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Effects of Differing Abundance Levels of Aphids[1] and of Certain Virus Diseases upon Yield and Virus Disease Spread in Potatoes

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INTRODUCTION

Potatoes, *Solanum tuberosum* L., in Maine are commonly infested by four species of aphids. These are 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).

These four species of aphids damage potatoes in two ways. When sufficiently abundant, their feeding damage will reduce yield (31, 41). They also have been reported to be vectors of several plant viruses that affect potatoes, including leaf roll, *Corium solani*, Holmes, (23, 10, 12, 22), and spindle tuber, *Acrogenus solani* var. *vulgaris* Holmes, (11, 15).

The aphids vary greatly in abundance from year to year and from one locality to another, as well as in the relative abundance of each species (40). They vary also in importance as vectors of the the leaf roll virus. The green peach aphid is by far the most important vector of leaf roll (23, 10, 12, 21, 42). It has also been reported to be a vector of spindle tuber (11, 22). While leaf roll virus is transmitted only by aphids, spindle tuber virus is spread largely (if not exclusively) by knives in cutting tubers into seed-pieces (16), by contact of machinery with infected plants when passing through the field, and by other similar mechanical means (5, 6, 20, 19). There are also reports of transmission by insects other than aphids (17, 22).

Infection with leaf roll virus causes a more serious disease of potatoes than does spindle tuber virus. Plants growing from seed-pieces in-

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fected with leaf roll virus have a 33 to 85% reduction in yield of tubers depending upon the variety of potato, location, and other conditions (23, 10, 8, 18). However, in several varieties a statistically significant reduction did not occur unless more than 10% of the stand consisted of leaf roll plants (4, 7). In addition to reducing yield, first-year infection in some varieties, notably Green Mountains (3), results, in many of the tubers, in a darkened netting of phloem tissue known as net necrosis. This makes them unsightly and objectionable as food and unfit for seed. Of the four potato varieties involved in this study, only Green Mountain shows net necrosis. Chippewa is the most susceptible of the four varieties to the leaf-roll virus. Green Mountain is next followed by Kennebec. Katahdin is least likely to become infected and then only in situations where peach aphids are unusually abundant or uncontrolled.

Infection with spindle tuber virus causes some reduction in yield as well as rough, elongated tubers. The effect of the disease upon yield varies greatly depending upon many factors, including strain of the virus, variety and strain of potato, location, and proportion of the stand of field-growing potato plants infected with the virus (15, 3, 7, 8, 18, 44). While the yield of infected plants may be reduced as much as 17-69%, under Maine conditions, a statistically significant reduction in total yield probably does not occur unless the stand contains more than 12-15% of infected plants (15, 7). Such a high percentage of infected plants seldom if ever occurs at the present time in commercial planting of potatoes in Maine.

An epizootic of the green peach aphid occurred generally over northeastern Maine in 1937 (39). This situation, coupled with adequate sources of leaf roll in the commercial plantings of potatoes, resulted in an epiphytotic of the leaf roll disease (3). Prior to 1937, leaf roll had been a virus problem of no great concern to the potato industry in Maine (13). However, in that year it became a very serious problem for commercial producers of potatoes for both seed and culinary purposes. The general abundance of the green peach aphid, although not in epizootic numbers every year thereafter, continued for many years to be found at high enough levels to cause leaf roll to be the virus disease problem of greatest concern to potato growers in Maine.

In eight years during the period 1944 to 1954, a study was conducted on Aroostook Farm, near Presque Isle, to develop ways of obtaining and maintaining varying levels of aphid abundance on potato plants. Methods for measuring aphid abundance and their effects on yield and virus transmission were devised. These techniques were then used to determine the effects of varying all-season levels of abundance of the aphids and of virus reservoirs of two potato diseases upon yield of potatoes and the spread of leaf roll and spindle tuber in four varieties of potatoes. The results of that study are reported in this bulletin.

MATERIALS AND METHODS

Experimental design

From 1944 to 1949, inclusive, the nine treatments were formed by combining each of the three abundance levels of aphids with each of the three abundance levels of leaf roll reservoirs. In 1950 and in 1953, the three aphid levels were combined with the three levels of abundance of reservoirs containing leaf roll and spindle tuber. This 3 x 3 factorial design was arranged each year in a 9 x 6 randomized complete block.

Varieties, plot size and separations, and cultural practices

Four varieties of potatoes were used in the experiment, viz., Katahdin in 1944 and 1945, Green Mountain in 1946 and 1947, Chippewa in 1948 and 1949, and Kennebec in 1950 and 1953.

Each plot consisted of eight rows 34-in. apart and 50 ft. long. The 2-oz. seed-pieces were spaced by hand 1 ft. apart in the planting furrow. The alleys between potato plots in rows (columns) were separated by strips of oats 9 ft. wide planted when the potatoes were planted in May. The 10 ft. alleys between blocks of plots were seeded with oats or Japanese millet when the last hilling of the potatoes had been made in late June or in early July. The seeding of alleys was done to inhibit inter-plot movement of apterous aphids infesting the potatoes (31).

Fertilization, at planting only, was at the rate recommended for the commercial production of potatoes by the Maine Cooperative Extension Service. It consisted of an in-row band of fertilizer on each side of the planting furrow. The rates per-acre varied from 1,400 lbs. to 2,650 lbs. depending upon the formulation used in relation to the recommended rates of N,P,K and Mg.

Cultivation included three row hillings except in 1945, 1949, and 1953 when only two were made. In some years a mechanical weeder was used before the first hilling and in other years, the row middles were cultivated once with a spade after the final hilling. When required, weeds were also pulled by hand.

Weekly applications of a fungicidal spray for the control of the late blight organism *Phytophthora infestans* (Mont.) De Bary were made in all plots, usually from about July 1 to September 10. Calcium arsenate was added to the spray mixtures during one or more applications in some years for control of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say). Otherwise, the only insecticide applied was nicotine-lime dust for obtaining and maintaining one or the other of two controlled levels of aphid abundance in certain plots.

Abundance of aphids and virus infector plants

There were three levels of abundance of aphids and three of virus infector plants. The uncontrolled level of aphid abundance was the high level. The intermediate and low levels of aphid abundance were obtained and maintained, in certain plots, throughout the season by making, as frequently as necessary, dust applications of hydrated lime-nicotine sulfate mixtures containing either 4% or 2% of nicotine. These were applied at different rates using rotary hand-operated machines. The dust applications were usually made in early morning when the air was calm, or below 2 mph; at times, late evening applications were required because wind movement in the morning prevented application at the intended time.

The three levels of virus reservoirs were obtained by randomly interplanting the appropriate numbers of healthy or healthy plus leaf roll or spindle tuber infected seed-pieces. The levels of virus reservoir abundance were 0%, 5%, or 10% of the stand in each plot. The healthy and virus-infected seed-pieces were of the same variety. When either level of infector plants was required, the appropriate numbers of healthy and virus-infected seed pieces for each row in the plot were randomly mixed before being placed in the rows. The numbers of seed-pieces were combined so as to have not more than 10% of the stand consisting of disease reservoirs in each plot when the three abundance levels of spindle tuber reservoirs (0%, 5%, 10%) were combined with those of leaf roll (10%, 5%, 0%). This was done to prevent a statistically significant loss in yield from having an excessive number of disease reservoirs in the plantings (4, 7, 8). The infector plants remained in the stands throughout the season. They were marked so that when samples were taken at harvest to study disease spread, these diseased hills could be avoided and thus only tubers from plants known to have grown from healthy seed-pieces were included in the samples carried over winter and planted the following year.

Determination of effects of treatments

Virus disease spread. Immediately prior to harvest, one tuber was taken from each of 100 sample plants per plot. The sample portion in each of the 8-row plots was the center 38 ft. on the four middle rows. The sample plants were located in a screen grid over the sample portion of each plot. The sample tubers were stored over-winter and planted in the field late in May. Disease symptoms were recorded when the plants were 12 to 18 inches tall.

Yield of tubers. At harvest, after the plants in the low aphid-level plots had been killed by frost, all tubers in the sample portion of each plot were dug and collected by hand, weighed in bulk, then graded and weighed by grades. Tuber counts by grades were also made. The weights and numbers by grades in the samples taken to study the spread of the virus diseases comprised part of the yield recorded for each plot.

Populations of aphids. During approximately one-third of the growing season, aphid counts were made at least weekly in one randomly-drawn 6-plot series representing each of the three levels of aphid abundance. Similar counts of aphids during the middle of the season were made in like series of plots randomly drawn from each of the remaining two series having the same level of aphid abundance. The aphid counts were made during the remaining one-third of the season in the three series of plots not previously used for that purpose. Throughout much of the summer and in most years, the counts were made twice each week in both the low and intermediate aphid-level plots. This was done especially during periods when frequent applications of the nicotine dusts were required to establish and maintain the desired aphid levels.

The aphid counts consisted of recording by species all apterous and alate forms observed on 25 plants per plot until the plants were about 8 in. tall; thereafter, only three leaves per plant (randomly located within the top, middle, and bottom thirds of stem length) or parts of these three leaves on 25 plants per plot were examined (24, 33). In all instances, the sample plants were located in a screen grid over the sample portion of a plot. Examinations were made of the potato leaves *in situ*.

Expressions of aphid abundance. The basic expressions of aphid abundance were average number per unit of leaf area, average number per whole plant when the plants were not over 8 in. high, and average number on three leaves per plant (top, middle, bottom) at other times (24). When the subunit of sample was less than three whole leaves per plant, conversions were made to the 3-leaf basis (33). The 3-leaf averages from plants over 8 in. high were converted to the whole-plant basis by using as a correction factor the average number of 3-leaf groups per plant as estimated for each count date.

Estimates of the average number of 3-leaf groups per plant or leaf area per plant were approximated by adjustments based on weekly leaf counts or leaf measurements made throughout the summers of 1967 to 1970 on field-growing plants of each variety of potato involved in this study (27). A study of these data indicated that the maximum or peak size, including average number of compound leaves or $in.^2$ of leaf area per plant, bore a close, positive linear relationship to the amount of rainfall during May and June for potatoes of the Katahdin, Green Mountain, and Chippewa varieties or from May 16 to June 30, inclusive, for Kennebec potatoes. It was also noted that the rates of increase in average number of leaves or in.^{2} of leaf area per plant were rather closely approximated on a graph by the slopes of lines drawn between two points in time representing plant emergence and peak number of leaves or in.^{2} of leaf area per plant.

The numbers of leaves and amount of leaf area per plant for a given variety of potato used in the present study were approximated, at each time of aphid count, by reading from graphs of estimated growth of that variety in the specified year. To make the graphs, straight lines were drawn between the points, in time, of emergence of the potato plants in the plots and the estimated seasonal peak number of leaves or peak amount of leaf area per plant in that year. The latter points on the graphs were approximated by multiplying the peak measurements for the appropriate variety growing in 1969 by the inches of rainfall during the appropriate period of each year (viz., May 1 to June 30, or May 16 to June 30, depending upon variety) divided by the inches of rainfall during the same period of 1969. For example, the average number of leaves or in.^{2} leaf area per plant at the seasonal peak in a specified year was considered to be 90% of the comparable 1969 figure when rainfall during the appropriate period of that year was 90% of the rainfall during the same period of 1969.

The all-season expression of aphid abundance was number of aphid-days of apterae per plant. This was determined by measuring the average height of the area beneath a curve (2) made by plotting against time the numbers of apterous aphids per plant of a given species or of all four species of aphids combined, as found at each aphid count during the summer. The average height of the curve was then multiplied by the number of days that the potato plants in the appropriate series of plots were infested by apterous aphids of that species or of all four species.

RESULTS AND DISCUSSION

Regulations of the levels of aphid abundance

Two regulated seasonal levels of aphid abundance on potatoes were established and maintained by properly timed applications of dust mixtures containing 2 or 4% of nicotine (Tables 1, 2, 3, Figures 1 to 8 incl.). Greater difficulty was experienced in establishing and maintaining the higher of these two regulated aphid levels than the lower one, referred to hereafter as the intermediate and low levels, respectively. Only two applications of the 2% dust were needed to establish and maintain the intermediate level in one year, three applications were needed in each of four years, and four applications in three years (Table 1). Five or six applications of the 4% dust were required to establish and maintain the low aphid-level except in 1945 when only four were needed.

The number and the timing of dust applications to establish and maintain the desired levels of aphid abundance were influenced by several factors. The most important factor was probably the size of the aphid population at the time control measures were started. Associated with this was the need for thorough plant coverage with the dusts if the needed reduction in the size of the aphid population was to be achieved. In addition, temperature and wind velocity during the dusting operation were important as were the application rates of the two dust mixtures.

Both regulated levels of aphid abundance were most successfully established and maintained when regulation was attempted near or shortly after the end of the aphids' spring migrations, when the numbers of aphids per plant and percentages of plants infested by aphids were small.

The low aphid-level was most readily established by directing the 4% nicotine dust to the lower half of the plants on both sides of every row in a given plot. This was double the amount of dust required for maintaining the level after successful initial establishment. Thereafter, little difficulty was experienced in maintaining a satisfactorily low level of aphid abundance with infrequent applications of the 4% dust at 25 to 30 lbs. per acre, applied to one side of each row, assuming that a very low aphid level was established at the end of the aphids' spring migrations. The average amount, expressed as lbs. per acre of the 4% dust applied each year (Table 1), included one application to both sides of every row in all plots receiving the same treatment.

The chief difficulties in regulating an intermediate level of aphid abundance included selecting the time and making a satisfactory application of the 2% nicotine dust to establish a level that would be neither too high nor too low. Experience showed that establishment of an initial level which was not low enough necessitated several supplemental applications to secure a gradual downward adjustment in aphid abundance. On the other hand, initial establishment of too low an aphid level, especially after the aphids' spring migrations were complete, resulted in a level that throughout the remainder of the season remained below the intermediate level desired. Generally, the most satisfactory intermediate aphid-level was obtained by applying the 2% nicotine dust to the upper half of the plants from one side of each row at a rate of 12 to 15 lbs. per acre. Considerable difficulty was experienced in making uniform applications of this dust mixture at so low a rate.

The unregulated aphid population trends

Rates of increase and decline. The rate of aphid increase in the unregulated populations (the high aphid-level plots in Figures 1, 3, 5, 7) was typically a straight line during the growth phase of the population when $\log_{n+1}$ of the average number of apterous aphids per plant was plotted against time (25, 29, 30, 37). Variability in the slope of this line from year to year was probably due in large measure to the general level of natural environmental resistance, including both physical factors, e.g. temperature, precipitation and relative humidity, and biological agents of aphid control, viz., entomogenous fungi, arthropod predators and parasites (34, 29, 32, 37). The slopes of the lines representing the increase in aphids per in.^{2} closely resembled those for average number per plant (Figures 2, 4, 6, 8).

There was considerable variability among years in slope of the line representing rate of decline in size and foliar density of the aphid population, as well as in the beginning of the decline (Figures 1 to 8, incl.) This variability was probably influenced largely by the timing and duration of increased activity of predators and entomogenous fungi (29, 37); however, variation among years in composition of the aphid population on the plants was also a contributing factor. For example, maturation on and flight of fall migrant forms from potatoes late in August and in September were responsible for much of the variation in the rate of decline in size of total aphid population in years when the buckthorn aphid comprised a large proportion of the aphid population (26).

Time of peak and abundance of aphids at the seasonal peak. In most years there was close agreement between the times of peak abundance and maximum density of aphids on foliage (Table 2). Only in 1946 was there a large difference in the times when these two phenomena occurred. In that year the persistence of large aphid populations per plant until late in the season caused a rapid loss of the potato foliage. This resulted in an increasing number of aphids per unit of leaf area as the leaf area per plant decreased. Excluding 1945, because of early termination of the experiment due to late blight, the seasonal peak of aphid numbers per plant during this 8-year study ranged from August 17 to 30. The comparable range for average number of aphids per in.^{2} was August 17 to September 12. Excluding 1945, at the peak there was a range of 9,200 to 55,700 aphids per plant, and a comparable range of 1.6 to 111 aphids per in.^{2} of foliage.

All-season abundance of aphids. There was much variability among years in the all-season abundance of apterous aphids in unregulated high-level populations (Table 3). The variability was considerable among years on the same variety of potato. Doubtless much of it resulted from differences among years in the productiveness of spring migrant aphids on their primary hosts, and in the size of the spring migrations of each species of aphids (45, 26, 35, 36); variability also resulted from differences among years in the effectiveness of natural agents of aphid control in the potato plantings, especially entomogenous fungi and arthropod parasites and predators (29, 32, 28, 30, 37). No estimates can be made of the amount or proportion of total variability from these sources.

The smaller aphid population on Katahdins in 1945 than in 1944 was due largely to the necessity of applying an herbicide to kill the plants in mid August because of an epiphytotic of the late blight fungus. Aphid populations rapidly increased until the latter part of August and became large on untreated potatoes in other nearby plots where an epiphytotic of the late blight fungus did not develop.

The regulated aphid population trends

Rates of increase and decline. The intermediate level, or the higher of the two regulated levels, exhibited characteristics of population growth and decline surprisingly similar to those of the unregulated level (Figures 1, 3, 5, 7). The similarity occurred despite the interruptive influence of the 2% nicotine-dust applications and the resulting reductions in overall size of the aphid population from such treatment.

The characteristics of aphid population growth and decline in the regulated, low-levels of aphid abundance were not similar to those of the unregulated, high levels of aphid abundance. However, there was a strong tendency for the characteristics of population growth to resemble those of the high aphid-level plots during the early stages of population growth, especially when the initial attempts to establish the low aphid-level were inadequate. In most instances successful establishment of the low aphid-level was not achieved unless a double-application rate of the 4% nicotine dust was made (25 to 30 lbs./acre to both sides of the potato rows). In 1946, the use of the double rate of the 4% dust was deferred until the third application, following which the low level was readily maintained (Figure 5). It appears that after a low level of aphid abundance was satisfactorily established, natural agents of aphid control were sufficiently effective to maintain low aphid levels thereafter with little need for dust applications.

Assessment of measurement of aphid abundance. There was much variability among years in the relative sizes of the intermediate and low regulated levels of aphid abundance (Table 4, Figure 1 to 8, incl.). A suitably low level in relation to the intermediate and high levels was maintained except in 1944 and 1945 (Table 3, Figures 1, 3, 5, 7). In 1944, the initial attempt to establish the low level was started too late; also, our knowledge of the ecology of the aphids was inadequate and we were inexperienced in the use of a short-lived aphidicide for establishing and maintaining a low level of aphid abundance. Some of the difficulty in 1945 was due to the epiphytotic of late blight resulting in the need for early application of an herbicide. The plants were killed before full expression of the differences in aphid abundance represented by the three levels could occur. Except possibly in 1949, the aphid population in none of the low aphid levels was large enough to cause a statistically significant reduction in yield of tubers.

The attempt to regulate an all-season level of aphid abundance intermediate to the low and unregulated, high, levels was fairly satisfactory although not entirely so (Table 3, Figures 1, 3, 5, 7). The size of the intermediate level was 30 to 35% of the high level in three of the eight years, 46 to 57% of it in three years, and 60 to 64% in two years (Table 4). The ideal level sought was just under 50% of the high, unregulated level of aphid abundance.

Effects of regulation upon composition of the aphid population

There were striking differences in the compositions of the aphid populations on potatoes depending upon the extent of regulation with nicotine (Table 5). Except in 1944, the proportion of the all-season total aphid population comprised by the buckthorn aphid decreased with a decrease in overall level of aphid abundance. The reason for the exception in 1944 is unclear, although it probably was associated in some way with the low level of buckthorn aphid abundance in the unregulated population. In contrast, except in 1944 there were sharp increases in the proportion of the population comprised by the potato aphid with decreasing levels of total aphid abundance, a selective response, no doubt, to the low rate of nicotine sulfate.

Comparable relationships for the foxglove and green peach aphids were not as consistent as for the buckthorn and potato aphids. In three of the seven years when present (1946, 1947, 1948), the percentage of aphid population comprised by foxglove aphids increased with decreasing levels of aphid abundance; in three years (1945, 1949, 1950), the intermediate level of aphid abundance had the highest proportion of foxglove aphids, while in 1953 the proportion in the intermediate level was below that of the low or high levels. The percentages of total aphid population comprised by the foxglove aphid were about equal in the high and low levels of aphid abundance in 1945 and in 1949, but larger in the low than high aphid-level plots in 1950 and in 1953.

The green peach aphid comprised an increasing percentage of the aphid population with decreasing levels of aphid abundance only in 1946 and in 1947. The percentages of total aphid abundance comprised by this aphid were larger in populations of the intermediate than in either the low or high levels of aphid abundance in five of the remaining six years, while it was smaller in 1945. During these six years, green peach aphids comprised a larger percentage of total aphid population in the high than in the low aphid-level plots in 1944, 1948, and 1950, while it was larger in the low than in the high aphid-level plots in 1945, 1949 and 1953.

The altered composition of the aphid population in the regulated levels of aphid abundance was associated to a considerable extent with the zonal stratification of the aphids on the potato plants (38, 33) in relation to the part of the plants toward which the nicotine dusts were directed, especially in the instances of the buckthorn and potato aphids. In most years a smaller proportion of aphid population was comprised by buckthorn aphids where the dust was directed at the lower half of the plants (low aphid level) than at the upper half where the aphid is least abundant. Some, but not all, of the reverse relationship in the instance of the potato aphid was due to its normally greater abundance on the upper than on the lower half of the plants; some may have been due to a difference in tolerance of the potato aphid for different strengths and application rates of the two dust mixtures.

We probably do not recognize all of the factors responsible for the substantial differences and variability among species in percentages of total aphid population comprised by each species. The factors operating in the instances of the buckthorn and potato aphids likely were of some importance for the other two species as well. However, no doubt, other factors must have had a significant influence. For example, the response of the foxglove aphid more closely resembled that of the potato aphid although the zonal distribution of the foxglove aphid on potato plants closely approaches that of the buckthorn aphid. The green peach aphid occurs most commonly on the lower one-third or one-half of the plants, yet the response of that aphid differed substantially from those of the other three species of aphids.

Effects of differing levels of aphid abundance

Appearance and condition of potato plants. There were distinct differences in the appearance of potato plants subjected to the three differing all-season levels of aphid abundance. Symptoms of direct aphid damage from feeding began to appear usually about two weeks sooner in the high aphid-level plots than in the intermediate aphid-level plots; they never developed in the low aphid-level plots. The principal symptoms of aphid damage were the appearance and rapid increase in amount of honeydew and accompanying fungal growth on the leaves, the abundance of cupped, crinkled, curled or rolled leaves, the relative abundance of discolored, darkened veins in the leaflets, the numbers of dead or drying bottom leaves, and the differences in general appearance of the plants from plot-to-plot as to color and vigor.

The time of first appearance, the rapidity of increase in, and ultimate severity of the aphid damage symptoms developing varied greatly among potato varieties, and also because of differing levels of aphid abundance, amounts of soil moisture, and weather conditions. Katahdins appeared to be most susceptible to aphid feeding, based on symptoms of feeding damage to the plants, followed by Green Mountains, Chippewas and the Kennebecs. There appeared to be little difference between Kennebecs and Chippewas. This ranking of Katahdin and Green Mountain agrees with observations by Burnham and MacLeod (9) and Adams (1). Figure 9 shows early September differences in appearance of Katahdin potatoes in plots subjected to one or another of the three all-season levels of aphid abundance.

Yield of tubers. The seasonal level of aphid abundance exerted a marked effect upon pounds of tubers per 100 ft. row sized above 1 7/8 or 2 inches in diameter at regular harvesttime, i.e., after the plants had died from aphid feeding damage or been killed by frost (Tables 6, 7). Excluding 1945, because of the necessity of applying an herbicide to the plants in mid-August, only in two years were the weights of tubers not significantly increased in plots having the two reduced levels of aphid abundance. In 1949, plots having either of the two regulated levels outyielded plots having the unregulated, high level of aphid abundance but the yield of plots having the low seasonal level of aphid abundance was not significantly larger ($P>0.05$) than that of the intermediate aphid-level plots. In 1953, the yield of the low aphid-level plots exceeded that of the high aphid-level plots, ($P<0.05$), but the yield of the intermediate aphid-level plots was not significantly less at the 5% level. In all other years, the increasing poundage of tubers over 1 7/8 inches or 2 inches in diameter was associated at a 5-percent or higher level of significance with a decreasing all-season level of aphid abundance.

The effects of the differing levels of aphid abundance upon average number of tubers over 1 7/8 inches or 2 inches in diameter per 100 ft. row were similar to those upon pounds of tubers of these sizes per 100 ft. of row.

Increasing yield (both pounds and numbers) of the larger sizes of tubers was more strikingly associated with decreasing levels of aphid abundance than was the yield of all tubers over 1 7/8 inches or 2 inches in diameter.

The data do not permit a critical appraisal of differential yield as a response to aphid abundance by variety of potato included in this study. However, our observations indicate that aphid feeding was more readily reflected as reduced yield of tubers in Katahdins than in the Green Mountain, Chippewa, or Kennebec varieties.

Threshold populations of aphids resulting in reduced yield of tubers. Correlation and regression analyses were made to determine whether reduction in yield of tubers was associated with the level of aphid infestation on the potato plants. The comparisons were between percentage of reduction in lbs. per 100 ft. row of tubers 1 7/8 or 2 inches in diameter, based on yield in the low aphid-level plots, and $\log_{n+1}$ of all-season average number of aphid-days of apterous aphids per plant in the comparable high and intermediate aphid-level plots (Table 8). The correlation was $r = 0.665$ ($P<0.01$). The regression equation was $Y = 12.56 - 29.97 + 13.16 X$. There was reasonably good fit of the data to the regression line except those for the Katahdin variety (Figure 10). Yield of Katahdins appeared to be more sensitive and affected to a greater extent by aphid abundance than that of the other varieties. Yield of Chippewas or Kennebecs was affected less than that of Green Mountains. Since the regression line represents an average reaction of four varieties having a wide range in degree of response to aphid feeding, it is not surprising that it did not closely fit all of these data.

The generalized threshold of aphid populations causing feeding damage to be reflected as reduced yield of tubers over 1 7/8 or over 2 inches in diameter was approximated by extending the regression line to the point where it intersected the ordinate of the graph (Figure 10); it was an all-season plant average of 20, 400 aphid-days per plant of infestation by apterae. This is the equivalent of about 272 aphids for the entire average period of 75 days per year that the plants were infested by aphids[7], during the 7-year period (Table 8). Assuming that the plants of the four varieties of potatoes had an all-season average of 37 leaves per plant which was one-half the average maximum number (27), this was equivalent to an all-season average of 22 aphids on three leaves per plant (top, middle, bottom).

This threshold estimate is only a generalized approximation since yield of tubers is affected by many factors in addition to level of aphid infestation and variety of potato, including fertilization, soil moisture, and size, age, and vigor of the plants when aphids are most abundant. For example, results of some of our studies revealed that an average of approximately 28 apterae of all species on three leaves per plant during mid-August was the threshold aphid population causing reduction of yield in Katahdins. Assuming an average of 51 leaves per plant during this period (27), this is the equivalent of between 475 to 500 apterae

[7] The length of this period was actually somewhat longer than this since aphid counts in most years did not extend to the time the plants were killed by frost.

per plant. Results of other studies, which we conducted over a period of more than 15 years, showed there was generally close agreement between the reduction in yield of tubers and the average number aphid-days per plant in excess of this number of aphids for the period during which the threshold level was exceeded.

Effects of virus-reservoir abundance upon yield

Leaf roll. The reduction in lbs. per 100 ft. row of tubers over 1 7/8 or 2 inches in diameter was not significant ($P>0.05$) as the percentage of the stand consisting of plants from leaf roll-infected seed-pieces increased from 0% to 5% to 10% (Tables 6, 7). However, excluding yields in 1945 for reasons given earlier in this bulletin, there appeared to be a tendency in some years for an increasing abundance of virus reservoirs to suppress yield. This is not surprising, although Bonde and Schultz (7) did not find a statistically significant reduction in yield in stands of potatoes containing as much as 10% of leaf roll-infected plants. Results of earlier studies (22) showed that yield of tubers by plants having chronic leaf roll was only 40 to 50% as much as that of healthy plants.

Spindle tuber. No reduction in lbs. per 100 ft. row of tubers over two inches in diameter occurred when the level of spindle tuber reservoirs in the plantings comprised up to 10% of the stand of Kennebec potatoes (Table 7).

Effects of abundance of aphids and of virus reservoirs upon spread of viruses

Spread of leaf roll. Excluding 1945, for reasons previously stated, the percentage of spread of leaf roll was significantly ($P<0.05$) affected by the relative abundance of aphids and of leaf roll reservoirs in the stands (Table 6, 7). In most years, the spread of leaf roll increased with increasing abundance of aphids and of leaf roll reservoirs in the plantings. The increase in leaf roll spread was significant ($P<0.05$) as the levels of leaf roll reservoirs increased from 0% to 5% to 10% except in 1946, 1947 and 1950. In 1946 and in 1950, the percentage of spread was significantly ($P<0.05$) less in plots having the 0% and 5% of leaf roll reservoirs than in plots having 10%, but did not differ from each other at the 5-percent level, while in 1947 leaf roll spread in plots having 5% or 10% diseased plants did not differ at the 5-percent level of significance but was greater than in plots having no leaf roll reservoirs in the plantings.

Except in 1944, the increase in spread of leaf roll in the high aphid-level plots over that in the low aphid-level plots was significant at the 5-percent level; however, only in 1947 was the spread in the intermediate aphid-level plots significantly less ($P<0.05$) than in the high aphid-level plots. Apparently, the difference between these two levels in abundance of the green peach aphid, which is the most important vector of leaf roll (21, 42), was in most years not great enough to result in differences in virus spread at the 5-percent level of significance.

In 1944, plant condition appeared to be largely responsible for lesser spread of leaf roll in plots of Katahdins subjected to the high levels of aphid abundance than to low levels of aphids. Before mid-August, the general appearance and condition of the plants began to deteriorate in the high aphid-level plots, while it was considerably later before such deterioration became apparent in the intermediate aphid-level plots. By September 10, most of the leaves were dead in the high aphid-level plots and the large aphid populations were concentrated on the stems and few yellowing leaves remaining. Apparently the plants in the high aphid-level plots became prematurely physiologically old and were incapable of being infected with leaf roll as a result of aphid feeding damage. On the other hand, the plants in the low aphid-level plots continued to exhibit a condition of vigor, with little loss of leaves, until killed by frost on September 24. Additionally, the large numbers of flying green peach aphids during August and September may have been responsible in part for the inordinate amount of leaf roll spread in the low aphid-level plots as shown in the samples from these plots grown in the following year.

Spread of spindle tuber. In 1950, the percentage of spread of spindle tuber increased as the level of abundance of spindle tuber reservoirs increased from 0% to 5% to 10% (Table 7). The percentage of spread recorded for the low aphid-level plots was significantly larger at the 5% level than in the high aphid-level plots but did not differ from the spread recorded in the intermediate level plots. This confusing situation was clarified by the studies of Bonde and Merriam (5) which showed that the spindle tuber virus can be spread mechanically. Likely, a major portion of the spread of spindle tuber in our 1950 experiment resulted from the frequent movement of machinery through the plots, including the tractor, implements of cultivation, and the duster used to apply fungicidal mixtures. The duster was equipped with a 12-ft. trailing canvas apron which covered all of the rows. Some spread may also have resulted from the cutting knife used in preparing the seed pieces.

There was very little spread of spindle tuber, and no spread of double infections in 1953, when no seed-pieces having double infections were planted, passage of the machinery of cultivation was restricted to the period during which the plants were small, and no application of fungicide was made. The results corroborate those of others which indicate that spindle tuber virus under field conditions is spread most readily by machinery of cultivation and by other similar mechanical means. If the virus is spread by insects, insects other than aphids are usually involved.

SUMMARY AND CONCLUSIONS

An 8-year study between 1944 and 1953, inclusive, was made of the effects of differing all-season levels of aphid infestation and of virus reservoirs upon yield of tubers and spread of two viruses, leaf roll and spindle tuber, in replicated small-plot plantings of four varieties of potatoes. The varieties were Katahdin, Green Mountain, Chippewa and Kennebec. The response of each variety was determined during two years, but most of the results from the second year's test with Katahdins could not be used in the comparisons because of the need to apply an herbicide to kill the plants before their full response had occurred.

The all-season levels of aphids abundance were high, intermediate and low. The high level was the natural aphid population in any given year. The intermediate and low levels were established and regulated by making applications of dust mixtures containing 2% or 4% nicotine, respectively, as frequently as needed. The most satisfactory levels were initially established by a calendar date near or soon after completion of the aphids spring migrations. The low level was readily maintained once it was established. Some difficulty was experienced in regulating the intermediate level so as not to be too low or too high in relation to the other two levels.

The all-season levels of virus reservoirs were obtained by planting randomly mixed healthy and virus-infected seed-pieces in appropriate ratios and by not disturbing the resulting stands of plants until harvesttime. The three levels of leaf roll or spindle tuber reservoirs were 0%, 5% and 10% of the planted seed-pieces. In all tests, these low, intermediate, and high levels of virus reservoir abundance, respectively, were subjected to each of the three levels of aphid abundance. Leaf-roll reservoirs were included in some of the plots in all years; spindle tuber reservoirs were included only in the two years of tests with Kennebecs.

Measures to ascertain the effects of these factorially-arranged treatments included counts, made weekly or more often, of aphids infesting the plants, yield of tubers after the plants had been killed by frost or died from aphid feeding damage, and the seasonal spread of the virus or viruses in all plots. Spread was determined the following year by observing for disease symptoms, field-growing plants that came from tubers which had been taken at harvesttime from the plants growing from healthy seed-pieces and stored over winter. The expressions of aphid abundance included the all-season average number of aphid-days per plant based on infestation by apterous aphids of all species, and the percentage composition of the population by species of aphids. Yield included average lbs. per ft. row of tubers over 1 7/8 or 2 inches in diameter. Virus spread was computed as percentage of healthy plants becoming infected during a given season.

The yearly average number of aphid-days of infestation per plant comprising the three levels of aphid abundance ranged from 1,400 to 27,200 in the low aphid-level plots, from 7,400 to 379,200 in the intermediate level plots, and from 11,600 to 1,245,000 in the high level plots.

The compositions of the total aphid populations as to species were affected substantially in plots having the regulated low and intermediate levels of aphid abundance. The nicotine as used in these experiments did not provide uniform reduction in the numbers of the four species of aphids infesting the plants. The proportion comprised by the buckthorn aphid decreased with decreasing levels of aphid abundance while, in all years except 1944, the proportion of the potato aphid increased with decreasing levels of aphid abundance. The changes in proportions of total population comprised by these species appeared to be related chiefly to zonal stratification of each species on the plants with respect to the part of the plants towards which the nicotine dusts were directed in establishing and maintaining the differing levels of aphid abundance. Similar proportions of the foxglove and green peach aphids were not consistent among years.

All four varieties of potatoes developed gradients in the severity of damage to the potato foliage and in the rate and ultimate extent of the deterioration of plant condition from aphid feeding which were associated with the all-season levels of aphid abundance. Katahdin plants appeared to exhibit these symptoms more readily than did the other three varieties, Green Mountains, Chippewas and Kennebecs in that order.

With few exceptions, the weight of tubers over 1 7/8 or 2 in. diameter increased ($P<0.05$) with decreasing all-season levels of aphid abundance but yield of the intermediate aphid-level plots did not always differ from that of the high or low aphid-level plots at the 5% level. Effects of aphid levels upon numbers of tubers of this size were similar to those upon pounds of tubers. Increasing weights and numbers of the larger sized tubers were especially associated with decreasing levels of aphid infestation.

Percentage reduction in pounds of tubers over 1 7/8 to 2 in. diameter was correlated with $\log_{n+1}$ of the average no. aphid-days per plant based on infestation by apterous aphids ($r = 0.665^{**}$). The regression equation was $Y = 12.56 - 29.97 + 13.16\ X$. Downward extension of the regression line gave an aphid damage threshold estimate of 20,400 aphid-days per plant. This is the equivalent of an all-season infestation of about 272 apterae per plant, or about 22 apterae on three leaves per plant (top, middle, bottom).

Percentage spread of leaf roll in most instances increased ($P<0.05$) with increasing abundance of aphids on the plants and with increasing levels of leaf roll reservoirs in the plots. However, the reverse occurred in one year of heavy aphid infestation when early plant deterioration apparently caused potato plants in the high and intermediate aphid-level plots to become incapable of being infected before the plants in the low aphid-level plots reached this condition.

Percentage spread of spindle tuber in one year of two years of tests increased significantly ($P<0.05$) as the abundance of spindle tuber reservoirs increased from 0% to 5% to 10% of the stand but was numerically less under conditions of high aphid levels than under those of either intermediate or low aphid levels. No difference in spread at the 5% level occurred in the other year, regardless of abundance levels of aphids or of spindle tuber reservoirs. We interpret the data as indicating that most of the spread of spindle tuber was caused by passage of machinery through the plots, and that at most only some small part of it may have been due to aphids.

Table 1

Application of nicotine sulfate dusts to plots of the population levels experiment to achieve the low and intermediate levels of aphids in the plots.

Year	Dates of Application 1st	2nd	3rd	4th	5th	6th	Avg lb per acre applied
			Low aphid levels plots (4% Nicotine)				
1944	Aug. 2	Aug. 8	Aug. 15	Aug. 24	Sept. 1		34.9
1945	July 23	July 30	Aug. 6	Aug. 14			36.4
1946	July 17	July 26	Aug. 6	Aug. 13	Aug. 21		39.7
1947	July 25	July 31	Aug. 7	Aug. 14	Aug. 28		38.4
1948	July 16	July 20	July 30	Aug. 6	Aug. 17	Aug. 24	35.5
1949	July 15	July 21	July 28	Aug. 4	Aug. 10	Aug. 18	30.4
1950	July 20	July 24	July 30	Aug. 17	Aug. 14	Sept. 1	34.9
1953	July 16	July 23	July 30	Aug. 7	Aug. 14	Aug. 21	34.6
			Intermediate aphid levels plots (2% Nicotine)				
1944	Aug. 2	Aug. 8	Aug. 15	Aug. 24			16.9
1945	July 23	July 30	Aug. 6	Aug. 14			13.6
1946	July 17	July 26			Aug. 21		20.0
1947	July 25	July 31	Aug. 7				17.9
1948	July 16	July 20	July 30	Aug. 6			13.6
1949	July 15	July 21	July 28				11.7
1950	July 20	July 24	July 30				14.1
1953	July 16					Aug. 23	11.6

Table 2

Time and size of peak aphid abundance and of peak aphid density on foliage of potatoes in plots having no regulation of aphid populations, 1944 to 1953.

Year	Variety	Apterous aphids per plant Date	Avg no.	Apterous aphids per in.² Date	Avg no.
			(000)		
1944	Katahdin	Aug. 30	21.7	Aug. 30	20.7
1945	Katahdin	Aug. 15	1.8	Aug. 15	1.6
1946	Green Mountain	Aug. 19	55.7	Sept. 12	111.1
1947	Green Mountain	Aug. 20	15.9	Aug. 20	12
1948	Chippewa	Aug. 30	14.8	Sept. 3	14
1949	Chippewa	Aug. 17	9.2	Aug. 17	9.8
1950	Kennebec	Aug. 24	22.0	Aug. 24	17.2
1953	Kennebec	Aug. 20	14.1	Aug. 22	19.4

Table 3

Aphid-days[a] of infestation per plant by levels of infestation on field growing potatoes. (See figures 1,3,5,7).

		Low level					Intermediate level					High level				
Year	Variety	Ba[b]	Gpa	Pa	Fa	All spp.	Ba	Gpa	Pa	Fa	All spp.	Ba	Gpa	Pa	Fa	All sp
							Numbers in thousands (000)									
1944	Katahdin	1.2	24.5	1.6	0	27.2	1.3	121.0	9.0	0	130.7	1.9	207.4	17.3	0	226.8
1945	Katahdin	.1	.9	.9	.2	2.1	.7	2.6	3.0	1.1	7.4	3.8	4.1	2.5	1.2	11.6
1946	Green Mountain	2.9	4.4	2.7	1.7	11.8	325.9	32.7	18.3	2.6	379.2	1185.5	34.8	20.7	4.1	124
	Green Mountain	.7	.6	2.7	.1	4.2	80.5	5.3	10.3	1.2	97.3	187.4	11.0	9.3	1.0	20
	Chippewa	.1	1.5	1.8	1.7	4.7	10.8	43.9	6.3	20.5	81.5	68.7	133.1	9.0	46.8	25
	Chippewa	T[c]	2.5	1.5	.1	4.1	11.5	49.2	11.6	1.9	74.2	86.1	112.1	11.5	2.6	21
	Kennebec	.3	.1	1.0	1.7	3.1	54.5	22.5	8.2	116.4	201.6	161.6	37.0	7.9	164.2	37
	Kennebec	.2	T	1.1	.1	1.4	126.3	3.4	6.5	7.1	143.3	212.4	3.5	6.6	13.3	23

lean number of apterous aphids per plant for the time that the potato plants were infested by the indicated species, multiplied by the number of he plants were infested by that species or, for the all-species grouping, by the number of days the plants were infested by any of the four aphid speci

a = Buckthorn aphid
pa = Green peach aphid
a = Potato aphid
a = Foxglove aphid

ess than 50 aphid-days of infestation.

Table 4

Year to year range in all-season size of aphid populations in the two variable, regulated levels of aphid abundance on potatoes, 1944-1953.

Year	Variety	No. apt. per plant High level	Percent of unregulated (High) level: Intermediate level	Percent of unregulated (High) level: Low level
		(000)		
1944	Katahdin	226.8	57.6	12.0
1945	Katahdin	11.6	63.8	18.1
1946	Green Mountain	1245.0	30.5	0.9
1947	Green Mountain	208.7	46.6	2.0
1948	Chippewa	257.5	31.7	1.8
1949	Chippewa	212.2	35.0	1.9
1950	Kennebec	370.6	54.4	0.8
1953	Kennebec	235.8	60.8	0.6

Table 5

Effect of nicotine dust applications, for obtaining two reduced levels of aphid abundance (inter. and low), upon the all-season composition of aphid population on potato plants, 1944 to 1953.

Year	Aphid level	Percent of total population: Buckthorn Aphid	Green peach Aphid	Potato Aphid	Foxglove Aphid
1944	High	.8	91.5	7.6	0
	Inter.	1.0	92.1	6.9	0
	Low	4.5	89.9	5.7	0
1945	High	33.1	35.6	21.2	10.1
	Inter.	8.9	34.6	40.2	15.4
	Low	2.9	42.7	43.9	10.5
1946	High	95.2	2.8	1.7	.3
	Inter.	86.0	8.6	4.8	.6
	Low	24.6	37.6	23.2	14.5
1947	High	89.8	5.3	4.5	.5
	Inter.	82.7	5.4	10.6	.3
	Low	16.2	14.7	66.1	3.0
1948	High	26.7	51.7	3.5	18.2
	Inter.	13.3	53.8	7.7	25.2
	Low	1.5	31.3	31.2	36.0
1949	High	40.6	52.8	5.4	1.2
	Inter.	15.5	66.3	15.6	2.5
	Low	.3	61.7	36.7	1.3
1950	High	43.6	10.0	2.1	44.3
	Inter.	27.0	11.2	4.1	57.7
	Low	10.1	2.3	32.4	55.2
1953	High	90.0	1.5	2.8	5.6
	Inter.	88.1	2.4	4.6	4.9
	Low	11.0	1.8	78.5	8.6

Table 6

Effect upon yield of tubers and spread of leaf roll disease from differing seasonal levels of abundance of aphids and of potato plants infected with leaf roll in field plantings of potatoes.

Treatments[1]: Level of aphids[2]	Treatments[1]: Level of leaf roll[3]	US 1 tubers (Avg lb/100 ft row)	Leaf roll spread (Avg %)	Levels of treatment factors: Level	US 1 tubers (Avg lb/100 ft row)	Leaf ro sprea (Avg %
KATAHDIN VARIETY			1944			
High	High	104.0	26.4	Aphids		
	Intermediate	105.4	21.0	High	106.2	18.0[4]
	Low	109.1	7.8	Intermediate	120.0	17.5[4]
Intermediate	High	112.9	26.3	Low	150.0	22.2[4]
	Intermediate	123.5	18.4			
	Low	123.6	9.0	Leaf roll		
Low	High	148.7	29.4	High	121.8	27.4[4]
	Intermediate	146.4	20.4	Intermediate	125.1	19.9[4]
	Low	155.0	17.3	Low	129.2	11.4[4]
LSD	P=0.05	15.2	NS		8.8	5.1
			1945[5]			
High	High	65.0	6.9	Aphids		
	Intermediate	69.6	5.7	High	64.9	4.5[6]
	Low	60.3	.5	Intermediate	63.1	3.8[6]
Intermediate	High	65.0	6.8	Low	63.0	3.4[6]
	Intermediate	61.2	4.2			
	Low	63.3	.5	Leaf roll		
Low	High	63.7	6.2	High	64.5	6.6[6]
	Intermediate	62.8	3.7	Intermediate	64.5	4.5[6]
	Low	62.3	.2	Low	62.0	.4[6]
LSD	P=0.05	NS	—		NS	—
GREEN MOUNTAIN VARIETY			1946			
High	High	151.6	25.1	Aphids		
	Intermediate	157.4	14.6	High	151.1	17.4
	Low	144.3	13.3	Intermediate	184.4	19.4
Intermediate	High	175.9	25.0	Low	209.7	24.4
	Intermediate	185.3	12.6			
	Low	192.5	20.9	Leaf roll		
Low	High	204.5	28.1	High	179.1	26.1
	Intermediate	207.6	20.8	Intermediate	181.5	16.0
	Low	217.1	24.5	Low	184.7	19.6
LSD	P=0.05	11.8	9.1		7.5	5.2

able 6 continued)

Treatment[1]		US 1 tubes	Leaf roll spread	Levels of treatment factors		
vel of phid[2]	Level of leaf roll[3]	(Avg lb/100 ft row)	(Avg %	Level	US 1 tubers (Avg lb/100 ft row)	Leaf roll spread (Avg %)
			1947			
igh	High	128.6	30.3	Aphids		
	Intermediate	123.9	33.5	High	125.2	25.6
	Low	123.2	14.1	Intermediate	138.0	16.7
itermediate	High	142.2	20.1	Low	146.4	5.0
	Intermediate	136.9	28.5			
	Low	134.8	2.5	Leaf roll		
ow	High	142.0	7.9	High	137.6	19.6
	Intermediate	145.6	6.9	Intermediate	135.5	23.0
	Low	151.8	.9	Low	136.6	5.8
LSD	P=0.05	10.6	17.7		6.1	10.4
HIPPEWA VARIETY			1948			
igh	High	178.2	74.0	Aphids		
	Intermediate	184.4	54.5	High	184.4	43.1
	Low	190.7	4.3	Intermediate	202.2	36.3
itermediate	High	204.1	58.9	Low	209.6	17.7
	Intermediate	203.3	49.9			
	Low	199.3	4.0	Leaf roll		
ow	High	205.5	36.7	High	195.9	56.6
	Intermediate	207.3	17.1	Intermediate	198.4	40.4
	Low	216.1	1.5	Low	202.0	3.3
LSD	P=0.05	13.0	13.5		7.4	7.8
			1949			
igh	High	170.9	93.3	Aphids		
	Intermediate	184.4	69.1	High	176.1	63.7
	Low	173.0	27.2	Intermediate	187.0	58.2
itermediate	High	179.3	79.7	Low	192.5	46.7
	Intermediate	192.9	76.7			
	Low	188.8	19.3	Leaf roll		
ow	High	202.2	61.3	High	184.1	78.2
	Intermediate	188.1	54.6	Intermediate	188.5	66.9
	Low	187.2	25.7	Low	183.0	24.0
LSD	P=0.05	16.9	13.9		9.8	8.1

Combinations of factor gradients.

See Figures 1-8, inclusive, and tables 2 and 3.

In all instances the amount introduced was 10%, 5%, or 0% of the seed-pieces planted for high, intermediate, or low levels, respectively.

In 1944, 0.4% of the seed-pieces planted as "healthy seed" were found to be infected with leaf roll; however, this amount, added to the known amounts introduced at planting to form the leaf roll levels, was excluded in computing percent spread.

All plants killed with an herbicide on August 16 because of severe late blight infection in all plots.

These figures represent all plants growing from sample tubers that had chronic symptoms of leaf roll; no exclusions were made for reservoir plants resulting from leaf-roll infected seed-pieces introduced at planting to form the leaf roll levels.

Table 7

Effect upon yield of tubers and spread of leaf roll or spindle tuber from differing seasonal levels of aphids and of potato plants infected with leaf roll or spindle tuber in field plantings of Kennebec potatoes.

Treatments			Yield	Percent spread			Treatment factors				
Level of aphids[1]	Level of leaf roll[2]	Level of spindle tuber[2]	Avg. lb tubers /100 ft row[3]	Leaf roll	Spindle tuber	Double infections[4]	Level	Avg lb tubers/100 ft row[3]	Avg percent spread: leaf roll	Avg percent spread: Spindle tuber	Avg percent spread: Double infections
					1950						
High	High	Low	206.1	56.0	14.0	9.8	Aphids				
	Interm.	Interm.	210.8	38.7	29.8	14.6	High	208.7	40.7	23.6	11.7
	Low	High	209.2	29.0	27.5	10.5	Interm.	222.2	46.8	31.5	16.7
Interm.	High	Low	224.2	61.1	18.5	12.1	Low	243.2	21.7	35.6	6.1
	Interm.	Interm.	221.2	34.6	28.9	11.2	Leaf roll				
	Low	High	221.3	45.6	48.1	26.5	High	233.4	50.9		14.1
Low	High	Low	199.4	35.4	20.7	9.3	Interm.	235.8	31.9		11.8
	Interm.	Interm.	244.9	22.6	32.5	9.5	Low	236.9	27.7		10.5
	Low	High	245.9	9.0	54.7	5.3	Spindle tuber				
							High	236.9		43.4	14.1
							Interm.	235.8		30.4	11.8
							Low	233.4		17.8	10.5
LSD	P=0.05		NS	16.4	8.4	7.4		9.0	9.4	4.8	4.3

(Table 7 continued)

					1953
High	High	Low	187.6	25.4	0.2
	Interm.	Interm.	187.0	20.6	1.7
	Low	High	192.2	1.5	1.9
Interm.	High	Low	184.0	29.1	.4
	Interm.	Interm.	194.6	17.8	1.6
	Low	High	191.8	.9	.8
Low	High	Low	210.6	6.8	.8
	Interm.	Interm.	203.2	2.8	1.5
	Low	High	207.3	.3	2.3
LSD	P=0.05		NS	8.8	NS

Aphids			
High	188.9	15.4	1.3
Interm.	190.2	15.4	1.0
Low	207.0	3.2	1.5
Leaf roll			
High	194.1	20.4	
Interm.	194.9	13.7	
Low	197.0	.9	
Spindle tuber			
High	197.0		1.7
Interm.	194.9		1.6
Low	194.1		.5
LSD P=0.05	12.0	5.1	NS

[1] For aphid levels, see tables 2 and 3, and figures 1 to 8.

[2] Approximately 10%, 5%, or 0% of the stand for high, intermediate, or low levels, respectively.

[3] Tubers over 2 in. diameter.

[4] Plants showing symptoms of both leaf roll and spindle tuber diseases. The figures in this column refer only to plants having double infections. The figures for leaf roll alone or spindle tuber alone include plants showing double infections, i.e. such plants were counted in the leaf roll figures and again in those for spindle tuber. Percent spread of double infections in 1950 was based on numbers of plants with double infections in the plots growing from the seed-pieces planted in 1950. In 1953 none of the seed-pieces planted had double infections.

Table 8

Relationship between level of aphid abundance on potato plants of five varieties and reduction in yield of tubers.

Year	Variety	Avg all-season aphid infestation: Level	Avg all-season aphid infestation: Aphid-days/plant[a] (X_1)	% Reduction in lb. U.S. 1 grade tubers[b] (X_2)
			(000)	
1944	Katahdin	High	226.8	29.2
		Inter.	130.7	20.0
1946	Green Mountain	High	1,245.0	27.9
		Inter.	379.2	12.1
1947	Green Mountain	High	208.7	14.5
		Inter.	97.3	5.7
1948	Chippewa	High	257.5	12.0
		Inter.	81.5	3.5
1949	Chippewa	High	212.2	8.5
		Inter.	74.2	2.9
1950	Kennebec	High	370.6	14.2
		Inter.	201.6	8.6
1953	Kennebec	High	235.8	8.7
		Inter.	143.3	8.1

Correlation coefficient: $r = 0.665$** [c]

[a] See Table 3 for aphid-days/plant in comparable low aphid-level plots.
[b] Based on yield in comparable low aphid-level plots (See Tables 6 & 7).
[c] Correlation between $\log_{n+1}$ of numbers in column X_1 and of percentages in column X_2.

References Cited

1. Adams, J. B. 1946. Aphid resistance in potatoes. Amer. Potato J. 23: 1-22.
2. Ascovitz, S. I. 1955. Rapid method for determining mean values and areas graphically. Science (Washington, D. C.) 121: 212-3.
3. Bonde, R. 1937-38. Spread of virus diseases in Aroostook County. *In* Maine Agr. Exp. Sta. Bull. 391: 233-340 (297).
4. ———. 1938-39. Observations on the prevalence of potato diseases in Maine during 1938. *In* Maine Agr. Exp. Sta. Bull. 397: 695-854 (804-5).
5. ———, and Merriam, D. 1951a. Studies on the dissemination of the potato spindle tuber virus by mechanical inoculation. Amer. Potato J. 28: 558-60.
6. ———, and ———. 1951 b. Potato spindle tuber control. Maine Agr. Exp. Sta. Bull. 487, 15 p.
7. ———, and E. S. Schultz. 1939-40 Effect on potato yield of different percentages of viruses. *In* Maine Agr. Exp. Sta. Bull. 400: 185-300 (262-3).
8. ———, ———, and W. P. Raleigh. 1943. Rate of spread and effect on yield of potato virus diseases. Maine Agr. Exp. Sta. Bull. 421, 28 p.
9. Burnham, J., and D. J. MacLeod. 1942. Varietal susceptibility of potatoes to aphid injury. Canad. Entomol. 74: 36.

10. Folsom, D. 1921. Potato leaf roll. Maine Agr. Exp. Sta. Bull. 297: 37-52.
11. ———. 1923. Potato spindle tuber. Maine Agr. Exp. Sta. Bull. 312: 21-44.
12. ———. 1932. Potato degeneration diseases: Natural and experimental transmission in Green Mountains in Central Maine. *In* Maine Agr. Exp. Sta. Bull. 363: 233-314 (276).
13. ———. 1938-39. Green Mountain seed plots. *In* Maine Agr. Exp. Sta. Bull. 397: 695-854 (788-92).
14. ———, W. C. Libby, G. W. Simpson, and O. L. Wyman. 1938. Net necrosis of potatoes. Maine Ext. Serv. Bull. 246, 12 p.
15. ———, E. S. Schultz, and R. Bonde. 1926. Potato degeneration diseases: Natural spread and effect upon yield. Maine Agr. Exp. Sta. Bull. 331: 57-112.
16. Goss, R. W. 1926. Transmission of potato spindle tuber by cutting knives and seed-piece contact. Phytopathology 16: 299-303.
17. ———. 1928. Transmission of potato spindle-tuber by grasshoppers (Locustidae). Phytopathology 18: 445-48.
18. LeClerg, E. L., P. M. Lombard, A. H Eddins, H. T. Cook, and J. C. Campbell. 1944. Effect of different amounts of spindle tuber and leaf roll on yields of Irish potatoes. Amer. Potato J. 21: 60-71.
19. Manzer, F., and D. Merriam. 1961. Field transmission of the potato spindle tuber virus and virus X by cultivating and hilling equipment. Amer. Potato J. 38: 346-52.
20. Merriam, D., and R. Bonde. 1954. Dissemination of spindle tuber by contaminated tractor wheels and by foliage contact with diseased plants. Phytopathology 44: 111 (Abstract).
21. Robert, Y. 1971. Epidemiologie de l'enroulement de la Pomme de terre: capacite vectrice de stades et de formes des pucerons *Aulacorthum solani* Kltb., *Macrosiphum euphorbiae* Thomas, et *Myzus persicae* Sulz. Potato Res. 14: 130-9.
22. Schultz, E. S., R. Bonde, and W. P. Raleigh. 1931. Potato degeneration diseases: Experimental transmission by insects in northeastern Maine. *In* Maine Agr. Exp. Sta. Bull. 360: 167-231 (196-97).
23. ———, and D. Folsom. 1920. Leafroll, net-necrosis, and spindling-sprout of the Irish potato. J. Agr. Res. 21: 47-80.
24. Shands, W. A., and G. W. Simpson. 1953. Survey methods: Aphid populations on potatoes in the Northeast. Plant Protection Programs, USDA, Coop. Econ. Insect Rep. 3: 181-82.
25. ———, and ———. 1959. Characteristics of aphid-population growth on potatoes in northeastern Maine. Ann. Entomol. Soc. Amer. 52: 117-21.
26. ———, and ———. 1971. Seasonal history of the buckthorn aphid and suitability of alder-leaved buckthorn as a primary host in northeastern Maine. Maine Life Sciences and Agr. Exp. Sta. Tech. Bull. 51, 24 p.
27. ———, ———, and C. C. Gordon. 1971. Growth characteristics of potato plants useful in studies of population dynamics and biological control of aphids. Amer. Potato J 48: 439-49.
28. ———, ———, and ———. 1972. Survey of parasites of potato-infesting aphids 1963 to 1969 in northeastern Maine. Maine Life Sciences and Agr. Exp. Sta. Tech. Bull. 60.

29. ———, ———, and I. M. Hall. 1963. Importance of entomogenous fungi in controlling aphids on potatoes in northeastern Maine. Maine Agr. Exp. Sta. Tech. Bull. 6, 42 p

30. ———, ———, I. M. Hall, and C. C. Gordon. 1972. Survey of entomogenous fungi affecting potato-infesting aphids in northeastern Maine, 1963 to 1969. Maine Life Sciences and Agr. Sta. Exp. Sta. Tech. Bull. 58.

31. ———, ———, P. M. Lombard, R. M. Cobb, and P. H. Lung. 1950. Control of aphids on potatoes with DDT when used with fungicides. Maine Agr. Exp. Sta. Bull. 480, 41 p.

32. ———, ———, C. F. W. Muesebeck, and H. E. Wave. 1965. Parasites of potato-infesting aphids in northeastern Maine. Maine Agr. Exp. Sta. Tech. Bull. 19, 77 p.

33. ———, ———, and L. B. Reed. 1954. Subunits of sample for estimating aphid abundance on potatoes. Jour. Econ. Entomol. 47: 1024-7.

34. ———, ———, F. S. Roberts, and C. F. W. Muesebeck. 1955. Parasites of potato-infesting aphids and of some other aphids in Maine. Proc. Entomol. Soc. Washington 57: 131-6.

35. ———, ———, and H. E. Wave. 1969. Canada plum, *Prunus nigra* Aiton, as a primary host of the green peach aphid, *Myzus persicae* (Sulzer), in northeastern Maine. Maine Agr. Exp. Sta. Tech. Bull. 39, 32 p.

36. ———, ———, and ———. 1972. Seasonal population trends and productiveness of the potato aphid on swamp rose in northeastern Maine. Maine Life Sciences and Agr. Exp. Sta. Tech. Bull. 52, 35 p.

37. ———, ———, H. E. Wave, and C. C. Gordon. 1972. Importance of arthropod predators in controlling aphids on potatoes in northeastern Maine. Maine Life Sciences and Agr. Exp. Sta. Tech. Bull. 54, 49 p.

38. Simpson, G. W. 1932. Spraying and dusting experiments for the control of potato aphids. J. Econ. Entomol. 25: 634-9.

39. ———. 1937-38. Insects in relation to the transmission of potato virus diseases. *In* Maine Agr. Exp. Sta. Bull. 391: 233, 340 (298-304).

40. ———. 1940. Aphids and their relation to the field transmission of potato virus diseases in northeastern Maine. Maine Agr. Exp. Sta. Bull. 403: 189-305.

41. ———, and W. A. Shands. 1954. Fewer applications of DDT with proper timing produce equal yields of potatoes at less cost. Maine Agr. Exp. Sta. Bull. 533, 28 p.

42. ———, and ———. Unpublished manuscript. Differential spread of potato leaf roll by three species of potato infesting aphids in northeastern Maine.

43. ———, ———, and H. E. Wave. Unpublished manuscript. Flight studies of aphids in northeastern Maine.

44. Singh, R. P., R. E. Finne, and R. H. Bagnell. 1971. Losses due to potato spindle tuber virus. Amer. Potato J. 48: 262-7.

45. Wave, H. E., W. A. Shands, and G. W. Simpson. 1965. Biology of the foxglove aphid in northeastern United States. Agr. Research Serv. U.S. Dept. Agr. Tech. Bull. 1338, 40 p.

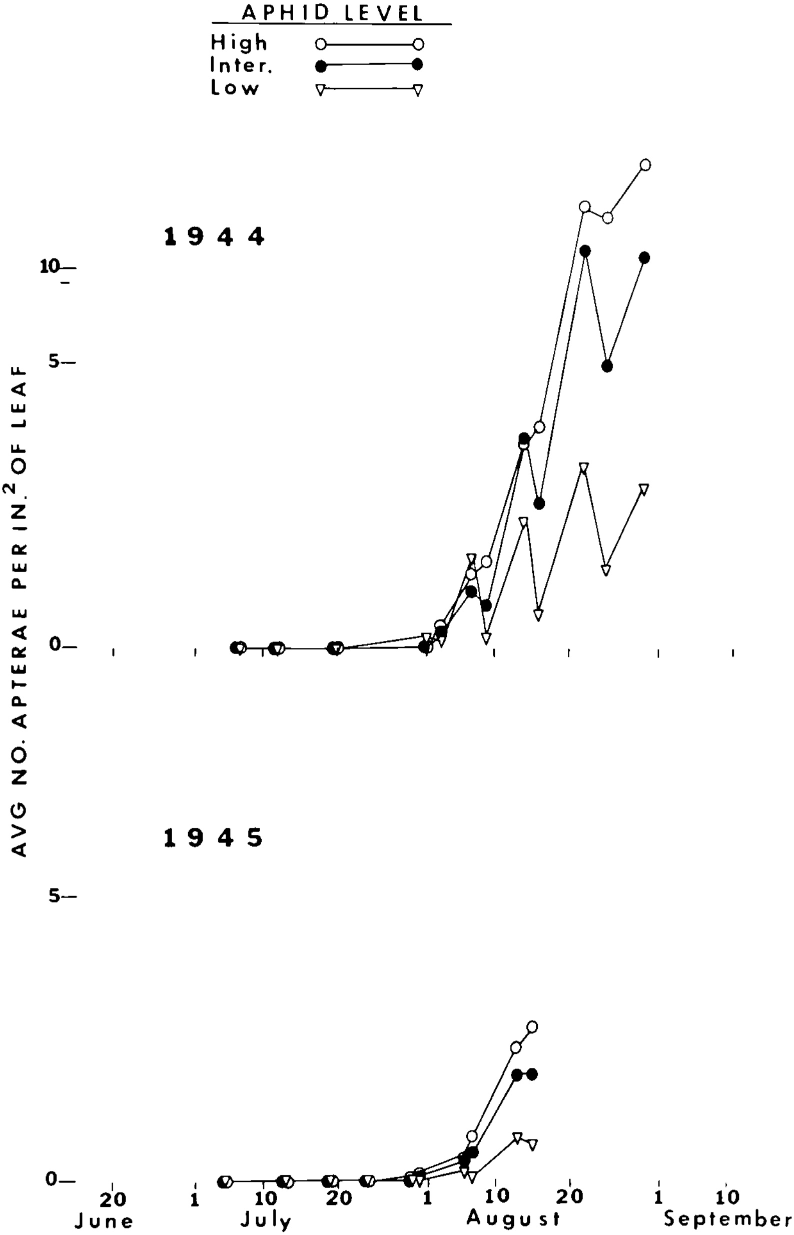

FIGURE 1. Seasonal trends of one natural (high) and two regulated levels of aphid abundance on field growing Katahdin potatoes. The open and shaded triangles show application dates of nicotine dust mixtures made to obtain and maintain the intermediate and low levels, respectively (See table 1).

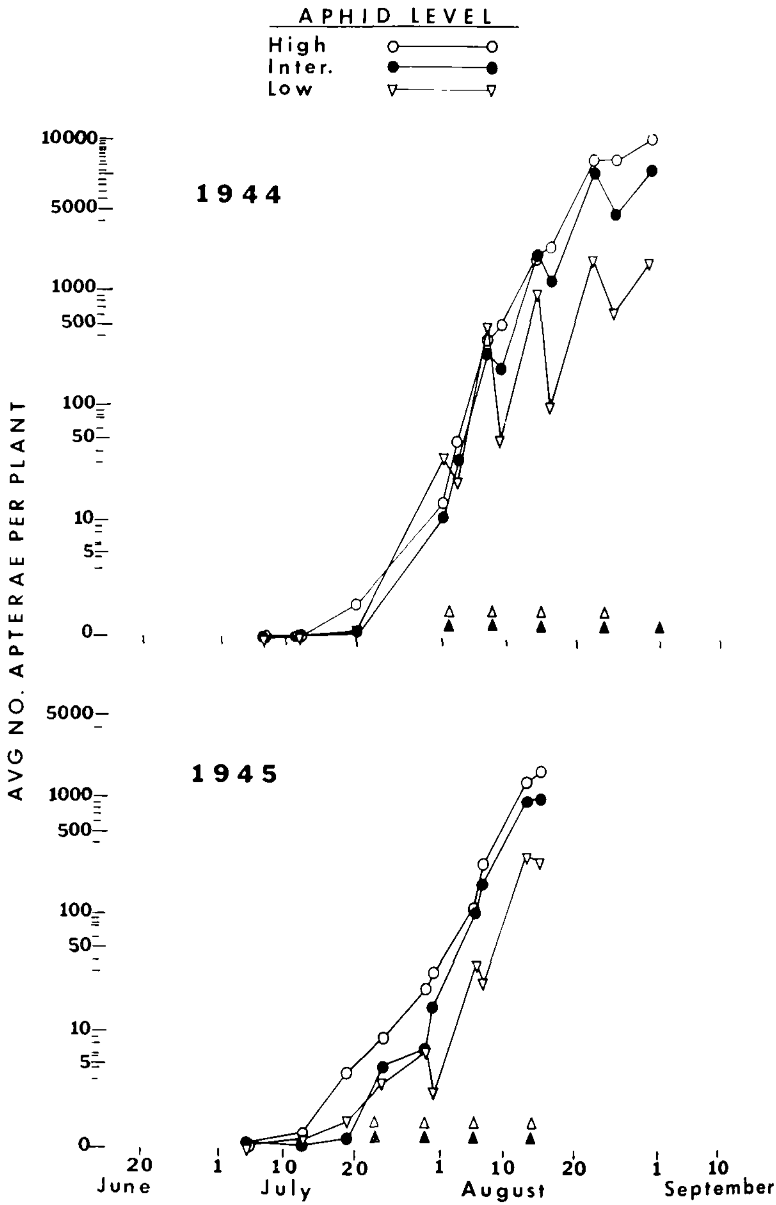

FIGURE 2. Seasonal trends of aphid density on foliage of Katahdin potatoes having the three levels of aphid abundance shown in figure 1.

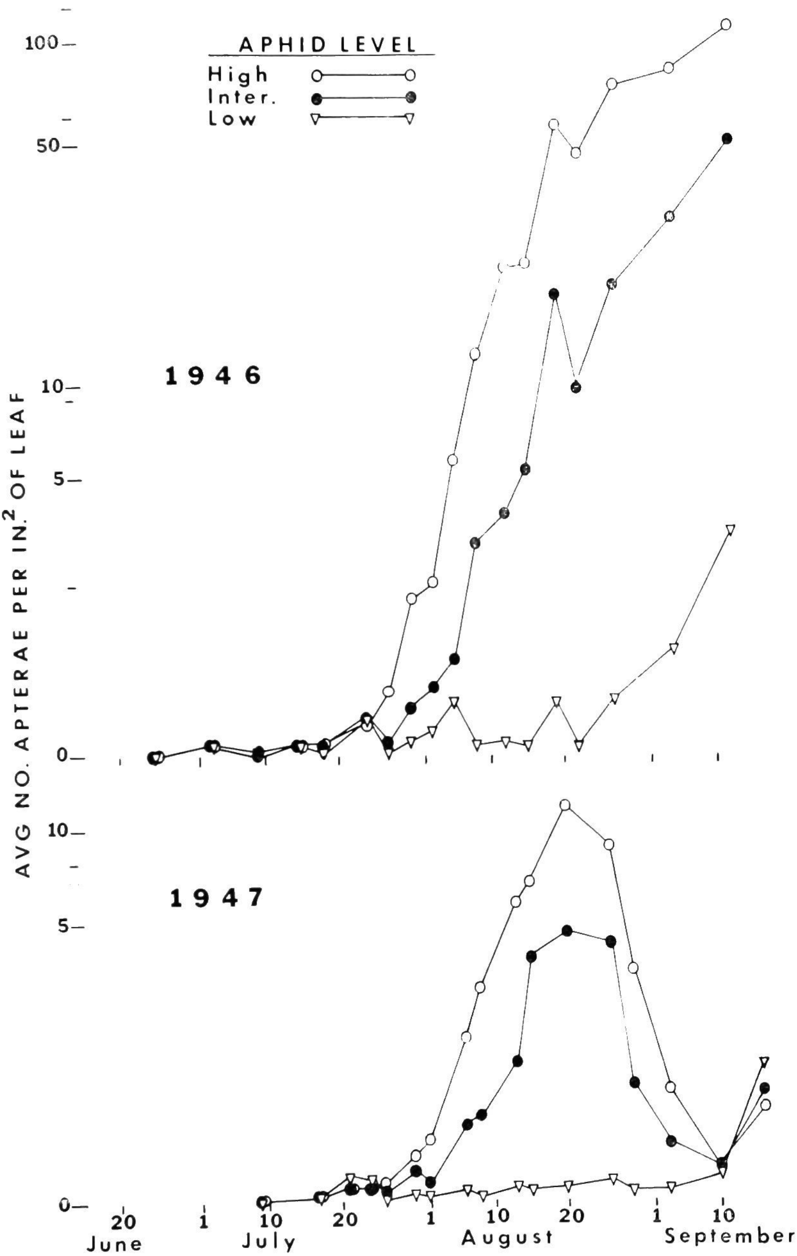

FIGURE 3. Seasonal trends of one natural (high) and two regulated levels of aphid abundance on field growing Green Mountain potatoes. The open and shaded triangles show application dates of nicotine dust mixtures made to obtain and maintain the intermediate and low levels, respectively (See table 1).

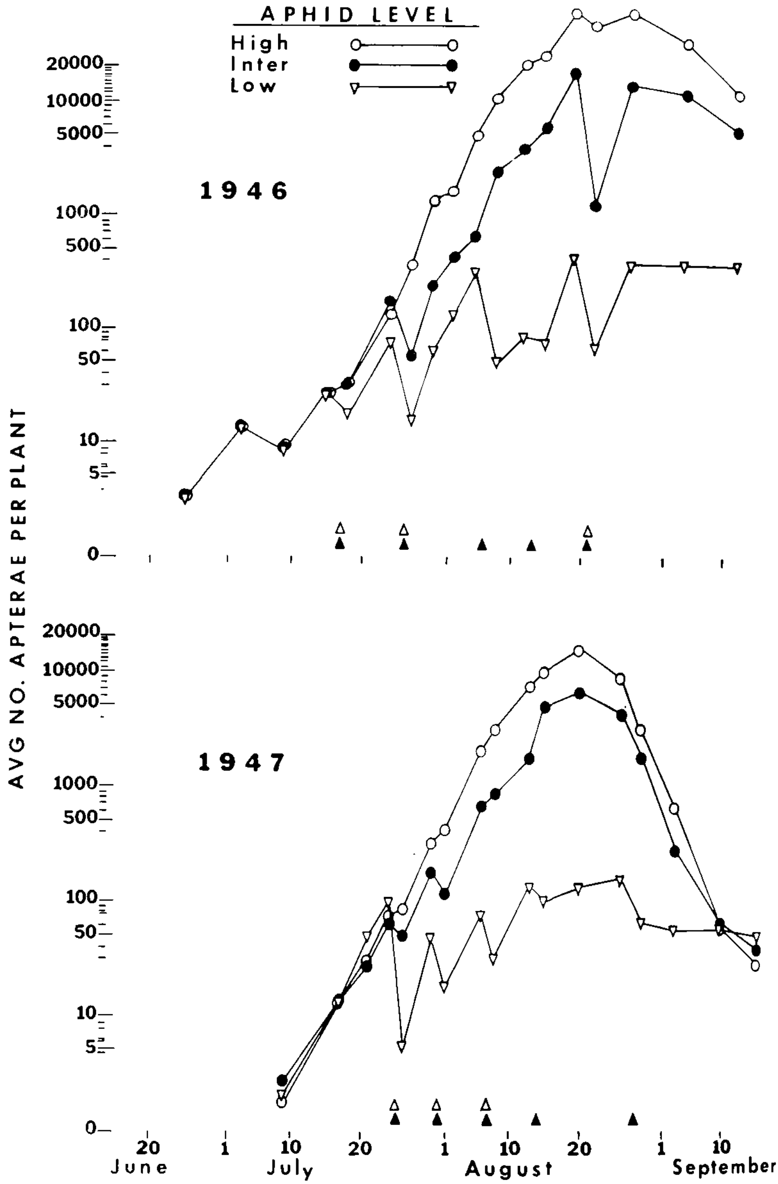

FIGURE 4. Seasonal trends of aphid density on foliage of Green Mountain potatoes having the three levels of aphid abundance shown in figure 3.

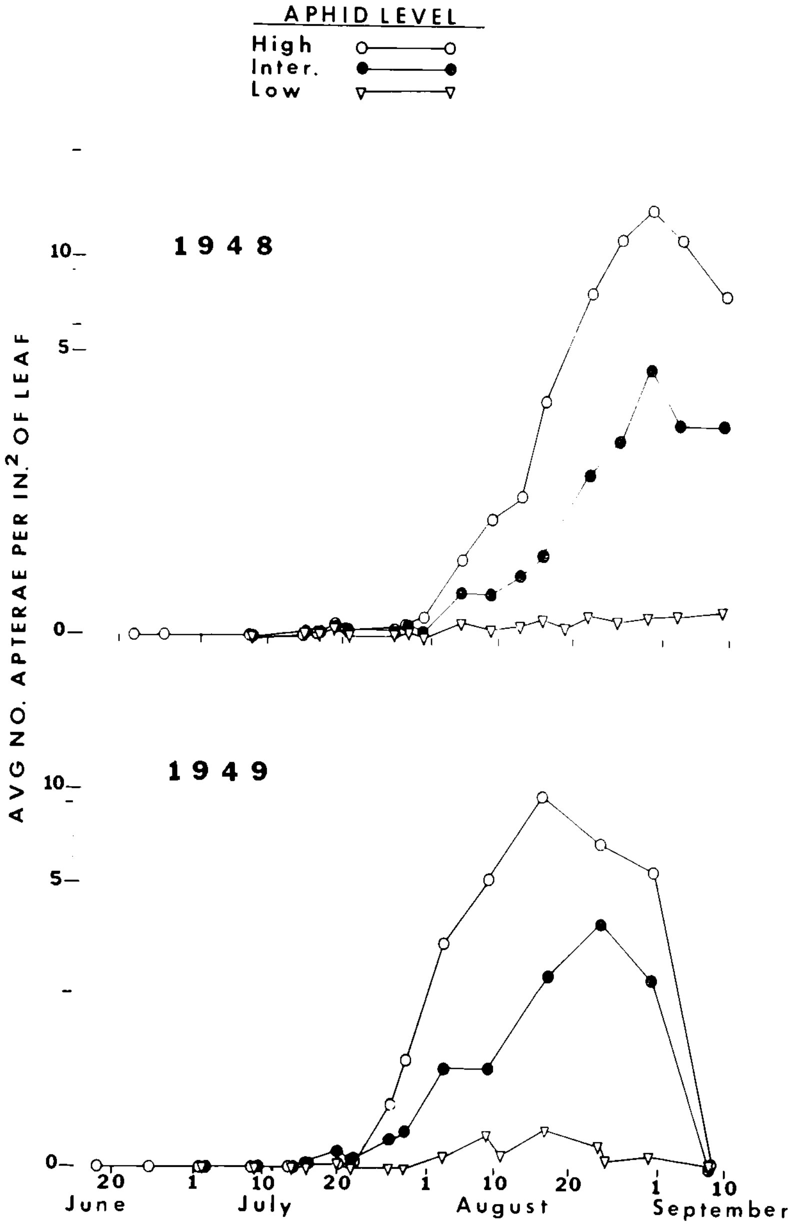

FIGURE 5. Seasonal trends of one natural (high) and two regulated levels of aphid abundance on field growing Chippewa potatoes. The open and shaded triangles show application dates of nicotine dust mixtures made to obtain and maintain the intermediate and low levels, respectively (See table 1).

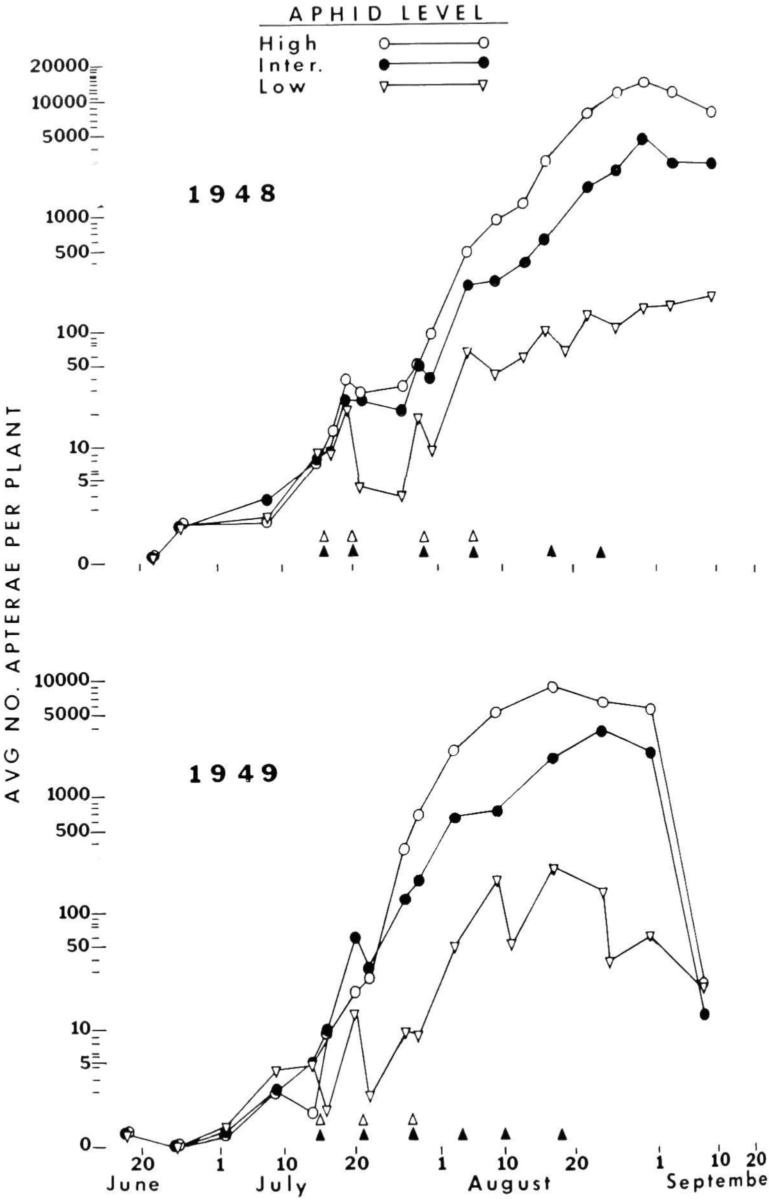

FIGURE 6. Seasonal trends of aphid density on foliage of Chippewa potatoes having the three levels of aphid abundance shown in figure 5.

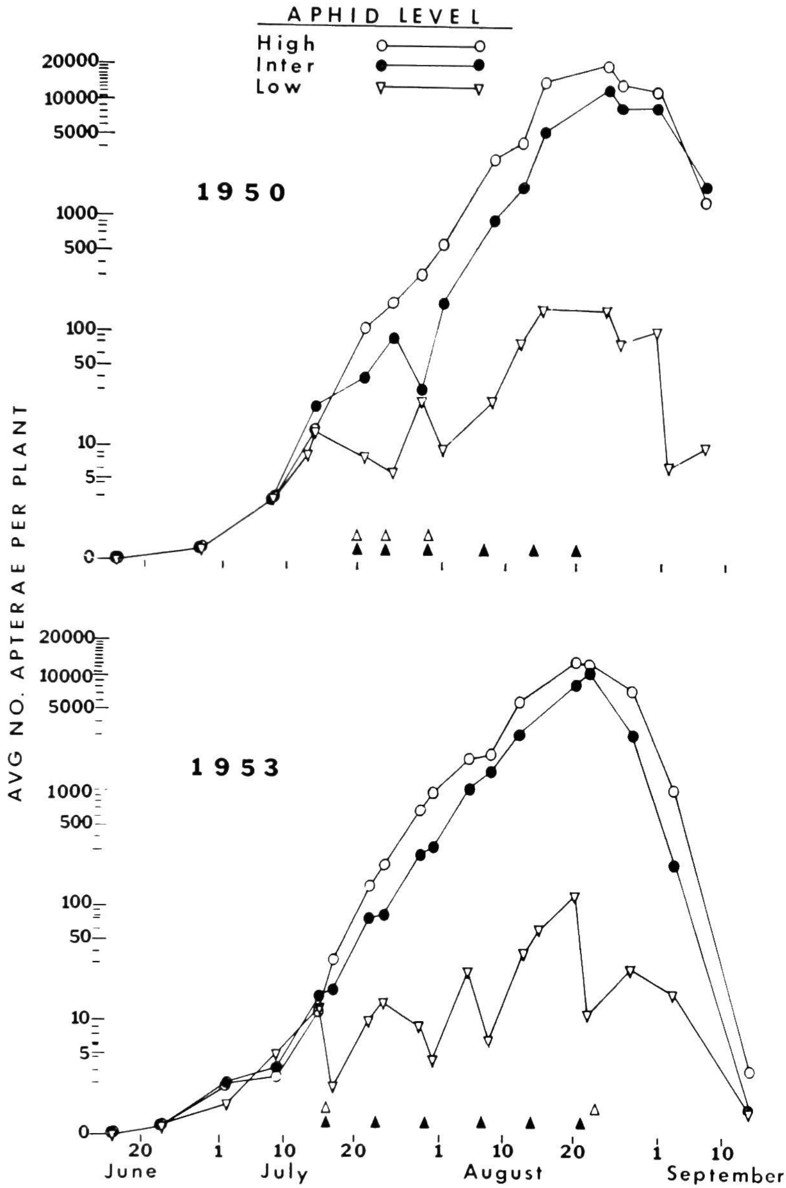

FIGURE 7. Seasonal trends of one natural (high) and two regulated levels of aphid abundance on field growing Kennebec potatoes. The open and shaded triangles show application dates of nicotine dust mixtures made to obtain and maintain the intermediate and low levels, respectively (See table 1).

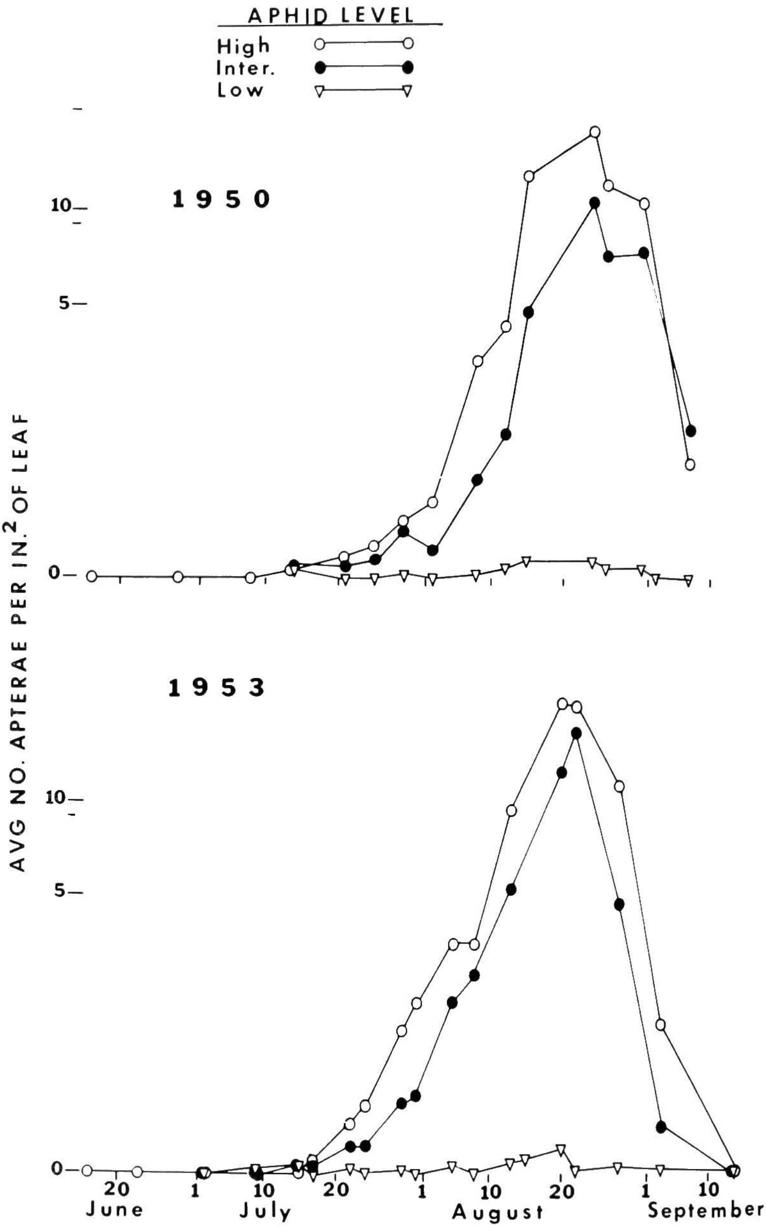

FIGURE 8. Seasonal trends of aphid density on foliage of Kennebec potatoes having the three levels of aphid abundance shown in figure 7.

FIGURE 9. Katahdin potatoes on September 11, 1944 which had been subjected to 3 all-season levels of aphid infestation. Plants in low level plots had a vigorous appearance with most leaves retained. Plants in intermediate level plots were in poor condition and had lost many leaves. Plants in high level plots were nearly dead, few leaves remaining.

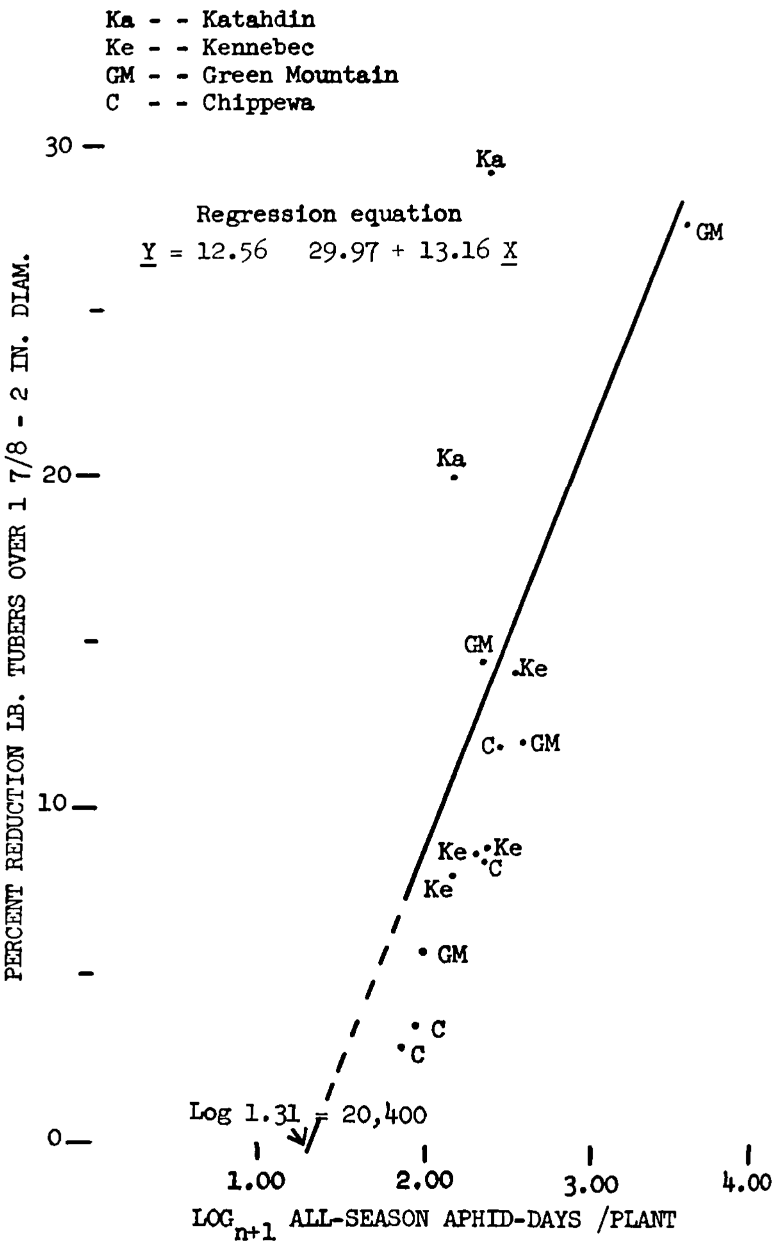

FIGURE 10. Yield response to aphid infestation by 4 varieties of potatoes.