids combined, viz., about July 10 and again, about August 14. In 1967, the date of the first departure, July 26, was the same for both groupings of aphids; but that of the second one for the potato aphid was August 17, while for the other grouping it was August 10.

In 1959, at the time of the first downward departure from the expected rate of population increase, the approximate average numbers of

aphids on three leaves per plant were 0.86 for the potato aphid and 0.24 for the other group; at the time of the second downward departure, the comparable numbers for the two aphid groupings were 1.93 and 4.59 respectively (Table 6). The percentages of plants (three leaves/plant) infested by mobile stages of predators on these two occasions were 1.3 and 8.0, respectively.

						Table 6			-		_	
dance	of pa	rasitized	and	dead,	diseased	aphids in	the	experim	iental	plantings	of potato	es for
	which	abunda	nce o	of the	mobile	stages of	pred	ators is	show	n in Figu	re 1.	

			Potato aphic	1	All other species of aphids			
		Avg no. on 3 leaves/plant ^a	Percent parasitized ^b	Percent dead, diseased ^b	Avg no. on 3 leaves/plant ^a	Percent parasitized ^b	Percent dead, diseased ^b	
				1959				
	12	0	0	0	0	0	0	
	19	0.05	0	0	0.01	0	0	
	26	0.14	0	0	0.30	0	0	
	3	0.15	0	0	0.03	0	0	
	10	0.86	3.6	0	0.24	0	0	
	17	2.09	3.4	0.31	2.91	0.03	0	
	24	4.34	5.0	0	7.07	0.04	0	
	31	1.78	3.6	0	3.25	0	0	
st	7	1.24	3.1	0	3.26	0	0	
	14	1.93	0	0.34	4.59	0.02	0.02	
	21	0.35	0	14.29°	0.77	2.00	0	
	28	0.08	0	0	0.28	0	0	
	4	0.17	0	0 1967	0.42	0	0	
	27	0.06	0	0	0.08	0	0	
	5	0.08	7.69	0	0.07	0	0	
	11	0.30	3.06	0	0.50	0	0	
	18	1.27	3.73	0.09	0.92	0.14	0	
	26	5.13	2.45	0.40	4.01	0.07	0	
st	2	1.24	2.59	17.11	1.19	0	0.11	
	10	0.11	3.23	11.81	20.16	0.01	0.08	
	17	0.36	1.01	24.49	12.15	0.01	0.13	
	24	0.19	0	22.28	5.99	0	0.99	
	5	0.12	0	12.00	4.78	0	0.69	

ng aphids.

nd to be dead, diseased by laboratory diagnosis.

The evidence strongly indicates that, in 1959, predators were principally responsible for both downward departures from the expected rates of population increase of both aphid groupings. No dead, diseased potato aphids were found until one week after the date of the first downward departure; none was seen from then until the date of the second downward departure, when only trace numbers again were found (Table 6). No dead, diseased aphids other than the potato aphid were found until the latter date. Likewise, only trace numbers of parasitized specimens of the other three aphids were found at any time.

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Parasitized potato aphids were not found before the date of the first downward departure; however, from 3.1% to 5.0% were parasitized between then and the date of the second downward departure. Earlier studies (Shands *et al.* 1965) indicated that this low percentage of parasitization probably had no appreciable suppressive impact on the population trend of the potato aphid. Furthermore, the population would not have increased between August 7 and 14 had parasitization, which ended about August 7, been substantially responsible for the sharp reduction in population noted (Figure 1, Table 6).

In 1967, the first downward departure from the expected trend in aphid population occurred for both aphid groupings about July 26 when the average numbers of aphids on three leaves per plant were five potato aphids and four of the other-species grouping; this occurred when 21% of the plants were infested by mobile stages of predators. The percentages of the plants infested by predators on the dates of the second departure for the other-species grouping (Aug. 10) or for the potato aphid (Aug. 17) were 8.3 and 12.6, respectively.

The first departure of the aphid population trend from the expected in 1967 was not due to entomogenous fungi or, at least in the instance of the three-species group of aphids, to parasites (Table 6, Figure 1). There was doubtless some depressive effect from parasites upon the rate of potato aphid increase but it was probably enough to affect only the slope of the line; the sharp downward departure on July 26 occurred only after three weeks of decreasing parasitization (Table 6).

The second downward departure in 1967 was not due to parasites in the instance of the three-species grouping of aphids, and very likely not in the case of the potato aphid because parasitization continued to decrease following the first downward departure from the expected population trend (Figure 1). On the other hand, entomogenous fungi contributed very substantially to the second downward departure and collapse of the population of the potato aphid, along with predators. In fact, the prevalence of either the predators or the entomogenous fungi was adequate to cause the collapse of the potato aphid population.

Entomogenous fungi had little influence upon the beginning of the second downward departure of the population trend of the three-species grouping of aphids in 1967. The first dead, diseased specimens of aphids in this grouping were found on that date also (Table 6); but at that time dead, diseased specimens were present only in small numbers. However, pathogenic fungi probably contributed to the collapse of the population of the three-species group of aphids.

In the examples from 1959 and 1967, arthropod predators were largely responsible for the downward departures of aphid population trends from the expected, although entomogenous fungi contributed substantially to reduced numbers of the potato aphid in August, 1967. When aphid populations were very small the departure from the expected rate of increase became evident when only 1.3% of the plants (three leaves per plant) were infested with mobile stages of predators, while sharp reductions in or collapse of the aphid population occurred when 8% to 36% of the plants were so infested (Figure 1). In all instances of both years, larvae and adults of coccinellids were by far the most abundant of the predators in these plantings of potatoes.

Other, more specific approximations of some of the predator-aphidhost plant relationships at the beginning of the downward departures (Figure 1) of aphid population trends from the expected are shown in table 7. The basis and methods of computing these relationships are described or indicated in the discussion of Table 6 and in footnote 2 of Table 7.

Depending upon aphid population, the average number of predators per plant (three leaves per plant) at the beginning of the downward departures ranged from 0.08 to 3.49. The corresponding range in number of aphids per predator at these times was 31 to 225. The potato leaf (searching) area per predator varied from 1,188 cm² to 18,138 cm², while the range in average leaf area per aphid was 19 cm² to 240 cm² (Robinson *et al.* 1970, Shands *et al.* 1971).

These relationships, together with others shown in Table 7, represent a rather wide range of conditions prevailing at the beginning of the downward departures. We cannot suggest with certainty what combination of predator-aphid-host plant threshold relationships will cause a downward departure in aphid population growth from the expected.

Neither in 1959 nor in 1967 did the suppressive effect upon the aphid population from naturally occurring predators continue long enough to cause a total collapse of the aphid population, even though as high as 36% of the plants (three leaves/plant) were infested by mobile stages of the predators. The factor chiefly responsible for this was the seasonal distribution of the coccinellid predators (Table 2). Over-wintered adults and first generation larvae were principally responsible each year for the first downward departure noted. The suppressive effect upon aphid increase from this cause largely ceased after the larvae pupated but was resumed when the first generation adults and, subsequently, second generation larvae began to appear and increase in abundance.

Total collapse of the aphid population was more nearly approached following the second downward departure than following the first one, both in 1959 and in 1967. This probably resulted from the supplementary suppressive effects from other biological agents of aphid control, prin-

	Departure dates								
	1	959		1967					
	July 10	August 14	July 26	August 10	August 17				
Mobile stages of predators ^b									
No/100 aphids	1.33	1.35	3.23	0.40	1.06				
No/plant	0.08	1.08	3.49	1.34	2.45				
No/hectare	3,038	41,000	135,500	50,9 00	93,000				
Apterous aphids, all speciesb									
No/predator	75	74	31	225	94				
No/plant	6	80	107	302	230				
No/hectare (in thousands) 227.8	3,048	4,064	11,468	8,734				
Leaf area of potatoes ^b									
cm ² /predator	18,138	4,013	1,188	4,313	2,664				
cm²/aphid	240	54	39	19	28				
cm²/plant	1,451	4,334	4,147	5,779	6.527				
cm ² /hectare (in thousands)	55,100.3	164,579.3	157,478.2	219,451.7	247,859.3				

Table 7

Some approximate predator-aphid-host plant relationships at the start of downward departures of aphid population trends from the expected on field-growing Katahdin potatoes infested with naturally occurring inundative populations of predatorsa.

^a See Figure 1.

^b Computations are based on 30-cm spacing of potato seed-pieces in 86-cm rows, using for 1967 actual leaf counts and leaf measurements; for 1959, the compu-tations were based on estimates of the numbers and areas of leaves per plant adjusted in relation to amount of rainfall during May and June (Shands *et al.* 1972. Amer. Potato J. 48: 439-49.

cipally entomogenous fungi, together with the natural reduction in aphid population on potatoes as the fall migrant aphids matured and left the potato plants for the primary hosts.

These examples (Figure 1) serve to illustrate the need for programmed, continuing supplementation of the populations of naturally occurring predators in potato fields to obtain adequate commercial control of aphid populations with coccinellids.

YEARLY VARIABILITY IN IMPORTANCE OF NATURALLY OCCURRING PREDATORS IN CONTROLLING APHIDS ON POTATOES NOT TREATED WITH INSECTICIDE

Much variablity among years has been observed in abundance and importance of entomogenous fungi and insect parasites as natural agents of aphid control on potatoes in northeastern Maine (Shands et al. 1963, 1965). As shown earlier in this bulletin, much variation among years has also occurred in abundance of the arthropod predators of aphids on potatoes. We attempt now to evaluate the importance of naturally occuring arthropod predators for controlling aphids on potatoes in the same area during the period 1952 to 1969, inclusive.

MATERIALS AND METHODS

All observations and counts of aphids and predators were made on potatoes growing in replicated small plots or small fields, located largely on Aroostook Farm. The size of the plots and the cultural procedures were indicated earlier in this bulletin; basically, they were similar in the small fields. No insecticide was applied to the growing plants.

The methods for determining abundance of predators and aphids on the growing plants were indicated earlier in this bulletin. Weekly records of abundance, usually over a period of 12 or 13 weeks, were made of the arthropod predators and of living, parasitized, and dead, diseased aphids on the same number of units or subunits of sample potato plants in each plot or small field. The number of sample plant units examined each week usually was 150 at a given location, but it varied from 100 to 150 depending upon location and year. The plantings in any given year were at 3 to 14 locations; the yearly average number of locations during the study was over 7. The weekly averages for abundance of aphids or predators were based on the examination of three subunits of sample (leaves, or parts thereof) on 450 to 2,100 plants; the weekly average for the 18-year period was 1,075 sample plants per week.

METHOD USED TO ASSESS IMPORTANCE OF PREDATORS

The basic procedure used in assessing the importance of arthropod predators was described in the immediately preceding two sections of this bulletin, viz., in delineating effects of the biological agents of aphid control, and the effects of inundative populations of predators upon aphid populations on potatoes. Two additional assumptions were made which aided in the present attempt to make yearly assessments as to the biological agent or agents principally responsible for the downward departure or departures of the aphid population trends from the expected one.

One assumption was that the suppressive effect of parasitization seldom, if ever, was large enough to cause a distinct downward departure of an aphid population trend from the expected; however, it may probably be enough to decrease the slope of the line representing the rate of aphid population growth. This assumption was based on the conclusions from observations during the period 1952 to 1962, inclusive (Shands *et al.* 1965), as well as from unpublished observations during the period 1963 to 1969, inclusive. Therefore, in the assessments which follow, no particular recognition is given to the suppressive effect upon aphid population growth from internal parasites.

The second assumption was that appearance of dead, diseased specimens of the potato aphid in populations on potato plants was cause to consider that entomogenous fungi may become a factor in suppressing the rate of population growth of the potato aphid in that field. This assumption was based on results of studies from 1952 to 1963, inclusive (Shands *et al.* 1963). Our observations have shown that entomogenous fungi also suppress population growth of the other three potato-infesting species of aphids, but that those three species may be somewhat less susceptible to infection than is the potato aphid.

RESULTS AND DISCUSSION

Weekly abundance records for mobile stages of arthropod predators and for two groupings of aphids (potato aphid, and the other three species) on potatoes not treated with insecticides are shown for the years 1952 to 1969, inclusive, in Figure 2-10. The averages for each week are shown on mid-week dates throughout although they were derived from field counts made throughout each week. Therefore, for any date the average is only an approximation, as also are the indicated beginnings of the downward departures from the expected trend of aphid population growth.

During the 18-year period 1952 to 1969, inclusive, the downward departure from the expected yearly population trend of the potato aphid or that of the other three species combined was of sufficient magnitude on 31 occasions to consider the departure as being due to substantial suppressive effects from the action of natural agents of aphid control (Figure 2-10). In 11 of the 18 years the beginning of downward departures of the three-species grouping of aphids from the expected differed from that of the potato aphid. There were two appreciable downward departures from the expected in population trends of the potato aphid in each of the two years (1955, 1958), but this occurred in only one year in the three-species grouping (1968).

The levels of predator abundance at the start of the downward departures from the expected aphid population trends differed among years for both species grouping of aphids and often, as well, between the two groupings of aphids in the same year. Thus, predators were not wholly responsible for all downward departures from the expected in population trends of the three-species grouping of aphids, even when the beginnings of these departures differed from those of the potato aphid; neither were the downward departures from the expected population trends of the potato aphid necessarily due wholly or even largely to the action of entomogenous fungi.

For a more intensive evaluation of the causes, the observed downward departures in population trends of the aphids from the expected were separated by years into two categories of probable cause, viz., those due largely to *predators* alone or those due probably to *predators and entomogenous fungi* acting together. The separations into probable cause categories were not based wholly upon whether or not the beginnings of the downward departures of the three-species grouping of aphids differed from those of the potato aphid. In addition, the decisions included consideration of the levels of abundance of predators at the start of each downward departure and the date that dead, diseased specimens in each species grouping of aphids were first found (Table 8). Prior to 1958 the decisions as to whether or not dead aphid specimens were "diseased" was based upon the experience and field indentification of the observer; thereafter, many were based, as well, on laboratory diagnosis of some of the specimens.

The downward departures in population trends of the three-species grouping in 10 of the 18 years, viz., 1953, 1958, 1959, and 1963 to 1969, inclusive (Figures 2, 5, 6, 7, 8, 9), were placed in the category of being due largely to *predators;* in the remaining eight years, they were placed in the category of probably being due largely to *predators and entomogenous fungi* acting together (Table 8). The timing of the downward departures for the three-species grouping of aphids differed from those for the potato aphid in eight out of the ten years when predators appeared to be responsible for the changes noted in the population trends. In 1968 they differed for the first downward departure, but were the same for the second one; in 1969 they were the same for both species groupings of aphids. In the other cause category, *predators plus fungi*, the beginnings of the downward departures for the three-species grouping of aphids were the same as those for the potato aphid in only five of the eight years.

More detailed consideration of the date on which the first observed dead, diseased specimens were found in each of the two aphid groupings and of the prevalence of predators at the start of the downward departures from the expected in their respective population trends, reveals additional reasons for placing each downward departure in one or the other of the two cause categories. Entomogenous fungi apparently had no effect upon the beginning of the downward departures from the expected in population trend of the three-species grouping of aphids during four of the ten years that were placed in the cause category of predators (1963, 1964, 1966, 1968); dead, diseased specimens among these three species of aphids were not found until after the start of the departures in three of these four years, while none was found in the fourth year (1968). In the remaining six years (1953, 1958, 1960, 1965, 1967, 1969) of these ten, entomogenous fungi probably had little effect upon the beginnings of the downward departures since in each of these years the dates of finding dead, diseased aphids of these three species were about the same as those for the beginnings of the downward departures in population trends. Our observations indicate that the species of aphids in this grouping appear to be affected by entomogenous fungi to a much lesser degree Effect of predators upon population growth of aphids on field-growing potatoes, not treated with insecticides, at Presque Isle, Maine, 1952 to 1969, inclusive.

		Potato	Aphid		Other species of aphids			
Year	Date	% plants infested with predators ^a	First dead, diseased found ^b	Date	% plants infested with predators ^a	First dead, diseased found ^b		
	A. Downw	ard departures of	population trends co	nsidered as be	ing due largely to p	predators.		
1953	July 17	0.2	July 17	July 22	1.5	July 21		
1958	Aug. 6	2.2	July 2	Aug. 13	3.1	Aug. 12		
1960	Aug. 3	4.2	July 6	Aug. 10	2.8	Aug. 8		
1963	July 31	1.7	July 29	Aug. 7	4.8	July 29		
1964	July 22	2.0	July 30	July 29	3.0	Aug. 10		
1965	Aug. 11	6.6	July 1	Aug. 11	6.6	Aug. 12		
1966	Aug. 3	1.3	Aug. 2	Aug. 10	2.0	Aug. 16		
1967	July 19	0.4	July 17	July 26	10.5	July 26		
1968	July 2	4.8	July 31	July 9	4.8	None found		
	Aug. 6	1.4	July 31	Aug. 6	1.4	None found		
1969	Aug. 6	2.7	July 24	Aug. 6	2.7	Aug. 7		
Avg % by pre	6 plants infeste dators (all year	d (s) 2.8			3.9			

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	B. Downwara	departures con	nsidered	as	being due	e to prea	lato <mark>rs</mark> and	d entomogenous	fungi.	
1952	Aug. 13	7.0	Aug	. 6		Aug.	13	7.0	June	28 ^d
1954	Aug. 4	0.8	July	27		Aug.	4	0.8	July	28
1955	July 14	0.1	July	14						
	Aug. 17	3.6	Aug	. 17		Aug.	17	3.6	July	20
1956	Aug. 15	2.6	Aug	. 8		Aug.	15	2.6	Aug.	6
1957	Aug. 7	3.2	July	31		Aug.	14	12.4°	July	27
1959	July 22	4.9	July	8		July 2	22	4.9	July	20
1961	Aug. 9	2.7	Aug	9		Aug.	16	2.5	Aug.	8
1962	July 18	0.6	July	18		Aug.	8	2.0	July	31
Avg %	plants infested									
by preda	tors (all years)	2.3						2.7		

^a Mobile stages on the 3-leaf-per plant basis.

^b Limited to species of the indicated grouping.

^c Excluded from the average since the level of predation obviously was large enough to have affected or caused the downward departure of population trend from the expected.

^d Questionable field diagnosis of buckthorn aphid.

than is the potato aphid. Furthermore, predators were of above-average abundance at the times of these departures during four of the ten years, two of which (1963, 1967) were among the six during which dead, diseased specimens were found about the same date as the corresponding beginning of the downward departure from the expected population trend.

There appears to be little question but that entomogenous fungi were important in six of the eight years in which the downward departures of the three-species group were placed in the cause category of predators plus fungi (Table 8). In each of these years dead, diseased aphid specimens of the three-species grouping were found well in advance of the start of each of the departures. There was doubt about placing a seventh year (1952) in this category since the June 28 date of finding the first dead, diseased specimen of a buckthorn aphid was unusually early. The determination of the cause of mortality of that specimen was based on field identification. Placement of this departure was done on the basis of that identification and, also, because dead, diseased potato aphids were found one week before the start of the downward departure for the threespecies grouping of aphids. For the latter reason, the downward departure of aphids of this grouping in 1959 was placed also in this cause category. Predator abundance was above average at the start of the departures in four of the eight years, one of which was 1959.

Irrespective of predator abundance, entomogenous fungi probably exerted a substantial influence upon the beginning of the downward departures from the expected trends of potato aphid populations during 16 of the 18 years. Dead, diseased potato aphids were found well in advance of the starting dates of the departures in three years (1958, 1960, 1965) of the ten placed in the cause category of *predators;* this was also the case at the time of the second departure observed in 1969. In four of these ten years (1953, 1963, 1966, 1967), the dates of finding the first dead, diseased potato aphids were coincident with the beginnings of the downward departures of the potato aphid population trends. Dead, diseased specimens of potato aphids were not found prior to the start of the departure in 1964, or before the first of the two departures observed in 1968. Predators were above average in abundance at the start of the downward departures in three of the ten years in this category, viz., 1960, 1965, and at the start of the first of the two departures in 1968.

The action of entomogenous fungi, doubtless, substantially influenced the beginning of downward departures from the expected potato aphid population trends in five of the eight years placed in the cause category of *predators and fungi* since during these years (1952, 1954, 1956, 1957, 1959) dead, diseased aphid specimens of this species were present on the potato plants before the departures were observed (Table 8). Fungal activity probably was of importance during the remaining three of these eight years, as well, since dead, diseased specimens of the aphid were first found near the date of the beginning of the departures. Predators were substantially above average in abundance at the beginning of the departures in three of the eight years in this category (1952, 1955, 1959), and slightly above average in 1961.

Some importance may be attached to the level of abundance of predators required to influence the beginning of the downward departure of the population trends placed in the two cause categories. An average of 2.8% of plants was infested by mobile stages of predators at the start of the downward departures of potato aphid population trends from the expected for the ten years placed in the cause category of *predators* (Table 8). The corresponding percentage for those of the three-species grouping was 3.9, or over one-third larger than for the potato aphid. For those departures considered as being due to *predators and fungi*, the average abundance of predators at the beginnings of the departures for both aphid groupings was somewhat less than on the corresponding dates of departures placed in the cause category of *predators*. Also, the percentages of plants infested by predators at the start of departures of the threespecies grouping of aphids was larger than it was for the potato aphid in both cause categories.

Several factors may have influenced in large measure the higher levels of predator abundance required to cause a downward departure from the expected in the population trends of the three-species grouping of aphids as opposed to the potato aphid. Ordinarily, populations of the potato aphid are smaller than those of the three-species grouping and thus may require fewer predators to decrease the populations of the potato aphids to the point where a departure would be evident. Populations of the potato aphid usually reach the seasonal peak on potatoes in early August, while the seasonal peak of the three-species grouping ordinarily occurs later in August when predator abundance is at a peak.

Thus far, consideration of the data in Figure 2-10, inclusive, and in Table 8 has shown that the actions of arthropod predators and entomogenous fungi were rather closely associated with the downward departures from the expected aphid population increase on potatoes not treated with insecticides. A somewhat indicative, but unsatisfactory, method differentiating the effects of these two agents of biological control was to consider predators as the causal agent when the beginning of the downward departure of the three-species grouping of aphids differed from that of the potato aphid. A better, but still not wholly satisfactory assessment resulted from considering predators *plus* entomogenous fungi as the cause for initiation of the downward departures. The most satisfactory approach was to consider either of these agents singly or acting together as possibly initiating the downward departures from the expected rates of increase of the potato aphid or of the three-species grouping of aphids, i. e., consideration of the abundance of predators and date of the first finding of dead, diseased specimens of that species grouping, in relation to the date of the beginning of the downward departure, related to a similar finding for the potato aphid. When this was done, it appeared that the beginnings of downward departures were associated largely with the action of predators in a number of instances, while in others pathogenic fungi, as well, appeared to be involved. In the instance of the potato aphid, predators appeared clearly to have been the causal agent in only two out of 20 instances; in 18, the downward departures from the expected were probably the result of joint actions of the two agents.

However, further study was required to determine whether or not the action of predators was a definite, significant initiating cause of the downward departures of aphid population trends from the expected. To make this determination, a correlation analysis was made between the size of aphid populations (X) at the beginning of the downward departure and the prevalence of mobile stages of predators (Y) on that date (Table 9). There was a positive relationship $(r=0.570^{**})$ which, although of rather a low order, was significant at a level considerably in excess of P=0.01. Thus, predator abundance was associated with aphid populations at the beginning of the downward departures from the expected rate of the population increase for both species groupings of aphids. The relatively low *r*-value probably indicates that the suppressive force was due partly, in many instances, to the action of one or more agents in addition to predators; the available evidence indicates it was chiefly entomogenous fungi.

This conclusion is substantiated by the highly significant (P=0.01) standard error (0.011743) of the regression coefficient in the linear regression equation: Y = 2.198 + 0.0370115 X (Table 9). It is further supported by the regression line, which when extended to the point of intersection of the Y-axis, indicates that a level of predator action characterized by approximately 2.35% of the three-leaf sample units being infested by mobile stages was required to effect a population suppression of a magnitude adequate to initiate a downward departure in the aphid population. This suggests that a downward departure which started when predator abundance was below the 2.35% level was caused by pressure exerted largely by the action of agents other than predators. If correct, this assumption shows that predators were the major initiating cause of the downward departures from the expected aphid population

growth curves in only 14 out of the 31 instances observed during the 18year period, while in the remaining 17 instances there were contributory factors other than or in addition to predators (Figures 2-10, inclusive; Tables 8, 9).

The validity of this conclusion depends in part upon the exactness of the estimates of predator abundance. The recorded estimates could have been low, especially for periods during which chrysopid larvae were abundant. Our observations showed that population estimates for this group of predators probably were lower than the actual situation because

Table 9 tion of abundance of mobile stages of arthropod predators to downward departure of aphic population trends from the expected on potatoes.

Start of down-	Avg no	Percent plants infested					
· ward departure	Potato aphid	three other species	Total	with predators ^b			
Aug. 13	12.31	180.46	192.77	7.0			
July 17	0.21	2.97	3.18	0.2			
July 22	1.00	17.37	18.37	1.5			
Aug. 4	9.94	11.17	21.11	0.8			
July 14	0.22	3.89	4.11	0.5			
Aug. 17	2.67	98.32	100.99	3.5			
Aug. 15	5.25	36.79	42.04	2.6			
Aug. 7	5.21	35.39	40.60	3.2			
Aug. 14	8.66	124.67	133.33	12.4			
Aug. 6	1.60	3.31	4.91	2.2			
Aug. 13	3.13	10.31	13.44	3.1			
July 22	5.14	5.74	10.88	4.9			
Aug. 3	8.03	2.36	10.39	4.2			
Aug. 10	8.38	7.83	16.21	2.8			
Aug. 9	0.71	16.42	17.13	2.7			
Aug. 16	3.47	62.47	65.94	2.5			
July 18	0.11	0.06	0.17	0.6			
Aug. 8	2.23	1.90	4.13	2.0			
July 31	3.96	11.13	15.09	1.7			
Aug. 7	7.19	33.61	40.80	4.8			
July 22	0.50	0.29	0.79	2.0			
July 29	1.17	0.92	2.09	3.0			
Aug. 11	10.13	4.41	14.53	6.6			
Aug. 3	3.08	0.81	3.89	1.3			
Aug. 10	3.90	2.96	6.86	2.0			
July 19	1.84	2.60	4.44	0.4			
July 26	7.78	15.78	23.56	10.5			
July 2	0.11	0.07	0.18	4.8			
July 9	0.18	0.13	0.31	0.6			
Aug. 6	0.82	0.16	0.98	1.4			
Aug. 6	5.19	1.92	7.11	2.7			
Correlation coefficient ^e : $r = 0.570^{**d}$ Regression equation ^e : $Y = 2.198 + 0.0370115X$ S. E. of regression coefficient ^e : 0.011743**							

n 3 leaves per plant.

tobile stages of predators on the 3-leaf-per-plant basis. atiables compared: Total apterous aphid population (X), % of plants infested by mobile stages f predators (Y).

< 0.01

of difficulty experienced by observers in seeing these larvae when making the aphid counts on potato leaves; the small chrysophid larvae in particular moved so rapidly and often fell or moved from the sample potato leaf as, or soon after, it was turned over for making the aphid count.

POTENTIAL USEFULNESS OF THE RESULTS

Realignment of the data in Table 9 showed that the starting dates of 12 of the 31 downward departures from the expected trends of aphid populations during the 18 years occurred during the period July 2 to 31, while 19 of them were between August 3 and 17. (The mean dates for the two periods were July 19 and August 9, respectively.) There were differences of considerable magnitude between these two periods in some of the predator-aphid-host plant relationships, consideration of which may be important in promoting the use of predators for control of aphids on field-growing crop plants (Table 10).

The average numbers of mobile stages of predators on three leaves per plant on the average dates for all beginnings of downward departures from expected trends of aphid populations were 0.293 or 0.685 for the first and second of the two periods, repectively; the average for all dates was 0.554. The ranges in average number of mobile stages of predators per plant within each of the two periods were large.

The average number of aphids per predator at the start of the downward departures during the two periods was 244 for the first one, and 980 for the second; the average for all departures was 702. Again, the range in numbers of aphids per predator (when predators were most abundant or least abundant) was from 148 to 280 during the first period, and 238 to 969 during the second period.

The average searching area, or leaf area, per predator at the start of the downward departures was about 9,200 cm² in the first period, and 7,700 cm² during the second period; the average for all departures was 7,900 cm². The ranges in average searching area per predator (when the predators were most or least abundant) was from 2,600 cm² to 138,800 cm² during the first period, and 2,500 cm² to 38,000 cm² in the second period.

The average leaf area per aphid at the start of the downward departures amounted to 38 cm² in the first period, while it was only 7.8 cm² during the second period; the average for all departures was 11.2 cm². The range in average leaf area per aphid when predators were most abundant was 9 cm² to 94 cm² during the first period, and 2.6 cm² to 14.5 cm² during the second period.

Additional predator-aphid-host plant relationships occurring during the 18 years included in this study are shown in Table 10.

Ta	ble	10

Some average, approximate, predator-aphid-host plant relationships at the start of the downward departures of aphid population trends from the expected on field growing potatoes^a not treated with insecticides, 1953 to 1969, inclusive.

	Period	!!		
	First (July 2-31) (12 examples)	Second (August 3-17) (19 examples)	average, both periods August 1	
Date (for average)	July 19	August 9		
Aobile stages of predators no/plant (minimum-maximum) ^b Average	0.021 - 1.456 0.293	0.139 - 2.692 0.685	0.554	
No/100 aphids (MinMax.) ^b Avg	0.358 - 0.676 0.410	0.103 - 0.422 0.102	0.142	
No/hectare (MinMax.) ^b Avg	800 - 55,297 11,128	5,279 - 99,847 26,016	21,040	
1pterous aphids No/plant (MinMax.) ^b Avg	31 - 408 71	331 - 2,547 671	389	
No/predator (MinMax.) ^b Avg	148 - 280 244	238 - 969 980	702	
No/hectare (MinMax.) ^b (thousands) Avg	1,177 - 15,495 2,711	12,587 - 96,717 25,493	14,772	
Leaf area cm ² /predator (MinMax.) ^b Avg	2,552 - 138,800 9,205	2,539 - 38,007 7,712	7 ,8 70	
cm ² /aphid (MinMax.) ^b Avg	9 - 94 38	3 - 15 8	11	

· See Figures 2 to 10, inclusive.

The minima and maxima relate to overall abundance of the mobile (aphid-consuming) stages of predators; they may not coincide with those for aphid abundance (see Table 9).

Many of the relationships that were determined during this study or would be kept current by measuring crop foliage and making field counts of predators and aphids at regular intervals as the season progresses may be valuable aids in devising and scheduling predator introductions in field experiments for controlling aphids on potatoes. Also of importance is a knowledge of the aphid (food) consumption requirements of the predator being introduced. Information of this nature has been determined for some species of predators (Blackman 1967, Clausen 1940, Cutright 1924, Dunn 1952, Ellingsen 1969, Gurney and Hussey 1970, Hagan and Sluss 1965, Hodek 1957, Hodek *et al.* 1965a, 1965b, Iperti 1965, Russel 1970, Smith and Hagan 1965, Savoiskaya 1965, Sundby 1966, Szumkawsksi 1955, Wadley 1931). These principles may be applicable for similar experiments in control of aphids with predators on other crops.

A few examples will suffice to illustrate some of the potential uses for data of this nature. One can estimate the general abundance of predators needed to initiate downward departures from the expected aphid population trends for particular levels of aphid abundance to be expected on the crop at different times during a season by knowing or determining the leaf area to be searched, the effective searching area of the naturallyoccurring predator populations, and the probable levels of natural abundance of these predators to be expected. One can develop advance estimates of the levels and frequencies of predator introductions required to establish and maintain the levels of suppression necessary for lowering the aphid population to and/or for holding it below a predetermined maximum permissible size. The levels and frequencies of predator introductions can be adjusted as the season advances on the basis of data being obtained on current abundance of aphids and predators on the crop, leaf area of the crop, and an estimate of the additional suppressive effect on population increase to be expected from entomogenous fungi and insect parasites.

SUMMARY AND CONCLUSIONS

Of the 18 identified species of arthropod predators commonly occurring on potatoes in northeastern Maine, the most abundant during this study, 1952 to 1969, inclusive, were six species of syrphids (Diptera: Syrphidae), two of chrysopids (Neuroptera:Chrysopidae), and, most abundant of the insects, 10 species of coccinellids (Coleoptera:Coccinellidae). An undetermined number of species of spiders (Arachnida) were also present. Field counts of the life stages occurring on potatoes indicated that annually, on this crop plant there were two generations per year of coccinellids but only one of syrphids or of chrysopids. The spiders were well distributed throughout the summer but appeared to be most abundant for a short time after the aphids' spring migrations.

The two common, and abundant, species of coccinellids occurring on potatoes were *Coccinella transversoguttata* Faldermann and *Hippodamia tredecimpunctata tibialis* (Say). During the 18-year study, the range in percentage of total population of adult coccinellids on field-growing potatoes comprised by *C. transversoguttata* or *H. tredecimpunctata tibialis* varied annually from 8.2 to 66.0 or 24.1 to 92.9, respectively. There was some tendency for these species to have cycles of relative and actual abundance.

Field studies revealed that the mobile stages of predators were more than twice as abundant on potatoes not treated with insecticides as on those receiving variable numbers of applications of insecticides of different kinds and at different rates.

None of the three methods used for expressing abundance of the predators in this study was entirely satisfactory. Indications were that on

the three-leaf-per-plant basis of count, the percentage of plants infested or the average number per 100 plants of the mobile stages about equally expressed predator abundance when aphid populations were small. However, the average number of predators per 100 aphids appeared to be a better measure of predator abundance when aphid populations were moderate-to-large in size.

The relationship between percentage of plants infested by mobile stages and their numbers on three leaves per plant was such that the number of mobile stages per plant was found to be equal to the percentage of plants infested (3-leaf basis: top, middle, bottom) X one-third of the number of leaves per plant X 1.11.

From a nine-year field test it was concluded that better control of aphids by coccinellids occurred in small-plot plantings of untreated potatoes bordered by untreated strips of oats than in those bordered by strips of oats receiving two or three applications of an aphidicide. However, aphid control from predators on untreated potatoes was often much below a commercially acceptable level. The adult coccinellids apparently moved from the treated oats to the untreated potatoes soon after landing because of the low aphid populations on the treated oats, whereas movement of coccinellid larvae or adults from untreated oats to potatoes occurred after the aphid population on the oats collapsed from predation. The coccinellid larvae, and to some extent the adults, were more abundant on the potatoes bordered by the untreated than by the insecticidetreated oats. Although not entirely consistent from year to year, a similar relationship between treated and untreated oats was found for the allseason abundance of the mobile stages of all predators on the potatoes.

Basic features of the method used to delineate the effect of predators upon aphid population trends on untreated potatoes consisted of plotting, against time, the log n + 1 of aphid numbers per unit of plant sample which, essentially, results in a straight line during the growth phase of the population unless or until suppressive forces become of sufficient magnitude to cause a downward departure of the population trend from the expected. The point of downward departure was considered to be the point where the actual population trend began the downward departure from a continuation of the straight line, irrespective of its slope. To illustrate the method used, a discussion was given of selected examples of aphid population trends on potatoes during two years. In both years inundative but natural populations of predators were present; in both years there were two downward departures from the expected population trends of the potato aphid and for the other three species of aphids on the plants, as a group. The discussion included, also, an assessment of the evidence indicating the nature of the cause of the suppressive force resulting in the observed downward departures of aphid population trends from the expected. Although predator abundance, alone, was adequate to have caused the downward departures in the examples chosen, the abundance and action of entomogenous fungi were great enough to have caused one of the four departures illustrated. Clearly, therefore, both predators and fungi contributed to the suppression causing that particular downward departure from the expected.

An intensive study was made to assess the importance of predators as a causal agent of the suppression resulting in downward departures of aphid population trends from the expected on untreated potatoes at Aroostook Farm, near Presque Isle, during the period 1952 to 1969 inclusive. (Earlier studies had shown that parasites, while not without some effect, were of relatively minor importance in suppressing the size of the aphid population at the peak.) A somewhat indicative, but unsatisfactory, method of differentiating the effects of predators or entomogenous fungi was to consider predators as the causal agent associated with the beginning of the downward departure for the three-species grouping of aphids when it differed from that for the potato aphid. (The potato aphid is especially susceptible to attack by pathogenic fungi.) A better, but still unsatisfactory, assessment of the probable causal agent or agents resulted when data regarding action of entomogenous fungi and predators formed the basis for separating the downward departures from the expected of the three-species grouping of aphids into two probable cause categories, viz., predators or predators plus entomogenous fungi. When this was done, the beginnings of downward departures for population trends of the three-species grouping of aphids apparently were associated largely with predator abundance in some instances, while in others the association was best when predators plus fungi were considered to be the cause of the departure from the expected trend. In only two of 20 instances were downward departures from the expected potato aphid population trends associated with predators alone; the other 18 appeared to be associated best with the joint action of predators and fungi.

A correlation coefficient of r=0.570, significant at P=0.01, was found between the size of the aphid population (X) at the start of the downward departure and the percentage of plants infested by mobile stages of predators (Y) on that date. The standard error of the regression coefficient, 0.011743, was significant at P=0.01. The linear regression equation was Y=2.198 + 0.0370115 X. The plotted regression line showed that a level of predator action characterized by 2.35% of the potato plants (3 leaves/plant: top, middle, bottom) infested by mobile stages of arthropod predators was required to initiate a downward departure of aphid population trend from the expected. These results showed that predators were largely the initiating cause of 14 of the 31 downward departures of aphid population trends observed during the 18year period, while in the remaining 17 instances there were contributory causes other than or in addition to predators. The indications are that entomogenous fungi were chiefly responsible for the initiation of these 17 downward departures.

Realignment and further analysis of the data for predator abundance at the beginning of the 31 observed downward departures from the expected aphid population trends showed that 12 of them occurred during the period July 2 to 31, while the remaining 19 occurred during the period August 3 to 17. There were large differences between the two periods in all predator-aphid-host plant relationships examined. Generally, at the start of the downward departures, the number of predators per plant and the number of aphids per predator were smaller during the first period than during the second one, while the searching area (leaf area) per predator was greater during the first period than during the second one. The level of aphid abundance and the numbers of aphids per unit of leaf area during the first period were below those of the second period.

Several examples were given of the potential uses of the results of this study in planning and conducting experiments on the control of aphids on potatoes or other crop plants by artificially supplementing the naturally occurring populations of predators through field introductions of laboratory reared predators.



FIGURE 1. Examples of the effect of naturally occurring inundative populations of arthropod predators upon population trends of aphids on potatoes not treated with insecticides. Presque Isle, Maine, 1959 and 1967.

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FIGURE 2. Abundance of mobile stages of arthropod predators in relation to aphid population trends on field-growing potatoes not treated with insecticide. Presque Isle, Maine, 1952 and 1953.



FIGURE 3. Abundance of mobile stages of arthropod predators in relation to aphid population trends on field-growing potatoes not treated with insecticide. Presque Isle, Maine, 1954 and 1955.



FIGURE 4. Abundance of mobile stages of arthropod predators in relation to aphid population trends on field-growing potatoes not treated with insecticide. Presque Isle, Maine, 1956 and 1957.



FIGURE 5. Abundance of mobile stages of arthropod predators in relation to aphid population trends on field-growing potatoes not treated with insecticide. Presque Isle, Maine, 1958 and 1959.



FIGURE 7. Abundance of mobile stages of arthropod predators in relation to aphid population trends on field-growing potatoes not treated with insecticide. Presque Isle, Maine, 1962 and 1963.

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FIGURE 8. Abundance of mobile stages of arthropod predators in relation to aphid population trends on field-growing potatoes not treated with insecticide. Presque Isle, Maine, 1964 and 1965.



FIGURE 9. Abundance of mobile stages of arthropod predators in relation to aphid population trends on field-growing potatoes not treated with insecticide. Presque Isle, Maine, 1966 and 1967.



FIGURE 10. Abundance of mobile stages of arthropod predators in relation to aphid population trends on field-growing potatoes not treated with insecticide. Presque Isle, Maine, 1968 and 1969.

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